RESEARCH ARTICLE

SABRAO Journal
of Breeding and Genetics
49 (4) 327-335, 2017

GENERATION MEAN ANALYSIS FOR GRAIN YIELD AND ITS COMPONENT TRAITS IN SUBMERGENCE RICE

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SUMMARY

An experiment was conducted to determine the mode of inheritance of submergence tolerance in six basic generations *viz.*, P_1, P_2, F_1, F_2, B_1, B_2 of cross HUR-105 x Swarna Sub1. The chi-square values for F_2, B_1 and BC_2 populations were 1.5, 0.33 and 0.05 respectively, showing non-significant at 5% level of significance indicating the observed data are in accordance with the expected data and following Mendelian pattern of inheritance to submergence tolerance. The ratio showed in different generation for tolerant and susceptible plants are showing the dominance pattern of inheritance for submergence tolerance gene. The scales A, B, C and D were found significant for most of the traits under both the conditions indicating presence of epistasis. Plant height, panicle length, panicle weight, spikelets per panicle, test weight, yield per plant and amylose content, 'h' and 'l' gene effect displayed opposite signs under irrigated condition, indicating duplicate epistasis. Productive tillers per plant, flowering time, maturity and gel consistency showed complementary epistasis. The additive genetic variance was predominant in all the traits except test weight under normal irrigated condition while under stress condition, except for test weight and panicle weight, explaining that it is associated with homozygosity and hence it is fixable in nature and selection for these traits will be very effective components in cross HUR-105 x Swarna-Sub1.

Key words: Inheritance, submergence, gene action, component of variances

Key findings: The gene action for submergence tolerance and yield attributing traits indicating additive, dominance and epistatic genetic components are important for the expression of traits and gives valuable information for researchers to planning and design the appropriate breeding procedure to develop high yielding rice submergence tolerance varieties with desirable yield and yield related traits.

Manuscript received: July 28, 2016; Decision on manuscript: June 5, 2017; Manuscript accepted: September 22, 2017.

Communicating Editor: Bertrand Collard

INTRODUCTION

Rice, *Oryza sativa* L., (2n = 24) an important cereal, belonging to the family *Graminae* and subfamily *Oryzoideae* is the staple food for half of the world's population and 90% of it is being produced and consumed in Asia. Rice is grown especially in the large areas of Asia, Latin America and Africa that are characterized by a semitropical climate with alternating rainy and dry seasons. Rice yields remain low (0.5–2.5 t ha^{-1}) and unstable due to two perennial natural problems: drought and flooding (IRRI, 2009, 2010). Among the several biotic and abiotic stresses affecting rice production, submergence has been identified as the third most important constraint for higher rice productivity causes total yield loss (Sarkar *et al.*, 2006). Prolonged submergence is a major constraint to rice production, affecting over 15 M ha in South and South East Asia and causing an annual yield loss of over US$ 600 million (Singh *et al.*, 2009). Flooding is a serious constraint to rice plant growth and survival in rainfed lowland and deep water areas because it results in partial or complete submergence of the plant. The average rice productivity of submergence-prone areas in eastern India is 0.5 - 0.8 t ha^{-1}, whereas it is about 2.0 t ha^{-1} for favorable rainfed lowlands, being much lower than the input-intensive irrigated system (5.0 t ha^{-1}). However, these flood-prone ecosystems have enormous potential for more food production to meet the ever increasing demands for rice supply because of the predominance of good soils and freshwater resources (Ismail *et al.*, 2013).

Submergence tolerance is controlled by a single major quantitative trait locus (QTL) on chromosome 9, along with a number of minor QTLs (Xu and Mackill, 1996; Nandi *et al.*, 1997; Toojinda *et al*., 2003). FR13A, which is one of the most submergence-tolerant donor variety. The major QTL, named Sub1, with a LOD score of 36 and an R^2 value of 69% (Xu and Mackill, 1996), provides tolerance to complete submergence for up to 2 weeks. Sub1 gene enables rice to survive and more importantly, recover after flooding (Mackill *et al.,* 2012). The varieties with Sub1 gene showed a yield advantage of 1 to 1.3 t/ha over the original varieties following submergence for a few days up to 18 days (Neeraja *et al.,* 2007; Singh *et al.*, 2009; Mackill *et al.*, 2012; Singh *et al.,* 2013). Swarna-Sub1 yields twice that of Swarna without Sub1 with about 15 days of submergence. The Sub1 QTL for submergence tolerance is being transferred into ten locally adapted popular rice varieties possessing either intolerant allele or absence of the Sub1A gene (Singh *et al.,* 2016). Therefore, in this study an attempt has been made to estimate the inheritance of various kinds of gene effects and their importance in the control of grain yield and its component characters in submergence tolerant rice. Grain yield is a complex polygenic trait and is dependent on the combination of its component traits *viz.*, number of filled grains, test grain weight, panicle length, panicle weight and effective tillers per plant. The information about the nature and magnitude of gene action prevailing in the breeding material would be a valuable tool for selecting breeding procedure and hence to achieve the desired genetic improvement through correlated response of selection.

MATERIALS AND METHODS

Plant material and experimental plan

The two *indica* rice varieties HUR-105 (Malviya Dhan-105) and Swarna-Sub1 were used in this study in which HUR-105 is most widely grown in North East India owing to its high yielding, semi dwarf, medium duration, with grain quality, but submergence intolerant and Swarna-Sub1 is a submergence tolerant variety. The crosses were made in *kharif* 2009 between HUR-105 x Swarna-Sub1 to raise the F_1. In the next, *off season* at ICAR-NRRI, Cuttack the F_1 were backcrossed with recurrent parent (P_1) and donor parent (P_2) to generate B_1 and B_2 population. In *kharif* 2010 the BC_1 plants were backcrossed to have the BC_2 plants. Six generations, namely, P_1, P_2, F_1, F_2, B_1 and B_2 along with BC_2 were raised in a complete randomized block design in both normal irrigated and submerged condition, with three replications at Agricultural Research Farm, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India during *kharif* 2011. Twenty-one days old seedlings were transplanted in separate plot size 3 × 1 m with spacing 20 × 15 cm apart. The recommended packages of practices were followed to raise healthy crops. Submergence screening was performed in controlled conditions that allow flooding with water depth of 1.0 meters for a period of 15 days. The plants were de-submerged and the survival of plants was scored after 20 days of recovery following the procedure of Pamplona *et al. (*2007).

Table 1. Estimation of variance components for eleven traits in submergence tolerant rice.

Traits	V_E		V_P		V_G		V_A		V_D	
Condition	N	S	N	S	N	S	N	S	N	S
Productive tillers per plant	1.08	2.13	9.25	5.91	8.16	3.78	14.86	9.81	-6.70	-6.03
Plant height	7.47	12.69	39.70	3.77	32.22	-8.92	66.40	3.83	-34.18	-12.76
Flowering time	4.08	2.03	2.68	8.31	-1.39	6.27	2.21	5.91	-3.60	0.36
Maturity	2.07	1.93	1.56	21.79	-0.50	19.86	0.65	28.54	-1.15	-8.68
Panicle length	0.53	0.78	0.17	2.72	-0.35	1.93	0.08	2.80	-0.43	-0.87
Panicle weight	0.06	0.02	0.29	0.08	0.23	-0.01	0.20	-0.20	0.03	0.19
Spikelet per panicle	14.29	26.20	102.64	145.28	88.34	119.07	190.17	233.76	-101.82	-114.68
Test weight	0.43	0.18	0.22	0.23	-0.21	0.05	-1.21	-0.42	0.99	0.47
Yield per plant	1.43	0.35	2.25	0.22	0.82	-0.12	3.23	0.32	-2.40	-0.45
Amylose content	0.64	0.38	4.96	2.72	4.31	2.33	4.60	3.19	-0.29	-0.85
Gel consistency	10.94	0.24	27.11	8.43	16.17	8.19	46.37	7.47	-30.20	0.72

Observation recorded

The phenotypic traits were assessed on each individual entry in the segregating generations and observations were recorded for eleven quantitative traits *viz.*, number of productive tillers per plant (PTP), plant height (PH), flowering time (DF), maturity (DM), panicle length (PL), panicle weight (PW), spikelet per panicle (SSP), test weight (TW), grain yield per plant (YPP), amylose content, and gel consistency (Table 1). Ten plants from both parents, 20 plants from F_1, B1 and B_2 and 400 plants from F_2 generation per replication were randomly selected and tagged for observing the traits under normal irrigated and stress condition.

Statistical analysis

Analysis of variance was carried out by following the procedure of complete randomized block design analysis described by Panse and Sukhatme (1967), for all six generations. The inheritance pattern and distribution of frequency for submergence tolerance was carried out by χ^2 test. The means were computed for each generation of P_1, P_2, F_1, F_2, B_1 and B_2. The variance and corresponding standard errors of the means were computed from the deviations of the individual values from the pooled mean for each of the generation in each cross. The generation mean analysis was performed according to Hayman (1958) and Jinks and Jones (1958) for the estimation of genetic components of variation, epistasis model and gene effects in two steps (i) testing for epistasis to determine the presence or absence of interallelic interaction through scaling test and (ii) estimation of gene effects, variances and the type of epistasis involved.

Scaling test for A, B, C and D scales as suggested by Hayman and Mather (1955) and Mather and Jinks (1971) was applied to test the adequacy of simple additive-dominance model. Utilizing the means of different generations, the values of A, B, C and D scales were calculated. The standard errors of A, B, C and D were obtained as square root of the variances V_A, V_B, V_C and V_D, respectively and utilized for testing the significance of the deviations of the respective scales from zero. To test the significance of the scales, the 'Student's t' values for each of these quantities were calculated. The significance of the scales was evaluated using calculated P values for respective calculated 't' values. To tests the adequacy of additive-dominance model using a $\chi 2$ test, Joint scaling test (Cavalli, 1952) was conducted which combines several scaling test into one. The generation means were analysed by the method suggested by Hayman (1958) to provide information on the inheritance of observed traits. The generation means were used to estimate the six genetic parameters *viz.*, m, d, h, i, j and l of digenic interaction model representing mean, additive genetic effect, dominance genetic effect, additive × additive gene interaction effect, additive × dominance interaction effect and dominance × dominance gene effects, respectively assuming that no linkage and no higher order gene interaction exists. Considering the generation means as reference values, the six genetic parameters were calculated. The least squares computation method was used for arriving at different gene effects.

RESULT AND DISCUSSION

Analysis of variance

The analysis of variance was performed for the generation of specific cross under irrigated and submerged conditions as well as pooled analysis performed. Results showed significant differences for most of the traits in pooled as well as individual irrigated and stress conditions. It is evident from the analysis of variance that the lines showed significant difference for most of the traits except days to flowering, maturity and panicle weight in pooled analysis. Under normal irrigated conditions, there was no significant difference for the traits except flowering time, maturity, panicle weight, amylose content and gel consistency, but under stress condition, productive tillers per plant, flowering time, maturity and panicle weight were found to be non-significant (Table 2). The significant difference in rice lines for yield traits were also reported by Singh *et al.* (2007).

Scaling and joint scaling tests

Scaling and joint scaling tests were performed to understand the adequacy of simple additive-dominance model. Further, joint scaling test was adapted to fit the data to three parameter model to estimate mean (m), additive gene effects (d) and dominant gene effects (h) and to evaluate adequacy of simple additive-dominance model. Chi square test was conducted to evaluate the goodness of fit of this model.

The scaling test showed all A, B, C and D scales were significant for panicle length and grain yield per plant indicating presence of epistasis. All the traits related to yield in both irrigated and submergence conditions in the present study were significant in either one of the scales or in combination representing the existence of epistatic interactions between the genes involved. The scaling test in irrigated condition showed significant for productive tillers per plant, plant height, days to flowering time, maturity, panicle length, test weight, yield per plant and gel consistency for Scale A, for Scale B all the trait except plant height and test weight showed significant result, for Scale C all traits were showed significant result and for Scale D days to flowering time, maturity, panicle length, panicle weight, spikelets per panicle, test weight, yield per plant and amylose content showed significant result. While in submergence condition, the scaling test showed significant for productive tiller per plant, plant height, maturity, panicle length, yield per plant and amylose content for Scale A, for B, C and Scale D all the traits except flowering time showed significant result (Table 3).

Further, joint scaling test in irrigated condition for cross HUR105 x Swarna-Sub1, the chi square value of nine traits *viz.*, productive tiller per plant, plant height, flowering time, maturity, panicle length, panicle weight, spikelets per panicle, amylose content and gel consistency were not significant indicating the absence of digenic nonallelic interaction. The adequacy of simple additive-dominance model suggests nonallelic interaction effect (epistasis) is absent and generation means depends only on additive-dominance effect of the gene. Chi square values were significant for remaining two traits in the present study indicating the data does not fit into simple additive-dominance model. In submergence condition, the chi square values for four traits *viz.*, flowering time, maturity, spikelets per panicle and amylose content were non-significant indicating the absence of digenic nonallelic interaction. The adequacy of simple additive-dominance model suggests nonallelic interaction effect (epistasis) is absent and generation means depends only on additive-dominance effect of the gene. Chi-square values were significant for remaining seven traits in this study indicating the data does not fit into simple additive-dominance model. The role of epistatic interactions was identified by lack of goodness of fit into three parameter models and the data was further subjected to six parameter models.

Table 2. ANOVA for individual environment for all eleven traits in submergence rice HUR 105- Sub1.

Source of variation	df	Mean Sum of Square																					
		Productive tillers per plant		Plant height		Flowering time		Maturity		Panicle length		Panicle weight		Spikelet per panicle		Test weight		Yield per plant		Amylose content		Gel consistency	
		N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S
Replicates	2	2.80	8.80	28.13	49.70**	1.70	0.70	1.20	4.70	0.70	1.20	0.20	0.04	37.30	125.10	0.20	1.60**	1.40	0.60	1.10	5.20*	16.40	9.00
Generations	5	21.00*	5.80	105.70**	259.80***	8.20	6.90	5.30	14.80	5.50***	11.90**	0.30	0.08	159.20*	365.00**	2.90*	3.70***	15.40**	5.80***	2.20	8.00**	25.90	22.60**
Error	10	4.30	2.30	15.80	6.00	4.30	7.30	2.50	11.70	0.50	2.00	0.20	0.08	37.20	59.40	0.80	0.20	1.90	0.33	3.30	0.80	18.20	3.70
Total	17	9.00	4.00	43.70	85.80	5.20	6.40	3.20	11.70	2.00	4.90	0.20	0.07	73.00	157.00	1.40	1.40	5.80	2.00	2.70	3.40	20.30	9.90

** and *: Significant at 1 and 5 per cent level, respectively; ***: Significant at 0.01; **N**: Normal Irrigated condition; **S**: Stress submergence condition

Table 3. Scaling tests and estimate of genetic parameters for all eleven traits in submergence rice.

Traits	Scaling test								Joint Scaling test							
	Scale A		Scale B		Scale C		Scale D		m		d		H		χ2	
	N	S	N	S	N	S	N	S	N	S	N	S	N	S	N	S
Productive tillers per plant	1.33**	-3.27***	-4.89 **	-1.74***	-3.72 **	4.51***	-0.12	4.78 ***	14.75	7.45	2.89	-1.26	4.24	1.75	1.37	9.49 **
Plant height	4.22***	8.00 ***	-0.56	-6.42***	8.13 **	54.03***	2.22	26.22 **	91.97	83.44	8.45	17.71	2.95	-0.56	0.93	149.63 *
Flowering time	6.00***	0.33	5.00 ***	0.33	13.00***	3.33*	1.00 **	1.33	103.20	121.88	-0.74	-1.98	1.81	1.49	2.99	6.75
Maturity	4.55***	4.33 ***	1.33 **	4.00***	11.20***	3.00	2.67 ***	-2.67 *	134.46	149.76	1.14	-1.98	0.55	2.93	0.26	0.06
Panicle length	2.88***	-6.69 ***	3.11 ***	-1.94***	5.07 ***	2.58***	-0.48***	5.56 ***	22.44	19.69	-0.24	-1.74	2.82	2.41	0.80	68.31 ***
Panicle weight	-0.10	0.13	-0.30***	-0.43***	-1.80***	1.05***	-0.68***	0.63 ***	3.67	2.78	0.17	0.11	0.55	-0.36	5.28	16.95 ***
Spikelet per panicle	-0.93	-1.96	4.56 ***	16.57***	24.60***	27.89***	10.59***	6.65 *	151.25	127.38	-0.38	-10.3	19.15	17.59	0.69	1.48
Test weight	-3.45***	0.39	0.33	-1.27***	1.33 ***	3.22***	2.26 ***	2.09 ***	17.79	12.83	0.29	-1.24	1.43	1.44	78.12***	34.94 ***
Yield per plant	1.99***	2.65 ***	3.54 ***	-2.19***	-2.37 **	-2.75***	-3.93***	-1.63 ***	20.46	11.29	1.11	-0.52	3.57	-0.34	15.57***	98.80 ***
Amylose content	-0.37	-0.86***	-1.39 **	-1.47***	-4.27***	-6.47***	-1.26 *	-2.83 ***	24.56	23.99	-0.9	-2.39	-0.17	0.58	2.92	1.72
Gel consistency	-4.83***	0.23	-6.83 ***	1.90**	-8.67***	11.73***	1.50	4.73***	74.68	75.93	4.18	3.72	5.82	-1.29	5.33	4.17*

** and *: Significant at 1 and 5 per cent level, respectively; ***: Significant at 0.01; **N**: Normal Irrigated condition; **S**: Stress submergence condition

Gene effect and component of variances involved

It was found that in all the generations, traits related to yield in both irrigated and submergence conditions was significant in either one of the scales or in combination representing the existence of epistatic interactions between the genes involved (Table 4). The epistatic effects involved in combination of fixed and non fixed genes were shown to contribute to the genotypic mean of any population and these effects define specific additive × additive and additive × dominant epistatic components (Viana, 2000). Hasib *et al.* (2002) observed both additive and non-additive gene action were important for the expression. Digenic nonallelic interaction model with six parameters namely m, d, h, i, j and l revealed that the epistatic interaction model was found adequate to explain the gene action for the traits, productive tillers per plant, days to flowering time, panicle length, panicle weight, test weight and yield per plant in irrigated condition while for stress condition it is adequate for all traits except for flowering time, spikelet per plant and amylose content. The estimates of gene effect clearly illustrate high variation in the observed traits. The 'h' and 'l' gene effect displayed opposite signs for the traits *viz.,* plant height, panicle weight, panicle length, spikelet per panicle, test weight, yield per plant and amylose content under irrigated condition and under submergence condition allthe trait displayed opposite sign, indicating duplicate epistasis. These results are consistent with the earlier reports of Hasib *et al.,* (2002); Divya *et al.,* (2014) for plant height, number of productive tillers, panicle length, flowering time, spikelet per panicle, test weight and yield per plant.

The values of dominance (h) and dominance x dominance (l) interaction were in the same direction for traits like productive tillers per plant, flowering time, maturity and gel consistency under irrigated condition only and the interaction fit into complementary epistasis model. Under stress conditions, no traits suggested complementary epistasis. It was reported that gene effects are known to be cross specific and fits into complementary recessive epistasis for grain yield (Kumar *et al.,* 2007). The sign associated with the estimates of additive (d) and dominance (h) indicates the parent that concentrates the highest number of genes for increasing the trait (Falconer, 1989). Additive effect was the only significant portion of gene controlling grain yield per plant of the rice. The positive sign in the additive gene effect implies that HUR-105 contributes positively to the trait as compared to Swarna-Sub1, and vice versa. The result is in conformity with the findings of Singh *et al*., (2016). For panicle length, panicle weight, test weight and yield per plant additive x additive interaction was observed, while dominance x dominance interaction was observed for productive tillers per plant and days to flowering under normal irrigated condition.

Variance estimation using the six generation values revealed that variation due to dominant genetic effect was predominant for the traits under study. Estimation of variance components in these six generation materials indicates that additive variance was higher than dominance variance for most of the traits under study under both the conditions. The additive gene action predominated in the inheritance of submergence tolerance, with one major gene or block of genes having partial dominance was earlier reported by Pathan and Miah (1989). This gene action can be exploited through simple selection for the said traits. Under irrigated condition, variance estimates also revealed that degree of dominance (H/D) was more than one for traits like productive tillers per plant, plant height, days to flowering, panicle length, panicle weight, spikelet per panicle, amylose content and gel consistency while under submerged condition it is more than one for productive tillers per plant, flowering time, panicle length, panicle weight, spikelet per panicle, test weight, yield per plant and gel consistency. The trait test weight under irrigated condition and panicle weight and test weight under stress condition expressed higher dominance variance than additive variance. Similar finding was earlier reported by Azizi *et al.,* (2006). It is concluded that these traits are governed by non additive gene action; it is also evident from the superior performance of F1s than advanced lines (Manickavelu *et al.,* 2006; Saleem *et al.,* 2010). The predominance of non additive gene action

Table 4. Estimation of gene effects based on six generation means for eleven traits in submergence tolerant rice.

Traits	M		D		H		I		j		l		Type of epistasis	
Condition	N	S	N	S	N	S	N	S	N	S	N	S	N	S
Productive tillers per plant	16.33 ***	10.00***	5.22 ***	-1.66 ***	4.55 ***	-7.50 ***	0.22	-9.54***	3.11	-0.77	3.33 *	14.56***	C	D
Plant height	94.66 ***	92.55***	10.03 ***	14.66 ***	-1.72	-44.33***	-4.44	-52.44***	2.39	7.22	0.78	50.88 ***	-	D
Flowering time	105.00 ***	122.33***	-0.33	-2.00 ***	-2.83 ***	-1.66	-2.00**	-2.67	0.50	----	-9.00 ***	2.00	C	-
Maturity	135.67 ***	151.66***	2.00 ***	-2.00 **	-6.39 ***	8.16 ***	-5.33***	5.33*	1.61	0.16	-0.55	-13.66 ***	-	D
Panicle length	23.93 ***	21.11***	0.11	-3.77 ***	3.42 ***	-9.16 ***	0.97 ***	-11.11***	-0.11	-2.37	-6.97***	19.67 ***	D	D
Panicle weight	3.58 ***	2.64***	0.36 ***	0.14 *	1.88 ***	-1.38 ***	1.36 ***	-1.26***	0.14	0.29	-0.88 *	1.47 ***	D	D
Spikelet per panicle	165.78 ***	142.33***	-2.54 ***	-18.22 ***	-3.89	3.51	-21.18 ***	-13.32*	-2.77	-9.27	17.55 ***	-1.24	--	--
Test weight	18.94 ***	14.19***	-1.33***	-0.55 ***	-2.61 ***	-2.69 ***	-4.52 ***	-4.11***	-1.88	0.81	7.64 ***	5.01 ***	D	D
Yield per plant	20.50 ***	10.73***	1.63***	0.47 ***	11.24 ***	4.78 ***	7.86 ***	3.26***	-0.77	2.40	-13.47 ***	-3.77 ***	D	D
Amylose content	23.55 ***	22.89***	-0.53 *	-1.91 ***	2.41 *	4.72 ***	2.52 *	4.16***	0.52	0.27	-0.79	-1.89	--	--
Gel consistency	77.33 ***	78.12***	4.16***	2.85 ***	0.33	-10.79 ***	-3.00	-9.52***	1.00	-0.80	14.66 ***	7.32 ***	--	D

** and *: Significant at 1 and 5 per cent level, respectively; ***: Significant at 0.01; **N**: Normal Irrigated condition; **S**: Stress submergence condition

Table 5. Genetics of submergence tolerance.

Treatment	Plants transplanted	Plants survived	% survival (Observed)	expected (Plant survival)	X^2 cal	X^2 tab (0.05)	D.F.	Mendelian data ratio
HUR 105	50	10	20	0	--	--	--	--
Swarna-Sub1	50	49	98	50	--	--	--	all
F_1	26	23	88.47	26	0.35	--	--	all
F_2	50	30	60	37.5	1.5	3.841	1	3:1
BC_1	24	10	41.67	12	0.33	3.841	1	1:1
B_2	26	24	92.3	26	0.16	--	--	all
BC_2	42	20	47.62	21	0.05	3.85	1	1:1

for these traits under study indicated that improvement of these traits could be possible through heterosis breeding. To obtain better genotypes through recombination breeding, hybridization followed by selection at later generations is suggested for exploiting dominance gene action. The additive genetic variance was predominant in all the traits except test weight under irrigated condition, and under stress except for test weight and panicle weight, explaining that it is associated with homozygosity and hence it is fixable in nature and selection for these traits will be very effective in the cross HUR-105 x Swarna-Sub1. The calculated chi square value for F_2, B_1 and BC_2 were less than the tabulated chi square value which indicate that observed data are in accordance with expected ratio and follow Mendelian pattern of inheritance to the submergence tolerance. In F_1 and B_2 generation tolerance phenotype is observed which indicate the presence of dominance gene for the submergence tolerance (Table 5).

CONCLUSION

Dominance gene effects played major role in controlling the genetic variance in most of the traits studied. However, additive gene effects were also found to be important for inheritance of panicle length, panicle weight, test weight and yield per plant. Biparental mating might be useful in exploiting both additive and non-additive gene actions to obtain desirable recombinants. The characters for which additive and dominance gene actions were observed recurrent selection breeding techniques may be appropriate. With regard to the negative values observed in most cases either with main effects [d] and [h] or epistatic interaction effects ([i], [j] and [l]), these might indicate that preponderance was towards the less value trait and alleles responsible for less value of traits were over dominant over the alleles controlling high values.

ACKNOWLEDGEMENT

Authors are thankful to Department of Biotechnology, New Delhi, Ministry of Agriculture, Government of India for their financial support required for complete the research work in a proper way.

REFERENCES

Azizi F, Rezai AM, Saeidi G (2006). Generation mean analysis to estimate genetic parameters for different traits in two crosses of corn inbred lines at three planting densities. *J. Agric. Sci. Technol.* 8: 153–169.

Divya B, Biswas A, Robin S, Rabindran R, Joel AJ (2014). Gene interactions and genetics of blast resistance and yield attributes in rice (*Oryza sativa* L.). *J. Genet.* 93: 415–424.

Falconer (1989). Introduction to quantitative genetics, 3rd ed., Longman Scientific and Technical, Harlow, pp. 463.

Hasib KM, Ganguli PK, Kole PC (2002). Genetic analysis of some quantitative resistances in aromatic rice involving induced mutant. *Trop. Agric. Res. Ext.*, 5: 1–6.

Hayman BI (1958). The separation of epistatic from additive and dominance variation in generation means. *Heredity.* 12: 371-390.

Hayman BI, Mather K (1955). The description of genic interaction in continuous variation. *Biometrics* 2: 69-82.

IRRI (2010) Global rice science partnership (GRisP) proposal for a CGIAR research program on rice based production systems, Los Banos, Philippines, pp. 84.

IRRI (International Rice Research Institute). (2009). http:// www.irri.org.

Mackill DJ, Ismail AM, Singh US, Labios RV, Paris TR (2012). Development and rapid adoption of submergence-tolerant (Sub1) rice varieties. *Adv. Agron.* 115: 303–356.

Manickavelu A, Nadarajan N, Ganesh SK, Gnanamalar RP (2006). Genetic analysis of biparental progenies in rice (*Oryza sativa* L.). *Asian J. Plant Sci.* 5: 33–36.

Mather K (1949). Biometrical genetics. Methuen and Co., London.

Nandi S, Subudhi PK, Senadhira D, Manigbas NL, Sen-Mandi S, Huang N 1997. Mapping QTLs for submergence tolerance in rice by AFLP analysis and selective genotyping. *Mol. Gen Genet.* 255: 1–8.

Neeraja C, Maghirang-Rodriguez R, Pamplona AM, Heuer S, Collard B, Septiningsih E, Vergara G, Sanchez D, Xu K, Ismail AM, Mackill D

(2007). A marker-assisted backcross approach for developing submergence-tolerance rice cultivars. *Theor Appl Genet.* 115: 767–6.

Pamplona A, Ella E, Singh S, Vergara GV, Ismail A, Mackill DJ (2007). Screening procedure for tolerance of complete submergence in rice. *Sub1 Rice News* 1 (2).

Panse VG, Sukhatme PV (1967). Statistical methods for agricultural workers. ICAR, New Delhi. 2nd ed., pp.381

Pathan MS, Miah NM. (1989). Inheritance of submergence tolerance in some rainfed lowland rice (*Oryza sativa* L.). *Bangladesh J. Agric.* 14:1-9.

Saleem MY, Mirza JI, Haq MA (2010). Combining ability analysis of yield and yield related traits in Basmati rice (*Oryza sativa* L.). *Pak. J. Bot.* 42: 627–637.

Sarkar RK, Reddy JN, Sharma SG, Ismail AM (2006). Physiological basis of submergence tolerance in rice and implications for crop improvement. *Current Science*. 91: 899–906.

Setter TL, Ellis M, Laureles ES. Senadhira D, Mishra S Sarkarung, Datta S (1997). Physiology and genetics of submergence tolerance in rice. *Ann. Bot.* 79: 67-77.

Singh AK, Singh PK, Ram M, Kumar S, Arya M, Singh NK, U.S. Singh (2016). Gene interactions and association analysis for sheath blight resistance in rice (*Oryza sativa* L.). *SABRAO J. Breed. Genet*. 48: 42-52.

Singh R *et al.* (2016). From QTL to variety-harnessing the benefits of QTLs for drought, flood and salt tolerance in mega rice varieties of India through a multi-institutional network. *Plant Science* 242: 278–287.

Singh RP, Kumar MS, Madhavilatha L (2007). Variability and relationship studies of yield and yield attributing traits in diverse lines of international irrigated observational nursery of rice (*Oryza sativa* L.). *J. Res. ANGRAU*. 35: 16-22.

Singh S, Mackill DJ, Ismail AM (2009). Responses of Sub1 rice introgression lines to submergence in the field: yield and grain quality. *Field Crops Res.* 113: 12–23.

Singh US, Dar MH, Singh S, Zaidi NW, Bari MA, Mackill DJ, Collard BCY, Singh VN, Singh JP, Reddy JN, Singh RK, Ismail AM (2013). Field performance, dissemination, impact and tracking of submergence tolerant (Sub1) rice varieties in South Asia. *SABRAO J. Breed. Genet*. 45: 112-131.

Thirugnanakumar S, Narassiman R, Senthil N, Eswaran R, Kumar CP (2007). Gene effects for grain yield and its component characters in rice (*Oryza sativa* L.). *Crop Imp.* 34: 19–23.

Toojinda T, Siangliw M, Tragroonrung S, Vanavichit A (2003). Molecular genetics of submergence tolerance in rice: QTL analysis of key traits. *Ann. Bot.* 91: 243–253.

Viana JMS (2000). Generation mean analysis to polygenic systems with epistasis and fixed genes. *Pesq. agropec. bras., Brasília,* 35: 1159–1167.

Xu K, Mackill DJ (1996) A major locus for submergence tolerance mapped on rice chromosome 9. *Mol. Breed.* 2:219–22.