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Generation mean analysis for submergence tolerant and yield traits in rice

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Abstract

Prior information on genetics and gene action of desirable traits in parents is prerequisite for development of strategies of breeding programs of the crop plants. The components of genetic variation are crucial factors determines destiny of breeding. Assessing genetic variation among genotypes to be utilized as parent in crossing program is paramount importance in harnessing accelerative genetic gain with precision. Results of the study shown the that numbers of gene involvement in breeding value, additive (d) effect and dominant \times dominant (l) gene interaction were the only significant portion of gene controlling plant height, number of effective tillers, grain yield per plant, spikelet fertility and percent survivability under submergence stress. The additive and dominance gene effects were found important in managing submergence stress in rice. The plus sign in the additive gene effect implies that rice variety Hasanta contributes positively to the trait as compared to Swarna Sub1 and *vice versa*.

Keywords: Generation mean analysis, scaling test, epistatic, gene action

Introduction

Rice (*Oryza sativa* L.) is prime source of livelihood in Asian countries, grown extensively across the regions and ecosystems in the world. In Asia, it covers ~50% of the area and ~90.4% of the whole rice production for ~ 2.7 billion peoples (Rout *et al.*, 2020) [28]. In addition, this sole crop provides employment for billions of people directly/indirectly (Dat, 2004). India has largest area (44.6 mha) under rice crop and ranked 2nd in production after China (Verma *et al.*, 2016) [4]. Rice has played great role in apprehension of 'Green Revolution' in the country (Kumar *et al.*, 2019) [17]. However, changing climate and demographic scenario (~9.0 billion people by 2030) creating challenge towards meeting food demand across the world which necessitates further breeding attention (Gurdev, 2006) [7]. In addition to that, the water scarcity, decreasing arable land, resurgence of minor insect pests and diseases coupled with climate changes going to be great challenge for sustainable rice production.

Frequent occurrence of abiotic stresses like submergence, drought and salinity are the most detrimental for rice production in rainfed ecosystem (Sekar and Pal 2012) [32]. Submergence due to flash flooding (FF) is third important abiotic stress in rainfed ecologies, hampers sustainability of crop plants and causes huge yield loss, annually (Iftekharruddaula *et al.*, 2015) [11]. In India, ~36% of the rice area are submergence prone, of that ~90% are distributed in eastern states where rice is major commodity of livelihood (Pradhan *et al.*, 2015) [23]. Being semi-aquatic in nature, rice plant is able to modulates in various ways to sustain under submergence (Khush *et al.*, 1997) [14]. However, intense and prolonged submergence is fatal for its substantiality (Kumar *et al.*, 2021) [16]. Submerged plant canopy faces several challenges like energy shortage, nutrient and oxygen deficiency which affects proper plant growth and survival (Pradhan *et al.*, 2019) [24]. Besides, submergence creates very conducive environment for the growth of several biotic stresses like bacterial blight (BB) and sheath blight which makes havoc to the rice sustainability under rainfed shallow-lowland. Changing climate scenario looking very distressing, predicting severe and frequent flooding down the line in coastal regions (Sanchez *et al.*, 2000) [30].

Development of climate resilient and multiple disease resistance cultivars found to be substantial to combat rice yield losses (Ronald *et al.*, 1992, Das *et al.*, 2016) [27]. Rice plants has inbuilt ability to sustain flooding up to one week (Adkins *et al.*, 1990, Palada *et al.*, 1972) [1, 22], however, beyond that only tolerant genotypes can survive (Catling *et al.*, 1992) [3].

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Tolerant plants make several adaptive changes to sustain under hypoxia/anoxia without major damage (Pradhan *et al.*, 2019 [23], Samanta *et al.*, 2020 [29], Sarkar *et al.*, 2014 [31]). Tolerant plants are able to manipulate synthesis/secretion of several plant growth regulators like ethylene, gibberellic acid (GA), abscisic acid (ABA) which regulates shoot elongation and leaf senescence, thus, enhances plant survival under flood (Rajpurohit *et al.*, 2011). Tolerant plants are able to switch on alcohol dehydrogenase (ADH) activity which controls judicious energy consumption and enhances plant survival under submergence (Kumar *et al.*, 2021) [16].

In rice, genomic blocks regulating adaptive modulations under flooding have been identified, validated and successfully deployed in several suitable genetic background (Singh *et al.*, 2016, Rout *et al.*, 2020) [33, 28]. The *Sub1* gene controlling two weeks' tolerance is mapped on chromosome-9 along with other minor QTLs in the Indian rice landrace FR13A (Xu *et al.*, 1996 and 2006) [37, 36]. In this context, genomics based improvement of plant resistance/tolerance has been proven as most promising strategies towards development of sustainable cultivars. Identification of suitable donors with nature of genetics and gene action with close genetic proximity and duration with recurrent parent is paramount important for precise and fast development of climate resilient cultivars. This study is aimed at assessment of genetics and gene action of traits contributing tolerant as well as yield under submergence for their judicious utilization in breeding programs. Generation mean analysis is used to determine the gene action governing quantitative traits, extent of additive, dominance and epistatic effects for designing appropriate breeding strategies.

Materials and Methods

The experiment was laid down at research farm of ICAR-National Rice Research Institute, Cuttack during both seasons from Kharif 2019 to Kharif-2021. The well fertile land with good irrigation and drainage facilities was selected to conduct the trials. The experimental plot was alluvial loam which is supplemented with per hectare 120 kg N, 60 kg P₂O₅ and 40 kg K₂O during both seasons. The F₁s were generated between Hasanta and Swarna *Sub1* (Submergence tolerant) where Hasanta was used as female. During Kharif, 2021 all crosses including F₁, BC₁, BC₂ and F₂ along with both parents, P₁ and P₂ were grown in three replications in RBD fashion. Twenty

days old seedlings of each generations and parents were grown in screening tank in three row with 22 plants per row at 20cm x 15 cm spacing. Subsequently, complete submergence was imposed for 14 days with 1.5-meter water depth. After fourteen days of submergence, water was removed from the tanks and regeneration was recorded after one week (IRRI, 2014) [12]. The data were recorded on five plants from each of the entries for the characters namely: days to 50% flowering (DFF), days to maturity (DM), plant height (PH), flag leaf length (FLL), flag leaf width (FLW), number of effective tillers per plant (NETPP), panicle length (PL), panicle weight (PW), number of grains per panicle (NGPP), number of chaffs per panicle (NCP), Spikelets fertility % (SF%), test weight (TW), grain yield per plant (GYPP) and % survival (% S). Data on agro-morphological and % survival traits were recorded after each one week of submergence (0, 7, 14 and 21 days) on randomly selected ten plants t in each generation.

Statistical Analysis

Analysis of variance was performed by using procedure of randomized block design analysis given by Panse and Sukhatme (1967), for all six generations. Scaling test was followed for estimation of genetic component of variation for studied traits (Mather, 1949 and Hayman and Mather, 1955) [19, 8]. Six parameter model (Hayman, 1958 and Jinks and Jones, 1958) [10, 13] was analyzed for all possible genetic components of variation. The 'weighted least square method' was utilized for estimation of the genetic parameters, m, d and h (Nelder, 1960 and Hayman, 1960) [21, 9]. Above estimates were utilized for calculation of expected generation means which compared the observed generation mean values by using χ^2 test. The significant χ^2 value indicates the non-adequacy of model and presence of non-allelic interactions.

Result and Discussion

Analysis of variance

The analysis of variance revealed that all six generations (F₁, BC₁, BC₂, F₂, P₁, P₂) under submergence stress differed significantly for all the traits (Table 1). It evidenced from analysis of variance that lines and treatments showed significant variation for all traits under all submergence regimes. Similarly, significant difference among lines for yield traits under submergence was reported by Rao *et al* 2017 [26].

Table 1: Analysis of variance for Agro-morphological traits in 11 rice genotypes under different submergence (0, 7, 14, 21 days) regimes

Source of variation	DF	DFF	DM	PH(cm)	FLL (cm)	FLW (cm)	NETP P	PL (cm)	PW (g)	NGP P	NCP	SF%	TW	GYPP (g)	KL (mm)	KW(m m)	L/B Ratio	HRR %	SV%
Replication	2	0.66	26.85*	10.09*	0.18	2.25*	362.05*	131.34**	0.10	3.21*	414.4*	18.88*	363.74**	49.91*	0.89	15.63*	0.05*	11.35*	22.50*
Genotype (a)	10	226.67**	357.81**	132.85**	28.74*	0.027*	6.49**	20.35*	11.61*	607.4**	341.75**	24.90*	10.34*	131.84**	0.549*	0.070*	0.671*	29.20**	490.73
Treatment (b)	3	0.94*	7.44**	17.98*	2.15*	4.47**	2207.40**	1328.91**	136.00**	1.31*	351.67**	236.10**	921.39**	39.95*	9.36*	11.45*	7.53**	2.38*	15.66**
a x b	30	15.44**	97.17*	171.24**	0.57	12.89**	105.30**	78.50*	100.12**	8.13*	42.23*	11.08*	101.89**	22.93*	8.22*	0.75	1.58*	9.36*	28.34**
Error	88	4.24	5.06	26.10	1.69	0.005	1.26	0.582	0.56	62.33	39.727	6.07	3.86	0.48	0.008	0.007	0.023	2.47	9.75

Estimates from scaling tests

The gene action of the traits undertaken in this study were investigated based on simple additive × dominance model to understand the pattern of the gene action of the target trait (*Sub1*) as well as basic traits of Hasanta to be recovered in end product (Table-2). The scaling test showed all scale, A, B,

C and D were significant for almost all the traits except panicle weight (B, C and D), Number of chaffs per plant (A, B and D), spikelets fertility percent (A and B), test weight and grain yield per plant (A, C and D), Kernel length (B, C and D), Kernel width (A, B and D), L/B ratio (A, C and D), HRR% (A, B and C). The all studied traits indicates the

presence of non-allelic interaction. All the basic traits like duration, plant height, fertility, grain type and value added trait, submergence tolerance were significant in more than

three scales or in combination indicates the presence of epistatic between the genes responding these traits.

Table 2: Scaling test and generation mean analysis for yield, quality and submergence traits in the parents P1, P2 and combinations F1, F2, B1 and B2 of Hasanta/Swarna Sub1

Traits/ Parameters	Scaling test				Generation mean analysis						X ² test
	A	B	C	D	m (Hayman)	d (Hayman)	h (Hayman)	i (Add × Add)	j (Add × Dom)	l (Dom × Dom)	
DFP	12.48**	1.22**	3.71**	2.32**	5.45**	22.65**	-15.55**	-1.82	18.65**	17.25**	142.13**
DM	16.45**	10.09**	-25.50**	-22.52**	49.21**	-16.01**	12.34**	57.74**	-2.9	2.17**	1604.87**
PH(cm)	13.6**	8.08**	-4.30**	22.36**	52.78**	2.92**	2.95**	3.18**	4.91**	23.42**	872.33**
FLL (cm)	37.89**	27.34**	24.32**	10.6**	31.07**	52.59**	1.78**	2.81**	-5.03**	1.69**	1034.27**
FLW (cm)	13.55**	-12.7**	15.08**	8.12**	1.44**	54.72**	37.89**	24.65**	13.88**	24.01**	1436.02**
NETPP	8.25**	6.88**	7.29**	-22.54**	11.44**	27.67**	-0.42	0.16**	-11.64**	4.88**	659.25**
PL (cm)	28.25**	48.17**	12.00**	8.66**	52.61**	4.13**	3.79**	-1.72	2.5**	85.33**	1120.45**
PW (g)	-4.11	23.65**	15.6**	0.48**	4.08**	12.08**	12.47**	5.18**	-0.18	1.55**	183.9**
NGPP	4.56**	23.4**	4.18**	10.75**	1.55**	1.88**	12.9**	5.19**	0.98**	1.09**	427.25**
NCPP	6.1**	-11.5**	-2.34	33.68**	49.93**	3.9**	3.75*	7.6**	-7.39**	17.71**	1955.85**
SF%	4.58**	0.6**	-0.48	-0.85	-14.87**	18.28**	-25.1**	23.42**	-1.98	-2.44	642.14**
TW	0.82**	-0.22	1.25**	1.57**	1.22**	2.85**	-3.65	-1.65	-0.31	1.86**	120.82**
GYPP (g)	0.36**	0.08	0.10**	0.09**	0.25**	1.62**	0.68**	-0.28	-0.14	0.87**	634.21**
KL (mm)	0.018	2.48**	2.03**	12.6**	12.56**	9.63**	4.55**	0.65**	22.9**	3.84**	244.085**
KW(mm)	6.24**	54.36**	-2.80	7.55**	61.25**	-4.87	3.21**	-1.62	2.038**	35.43**	953.57**
L/B Ratio	1.15**	-0.11	0.42**	0.17**	2.58**	1.47**	2.35**	1.98**	0.87**	1.68**	56.47**
HRR%	8.45**	33.08**	7.25**	-2.44	22.78**	-2.55	40.9**	-2.44	-8.56**	1.76**	139.6**
%SV	10.08**	10.95**	1.86**	3.95**	8.06**	7.22**	47.56**	4.36**	14.7**	0.92**	1208.52**

In addition, goodness of fit of this model was confirmed by chi-square analysis. The abundance of simple additive-dominance model suggests the absent of non-allelic interaction effect (epistasis) and means value of different generations depends only on additive × dominance gene interaction or effect of the gene. The chi-square analysis showed that all the 19 studied traits of cross derivatives of Hasanta and Swarna Sub1 had significant value, indicates existence of epistatic effect among these traits. The results of this study revealed that the data does not fit into simple additive × dominance model; role of epistatic is prevalent which is not fit into three parameter model, hence further subjected for six-parameter model analysis.

Six-parameter analysis

Digenic non-allelic interaction model consisting six parameters, m, d, h, i, j and l showed adequacy of the epistatic model to explain the gene action in the traits days to fifty percent flowering, days to maturity, plant height, flag leaf length, flag leaf width, number of effective tillers, panicle length, panicle weight, spikelets fertility, test weight, grain yield per plant, quality traits and percent survivability. The gene effect value was clearly illustrated the high variation among the observed agro-morphological traits (Table-2). The means and additive components for all studied traits were found highly significant.

The six-parameter analysis of Hasanta/Swarna Sub1 revealed the dominance (h) and dominance × dominance (l) gene interaction or effects opposite signs for the traits *viz.*, days to fifty percent flowering, number of effective tillers per plant and test weight were fit into the duplicate type of epistatic. Whereas, values of most of the traits showed same sign for h and l scale were fit into complementary non-allelic model.

The type of the gene interactions is depending on weight and sign of the estimates of 'h' and 'l' scale or effects in the case

many genes pair interacting. The sign of the estimates of 'd' and 'h' scale indicates about the parent which involves high number of genes for a trait. The additive effects and dominant × dominant (l) interaction are found to be significant part of gene controlling grain yield and spikelets fertility in rice. The results of this study revealed that additive and dominance effects were substantial in expression of submergence tolerant in rice. The plus sign of additive gene effect infers that Hasanta contributes positively to the trait. The positive sign for the scale 'd' was in most of the traits except days to maturity, kernel length and HRR%, whereas, it was recorded negative 'h' in the traits days to fifty percent flowering, number of effective tillers, spikelets fertility and grain yield per plant (Table-1).

Characterizing genetics of the yield and contributing traits is prerequisite for planning successful breeding strategies in crop plants. The fundamental concept for analyzing genetics and gene action in crop plants is based on 'generation mean analysis' (Hayman, 1958 and Jinks and Jones 1958) [10, 13] which can detect epistasis/non-allelic effect of genes. It is reported that additive and dominance and epistatic effects contributes substantially towards mean of the population (Viana, 2000) [35]. Though, epistatic effects creates biasness in the estimation of additive and dominance components which depends mainly on the relative values of epistatic. Analyzing epistasis is very critical, hence analyses priorly before advance estimation for gene effect.

The traits studied were significant for more than two scale representing the presence of non-allelic interactions among the genes. The abundance of simple additive-dominance-model advocates the absent of epistasis effects. The means value of different generations is depending on additive × dominance gene interaction or effect. The chi-square test showed all 19 traits of the Hasanta/Swarna Sub1 derivatives (all six generations) were significant which indicates presence

of epistatic among these traits. This finding has full corroboration with the findings of Mahalingam and Nadarajan, 2010; Gnanamalar and Vivekanandan, 2013; and Kiani, 2013^[18, 6, 15].

Epistatic model with six-parameters revealed that it was adequate to elucidate the gene action in most of the traits studied. The assessed gene effect evidently explains the high variation in all traits. The mean and additive variances for days to fifty percent flowering, days to maturity, plant height, number of ear bearing tillers, panicle length, number of grain per panicle, spikelets fertility, test weight, grain yield per plant, % survivability, head rice recovery, kernel length, kernel breadth, and kernel L/B ratio were highly significant (Murugan and Ganesan 2006)^[20]. These results are in conventionality with the previous findings of Kiani *et al.* (2013)^[15] and Divya *et al.* (2014)^[5] for plant height, number of tillers, panicle length, days flowering, etc. It is found in this study that genic effects were cross-specific and fits to the complementary recessive interaction for most of the traits (Thirugnanakumar *et al.*, 2007, Divya *et al.* 2014)^[34, 5].

The result of our study has full corroboration with the findings of Divya *et al.* (2014)^[5] who has reported complementary interaction for most of the quantitative traits.

Conclusion

The results of this study has revealed the presence of high number of genic factors are involved in breeding value. Additive (d) effect and dominant × dominant (l) epistatic were the significant part of gene controlling grain yield per plant, spikelet fertility and survivability under submergence. The additive and dominance genic effects were found substantial in controlling submergence tolerance in rice. The plus sign in the additive gene effect implies that Hasanta contributes positively than the Swarna.

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