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Research Article

Generation mean analysis for yield and submergence tolerance in high yielding varieties of rice (*Oryza sativa* L.)

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Abstract
An investigation in rice (*Oryza sativa* L.) was carried out by utilizing two cosmopolitan rice varieties of Tamil Nadu namely ADT 43 and Improved White Ponni along with the donor submergence tolerance FR13A to reveal the genetics and gene action for submergence tolerance. The generation mean study was done by developing six generations *viz.*, P_1, P_2, F_1, F_2, B_1 and B_2 for two cross combinations namely ADT 43 × FR 13A (Cross 1), IWP × FR 13A (Cross 2).Gene action studies for submergence tolerance through generation mean analyses revealed that all the yield and yield component traits under submergence condition were mostly influenced by dominance gene action, except for number of filled grains per panicle, total number of grains per panicle and spikelet fertility in cross 1. Regarding 1000 grain weight epistatic gene action was predominant in cross 1. In cross 2, dominant gene action alone was predominant for the trait number of productive tillers per plant whereas, the epistatic gene effects were predominant for the traits number of filled grains per panicle and total number of grains per panicle. The traits, days to flowering, plant height, number of tillers per plant, spikelet fertility, 1000 grain weight and single plant yield were controlled by additive, dominance followed by epistatic gene action. The generation mean analysis also revealed that number of filled grains per panicle, 1000 grain weight and single plant yield in cross 2 under submergence condition were much influenced by different types of gene action *viz.*, additive, dominance and epistasis with complementary epistatic interaction. These crosses would be utilized for yield improvement through single plant selection in segregating generations. To obtain desirable segregants, the appropriate breeding method would be bi-parental mating or one or two cycles of recurrent selection followed by pedigree breeding will be effective and useful method to obtain expected improvement in rice under submergence tolerance.

Key words
Generation mean analysis, epistasis, additive gene action, submergence tolerance

Introduction

Rice (*Oryza sativa* L.) is the staple food crop and consumed by more than 50 per cent of the global human population (Mohanty 2013). The current status of the global rice production is 495.63 million tonnes (MT) (2016-2017) which was increased only nine MT in the preceding four year block (2011–2014) as compared to 80 MT increase in two such four year blocks during 2004–2011. In contrast, the global population is projected to increase by 25 % (9.2 billion) by 2050 (Schroeder *et al.* 2013). The reason for the marginal increase or decline in rice production is due to biotic and multiple abiotic stresses like flood, salinity, drought etc. Rice is a semi aquatic species which is generally cultivated under partially flooded condition. It is the only cereal that can be grown in flood prone ecosystem. However, uncertain rainfall is a major factor in India and Bangladesh; the challenges facing rice production in this areas are becoming ever more intricate with the enduring adverse climate changes and the ensuing increase in storms and sea level rise in coastal areas, where rice-based systems predominate.

Rice adapts to adverse condition depending upon the nature of flood or water level. Quiescence and elongation (escape) are the two different strategies by which rice adapts to water level. In deepwater areas, water level is usually increases gradually throughout the year and it can remain above 50 cm for longer periods. Rapid elongation ability is necessary for plants to keep up with rising water level. On the other hand, quiescence occurred when flash flood cover the entire rice plants for longer period. Deep water rice responds to submergence by promoting internode elongation, whereas, submergence tolerant lowland rice prevents elongation growth and optimize carbohydrate reserves so as to enable the development of new leaves upon de submergence.

The yield loss due to submergence was also observed in recent years due to unexpected rain and

flood throughout the world because of the climate change. Submergence stress is considered as a major challenge for rice production in South and Southeast Asia, causing annual loss of over one billion US dollars (Xu *et al.* 2006 and Khanh *et al*. 2013). Every year over 20 million ha in rainfed lowland areas are adversely affected by floods. Rice in theseareas is the major crop providing food for millions of subsistence farmingfamilies. South and Southeast Asiaare subjected to either frequent flash floods or submergence, longer-term flooding of 20-50 cm (partial/stagnant, semi-deep), deep water of more than 100 cm (deepwater rice) or very deep water of 3 to 4 meters, as in floatingrice areas. Thus, submergence, drought, and the sequential events (submergencefollowed by drought and *vice versa*) are the major constraints under rice production in rainfed lowlands (Mackill *et al*. 2010).

Materials and Methods

A major QTL (*Sub1*) explaining about 70% of phenotypic variation in submergence tolerance has been identified and fine mapped on chromosome 9 in the submergence tolerant cultivar FR13A (Xu and Mackill 1996, Nandi *et al*. 1997 and Xu *et al.* 2000). Three related ethylene response factor (ERF)-like genes at this locus were identified, *Sub1A*, *B* and *C*, although japonica cultivars and some indicas do not have the *Sub1A* gene (Xu*et al*. 2006). *Sub1A* and *Sub1C* were up-regulated by submergence and ethylene (Fukao *et al*. 2006). *Sub1A* was strongly induced in the tolerant cultivars in response to submergence, whereas intolerant cultivars had weak or no induction of the gene. Over expression of *Sub1A* conferred submergence tolerance in an intolerant japonica cultivar and down-regulation of *Sub1C* (Xu *et al.* 2006). The *SUB1* is a robust quantitative trait locus which has been mapped from submergence tolerant landrace FR13A. Tolerance in these varieties is controlled by the *SUB1* locus on chromosome 9 (Xu and Mackill 1996), which includes three ethylene response factor (ERF)–like genes (*SUB1A*, *SUB1B*, *SUB1C*) (Xu and Mackill 1996, Xu *et al*. 2006). The major determinant of submergence tolerance is the *SUB1A* gene (hereafter referred to as *SUB1*) (Xu *et al*. 2006 and Septiningsih *et al*. 2009).

The six generations *viz.*, P_1, P_2, F_1, F_2, B_1 and B_2 of the two cross combinations (cross 1 (ADT 43 x FR 13A) and cross 2 (IWP x FR 13A)) were raised in nursery bed. Twenty five days old seedlings were transplanted to main field at Agricultural College and Research Institute, Madurai in Randomized Block Design under submerged condition of 40 cm depth with two replications, adopting a spacing of 20cm between rows and 15cm between plants. The parents along with F_1, F_2, B_1 and B_2 were transplanted in the main field at the water level of 40 cm. The water level was monitored periodically and maintained for 14 days. After 14 days of complete submergence, the field was de submerged and survival of the plants was scored after 14 days of recovery.The scoring was done as per the standard evaluation system of rice (SES) developed by IRRI (1988) based on the per cent plant survival (PPS). Ten plants each in P_1, P_2 and F_1, 250 plants in F_2 and 150 plants each in B_1 and B_2were maintained for each cross per replication for the study. The phenotypic scoring was done at 21 days after de submergence of water as per the standard evaluation system of rice (SES) developed by IRRI for submergence in all the six generations. Observations were recorded on biometrical traits in all the available plants in P_1, P_2, F_1, F_2, B_1 and B_2 generations.

Result and Discussion

The greatest merit of generation mean analysis is that it helps in the estimation of epistatic gene effects namely additive × additive (i), additive × dominance (j) and dominance × dominance (l). Generation means analysis (Mather and Jinks, 1982) is a useful technique that provides the estimation of main genetic effects *viz.*, additive, dominance and their digenic interactions involved in the expression of quantitative traits.The nature of gene action governing the inheritance of yield and its components was therefore studied using generation mean analysis.The estimates of mean for six generations was carried out for P_1, P_2, F_1 F_2 B_1 and B_2, the scaling tests (A, B and C scales) and the gene effects *viz*., additive, dominance and epistatic interaction for the crosses namely cross 1 (ADT43 x FR13A) and cross 2 (IWP x FR 13A) under submerged environment. Based on the results obtained for yield and its attributing traits under submergence condition the results are furnished (Tables 1 and 2).

The generation mean analysis was carried out in selected two crosses obtained from the hybridization programmes. The variation among the means of different generation in all the ten characters studied suggesting the usefulness of the estimation of additive, dominance and epistatic interaction. Significant differences among six generation means were noticed for for days to 50 per cent flowering, plant height, number of tillers per plant, number of productive tillers per plant, panicle length, number of filled grains per panicle, total number of grains per panicle, 1000 grain weight and single plant yield.

The A, B and C scaling test for almost all the characters in the two crosses showed that atleast

one, two or all the three scales were found significant indicating the presence of non-allelic interaction in the inheritance of the characters under study. However, the character number of productive tillers per plant of cross 2 showed non-significant values for all the three scales indicating the non-interacting mode of inheritance. Any one or both the scaling tests were found to be significant in all the traits indicating the presence of epistasis (Table 1).

In cross 1 and 2, the scaling test revealed that, all the three scales *viz.*, A, B and C were significant for all the characters studied under salinity condition except for number of productive tillers per plant in cross 2. Hence, a simple additive-dominance model was inadequate to explain the above crosses except for number of productive tillers per plant in cross 2.The type of epistasis was determined as complementary when dominance (h) and dominance × dominance (l) gene effects have same sign and duplicate epistasis when the sign was different. Hence, the present study shows that significant additive and epistatic effects exist in all the six generations.A or B or all the three scaling was found significant for all the traits except number of productive tillers in cross 2 (Table 1).Both the crosses exhibiting non-allelic interaction for inheritance of almost all the traits studied. In general, the interaction effect together i.e., additive × additive (i) and dominance × dominance (l) found in higher magnitude than the combined main effects of additive (d) and dominance (h) effects for all the traits in both the crosses.

Studies on gene effects in generation mean analysis revealed that additive gene effect (d) was significant in cross 1 for the traits days to flowering, number of tillers per plant, number of productive tillers per plant, number of filled grains per panicle, total number of grains per panicle, spikelet fertility and single plant yield (Table 2).The predominance of additive gene action for days to flowering was earlier reported by RitheshBalan (2005), Anbumalarmathi (2005) and Kumar *et al.* (2007).The results are in accordance with the earlier findings of Gnanasekaran*et al.* (2006) and Senthil Kumar (2012) with the presence of non-additive gene action operating the trait number of tillers per plant.

The dominance gene effect (h) was significant in cross 1 for the traits days to flowering, plant height, panicle length,number of tiller per plant, number of productive tillers per plant and single plant yield whereas in the case of cross 2 it was observed significant effect for all the traits studied except number of filled grains and total number of grains per panicle.Dominance gene effect for number of productive tillers plant was earlier reported by Kumar et al (2007) and Priya (2003) and for the trait number of filled grains per panicle was reported by Subbulakshmi*et al.* (2016) and Kannan and Ganesh (2017).

The additive × additive (i) interaction effect was significant in cross1 for the traits days to flowering, plant height, panicle length, number of productive tillers per plant and single plant yield but in the case of cross 2 the significant effect was noticed for all the traits except plant height (Table 2). These results were in conformity for the trait number of productive tillers per plant, Robin (1997) for the trait number of grains per panicle, Kumar et al (2007), and Robin (1997), Yogameenakshi (2002).Additive gene action for single plant yield was noted by Panwar (2005), Sanjeev Kumar *et al.* (2005), Anbumalarmathi (2005) and Kumar *et al.* (2007), while non-additive gene action was registered by Mahalingam (2003), Priya (2003), Malini*et al.* (2006), and Raju *et al.* (2006) to govern the trait single plant yield.

The dominance × dominance (l) interaction effect had significant effect in cross 1 for all the traits whereas in the case of cross 2 the 1000 grain weight and single plant yield were observed non-significant (l) effect (Table 2). Similar results were earlier reported number of grains per panicle (Robin, 1997), 1000 grain weight (Mahalingam, 2003) and for grain yield (Kumar *et al.*, 2007). The dominance (h) and dominance × dominance (l) had opposite sign in cross 1 for all the traits (Table 2). It indicated the presence of duplicate dominance epistasis. In the cross 2 the predominance of duplicate epistasis was noticed from opposite sign of (h) and (l) for the expression of days to flowering, plant height, panicle length, number of tillers per plant, total number of grains per panicle and spikelet fertility. In cross 2 the traits number of filled grains per panicle, 1000 grain weight and single plant yield showed the presence of complementary type of epistasis (Table 2).

It could be noted that the presence of additive, dominance, additive × additive, additive x dominance and dominance × dominance interaction effects were present along with either duplicate dominant epistasis or complementary recessive epistasis for grain yield and most of its contributing traits. Hence, selection in the early segregating generations may not give desirable recombinants. Therefore selection may be delayed to later segregating generations when the dominance and epistasis disappear and resorting to intermating of segregants followed by recurrent selection.

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duplicate dominant epistasis or complementary recessive epistasis for grain yield and most of its contributing traits. Hence, selection in the early segregating generations may not give desirable recombinants. Therefore selection may be delayed to later segregating generations when the dominance and epistasis disappear and resort to intermating of segregants followed by recurrent selection.

Both additive and dominance gene actions play major role in several characters. In such circumstances biparental mating design or reciprocal recurrent selection can be followed for further recombination of alleles to produce desirable segregants. These methods can also be well adopted in order to harness the epistatic interactions by way of breaking the undesirable linkages. Diallel selective mating system proposed by Jensen (1970) could also be followed to break such undesirable linkages between two or more genes and to produce desirable recombinants.

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Table 1. Scaling test of quantitative traits of two crosses for submergence tolerance in rice

Crosses/scales	Cross 1 (ADT43 x FR13A)	Cross 2 (IWP x FR13A)
Days to flowering		
A	-14.96*±0.99	-14.47*±1.11
B	-9.48*±1.19	11.77*±0.98
C	33.80*±1.55	14.82*±1.90
Plant height (cm)		
A	-10.82*±1.42	-9.56*±1.13
B	-11.88*±1.38	21.10*±1.15
C	33.58*±2.56	9.78*±1.56
Panicle length (cm)		
A	0.08 ± 0.64	-0.10 ± 0.55
B	2.40*± 0.67	1.93*± 0.65
C	0.54 ± 0.99	-1.45 ± 0.89
Number of tillers per plant		
A	0.12±0.99	2.34*±0.88
B	-0.95±0.78	0.58±0.76
C	4.05*±1.42	-3.24*±1.24
Number of productive tillers per plant		
A	1.69*±0.75	0.70 ±0.59
B	-1.12±0.60	0.34±0.55
C	5.13*±1.14	-1.44±0.88
Number of filled grains per panicle		
A	-64.52*±7.94	-105.56*±14.11
B	-32.60*±6.81	38.08*±11.99
C	-66.20*±15.80	-5.04±14.47
Total number of grains per panicle		
A	-40.11*±8.26	-129.50*±15.28
B	-35.98*±7.03	49.32*±13.08
C	-49.65*±16.03	33.78*±16.42
Spikelet fertility (%)		
A	-17.34*±2.71	1.43±1.32
B	-1.83±1.82	-0.51±1.85
C	-15.83*±3.95	-10.79*±2.61
1000 grains weight (g)		
A	2.63*±0.97	4.58*±0.47
B	-6.43*±0.59	-10.33*±0.50
C	-3.76*±0.95	-10.76*±0.94
Single plant yield (g)		
A	-5.19*±2.56	-5.64±3.49
B	-19.01*±1.99	-10.13*±2.77
C	-5.30*±4.60	-25.10*±3.95

***Significant at 5% level**

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Table 2. Genetic components of generation mean for quantitative traits for Submergence tolerance in rice

Genetic effects	Cross 1 (ADT43 x FR13A)	Cross 2 (IWP x FR13A)
Days to flowering		
m	100.80*±0.31	109.98*±0.37
(d)	-2.04*±0.67	-1.32*±0.56
(h)	-51.14*±1.90	-4.77*±1.96
(i)	-58.24*±1.84	-17.52*±1.86
(j)	-2.74*±0.73	-13.12*±0.66
(l)	82.68*±3.12	20.22*±2.94
Plant height (cm)		
m	111.67*± 0.47	117.77*± 0.21
(d)	-0.92±0.69	-3.98*±0.56
(h)	-45.13*±2.50	11.41*±1.57
(i)	-56.28*±2.35	1.76±1.43
(j)	0.53±0.87	-15.33*±0.74
(l)	78.98*±3.76	-13.30*±2.75
Panicle length (cm)		
m	21.98*±0.12	22.02*±0.13
(d)	0.03±0.29	0.51±0.28
(h)	3.15*±0.88	4.90*±0.87
(i)	1.94*±0.77	3.28*±0.79
(j)	-1.15*±0.40	-1.01*±0.39
(l)	-4.42*±1.52	-5.11*±1.46
Number of tillers per plant		
m	14.30*± 0.24	12.19*± 0.18
(d)	1.16*± 0.457	1.38*± 0.41
(h)	-4.05*± 1.42	6.66*± 1.22
(i)	-4.88 ± 1.32	6.16*± 1.12
(j)	0.53 ± 0.55	0.88*± 0.51
(l)	5.71*± 2.32	-9.08*± 2.08
Number of productive tillers per plant		
m	12.37*± 0.18	8.5*2 ± 0.87
(d)	0.98*± 0.34	0.30 ± 0.19
(h)	-2.93*± 1.09	6.20*± 2.27
(i)	-4.56*± 1.00	-
(j)	1.40*± 0.39	-
(l)	3.99*± 1.79	-
Number of filled grains per panicle		
m	137.00*± 3.63	228.34*± 3.05
(d)	12.34*± 4.62	1.98 ± 8.70
(h)	-15.72 ± 17.49	13.86 ± 21.62
(i)	-30.92 ± 17.21	-62.44*± 21.27
(j)	-15.96*± 4.87	-71.82*± 8.98
(l)	128.04*± 24.32	129.92*± 37.71
Total number of grains per panicle		
m	168.80*±3.60	279.02*±3.32
(d)	24.86*±4.67	-7.26±9.32
(h)	-5.26±17.55	-24.51±23.40
(i)	-26.44±17.20	-113.96*±22.90
(j)	-2.06±4.98	-89.41*±9.60
(l)	102.53*±24.63	194.13*±40.74
Spikelet fertility (%)		
m	80.61*±0.83	81.78*±0.48
(d)	-4.49*±1.39	3.137*±0.87
(h)	-4.34±4.48	12.73*±2.76
(i)	-3.34±4.36	11.71*±2.62
(j)	-7.75*±1.52	0.97±1.02
(l)	22.52*±6.83	-12.63*±4.37
1000 grains weight (g)		
m	18.10*±0.15	14.96*±0.12
(d)	0.36±0.50	1.85*±0.18
(h)	-2.45±1.23	2.70*±0.73
(i)	-0.03±1.17	5.02*±0.61
(j)	4.53*±0.51	7.46*±0.20
(l)	3.83*±2.22	0.71 ±1.19
Single plant yield (g)		
m	31.24*±0.92	36.71*±0.68
(d)	5.55*±1.24	6.13*±1.92
(h)	-11.33*±4.67	25.24*±4.93
(i)	-18.90*±4.47	9.33*±4.72
(j)	6.91*±1.37	2.24±2.04
(l)	43.11*±6.78	6.44±8.67

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