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Inheritance of submergence tolerance in rice

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Summary

Inheritance of submergence tolerance in rice (*Oryza sativa* L.) was investigated in an 8 × 8 diallel cross. Duration to 50% mortality of the diallel populations (F_1's + parents) under completely submerged conditions at the seedling stage was used to characterize submergence tolerance instead of the usual submergence survival percentages.

A strong prepotency of parents was found in transmitting the character to their offspring. Additive and nonadditive gene effects were highly significant. Parents highly tolerant to submergence also had high gca effects, and F_1's between two tolerant parents were found to be the most tolerant of the diallel combinations. A high narrow-sense heritability was also observed.

The additive-dominance model was found valid for this diallel cross. Submergence tolerance was partially dominant over susceptibility and recessive alleles were more concentrated in the susceptible parents IR42 and IR11288-B-B-69-1.

Introduction

Some seven million hectares of naturally flooded rice land in south and southeast Asia may be classified, depending on the prevailing flooding depths during the main cropping season, as 'very deep' water (100 cm and above), and 13 million hectares are 'deep' (50 to 100 cm) (HilleRisLambers & Seshu, 1982). When semi-dwarf lowland rices are planted in the latter areas, they are frequently partly or completely submerged by abrupt flooding, causing drastic reduction in yield, or even total crop loss.

Complete submergence is tolerated for a limited time by both 'susceptible' and 'tolerant' rices. They do differ in that susceptible varieties are destroyed at a more rapid rate during total submergence than the tolerant ones (HilleRisLambers & Vergara, 1982). Incorporation of improved submergence tolerance could greatly improve the adaptation of varieties of rainfed lowland and deepwater rice.

The genetics of submergence tolerance is not entirely known: a few genetic studies have been made on tolerance to complete submergence in rice (Mohanty et al., 1982), and breeding for submergence tolerance has already started (HilleRisLambers et al., 1984). Knowledge of the genetics of submergence tolerance in rice will increase efficiency in breeding submergence tolerant varieties. But it is felt that there is a lack of suitable screening methods for genetic studies. The usual procedure of submerging parents and offspring for a predetermined period of 5–10 days often results in either universal survival, or wholesale destruction due to the incomplete predictability of relevant environmental factors that also influence submergence tolerance. For this reason, a range of treatments likely to include these extremes of survival and destruction and their utilization to derive a '50% lethal dose' measured in days was employed.

A second novel feature of the present work was the exclusive utilization of lines with improved plant type, some of them bred for submergence tolerance from the parents used in the aforementioned studies.

Materials and methods

In 1985, eight rainfed lowland rices which differed in their reaction to submergence (Table 1) were used to produce a diallel cross excluding reciprocals. The 28 F_1's + 8 parents were grown in a greenhouse. Ten days after germination, seedlings were submerged in 30 cm water. They were submerged for 5, 7, 9 and 11 days in two identical metal tanks. The experiment used a split-plot design with two replications. Duration of submergence was the main plot and genotypes, the sub plots. Water temperature was maintained at 30° C and light intensity was kept constant at 400 lux during submergence. After a 7-day recovery in a drained condition, a survival count was made for the four submergence durations. All entries died completely after submergence for 11 days. Duration to 50% destruction was calculated by linear interpolation between the two durations of submergence corresponding to the next higher and lower mortality than 50%. In some cases, less than 50% survival was recorded at the shortest duration (5 days) of the experiment. Where this happened, the estimation was made by assuming the next shortest duration (3 days) to have 100% survival – then subsequent interpolation. Genetic analyses followed the methods of Griffings (1956) and Hayman (1954).

Results and discussion

An analysis of variance indicated the presence of considerable genetic variation within the diallel populations for calculated duration to 50% mortality as an index of submergence tolerance (Table 2).

The longer mean duration of F_1's compared to that of parents (7.3 vs 6.9) indicated dominance in the direction of tolerance. The correlation between parental means and their offspring array means had a value r = 0.84**, suggesting a high prepotency of the parents in transmitting submergence tolerance to their progenies. Table 3 lists pertinent parental and F1 cross values for calculated duration (in days) to 50% mortality. Parents varied between 4.89 and 9.4 days. This range was exceeded by the F1's: 4.86–9.66.

Table 4 gives general and specific combining ability values of parents and crosses. As a group, the best-surviving parents of Table 3 also had the higher general combining abilities in Table 4. But the correlation was far from 100%: entry 5, with good survival in its own right, had poor combining ability compared to entries 3, 4, and 6. This latter group derives its submergence tolerance from

Table 1. Parents in the 8 × 8 diallel cross, their submergence tolerance ratings and origin.

Designation	sub tol[a]	Parentage
IR21567-16-2-2	MR	IR5857-4-1E-1/KLG6986-133-4P//IR2071-586-5-6-3
IR29012-4-1-3	MR	JAGANNATH/FR13A//IR42
IR31406-333-1	R	KURKARUPPAN/CR1002//IR13415-9-3
BKNFR76106-13-2	MR	IR1561-228-3-3/FR13A
IR8234-0T-9-2	MR	NAM SAGUI 19/IR1721-11-6-8//IR2061-213-2-16
BKNFR76106-16-0-1	R	IR1561-228-3-3/FR13A
IR11288-B-B-69-1	S	IR2071-625-1-251/LEB MUE NAHNG 111
IR42	S	IR1561-228-1-2/IR1737//CR94-13

[a] R = resistant. MR = moderately resistant, S = susceptible.

either FR13A or Kurkaruppan, both varieties renowned for this trait, whereas the submergence tolerance of entry 5 can not be attributed to any particular ancestor (Table 1), and its genotypic makeup for the trait is presumably different from (at least less dominant than) that of entries 3, 4 and 6. Of interest is also, that the longest submergence duration was obtained for the hybrid between two of these three best performing lines (entries 3 and 6). The analysis of variance for duration to 50% mortality showed highly significant effects of genotypes, but also of parents vs hybrids (Table 5). In this connection Table 3 indicates heterosis for long submergence duration, attributable to recombination with dominant submergence tolerance genes present in even susceptible varieties like entry 8.

Table 2. Analysis of variance of calculated duration as an index of submergence tolerance.

Source of variation	DF	SS	MS	F value
Total	71	161.31		
Replication	1	2.89	2.89	9.51**
Genotypes	35	147.77	4.22	13.88**
Parents	7	37.94	5.42	17.82**
Hybrids	27	107.81	3.99	13.12**
P vs H	1	2.02	2.02	6.65*
Error	35	10.85	0.30	

cv = 7.6%.

In the regression graph of array covariance and array variance, the position of the point intercept above the origin indicates partial dominance for submergence tolerance (Figure 1).

In the test for the validity of the additive-dominance model, the regression coefficient b was significantly different from zero and its deviation from unity was barely significant, indicating the presence of non-allelic interaction at a very low intensity. The t^2-test left intact the hypothesis of an additive-dominance model with independent dis-

Table 3. Mean of the calculated duration of submergence, array total (xi.), and array mean (x) in an 8 × 8 diallel cross in rice.

Parent	1	2	3	4	5	6	7	8	Xi.	Xi + Xii	X
1. IR21567-16-2-2	6.50	6.00	7.07	9.26	6.07	7.38	4.86	5.24	52.36	58.86	6.54
2. IR29012-4-1-3		5.57	7.55	8.68	6.55	7.70	5.48	6.24	53.75	59.31	6.72
3. IR31406-333-1			9.40	9.59	7.73	9.66	6.94	7.26	65.17	74.56	8.14
4. BKNFR76106-13-2				7.84	8.76	9.14	8.08	9.02	70.36	78.20	8.79
5. IR8234-0T-9-2					8.03	7.82	6.21	6.29	57.44	65.47	7.18
6. BKNFR76106-16-0-1						8.07	8.23	7.50	65.48	73.54	8.18
7. IR11288-B-B-69-1							4.89	4.86	49.54	54.43	6.19
8. IR42								5.10	51.50	56.60	6.44

X . . = Xij^2 = 260.47; Xij^2 = 1958.53; Xi + Xii^2 = 34514.67.
Grand Mean = 7.23; Mean of Parents = 6.90; Means of F_1s = 7.33.

Table 4. (gca) (diagonal) and (sca) (off diagonal) effects of calculated durations of submergence in an 8 × 8 diallel cross in rice.

Parent	1	2	3	4	5	6	7	8
1. IR21567-16-2-2	− 0.6264	− 0.0332	− 0.4882	1.3383	− 0.5687	− 0.0762	− 0.6797	− 0.5172
2. IR29012-4-1-3		− 0.5809	− 0.054	0.7178	− 0.0977	0.1983	0.1052	0.4373
3. IR31406-333-1			0.9441	0.0978	− 0.4873	0.6333	− 0.1752	− 0.0727
4. BKNFR76106-13-2				1.3076	0.1823	− 0.1912	0.2483	1.3238
5. IR8234-0T-9-2					0.0346	− 0.2622	0.0019	− 0.1282
6. BKNFR76106-16-0-1						0.8421	1.2218	0.2743
7. IR11288-B-B-69-1							− 1.0694	− 0.4542
8. IR42								− 0.8519

CD(gi–gj) = 0.3543; CD(Sij-Sik) = 1.0629; DC(Sij-skl) = 1.0022.

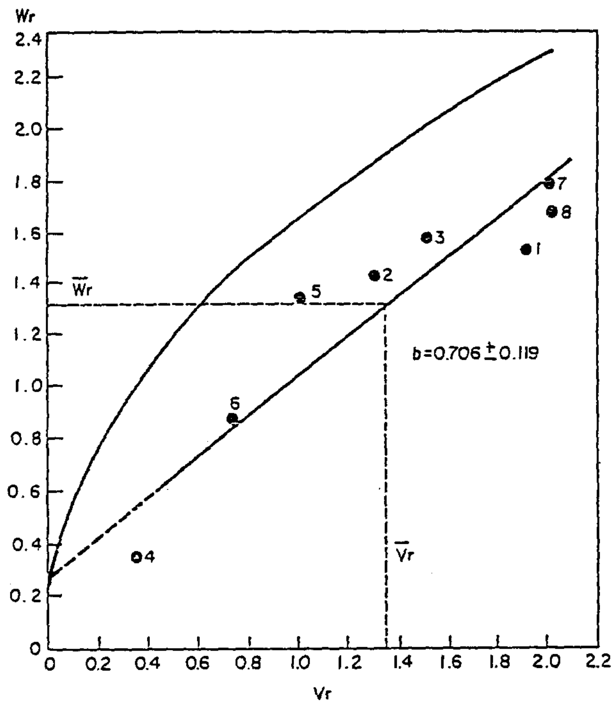

Fig. 1. Covariance (Wr)/Variance (Vr) regression graph of the submergence tolerance of rice in Study 2. The parents are (1) IR21567-16-2-2, (2) IR29012-4-1-3, (3) IR31406-333-1, (4) BKNFR76106-13-2, (5) IR8234-0T-9-2, (6) BKNFR76106-16-0-1, (7) IR11288-B-B-69-1, and (8) IR42.

tribution of genes among the parents for this diallel cross.

The estimated genetic components are given in Table 6, based on the calculating procedures given by Hayman (1954). Significance of the effects D and H_1 indicates the importance of both additive and dominant genetic effects, which supports the importance of general (gca) and specific (sca) effects in the combining ability analysis. These results are in agreement with those of Mohanty et al. (1982) who found both additive and non-additive gene effects highly significant for submergence tolerance in rice.

The estimate of dominance ratio (H_1/D) was 0.94, denoting partial dominance which was also supported by the graphic analysis. This result is not the same as that obtained by Mohanty et al. (1982) who found average dominance within the range of overdominance.

The proportion of the genes with positive and negative effects in the parents $H_2/4H_1$ was 0.13 which was less than the theoretical value of 0.25. This indicates a considerable degree of gene asymmetry over all loci, favoring the recessive alleles as evidence by the negative sign of F. The estimate of the ratio $\frac{\sqrt{(4DH_1)}+F}{\sqrt{(4DH_1)}-F}$ was 0.93, indicating that dominant and recessive genes were present in equal proportion in the parents.

The estimate of the ratio $\frac{h^2}{H^2}$ was 0.34, suggesting the involvement of one major gene or one block of genes showing dominance.

A high narrow sense heritability value (0.79) was obtained showing the importance of additive gene action in submergence tolerance. This agrees will with the result of Mohanty et al.'s inheritance study of submergence tolerance in rice (1982).

The correlation between the parental order of dominance (Wr + Vr) and the parental measurement of Yr was −0.58 (Figure 2). Except for parent 3, the higher submergence duration of the parents corresponds to lower (Wr + Vr) values, showing that the genes for tolerance (increasing alleles)

Table 5. Analysis of variance of submergence tolerance.

Source of variation	DF	SS	MS	F value
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Parents	7	37.94	5.42	17.82**
Hybrids	27	107.81	3.99	13.12**
P vs H	1	2.02	2.02	6.65**
Error	35	10.85	0.30	

Table 6. Estimated genetic components of variation.

Component	Std error	
D	2.522**	0.196
H_1	2.246**	0.451
H_2	1.196**	0.392
h_2	0.415	0.263
F	−0.163	0.463

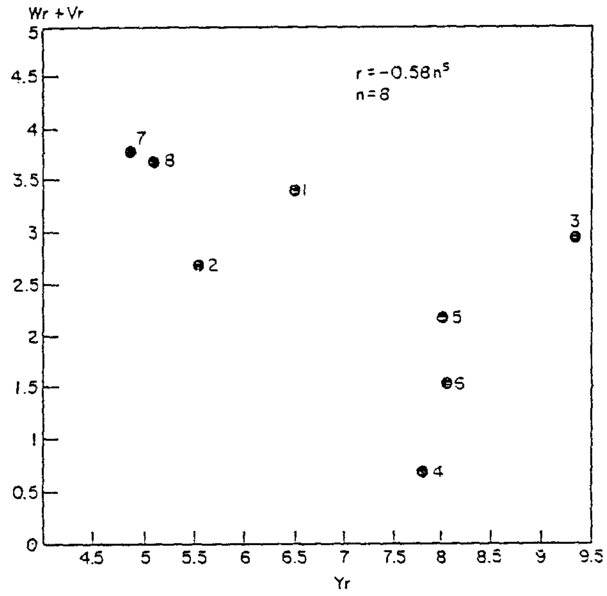

Fig. 2. Correlation of Parental Mean Yr with corresponding Wr + Vr showing the direction of dominance. The parents are (1) IR21567-16-2-2, (2) IR29012-4-1-3, (3) IR31406-333-1, (4) BKNFR76106-13-2, (5) IR8234-0T-9-2, (6) BKNFR76106-16-0-1, (7) IR11288-B-B-69-1, and (8) IR42.

were generally dominant. Mohanty et al. (1982) likewise found tolerance to be dominant.

Conclusions

Three parents, BKNFR76106-13-2, IR31406-333-1, and BKNFR76106-16-0-1, were the best: i.e., they took the longest time to arrive at 50% mortality. These parents with high values of submergence tolerance had high gca effects as well. Therefore, crosses between tolerant parents are recommended for faster improvement of tolerant varieties.

The high breeding value (heritability) recommends the utilization of better varieties for extensive crossing and selection in a conventional breeding program to improve varieties for submergence tolerance.

The significant dominance effect of genes suggests the potential use of hybrid rice in submergence-prone areas where production of hybrid rice is feasible.

The tolerant lines IR31406-333-1 and BKNFR 76106-16-0-1 showed high specific combining ability as well as high general combining ability effects. Therefore, and given the fact that the submergence tolerance of these two lines comes from two distinct parents and countries – Kurkaruppan from Sri Lanka and FR13A from India – the progenies from the cross between these two parents could be expected to give recombinations for higher submergence tolerance.

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