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S. P. Khatiwada · D. Senadhira · A. L. Carpena
R. S. Zeigler · P. G. Fernandez

Variability and genetics of tolerance for aluminum toxicity in rice (*Oryza sativa* L.)

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Abstract A study was undertaken to investigate the variability among lowland rice cultivars and the mode of gene action of aluminum (Al) toxicity tolerance in rice. Pregerminated seeds were grown in a nutrient solution containing 30 ppm Al and in normal nutrient solution, and relative root length (RRL) was determined at the 14-day-old stage to characterize genotypes for tolerance. Sixty-two traditional rice cultivars grown on lowland acid sulfate soil areas of Asia and West Africa were tested. Tolerant varieties 'Azucena', 'IRAT104', and 'Moroberekan', moderately sensitive 'IR29' and 'IR43', and sensitive 'IR45' and 'IR1552' were used to investigate the genetics of tolerance by diallel analysis. Of the 62 cultivars tested, only 3 were found to be sensitive to Al toxicity. Among the tolerant cultivars identified, 11 ('Siyam Kuning', 'Gudabang Putih', 'Siyam', 'Lemo', 'Khao Daeng', 'Siyamhalus', 'Bjm-12', 'Ketan', 'Seribu Gantang', 'Bayer Raden Rati', and 'Padi Kanji') were found to possess higher levels of tolerance than the improved tolerant upland cultivar 'IRAT104'. Diallel analysis revealed that high RRL is governed by both additive and dominance effects with a preponderance of additive effects. The trait exhibited partial dominance, and one group of genes was detected. Heritability was high, and environmenal effects were low. Findings suggest that when breeding for Al toxicity tolerance, selection can be made in early generations. The pedigree method of breeding would be suitable. Combining ability analysis revealed the importance of both general combining ability (GCA) and specific combining ability (SCA) in the genetics of Al toxicity tolerance in rice. GCA was more prevalent than SCA. Tolerant parens 'Azucena', 'IRAT104', and 'Moroberekan' were the best general combiners. The presence of reciprocal effects among crosses suggested the proper choice of parents in hybridization programs. Results indicated that 'Azucena', 'IRAT 104', and 'Moroberekan' should be used as the female in crosses for Al toxicity tolerance.

Key words Aluminum toxicity · Diallel analysis · Genetics · Rice · Variability

Introduction

Aluminum (Al) toxicity is a problem for rice grown on acid soils. It is considered as one of the primary causes of low rice productivity on acid upland and lowland acid sulfate soils (IRRI 1978). Toxic concentrations of Al are generally found in acid soils (pH 5.0 and below). A reduction in the amount of available phosphorus at low soil pH increases Al toxicity stress. A severe inhibition of root growth is the principle direct effect of Al on plants (Lu-Ning and Hou-Tian 1989). This reduction in root growth restricts water and nutrient uptake and leads to poor growth and yield.

The application of lime and phosphate fertilizers has been recommended as a remedial measure for Al toxicity (Hartwell and Pember 1918). Evans and Cate (1962) suggested that toxic Al could be drained by using sea water for reclaiming coastal acid sulfate soils. Quyen and Yoshida (1982) found the use of old-age seedlings as a possible practice to minimize the effect of Al toxicity in transplanted rice. However, liming or the use of soil amendments is not always economical, and practices such as drainage and transplanting are not practical in upland rice.

Field and laboratory experiments have indicated that rice shows a variability for Al toxicity (Ponnamperuma 1975; Konzak et al. 1976; Fageria and Zimmermann 1979; Fageria 1982; Fageria and Barbosa-Filho 1983; Fageria et al. 1988; Camargo et al. 1983; Alluri 1986; Sarkarung 1986; Sivaguru et al. 1992). Almost all of the

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S. P. Khatiwada · D. Senadhira (✉) · R. S. Ziegler
International Rice Research Institute, P. O. Box 933, 1099 Manila, Philippines

A. L. Carpena · P. G. Fernandez
Department of Agronomy, University of the Philippines, Los Banos, Laguna 4031, Philippines

varieties evaluated so far have been upland rice types. There are, however, about 5 million hectares of lowland acid sulfate soils under rice cultivation, and these rices are prone to Al toxicity. There are also large areas of unused acid sulfate soils. Most of these lie near densely populated coastal areas or river plains and in a favorable climate for food production (Beek et al. 1980). Upland cultivars with tolerance for Al toxicity have been identified. However, being japonicas, their direct use or role in breeding programs for use on lowland acid sulfate soils of Asia and West Africa–where indicas are grown–is limited. As the genetics of Al toxicity tolerance in rice is not well-understood, this study was conducted to determine the variability of Al tolerance among lowland rice cultivars and to gain an understanding of the genetics of Al toxicity tolerance in rice.

Materials and methods

The study consisted of two experiments conducted at the International Rice Research Institute (IRRI) in the Phytotron glasshouse maintained at 29°/21°C day/night temperature and 70% maximum relative humidity.

Experiment 1. evaluation of lowland rice cultivars for Al toxicity tolerance

Traditional indica cultivars–which are used in IRRI's breeding program for acidity tolerance and which originate from the acid sulfate soil areas of Asia and West Africa–were evaluated. Seeds were obtained from the working collection of the Plant Breeding, Genetics, and Biochemistry Division, IRRI These cultivars had not previously been screened for Al toxicity.

A total of 62 cultivars (see Table 1) were tested to determine the degree of tolerance for Al toxicity. The screening methodology followed was as described by Coronel (1980) and Coronel et al. (1980). 'IRAT104' and 'IR1552', previously identified as tolerant and susceptible, respectively (IRRI 1982, 1984, 1985), were used as checks. The experiment was conducted in January-February 1995 using randomized complete block design (RCBD) with two replications.

The dormancy of the seeds was broken by heat treatment at 45°C for 3 days in a forced draft oven. The seeds were then surface-sterilized with 0.1% $HgCl_2$ for 2–3 min and rinsed thoroughtly with distilled water. The sterilized seeds were soaked in water for 24 h and incubated for 48 h at 30°C. The pregerminated seeds were sown, 1 seed per hole with one row per cultivar, on a styrofoam sheet with 100 holes (10 × 10) and a nylon net bottom. The sheet was floated on nutrient solution (Yoshida et al. 1976) in a plastic tray (32 × 24 × 18 cm). In a tray there were 10 test entries with ten plants each. There were two trays for every 10 entries, one had normal nutrient solution and the other contained nutrient solution supplemented with 30 ppm Al. The Al treatment was applied immediately after seeding. Each pair of trays was kept adjacent to one another. Because of space limitations, the two replications were tested at two different times. The culture solution was renewed weekly and the pH of the solution (in both treated and untreated experiments) was maintained daily at 4.0 with 1 *N* HCl or NaOH. After 2 weeks eight plants (excluding the two border plants) of each row were measured for maximum root length. The relative root length (RRL) of each genotype was computed as follows:

$$\mathrm{RRL} = \frac{\text{Mean maximum root length (mm) of eight plants at 30 ppm Al}}{\text{Mean maximum root length (mm) of eight plants at 0 ppm Al}}$$

Analysis of variance for the 64 genotypes was done for RRL, and the means were compared by least significant difference using tolerant variety 'IRAT104' as the check.

Table 1 Relative root length (RRL) of some traditional rice varieties when grown in a normal and an Al toxic nutirent solution

Variety	Origin	RRL (mean of two repeats)
Siyam Kuning	Indonesia	1.159
Gudabang Putih	Indonesia	1.135
Siyam	Indonesia	1.105
Lemo	Indonesia	1.088
Khao Daeng	Thailand	1.083
Siyamhalus	Indonesia	1 059
Bjm-12	Indonesia	1.058
Ketan	Indonesia	1.056
Seribu Gantang	Malaysia	1.050
Bayer Raden Rati	Indonesia	1.047
Padi Kanji	Indonesia	1.043
Bjm-13	Indonesia	1.040
Batang Pane	Indonesia	1.039
Bjm-14	Indonesia	1.038
Ca Dung Do	Vietnam	1.037
Bjm-10	Indonesia	1.035
Padi Jambi	Indonesia	1.032
Gablak Cablak	Indonesia	0.956
Barito	Indonesia	0.944
Engatek	Malaysia	0.930
Bjm-15	Indonesia	0 928
Siyam-Kuning	Indonesia	0.925
Quisidugo	W. Africa	0.922
Lua Thuoc	Vietnam	0.918
Gudabang Kuning	Indonesia	0.916
Bjm-17	Indonesia	0 903
Kutik Putih	Indonesia	0.902
Kapuas	Indonesia	0.886
Baiang 6	Indonesia	0.886
Pontianak	Indonesia	0.853
Nang Coi	Vietnam	0.850
Bayar Kuning	Indonesia	0.848
Bjm-11	Indonesia	0.845
Thung Hoa Binh	Vietnam	0.845
Alabio	Indonesia	0.807
Khao Seetha	Thailand	0.807
Gaw Diaw Bow	Indonesia	0.801
Khao Taeng	Thailand	0.800
Lua Thuoc Co	Vietnam	0.794
Talang A	Indonesia	0.784
Mahakam	Indonesia	0.783
Galambong	Indonesia	0.773
Tai Nguyen	Vietnam	0.768
Ketumbar	Indonesia	0.742
Thom Ran	Vietnam	0.738
Talang B	Indonesia	0.729
Duvi Trau	Vietnam	0.701
Ca Dung Phen	Vietnam	0.700
Gogo Ranceh	Indonesia	0.698
Doc Phung	Vietnam	0.676
Nang Gao	Vietnam	0.671
Mansirit	Indonesia	0.670
Kapus	Indonesia	0.622
Yaca	W. Africa	0.661
S-1	W. Africa	0.659
Atanha	W. Africa	0.623
Nang Co	Vietnam	0.623
Than Nang Do	Vietnam	0.621
Pokkali	India	0.617
Soc Nau	Vietnam	0.587
Silla	W. Africa	0.573
S-4	W. Africa	0.450
IRAT104 (tolerant check)		0.828
IR1552 (susceptible check)		0.572
	CV%	12.5
	LSD (0.05)	0 213

Experiment 2: genetic analysis of Al toxicity tolerance

The experiment consisted of a complete diallel set of seven parents chosen from previous screening tests (IRRI 1982, 1984, 1985). The parents were 'IR45' and 'IR1552' (susceptible), 'IR29' and 'IR43' (moderately sensitive), and 'Azucena', 'IRAT104', and 'Moroberekan' (tolerant)

The seven parents were crossed in all possible combinations including reciprocals during the 1994 wet season. The donor parents were planted in the hybridization block of the Plant Breeding, Genetics and Biochemistry Division at three different dates at 2-weeks intervals to synchronize flowering. Crosses were made with at least 100 seeds for each cross. Seeds similar to F_1 seeds (naked seeds) were produced for the parents.

Breaking of seed dormancy, soaking, incubation, seeding, and other operations were as in Experiment 1. The experiment consisted of 49 test entries (7 × 7 diallel cross) and was established in a RCBD with four replications. Each plant was measured for maximum root length at the 14-day-old stage The number of plants measured for each treatment per replication was eight The RRL of each test entry was calculated as in Experiment 1

RRL data were subjected to Hayman's (1954b) method of diallel analyses The hypothesis of no difference between the reciprocal crosses was also tested by Hayman's (1954a) method. Absence of epistasis was tested by the analysis of regression coefficients as described by Hayman (1954b), Jinks (1954), and Mather and Jinks (1982). Genetic components of variation were estimated following Hayman's procedure (1954b) and those of Mather and Jinks (1982) as presented by Singh and Chaudhary (1985). Heritability (narrow sense and broad sense) estimates were done using the formula illustrated by Mather and Jinks (1971). The general combining ability (GCA) and specific combining ability (SCA) analysis was performed according to the procedure given by Griffing (1956), using method I (full set of diallel including reciprocals; fixed statistical model).

Results and discussion

Experiment 1 : evaluation of lowland rice cultivars for Al toxicity tolerance

The differential tolerance for Al among cultivars was found to be highly significant for RRL. RRL ranged from 0.45 in 'S4' to 1.159 in 'Siyam Kuning' (Table 1). Seventeen cultivars showed an RRL of 1.0 or greater than 1.0, indicating that they were not affected by 30 ppm Al or that they responded by increasing root length and achieving higher growth. An increase in root length in rice cultivars tolerant of 3 ppm Al was reported by Howler and Cadavid (1976) and Sarkunan and Biddapa (1982). Thanwornwong and Diest (1974) also noted an Al-induced promotion of seedling growth. Sivaguru and Paliwal (1993) found an increase in root length and shoot length at 6 ppm Al in tolerant cultivars 'Basmati 370' and 'CO 37'. An initiation of growth in tolerant cultivars by Al has also been reported in other crops. Berzonsky and Kimber (1986) reported that tolerant wheat variety 'Atlas 66' showed increased root regrowth in 12 ppm Al in nutrient solution. They further noted that wild species *Triticum ventricosum* showed regrowth at 72 ppm, while *T. triaristatum* showed both regrowth and induction of lateral roots at both 72 and 96 ppm Al concentration in solution.

The results of this study indicated that Al affects root length. In the susceptible check, root growth was reduced by almost 50%. Coronel et al. (1990) reported that RRL is a better expression of varietal differences than root weight and shoot weight. Of the 62 cultivars tested, only 3 were found to be susceptible in terms of RRL, indicating that the majority of traditional cultivars presently grown on acid sulfate soil areas possess tolerance for Al toxicity. The difference in RRL between 'IRAT104' and 9 of the cultivars tested was significant ($P = .05$) and that with 2 other cultivars was highly significant ($P = .01$). The differences suggest that these cultivars have higher degrees of tolerance than 'IRAT104' with respect to root growth. Ten of these varieties originate from South Kalimantan and South Sumatra, Indonesia, where stresses due to acid sulfate soil conditions are severe. The other cultivar, 'Khao Daeng', is a popular rainfed lowland type in acid sulfate areas of the Central Plain in Thailand. The results show that some of the lowland traditional cultivars grown on acid sulfate soils are good sources of tolerance for Al toxicity.

Table 2 Relative root length of 7 × 7 diallel cross (mean of four replications)

Male parent	Female parent						
	P1	P2	P3	P4	P5	P6	P7
P1 (IR29)	*0.705*	0.672	0.552	0.458	0.627	0.780	0.735
P2 (IR43)	0.657	*0.610*	0.572	0.513	0.749	0.691	0.713
P3 (IR45)	0.582	0.663	*0.484*	0.438	0.600	0.698	0.839
P4 (IR1552)	0.576	0.544	0.481	*0.424*	0.621	0.672	0.649
P5 (Azucena)	0.660	0.627	0.579	0.570	*0.719*	0.695	0.720
P6 (IRAT104)	0.728	0.605	0.670	0.555	0.739	*0.734*	0.799
P7(Moroberekan)	0.636	0.590	0.612	0.599	0.696	0.763	*0.758*

Experiment 2 : genetic analysis of aluminum toxicity tolerance

Performance of parents and F_1s

The mean RRL of the F_1s including reciprocals of the full diallel set consisting of seven parents are presented in Table 2. The analysis of variance among genotypes (parents, F_1s, and reciprocals) showed significant genotypic differences among the parents and hybrids (Table 3). There was no significant difference between

Table 3 Mean square values of anlaysis of variance among genotypes (Parents and F_1) for relative root length (CV = 8.7%)

Source of variation	*df*	Mean squares
Replication	3	0.00396
Genotypes	48	0.03665**
Parents (P)	(6)	0.06983**
F_1	(41)	0.03266**
P vs F_1	(1)	0.00128
Error	144	0.00309

** Significant at $P < 0.01$

Table 4 Analysis of variance of 7 × 7 diallel for relative root length

Source of variation	*df*	MS
Additive (a)	6	0.20764**
Dominance (b)	21	0.00992**
Directional (b1)	1	0.00128
Gene asymmetry (b2)	6	0.00694
Residual (b3)	14	0.01182**
Maternal (c)	6	0.03415**
Reciprocal (d)	15	0.00668*

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

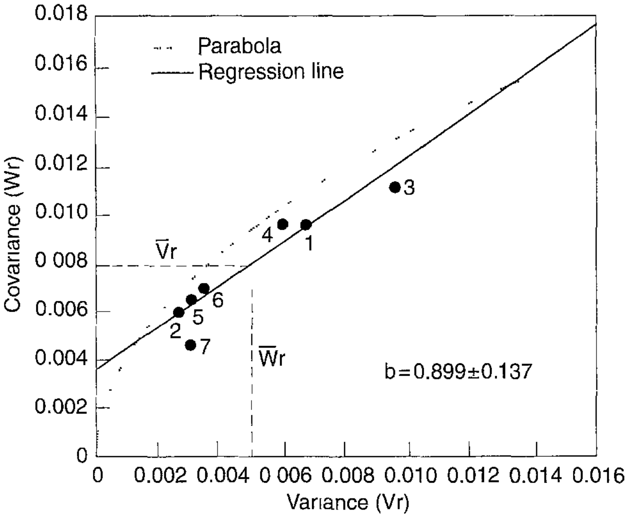

Fig. 1 Variance and covariance (Vr-Wr) regression graph of the 7 × 7 diallel analysis for relative root length. *Array 1* 'IR29', *2* 'IR43', *3* 'IR45', *4* 'IR1552', *5* 'Azucena', *6* 'IRAT104', *7* 'Moroberekan'

the parents and hybrids, indicating that the hybrids were similar to the parents. Estimates of variances and covariances (not shown) also confirmed these results.

Analysis of variance of diallel table

The analysis of variance of the diallel is presented in Table 4. The error variances were tested for homogeneity using Bartlett's test. The test of significance indicated that the variation in the F_1 phenotype was due to additive effect, dominance, and maternal and reciprocal differences. The result indicated that the significance of dominance was brought by the residual component only. The significance of the residual component showed that the dominance deviation was unique to each F_1, which is equivalent to the specific combining ability given by Griffing (1956). The nonsignificance of directional dominance indicated that the mean deviations of the F_1s were not different from their midparental values. This means that the dominance effect was not unidirectional. The nonsignificance of gene asymmetry indicated the presence of symmetrical distribution of genes among the parents. This result showed that the mean dominance deviation of the F_1 from their midparental values within each array did not differ over arrays, indicating that no parent had more dominant alleles than the others.

Test of hypothesis for simple-additive dominance model

The validity of the simple additive-dominance model was confirmed by testing the regression coefficient (Hayman 1954b; Jinks 1954). The *t*-test showed that the regression coefficient ($b = 0.899 \pm 0.137$) was significantly different from zero ($t = 6.563$) but not from unity ($t = 0.736$) at $n = 2$ degrees of freedom, indicating the absence of nonallelic interactions or epistasis.

Graphic analysis

The adequacy of the simple additive-dominance model was further satisfied as the Wr and Vr graph showed a linear regression of unit slope (Fig. 1). The regression line cuts the Wr axis above the origin, indicating partial dominance of the trait. 'Moroberekan', 'IR43', 'Azucena', and 'IRAT104' were located closest to the origin, suggesting that they are the most tolerant of Al toxicity and have most of the dominant genes for tolerance. The distribution of these parents on the regression line indicated that they contain similar genes for tolerance. The position of 'IR45', farthest from the origin, is an indication that it has most of the recessive genes for tolerance for Al toxicity, followed by 'IR29' and 'IR1552'.

Genetic components of variation

The estimation of the genetic components for Al toxicity tolerance using RRL as the criterion was made as the adequacy of the additive-dominance model was satisfied. The estimates of genetic effects and proportional values for RRL are presented in Table 5.

Additive effects (D), dominance effects (H_1 and H_2), and environmental effects (E) were found to be significant, while gene distribution (F) and dominance due to heterozygous loci (h^2) were not significant. The variations observed could be attributed mainly to additive and dominance effects of the genes as estimated by D, H_1, and H_2 variances as well as the environmental effects. This suggested the importance of both additive and dominance type of gene action in the inheritance of RRL as an indicator of tolerance for Al toxicity.

The mean degree of dominance $[(H1/D)^{1/2}]$ was within the range of partial dominance and was in agreement with results obtained from the Wr-Vr graphic analysis. This result was also in agreement with Camargo (1984). Similar results have also been reported in wheat (lorczeski and Ohm 1977) and in alfalfa (Campbell et al. 1994). The average frequency of positive and negative alleles in the parents ($H_2/4H_1$) was 0.21. This

Table 5 Estimates of genetic parameters for relative root length in 7 × 7 diallel cross

Genetic parameters	Estimate ± SE
(D) Additive effects	0.0167 ± 0.0006*
(H) Dominance effects	
H_1	0.0041 ± 0.0015*
H_2	0.0034 ± 0.0013*
h_2	0.0002 ± 0.0009*
(F) Gene distribution	0.0028 ± 0.0015
(E) Environmental effects	0.0008 ± 0.0002

	Proportional values	
$(H_1/D)^{1/2}$	Mean degree of dominance	0.4954
$(H_2/4H_1)$	Proportion of genes with + or − effects on parents	0.2082
$(KD/KR)^a$	Proportion of dominance and recessive genes in the parents	1.4001
r	Correlation between (Wr + Vr) and Yr	0.6618
r^2	Prediction for measurement of completely dominant and recessive parents	0.4380
(h_2/H_2)	Number of gene groups that control tolerance and exhibit dominance	0.0654
(h_{ns})	Heritability (narrow sense)	0.8177
(h_{bs})	Heritability (broad sense)	0.9106

* Significant at $P < 0.05$

[a] $KD/KR = [(4DH_1)^{1/2} + 1/2F]/[(4DH_1)^{1/2} - 1/2F]$

value (lower than 0.25) suggested unequal mean allelic frequencies at the loci with dominant and recessive genes. The proportion of dominant and recessive genes in the parents [KD/KR] was 1.4, indicating an excess of dominant genes. The negative correlation between (Wr + Vr) and Yr expressed by r showed that the genes with positive effects (higher RRL) were dominant over genes with negative effects (lower RRL). The gene asymmetry was confirmed by the ratio estimate $H_2/4H_1$, suggesting unequal mean allelic frequencies at the loci representing Al toxicity tolerance. This implied that positive and negative genes were not present in equal proportions in the parents.

The h_2/H_2 ratio estimated the number of effective factors as defined by Mather (1949), and it measured only those factors showing some degree of dominance. As h_2/H_2 was less than 1, this reveals the involvement of only one group of genes having dominance that influence the inheritance of Al toxicity tolerance.

The variance due to additive gene effect (D) was more than twice the variance due to dominance effects (H_1 and H_2), indicating the preponderance of additive effects. which were reflected in the high narrow-sense and broad-sense heritability (0.817) and the small difference between narrow-sense and broad-sense heritability (0.910). Selection for Al toxicity tolerance could be done in the early-segregating generations. These findings were in agreement with Camargo (1984). Aniol (1984) mentioned that Al tolerance in wheat was not simply inherited but that the expression of Al tolerance was additive with higher values of heritability. The significance of environmental variance suggests that better results could be expected if selection is done under controlled conditions. The pedigree method of breeding with selection in early-segregating generations done under controlled environmental conditions would be the must suitable method in developing Al toxicity-tolerant rice varieties.

Estimates of combining ability effects

Estimates of combining abilities were made based on the fixed model, method I, given by Griffing (1956). Five out of the seven parents used in the present study are frequently used by breeders for Al toxicity tolerance. Therefore, combining ability effects were determined to estimate the breeding value of the parents and to identify superior combinations.

Table 6 Analysis of variance for combining ability tests for relative root length

Source of variation	*df*	Sum of squares	Mean squares
GCA	6	0.311460	0.051910**
SCA	21	0.052100	0.002481**
Reciprocal	21	0.152544	0.007264**
Error	144	0.000004	0.000004

** Significant at $P < 0.01$

Table 7 General combining ability effects (underlined). specific combining ability effects (above diagonal) in 7 × 7 diallel cross

Parent	1	2	3	4	5	6	7
IR29	0.00807	0.02656	−0.03080	−0.02828	−0.03055	0.04136	−0.02755
IR43		−0.01034	0.03798	0.00125	0.03273	−0.04635	−0.04302
IR45			−0.05036	−0.02748	−0.02587	0 03004	0.07100
IR1552				−0.10250	0.03227	0.01131	0.02152
Azucena					0.02577	−0.01359	−0.02237
IRAT 104						0.06448	0.01179
Moroberekan							0.06489
SE (gi) = 0.00049				SE (sij) = 0.00122			

Table 8 Reciprocal effects and average reciprocal effects (underlined) of relative root length in a 7 × 7 diallel cross

Parent	1	2	3	4	5	6	7
IR29	$\underline{0.00107}$						
IR43	−0.00738	$\underline{-0.01378}$					
IR45	0.01525	0.04562	$\underline{-0.02529}$				
IR1552	0.05912	0.01575	0.02150	$\underline{-0.02936}$			
Azucena	0.01638	−0.06100	−0.01012	−0.02513	$\underline{0.01286}$		
IRAT104	−0.02625	−0.04312	−0.01375	−0.05838	0.02200	$\underline{0.01443}$	
Moroberekan	−0.04950	−0.06112	−0.11362	−0.02525	−0.01188	−0.01825	$\underline{0.04000}$

SE (rij) = 0.00140

Analysis of variance for combining ability showed that GCA, SCA, and reciprocal effects were highly significant (Table 6). The significance of GCA and SCA effects suggested the presence of both additive and nonadditive gene action. The mean sqaures for GCA were almost 21 times higher than for SCA effects, indicating the predominance of additive gene action. The GCA effects for each parent are presented in Table 7. The best combiners–those having high positive GCA effects–were the tolerant parents 'Moroberekan' and 'IRAT104'. 'Azucena', which is adapted to both uplands and lowlands, showed positive GCA effects, but the values were lower than those of upland types 'Moroberekan' and 'IRAT104'. The poor combiners were the sensitive parents 'IR1552' and 'IR45', followed by 'IR43'.

The estimates of SCA effects for all crosses are summarized in Table 7. Of the 21 cross combinations, 11 exhibited desirable positive SCA effects for RRL. 'IR42' × 'Moroberakan' and 'IR29' × 'IRAT104' produced the highest positive SCA effects.

The significance of reciprocal effects indicated that there should be a proper choice of male and female parents in hybridization to improve their GCAs. Table 8 shows the values of reciprocal values, suggesting that these varieties must be used as male parents. The desirable higher positive reciprocal values of 'Moroberekan', 'IRAT104' and 'Azucena' indicated that these varieties should be used as female parents. The choice of parents as male or female is not critical for 'IR29', since it was found to have a lower reciprocal effect.

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