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Genetic analysis of salinity tolerance in rice (*Oryza sativa* L.)

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Summary. The genetics of salinity tolerance in rice was investigated by a nine-parent complete diallel including reciprocals. Test materials involved susceptible (IR28, IR29, and M1-48), moderately tolerant (IR4595-4-1-13, IR9884-54-3-1E-P1, and IR10206-29-2-1), and tolerant ("Nona Bokra", "Pokkali", and SR26B) parents. Two-week-old seedlings were grown in a salinized (EC = 12 dS/m) culture solution for 19 days under controlled conditions in the IRRI phytotron. Typical characteristics of salinity tolerance in rice were found to be Na^+ exclusion and an increased absorption of K^+ to maintain a good Na-K balance in the shoot. Genetic component analysis (GCA) revealed that a low Na-K ratio is governed by both additive and dominance gene effects. The trait exhibited overdominance, and two groups of genes were detected. Environmental effects were large, and the heritability of the trait was low. Our findings suggest that when breeding for salt tolerance, selection must be done in a later generation and under controlled conditions in order to minimize environmental effects. Modified bulk and single-seed descent would be the suitable breeding methods. Combining ability analysis revealed that both GCA and specific combining ability (SCA) effects were important in the genetics of salt tolerance. Moderately tolerant parents – e.g., IR4595-4-1-13 and IR9884-54-3-1E-P1 – were the best general combiners. Most of the best combinations had susceptible parents crossed either to moderate or tolerant parents. The presence of reciprocal effects among crosses necessitates the use of susceptible parents as males in hybridization programs. Large heterotic effects suggest the potential of hybrid rice for salt-affected lands.

Key words: Genetics – Rice – Salinity – Tolerance – Na-K ratio – Diallel

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Introduction

Soil salinity limits rice production. While various methods such as reclamation, irrigation, and drainage are used to reduce soil salinity, they are not always economical or practical. Other strategies have to be developed, and one such strategy is the development of varieties with a tolerance for salinity.

Rice (*Oryza sativa* L.), one of the world's most important cereal crops, is moderately sensitive to salinity (Akbar et al. 1972; Korbe and Abdel-Aal 1974; Maas and Hoffman 1977). To effect and increase salinity tolerance, the rice plant itself is now being genetically modified. However, progress is slow, primarily due to an inadequate knowledge of the genetics and mechanism of salinity tolerance.

The mechanism of salinity tolerance has to be understood first before a plant can be modified or bred for this trait. Early studies reported that salt injury in rice plants is caused by both osmotic imbalance and an accumulation of the chloride ion (Akbar 1975; Iwaki et al. 1953; Ota and Yasue 1958; Shimose 1963; Tagawa and Ishizaka 1963; Murty and Janardhan 1971). More recent studies, however, have reported that the cause of the injury is more likely to be from excessive sodium (toxicity) and that chloride, being essentially a neutral anion, is tolerated over a wide range of concentrations (Clarkson and Hanson 1980). Biochemical evidence has shown that the disruptive effect of Na^+ in the conformation of the macromolecular structure and its interference with the roles of cytoplasmic K^+ will preempt Cl^- toxicity. Moreover, a Na-K imbalance adversely affected grain yield (Devitt et al. 1981). The potassium ion, which plays an important role in activating enzymes and which affects opening and closure of the stoma, correlated well with salt tolerance through its accumulation in the shoots (Ponnamperuma 1984).

A comparison of salt tolerance during germination and emergence with that during succeeding growth stages is difficult because different criteria are used to evaluate plant responses. However, several studies have shown that while rice is very tolerant of salinity during the germination process, it is very sensitive to it during the first to second leaf stages. Its tolerance progressively increases during tillering and elongation and decreases at flowering. Ripening appears to be less affected by salinity (Pearson 1959, 1961).

Several workers have reported the presence of considerable genetic variation in salinity tolerance among rice varieties (Akbar et al. 1972; Akbar and Yabuno 1975; Ikehashi and Ponnamperuma 1978). Aslam (1989 unpublished paper) confirmed intravarietal differences in rice tolerance for salt stress. His findings showed that a tolerant rice, compared with a salt-sensitive variety, maintains a lower concentration of Na^+ and Cl^-, a higher concentration of K^+ and Zn^{2+}, and lower Na-K and Zn-P ratios in the shoot. Compartmentalization of ions exists in every leaf. Na^+ and Cl^- concentrations are higher in older leaves, while that of K^+ is greater in younger leaves. K^+ selectivity in a tolerant variety is also higher. Furthermore, the relative growth rate of the shoot decreases with salinity; a tolerant variety has a relatively faster growth rate, and thus the absorbed Na^+ undergoes a greater diluting effect, than a sensitive variety. The rates of Na^+ and Cl^- transport are much higher in salt-sensitive varieties at the initial seedling stage, causing a greater accumulation of salt ions in the shoot. These studies on genotype variability support the theory that the exclusion of Na^+ and Cl^- from the shoot and an assured supply of K^+ in the tissues are the most important mechanisms of salinity tolerance in rice.

The response of the rice plant to soil salinity is a complex phenomenon. Some plant breeders have reported that salinity tolerance is governed by polygenes (Akbar and Yabuno 1975, 1977; Akbar et al. 1985). Consequently, it has been suggested that several donor parents be included for contributory characteristics in a breeding program so as to construct a phenotypically salt-tolerant variety through the pyramiding of desirable genes (Yeo and Flowers 1984).

Reports on diallel analysis have indicated significant additive and dominance genetic effects and a high degree of heritability values in most trait studies (Moeljopawiro and Ikehashi 1981; Akbar et al. 1985; Mishra et al. 1990 unpublished paper; Narayanan et al. 1990). Most of these studies had used partial diallel analysis and had large environmental interaction. This interaction often diffuses or masks the phenotypic difference in tolerance, thus complicating inheritance studies.

The study on genetic components of salinity tolerance in rice presented here was undertaken using a nine-parent full diallel analysis under a controlled experimental setup. It was conducted to confirm previous findings and to add new information to the genetics of salinity tolerance in rice. Knowledge of the possible sources of desirable genes and the type and amount of gene action will help rice breeders design effective breeding programs to develop high-yielding rice varieties with salt tolerance.

Materials and methods

Test materials

Genetic components of combining ability estimates of salinity tolerance in rice were investigated using a nine-parent complete diallel analysis. The parents involved were susceptible (IR28, IR29, and M1-48), moderately tolerant (IR4595-4-1-13, IR9884-54-3-1E-P1, and IR10206-29-2-1), and tolerant ("Nona Bokra", "Pokkali", and SR26B) (Table 1). The reaction to salinity of these parents has been confirmed by laboratory, greenhouse and field experiments conducted at IRRI over many seasons and years. These nine rice genotypes were used to produce a complete diallel cross including reciprocals. Seeds of 72 F_1s and nine parents were surface sterilized with 0.1% $HgCl_2$, then rinsed with distilled water. Sterilized seeds were soaked in water for 24 h and incubated for another 48 h at 30 °C. Pregerminated seeds were sown – 1 seed per hole – on a styrofoam sheet having 100 holes with a nylon net bottom. The sheets were floated on a nutrient solution recommended by Yoshida et al. (1976). After 14 days, the seedlings were subjected to salinization (EC = 12 dS/m) by adding a 16:1 mixture of NaCl and $CaCl_2$ to the nutrient solution. The nutrient solution was renewed once a week, and its pH was maintained daily at 5.5 (by adding either 1 *N* NaOH or HCl). The seedlings were grown in the IRRI phytotron glasshouse maintained at 27°/21 °C day/night temperature and a minimum relative humidity of 70% during the day. Irradiance inside the glasshouse was at least 80% of incident solar radiation. The experiment was conducted in a randomized complete block design (RCBD) with four replications. Each experimental unit consisted of 10 plants. Shoot sampling was done 19 days after salinization, when susceptible parents were severely affected. Shoot samples were oven-dried for 3 days at 70 °C. Dried samples were finely ground, and 1 g in powder form from each sample was taken for Na^+ and K^+ analysis using atomic absorption.

Statistical analysis

The diallel analysis of Hayman (1954) was used to compute for the array variance (Vr) and parent-array progeny covariance

Table 1. Mean of Na^+, K^+, and Na-K ratio uptake of parents under salinized conditions

Parent	Reaction to salinity	Na^+	K^+	Na-K ratio
IR28	Susceptible	0.652	1.935	0.359
IR29	Susceptible	0.835	2.410	0.350
M1-48	Susceptible	0.582	2.080	0.284
IR4595-4-1-13	Moderate	0.510	2.435	0.209
IR9884-54-3-1E-P1	Moderate	0.526	2.630	0.200
IR10206-29-2-1	Moderate	0.599	2.295	0.261
Nona Bokra	Tolerant	0.456	2.540	0.180
Pokkali	Tolerant	0.397	2.480	0.159
SR26B	Tolerant	0.452	2.850	0.159

Table 2. Mean over replication of Na-K ratio in a 9 × 9 diallel set under salinized conditions

Male parent	Female parent								
	1	2	3	4	5	6	7	8	9
1. IR28	0.359	0.200	0.256	0.185	0.197	0.268	0.147	0.210	0.175
2. IR29	0.279	0.350	0.221	0.145	0.146	0.184	0.157	0.158	0.189
3. M1-48	0.310	0.209	0.284	0.283	0.253	0.280	0.248	0.176	0.301
4. IR4595-4-1-13	0.235	0.172	0.166	0.209	0.130	0.185	0.206	0.208	0.241
5. IR9884-54-3-1E-P1	0.243	0.144	0.286	0.125	0.200	0.189	0.202	0.270	0.285
6. IR10206-29-2-1	0.240	0.247	0.266	0.293	0.217	0.261	0.214	0.231	0.289
7. Nona Bokra	0.241	0.281	0.222	0.169	0.201	0.248	0.180	0.358	0.194
8. Pokkali	0.221	0.185	0.270	0.222	0.193	0.315	0.169	0.159	0.218
9. SR26B	0.228	0.253	0.226	0.217	0.236	0.174	0.360	0.139	0.159

(Wr) for the Na-K ratio of the F_1 data. The calculated Wr values were regressed on the Vr values, and the relationship was plotted to make the Wr, Vr graph. This graph was used to determine the genetic order of dominance in salinity tolerance. The genetic components of variation were then calculated following Hayman's procedure (1954) as presented by Singh and Chaudhary (1979). The general combining ability (GCA) and specific combining ability (SCA) analyses were carried out according to the procedure outlined by Griffing (1956) using Method I (full set of diallel including reciprocals) Model I (fixed effects for genotypes). The heritability estimates were computed following the formula of Mather and Jinks (1982).

Results and discussion

Performance of parents to salinity

The mean performance of the parents for Na^+, K^+, and Na-K ratio absorption are presented in Table 1. Tolerant parents usually excluded Na^+ and absorbed more K^+ to maintain a good Na-K balance in the shoot, but there were exceptions. On the basis of absorbed Na^+, one susceptible parent (M1-48) could be classified as being moderately tolerant. With respect to K^+ absorption, one tolerant parent ("Pokkali") demonstrated moderately tolerant behavior and one moderately tolerant parent (IR9884-54-3-1E-P1), tolerant behavior. As seen in Tables 1 and 2, a ranking according to Na^+ or K^+ absorption only is not a reliable tool. However, the classification of susceptible, moderately tolerant, and tolerant based on field, laboratory, and greenhouse tests is clearly related to the Na-K ratio. The Na-K ratio, which is the balance between Na^+ and K^+ in the shoot, could then be a valid criterion in measuring salinity tolerance in rice. Thus the parents have been classificed according to the Na-K absorption ratio because of their metabolic interaction.

Test of assumptions for the additive-dominance model

The array variance (Vr) and parent-array progeny covariance (Wr) values represent the parental array points along the regression line in the geometric presentation of the diallel data. In the absence of non-allelic interaction, Wr is related to Vr by a straight regression line with unit slope. The validity of the additive-dominance model was satisfied as the uniformity test ($t^2 = 1.701$) shows non-significance; there is thus a homogeneity of Vr and Wr values. The assumption that genes are independently distributed among the parents was fully supported by the test. This implies that the presence or absence of an allele at a particular locus is statistically independent of the presence or absence of an allele at other loci. The regression coefficient for Na-K ratio ($b = 0.998$) was significant different from zero, and its deviation from unity is not significant. This also conformed with the assumption of absence of non-allelic interaction (epistasis); thus the data set fits the simple additive-dominance model. These results permitted further estimation of various genetic components of salinity tolerance.

To improve the linear fit (b) and to identify the parents that deviated from it, each parental array was omitted in turn, and the remaining eight arrays were re-analyzed. Up to two parental arrays were omitted and re-analyzed, but this did not yield a better graph (Fig. 1).

Diallel graphic analysis (order of dominance)

The regression graph (Fig. 1) of Wr and Vr in a diallel cross provides a useful means for assessing the genetic relationship among homozygous parents. Jinks (1954) and Hayman (1954) have shown that if there are only two alleles at each locus, the non-additive genetic variance is in the form of dominance only if their genes are distributed independently among the parents. The linear regression of Wr and Vr then has a unit slope. The estimate of mean Na-K ratio over replications and reciprocal crosses was used to obtain a set of nine Vr and Wr values. The graph of the nine Vr-Wr arrays produced a regression line with $b = 0.998 \pm 0.370$ (Fig. 1) that cut the Wr axis below the point of origin, indicating overdominance as its average degree of dominance (major and minor gene

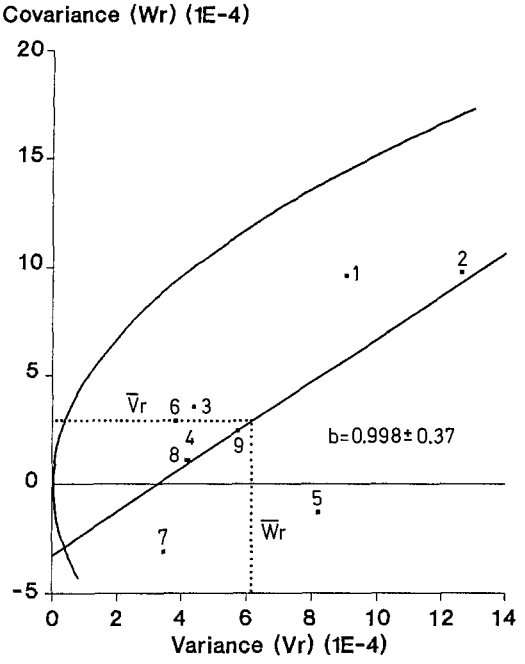

Fig. 1. Variance and covariance (Vr-Wr) regression graph of the 9 × 9 diallel analysis for the Na-K ratio. *Array 1* IR28, *2* IR29, *3* M1-48, *4* IR4595-4-1-13, *5* IR9884-54-3-1E-P1, *6* IR10206-29-2-1, *7* "Nona Bokra", *8* "Pokkali", *9* SR26B

effects). The positions of the array points suggest the distribution of dominant and recessive genes in the parental arrays. Parent 7 ("Nona Bokra") is very near the point of origin, indicating excessive dominant alleles that either increase or decrease the direction of tolerance. Both parents 1 and 2 (IR28 and IR29) are located at the upper end of the regression line, thus exhibiting excess recessive genes and possessing rarely (if any) dominant genes for salinity tolerance. Parent 9 (SR26B) is at the midpoint, indicating an equal proportion of dominant and recessive genes in SR26B for salinity tolerance. The proximity of array points corresponding to parents 3, 4, 6, 8, and 9 (M1-48, IR4595-4-1-13, IR10206-29-2-1, "Pokkali", and "Nona Bokra") is an indication of their genotypic similarity, and their differences were due to genes with very small effects. However, the pronounced discontinuity with some arrays relates to genes with remarkable effects on salinity tolerance.

Genetic components of salinity tolerance

The estimated genetic components of variation and proportional values are presented in Table 3. Variations due to additive (D) and dominance (H_1) gene effects were significant, indicating that the low Na-K ratio in the shoots is governed by both D and H_1 gene effects. Environment effects were large. These results reveal the complexity of the inheritance of salinity tolerance. The significance of gene distribution (F) means the presence of gene asymmetry, and its positive value indicates that

Table 3. Estimates of genetic parameters for Na-K ratio in 9 × 9 diallel cross

Genetic parameters		Estimate ± SE
(D)	Additive effect	0.0014 ± 0.0002 *
(H)	Dominance effect	
	H_1	0.0016 ± 0.0005 *
	H_2	0.0007 ± 0.0004 ns
	h^2	0.0011 ± 0.0003 *
(F)	Gene distribution	0.0019 ± 0.0005 *
(E)	Environmental effect	0.0006 ± 0.0001 *
		Proportional value
(H_1/D)	Mean degree of dominance	1.0701
$(H_2/4H_1)$	Proportion of genes with + or − effects in parents	0.1094
(K_D/K_R) [a]	Proportion of dominant and recessive genes in the parents	4.5623
r between (Wr + Vr) and Yr	direction of dominance	0.6670
(r^2)	Prediction for measurement of completely dominant and recessive parents	0.4449
(h^2/H_2)	Number of gene groups which control tolerance and exhibit dominance	1.6273
(h_{ns})	Heritability narrow sense	0.1918
(h_{bs})	Heritability broad sense	0.3673

* Significant at $P < 0.05$; ns, not significant

[a] $K_D/K_R = [(4DH_1)^{1/2} - 1/2F]/[(4DH_1)^{1/2} - 1/2F]$

more dominant alleles were present in the parents than recessive alleles, irrespective of increasing or decreasing effects. Gene asymmetry was confirmed by the ratio estimate $H_2/4H_1 = 0.1094$, indicating unequal mean allelic frequencies at the loci influencing salinity tolerance. This ratio implies that positive and negative genes are not present in equal proportion in each parent. The proportion of dominant to recessive genes in the parents ($K_D/K_R = 4.5623$) also suggests the predominance of dominant alleles. A value of $h^2/H_2 > 1$ reveals the involvement of two groups of genes exhibiting dominance in the inheritance of salinity tolerance. The first group may control Na^+ exclusion and the other, K^+ absorption. The mean degree of dominance $(H_1/D)^{1/2} = 1.0701$ at each locus was within the range of overdominance. These results confirm closely to the graphical analysis of Fig. 1. Narrow sense heritability, $h_{ns} = 0.1981$, was low, and the relatively large increase in broad sense heritability, $h_{bs} = 0.3673$, showed that both additive and dominance gene actions are operating in the inheritance of salinity tolerance.

The results reveal that the salt-tolerant phenotype selected at an early generation may not maintain its tolerance in subsequent generations and that this phenomenon is greatly affected by environmental factors. These findings imply that (1) early-generation breeding

materials must be large and replicated, (2) selection for tolerance must be delayed to later generations when dominance gene effects are dissipated, and (3) selection must be done under controlled conditions to minimize environmental effects. Modified bulk and single-seed descent would be suitable breeding methods to develop salinity-tolerant rice varieties.

Combining ability estimates

The notion of good combining ability implies the capacity of a parent to produce superior progenies when combined with another parent. In analyzing the combining ability of diallel data, the breeder breaks down the average performance of each progeny into components relating to general combining ability (GCA) as main effects and to specific combining ability (SCA) as interactions. GCA is the average performance of a parent estimated on the basis of its salinity tolerance when combined with other parents. GCA effects represent fixable (additive gene action) genetic components. SCA is used to designate cases in which a certain specific combination performed better on the basis of the average performance of the parents involved. SCA effects represent pre-dominance or non-additive gene action.

The analysis of combining ability estimates for salinity tolerance shows a highly significant difference in GCA and significant difference in SCA effects at the 5% level (Table 4). The mean squares of GCA is 2 times larger than those of SCA, suggesting the greater influence of additive gene action in the inheritance of salinity tolerance compared with the non-additive gene action (dominance and epistasis). Significant reciprocal effects indicated the influence of maternal or residual heterozygosity on salinity tolerance.

Estimates of GCA and SCA effects are presented in Table 5. Among the parents tested, IR4595-4-1-13 was the best combiner. Highly desirable negative GCA values in IR9884-54-3-1E-P1, "Pokkali", IR29, and "Nona Bokra" were also found, which makes them good combiners. These good combiners could produce salt-toler-

Table 4. Analysis of variance of 9 × 9 combining ability tests for Na-K ratio under saline conditions

Source of variation	Degrees of freedom	Mean square	F value
General combining ability (GCA)	8	5.668×10^{-3}	3.05 **
Specific combining ability (SCA)	36	2.808×10^{-3}	1.51 *
Reciprocal effect	36	5.417×10^{-3}	2.92 **
Error	240	1.858×10^{-3}	

*,** Significant at $P < 0.05$ and $P < 0.01$, respectively

Table 5. General combining ability (GCA) effects (*underlined*) and specific combining ability (SCA) effects (*above diagonal*) in 9 × 9 diallel cross under saline conditions

Parent	1	2	3	4	5	6	7	8	9
1. IR28	0.0176	0.0067	0.0133	−0.0076	−0.0037	−0.0060	−0.0447	−0.0166	−0.0405
2. IR29		−0.0091	−0.0279	−0.0326	−0.0519	−0.0174	0.0073	−0.0340	0.0056
3. M1-48			0.0280	−0.0034	0.0346	0.0026	−0.0141	−0.0193	0.0106
4. IR4595-4-1-13				−0.0243	−0.0549	0.0211	−0.0090	0.0248	0.0285
5. IR9884-54-3-1E-P1					−0.0177	−0.0220	−0.0016	0.0350	0.0534
6. IR10206-29-2-1						0.0182	−0.0081	0.0401	−0.0111
7. Nona Bokra							−0.0034	0.0522	0.0555
8. Pokkali								−0.0098	−0.0362
9. SR26B									0.0004

SE $(g_i) = 0.0096$, SE $(s_{ij}) = 0.0273$

Table 6. Reciprocal effects and average reciprocal effects (*underlined*) of Na-K ratio in a 9 × 9 diallel cross under saline conditions

Parents	1	2	3	4	5	6	7	8	9
1. IR28	0.0199								
2. IR29	−0.0397	0.0117							
3. M1-48	−0.0266	0.0059	−0.0081						
4. IR4595-4-1-13	−0.0246	−0.0135	−0.0586	0.0053					
5. IR9884-54-3-1E-P1	−0.0229	0.0010	0.0165	0.0023	−0.0095				
6. IR10206-29-2-1	0.0142	−0.0316	−0.0066	−0.0538	−0.0140	−0.0086			
7. Nona Bokra	−0.0468	−0.0615	−0.0131	0.0188	0.0002	−0.0171	−0.0117		
8. Pokkali	−0.0056	−0.0135	0.0467	−0.0068	0.0388	−0.0419	0.0947	−0.0023	
9. SR26B	−0.0261	−0.0320	−0.0376	0.0121	0.0243	0.0567	−0.0829	0.0396	0.0034

SE $(r_{ij}) = 0.0305$

ant progenies when crossed with other parents. On the other hand, M1-48, a susceptible parent, was the poorest combiner, with a very high undesirable, positive GCA value. Large reciprocal effects suggest the need for proper choices of male and female parent in hybridization programs to improve their GCAs. Table 6 shows the reciprocal effect values of parents and their crosses. IR29 exhibited a large positive reciprocal value and must be used as a male parent. Moreover, "Nona Bokra" must be used as a female parent since it possesses a large negative reciprocal value. The choice of male and female for other good combining parents is not critical since they have low reciprocal effects.

The estimates of SCA effects for all possible crosses are summarized in Table 6. Of the 36 cross combinations, 19 exhibited desirable negative SCA effects for the Na-K ratio. The best general combiners – e.g., IR9884-54-3-1E-P1 and IR4595-4-1-13 (both moderately tolerant parents) – produced a highly significant SCA value when crossed. Other good combiners (e.g., IR9884-54-3-1-1E-P1 × IR29 and "Pokkali" × IR29) produced good specific combinations. Desirable negative SCA effects were also obtained from crosses between good and poor combiners (e.g., "Nona Bokra" × IR28 and SR26B × "Pokkali"). Nevertheless, combinations of poor combining parents produced good specific combinations like SR26B × IR28. On the basis of the results obtained, parents with good GCAs produce good SCA more frequently than do parents with poor GCAs. However, susceptible parents like IR28 and IR29 could combine well with moderately tolerant and tolerant parents to produce tolerant progenies.

Significant reciprocal effects for SCA imply that a porper choice of male and female parents must be made to obtain a better SCA in the selected crosses. However, for the two best combinations (e.g., IR9884-54-3-1E-P1 × IR4595-4-1-13 and IR9884-54-3-1E-P1 × IR29), the choice of male and female parents is not critical because they have very low reciprocal effect values (Table 6). For the other good specific combinations, susceptible parents (IR28 and IR29) must be used as males and tolerant parents ("Nona Bokra", "Pokkali", and SR256B) must be used as females in order to improve their SCAs. These large heterotic effects also suggest the high potential of developing hybrid rice for salt-affected lands.

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