Inheritance of aluminum tolerance in maize

R. MAGNAVACA,
National Corn and Sorghum Research Center, EMBRAPA, C.P. 151, 35,700 Sete Lagoas, M.G., Brazil

C.O. GARDNER and R.B. CLARK
Department of Agronomy and U.S. Department of Agriculture, Agricultural Research Service, University of Nebraska, Lincoln, NE 68583, USA

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Summary The inheritance of Al tolerance in maize (*Zea mays* L.) was studied in nutrient solution. Analysis of relative seminal root lengths of six generations (P_1, P_2, F_1, F_2, BC_1, and BC_2) derived from crosses between tolerant and non-tolerant inbred lines showed that additive gene effects contributed most to genetic variation for Al tolerance of the materials included in this study. Dominance effects accounted for only half as much variation as did additive effects. Effects of epistasis contributed little compared to other gene effects. The frequency distributions of plants within the F_2 generations were continuous, unimodal, and typical for quantitatively inherited traits. There was some tendency for non-tolerance to be dominant over tolerance, but it was not consistent. In a diallel cross among inbred lines, the analysis of F_1 crosses indicated that the variance for general combining ability explained most of the variation, but specific combining ability was statistically significant in each case.

Introduction

The inheritance of Al tolerance in maize (*Zea Mays* L.) has been studied by several authors using different techniques to induce and assess Al toxicity[8,9,14,19,22,24,25]. Rhue *et al.*[22] grew plants of F_2 generations and the backcrosses of more sensitive parental lines in nutrient solutions with 250 μmol Al L^{-1} (126 μmol P L^{-1}) at different concentrations of Ca. Because of the tendency for a 3:1 segregation in the F_2 generations and a 1:1 segregation in the backcross generations among the maize inbred lines, they concluded that Al tolerance was controlled by a single locus. However, additional evidence by these authors indicated control of Al tolerance to be by a multiple allelic series[21].

Three tolerant and two non-tolerant maize lines were used to develop F_1, F_2, and backcross generations studied by Garcia *et al.*[9]. Seeds from these generations were planted in sand and irrigated with nutrient solution containing 0 and 2780 μmol Al L^{-1}. Seven days after germination, root lengths of seedlings grown with and without Al were measured to determine relative root lengths among the genotypes. The three F_1 hybrids studied and their backcrosses to the Al tolerant parents were relatively tolerant to Al. Backcrosses to the non-tolerant parents showed

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an approximate 1:1 segregation. In the F_2 generations, a bimodal distribution was observed with approximately a 3:1 segregation. These investigators concluded that Al tolerance in maize was controlled by a single dominant gene with possible alterations by modifiers.

Variance component estimates for Al tolerance were determined for the maize variety 'Piranao'[8]. A total of 144 progenies were produced according to the Comstock and Robinson[3] mating design I. Progenies were evaluated in a pot experiment with an acid soil. Based on shoot and root dry weights, it was reported that the most important component of genetic variability was dominance variance.

Naspolini *et al.*[19] obtained estimates of general and specific combining abilities from a diallel cross of 10 inbred maize lines previously selected for Al tolerance. The 45 possible single crosses were tested in a field experiment on acid soil with three levels of Al saturation (0, 45, and 64%). The estimates of the combining ability variances for grain yield were signficant even though they were variable among Al saturation levels. The magnitudes of general combining ability variances were higher than those of the specific combining ability variances, indicating the importance of additive gene effects.

Maize populations were tested for Al tolerance using nutrient solutions in a complete diallel cross involving the parental populations, F_1 crosses, and reciprocals[14]. The variance for general combining ability explained most of the variation, but specific combining ability was also significant.

Since information is somewhat limited, a better understanding of the genetic control of Al tolerance in maize is needed. Such information would be useful to help evaluate the potential of improving maize through selection and to greatly improve the efficiency of breeding programs aimed at helping to solve maize production problems in Al toxic acid soils. The objective of the research reported here was to obtain additional information on the inheritance of Al tolerance in maize and to assess the relative importance of additive and dominance effects and epistasis on Al tolerance.

Materials and methods

Growth of plants

Captan [N-(trichloromethylthio)-4-cyclohexene-1,2-dicarboximide] treated maize seeds were germinated between rolled paper towels kept moist with aerated water. Seven-day-old uniform sized seedlings without visual root injury were transferred to a plastic plate (42 plants per plate) and grown in 6.5 L of aerated nutrient solution containing 185 μmol Al L^{-1} as $KAl(SO_4)_2$. The nutrient solution and techniques used for growing plants have been described[1,15]. The composition of the nutrient solution (μmol element L^{-1}) was 10 900 NO_3-N, 3500 Ca, 2300 K, 1300 NH_4-N, 850 Mg, 590 Cl, 580 S, 45 P, 25 B, 9.1 Mn, 2.29 Zn, 0.83 Mo, 0.63 Cu, and 77 Fe as FeHEDTA (ferric hydroxyethyl-ethylenediaminetriacetate). The pH of nutrient solutions was adjusted initially to

4.0 ± 0.1 and maintained at this pH throughout the experiment. Water was added daily to maintain solution volumes.

Plants were grown in a controlled environment room with 16 h light at 27 ± 1°C and 8 h darkness at 19 ± 1°C. The photosynthetic photon flux density was 150 μE $m^{-2} s^{-1}$ at plant height (40 cm below the lamps) provided by fluorescent lamps (Agro-Life cool white, F40)*.

Handling of plants and traits measured to assess Al tolerance

When seedlings were transferred to treatment solutions, the initial lengths of seminal roots were measured. Plant were grown in Al treatment solutions for 10 days, when the experiments were terminated and the final seminal root lengths measured. Relative seminal root length (RSRL) was used to evaluate plants for Al tolerance. RSRL values were determined by dividing the final seminal root length by the initial length. This trait was chosen to assess Al tolerance because it has been found to be one of the better traits to assess Al toxicity[6,16]. The greater the RSRL value, the greater the Al tolerance.

Germplasm, experimental design, and statistical analysis of experiments

Experiment 1. Six generations (P_1, P_2, F_1, F_2, BC_1, BC_2) from each of six sets of crosses (B37 × A635, B37 × C103, Mo17 × B37, Mo17 × H84, W117 × A554, and W117 × A635) were used. The experimental design was a modified randomized complete block with three replications. Mean RSRL values were determined using six plants per plot, except for the F_2 generation in which 12 plants per plot were used.

Subdivision of the degrees of freedom and sums of squares for generations within each set were handled according to Mather and Jinks[17] generation means model. The following coefficients for parameters of the complete model were used to obtain the sums of squares:

Generation	Coefficients for parameters					
	m	[d]	[h]	[i]	[j]	[l]
P_1	1	1	0	1	0	0
P_2	1	−1	0	1	0	0
F_1	1	0	1	0	0	1
F_2	1	0	1/2	0	0	1/4
BC_1	1	1/2	1/2	1/4	1/4	1/4
BC_2	1	−1/2	1/2	1/4	−1/4	1/4

where m = the mean of the two parents; [d] = the cumulative additive gene effects; [h] = the cumulative dominance gene effects; [i] = the cumulative additive × additive epistatic effects; [j] = the cumulative additive × dominance epistatic effects and [l] = the cumulative dominance × dominance epistatic effects.

The estimates of the six parameters were obtained by using the equations:

$$m = 1/2\bar{P}_1 + 1/2\bar{P}_2 + 4\bar{F}_2 - 2\overline{BC}_1 - 2\overline{BC}_2$$

$$[d] = 1/2\bar{P}_1 - 1/2\bar{P}_2$$

$$[h] = 6\overline{BC}_1 + 6\overline{BC}_2 - 8\bar{F}_2 - \bar{F}_1 - 3/2\bar{P}_1 - 3/2\bar{P}_2$$

$$[i] = 2\overline{BC}_1 + 2\overline{BC}_2 - 4\bar{F}_2$$

$$[j] = 2\overline{BC}_1 - \bar{P}_1 - 2\overline{BC}_2 + \bar{P}_2$$

$$[l] = \bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4\overline{BC}_1 - 4\overline{BC}_2.$$

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Experiment 2. Four sets of F_2 progenies involving maize parental lines in the crosses A554 × W117, B37 × A635, B37 × C103, and Mo17 × H84 were used. The experimental design was a randomized complete block with four replications. The statistical analysis of RSRL values was conducted using indidivual plant data.

Experiment 3. Eight parental inbred maize lines (A554, A635, B37, C103, C164, H84, Mo17, and W117) and progenies of their diallel crosses (28 F_1 crosses without reciprocals) were tested for Al tolerance in nutrient solutions. The experimental design was a 6 × 6 triple lattice (three replications). The lattice analysis for RSRL was performed according to procedures outlined by Cochran and Cox[2]. Based on the effective error variance from the lattice analysis and the experimental error from the randomized complete block analysis, the relative efficiency of the lattice was determined. Where the relative efficiency of the lattice was less than 10%, the data were analyzed as a randomized complete block design and means were not adjusted.

Since the 36 treatments consisted of 28 F_1 progenies and eight parental lines, the sum of squares for treatments was subdivided into parents, parents *vs.* crosses, and among crosses according to procedures of Gardner and Eberhart[10]. The parents were excluded from the diallel cross part of the analysis which was then analyzed according to experimental method No. 4 of Griffing[11], involving one set of F_1 progenies with no parents and excluding reciprocal crosses. Only the $p(p-1)/2$ (p = number of parental inbred maize lines) different F_1 mean values were used in estimating general and speciifc combining ability variances.

Results and discussion

Experiment 1

Means of RSRL values measured in the different generations of six crosses are presented in Table 1. In Sets 1 and 2, F_1, F_2, and backcross generations were similar to the susceptible parents, but in Sets 3, 4, 5, and 6, the F_1, F_2, and backcross generations were similar to the more Al tolerant parents. The greatest amount of heterosis was exhibited in Sets 3 and 5.

The analysis of variance for the RSRL values measured in different generations of the six crosses (Table 2) indicated statistical significance among generation means in all six sets. Subdivision of the sums of squares for generations within sets into those attributable to each of the different kinds of gene effects is presented in Table 3. Estimates of genetic parameters in each set are shown in Table 4.

Table 1. Mean relative seminal root lengths (RSRL) measured in different generations derived from six maize crosses and grown in nutrient solutions (Experiment 1)

Set	Generation					
	P_1	P_2	F_1	F_2	BC_1	BC_2
1	$\frac{B37}{1.24}$	$\frac{A635}{1.62}$	1.20	1.32	1.26	1.37
2	$\frac{C103}{1.65}$	$\frac{B37}{1.21}$	1.24	1.24	1.25	1.19
3	$\frac{W117}{1.42}$	$\frac{A635}{1.69}$	1.74	1.59	1.55	1.63
4	$\frac{Mo17}{1.33}$	$\frac{B37}{1.25}$	1.39	1.35	1.44	1.43
5	$\frac{A554}{1.24}$	$\frac{W117}{1.35}$	1.48	1.39	1.41	1.55
6	$\frac{H84}{1.64}$	$\frac{Mo17}{1.29}$	1.54	1.52	1.46	1.39

Table 2. Analysis of variance of relative seminal root length (RSRL) obtained from six maize generations derived from six different crosses grown in nutrient solutions (Experiment 1)

Source of variation	df	Mean squares
Replications	2	0.0124
Sets	5	0.2188**
Replications × sets	10	0.0032
Generations within sets	30	0.0486**
Generations within Set 1	5	0.0688**
Generations within Set 2	5	0.0914**
Generations within Set 3	5	0.0373**
Generations within Set 4	5	0.0163**
Generations within Set 5	5	0.0341**
Generations within Set 6	5	0.0437**
Error	60	0.0030
Total	107	
CV (%)		3.9

** Statistical significance at $\alpha = 0.01$.

Sets 1, 2, 3, and 6 involved generations derived from crosses between tolerant and non-tolerant lines. In these sets, additive gene effects explained most of the genetic variation, but dominance contributed a significant amount of variance except in Set 6. Dominance accounted for about half as much of the total genetic variance as did additive gene effects in Sets 1, 2, and 3. Epistasis was significant in Sets 2 and 6. Each of the three kinds of epistasis variance in Set 2 was significant, although small compared to the variances due to additive and dominance effects. Dominance × dominance epistasis was significant in Set 6, but it was small compared to the variance due to additive effects. The model with epistasis effects included substantially increased the amount of genetic variance that could be explained compared to the model with only additive and dominance effects, except for Set 1 (see multiple r^2 values in Table 4).

Table 3. Mean squares of relative seminal root length (RSRL) obtained from six maize generations derived from six different sets (Experiment 1)

Source of variation†	df	Mean squares of set nos.					
		1	2	3	4	5	6
Generations within set	5	0.06880**	0.0914**	0.0373**	0.0163**	0.0341**	0.0437**
Additive	1	0.22188**	0.2688**	0.1128**	0.0994	0.0382**	0.1733**
Dominance	1	0.1114**	0.1107**	0.0568**	0.0351**	0.0904**	0.0080
Epistasis	3	0.00270	0.0258**	0.0056	0.0123*	0.0140**	0.0124**
Additive × additive	1	0.00001	0.0319**	0.0110	0.0040	0.0041	0.0008
Additive × dominance	1	0.00800	0.0314**	0.0034	0.0012	0.0097	0.0116
Dominance × dominance	1	0.00007	0.0141*	0.0024	0.0318**	0.0283**	0.0249**

*, ** Statistical significance at $\alpha = 0.05$, and $\alpha = 0.01$, respectively.
† Parameters defined by Mather and Jinks[17].

Table 4. Estimates of the additive, dominance, and epistasis effects for relative seminal root length (RSRL) obtained from six maize generations derived from six different sets (Experiment 1)

Set model†	Additive	Dominance	Additive × additive	Additive × dominance	Dominance × dominance	Multiple R^2 100 (%)
Set 1						
3 Parameters‡	−0.172	−0.232	–	–	–	92.7
6 Parameters‡	−0.188	−0.295	−0.027	0.163	0.037	94.9
Set 2						
3 Parameters	0.189	−0.228	–	–	–	80.5
6 Parameters	0.222	0.762	−0.067	−0.323	0.503	96.9
Set 3						
3 Parameters	−0.123	0.163	–	–	–	61.3
6 Parameters	−0.133	−0.010	0.013	0.107	0.207	88.5
Set 4						
3 Parameters	0.035	0.129	–	–	–	34.7
6 Parameters	0.042	1.228	0.367	−0.063	−0.757	62.2
Set 5						
3 Parameters	−0.073	0.206	–	–	–	67.3
6 Parameters	−0.053	1.237	0.340	−0.180	−0.713	89.0
Set 6						
3 Parameters	0.152	0.061	–	–	–	70.9
6 Parameters	0.172	−0.952	−0.360	−0.197	0.670	83.6

† Parameters defined by Mather and Jinks[17].
‡ The 3 parameter model excludes epistasis; the six parameter model includes epistasis.

In crosses between lines susceptible to Al (sets 4 and 5), dominance gene effects and dominance × dominance epistasis explained most of the genetic variation. Additive gene effects were of some importance in Set 5, but not in Set 4.

Experiment 2

The four F_2 progenies of single crosses A554 × W117, B37 × A635, B37 × C103, and Mo17 × H84 (Sets 1, 2, 5, and 6 of Experiment 1) differed in their mean Al tolerance when grown in nutrient solutions (Table 5). They also differed in the amount of plant-to-plant variation within the F_2 generations; Mo17 × H84 had the greatest variance and B37 × C103 had the least. The magnitude of the variances among plants within F_2 generations was not related to the magnitude of the differences between their parents in Al tolerance. A554 and W117 differed the least in RSRL values (0.11, Table 1), but had next to the highest variance in their F_2 generation; and B37 and C103 differed the most (0.44), but had the lowest F_2 generation variance. The two crosses involving B37 had the lowest variances among F_2 generation plants.

The frequency distributions of the F_2 generations are presented in

Table 5. Analysis of variance for relative seminal root length (RSRL) in F_2 maize generations of four different crosses grown in nutrient solutions (Experiment 2)

Source of variation	df	Mean squares
Replications	3	0.0088
F_2 generations	3	0.0420**
Error	9	0.0017
Total	15	
CV (%)		3.1
Among plants	656	0.0259
F_2 generation 1 (B37 × A635)	164	0.0185
F_2 generation 2 (B37 × C103)	164	0.0163
F_2 generation 3 (A554 × W117)	164	0.0294
F_2 generation 4 (Mo17 × H84)	164	0.0397

** Statistical significance at $\alpha = 0.01$.

Figure 1. The figure shows susceptible plants were more frequent than tolerant ones. The highest frequencies of Al-tolerant plants occurred in the cross involving Mo17 × H84. All frequency distributions were continuous, unimodal, and typical for a quantitatively inherited trait. Higher frequencies in the susceptible ranges for three crosses (numbers closer to 1.0), indicated a preponderance of genes dominant for susceptibility to Al tolerance. Plants in the F_2 generation of Mo17 × H84 showed the most nearly normal distribution.

Experiment 3

The analysis of variance for RSRL of eight parental lines and their 28 single-cross hybrids (diallel crosses) grown in nutrient solution are

Table 6. Analysis of variance for relative seminal root length (RSRL) in eight maize parents and their 28 F_1 crosses (diallel) grown in nutrient solution (Experiment 3)

Source of variation	df	Mean squares
Replications	2	0.0121
Treatments (unadj.)	35	0.3301**
Parents	7	0.1778**
Parents *vs* crosses	1	1.5699**
Crosses	27	0.3237**
General combining ability	7	0.8911**
Specific combining ability	20	0.1251**
RCBD error	70	0.0481
Blocks within replications (adj.)	15	0.0544
Intra-block error	55	0.0464
Total	107	
Average effective error		0.0479
Relative efficiency of lattice (%)		100.4
CV (%)		11.8

** Statistical significance at $\alpha = 0.01$.

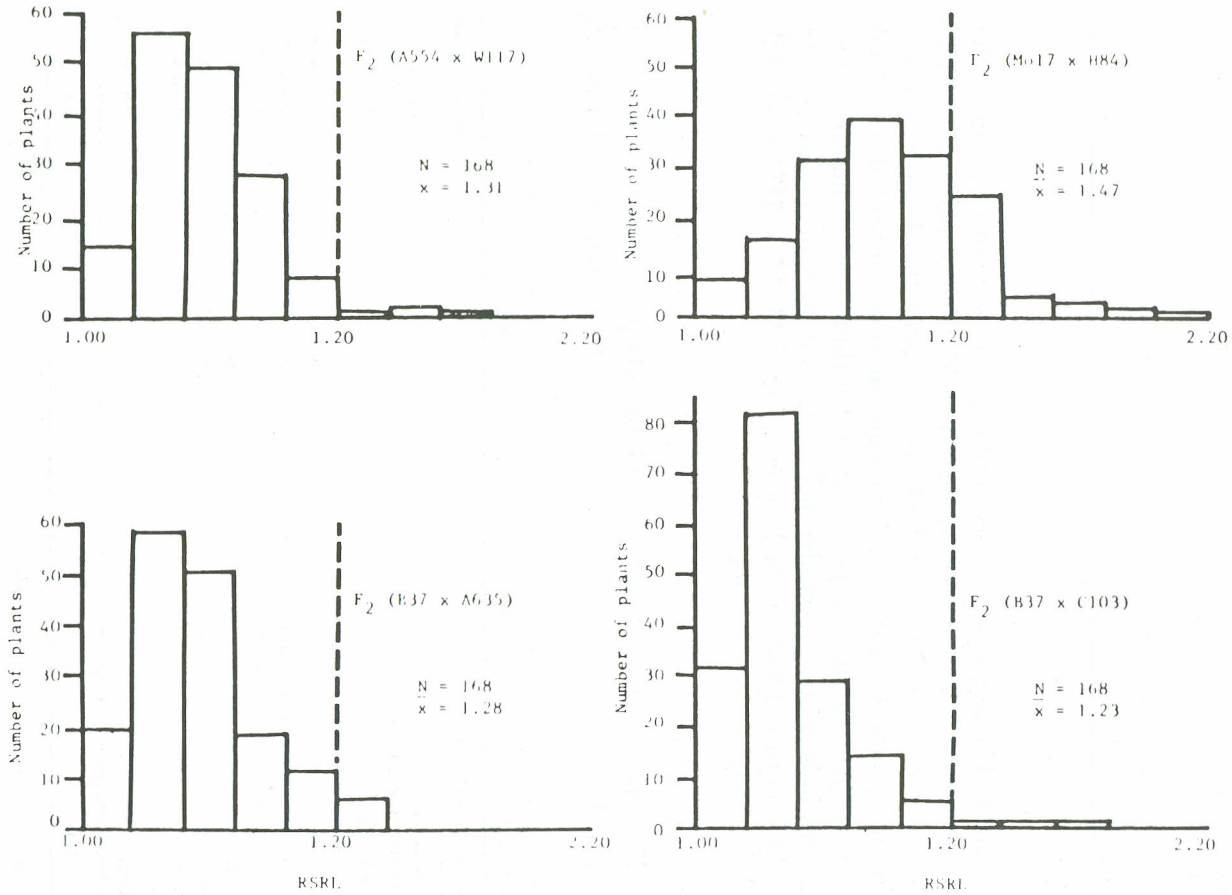

Fig. 1. Frequency distributions for relative s(al root length (RSRL) of plants from four different F_2 maize g(tions grown in nutrient solution (Experiment 2). (The dotted line represents genotypes considered to have good Al tolerance).

Table 7. Parental and F_1 means for relative seminal root length (RSRL) of maize grown in nutrient solution (Experiment 3)

Inbred lines	F_1 means									Parental† means
	Mo17	C103	H84	CI64	B37	W117	A635	A554	Cross mean	
Mo17		1.75	1.67	1.75	1.64	1.46	1.78	1.99	1.72	1.57 bcde
C103			1.81	1.82	1.72	1.63	1.85	2.37	1.85	2.06 a
H84				2.23	1.55	1.92	1.85	2.67	1.96	1.79 ab
C164					1.79	2.13	2.01	2.83	2.08	1.74 abc
B37						1.78	1.49	1.86	1.69	1.71 abcd
W117							2.27	2.03	1.89	1.39 cde
A635								2.19	1.92	1.50 bcde
A554									2.28	1.30 e

† For parents, means followed by a common letter are not significantly different at = 0.05, according to Duncan's New Multiple Range Test.

presented in Table 6. Statistical significance was noted for differences among parental lines, for parental lines *vs.* crosses, and for general and specific combining abilities. The parental lines *vs.* crosses comparison was an indication of heterosis in the F_1 generation crosses, which suggested a preponderance of genes dominant for tolerance in this set of lines. The variance for general combining ability explained most of the variation for each of the six variables studied, but specific combining ability was also important. As in Experiment 1, additive gene effects were the most important for controlling tolerance but dominance was also important.

The parental and F_1 generation means and estimates of general and specific combining ability effects are presented in Tables 7 and 8. Line C103 possessed the greatest tolerance to Al toxicity, adn B37, C164,and

Table 8. Estimates of general combining ability (GCA) and specific combining ability (SCA) effects for relative seminal root length (RSRL) of maize generations grown in nutrient solution (Experiment 3)

Inbred lines	SCA effects								GCA effects
	Mo17	C103	H84	C164	B37	W117	A635	A554	
Mo17		0.1484	−0.0585	−0.1158	0.2232	−0.1877	0.0965	−0.1063	−0.2373
C103			−0.0694	−0.1999	0.1523	−0.1699	0.0199	0.1195	−0.0847
H84				0.0865	−0.1380	−0.0022	−0.1113	0.2926	0.0403
C164					−0.0485	0.0639	−0.0952	0.2087	0.1843
B37						0.1727	−0.1563	−0.2057	−0.2713
W117							0.3895	−0.2666	−0.0417
A635								−0.1424	−0.0047
A554									0.4151

Standard errors of differences: Between two GCA effects = 0.0730
Between two SCA effects with one common parent = 0.1633
Between two SCA effects with no parents in common = 0.1461

H84 tended to be intermediate in Al tolerance. Results of Experiment 3 were somewhat in agreement with those of Experiment 1 in that higher Al tolerance was noted for C103 and H84 and lower Al tolerance was noted for A554, Mo17, and W117. However, the results for A635 and B37 were not consistent. Differences in seed quality between the two experiments may have been important. A635 seedlings with greater vigor were used in Experiment 3 than in Experiment 1. Rhue and Grogan[21] and Rhue *et al.*[22] reported low Al tolerance for A554, B37, and Mo17 tested in their nutrient solution studies.

A554 had the highest general combining ability and consistently performed well in crosses with the other lines. As a line, A554 had a low level of Al tolerance. Similar types of responses were noted for A554 when it was used in crosses by Rhue *et al.*[22], who suggested that specific factors existed in the Al non-tolerant A554 which enhanced the expression of Al tolerance in the F_1 generation, but their nature was not understood. In our study, the better than expected performance of A554 for Al tolerance was expressed particualrly in crosses with the more Al-tolerant lines A635, C103, C16, and H84.

Specific combining ability effects were highest for the crosses C164 × A554, H84 × A554, and W117 × A635, and lowest for B37 × A554, C103 × C164, and W117 × A554. The results described for the inheritance of Al tolerance by many authors were not in complete agreement with the results of the studies reported here. The differences may be explained by differences in genotypes and techniques used. Rhue[20], Rhue *et al.*[22], and Stockmeyer *et al.*[25] used 250 μmol Al L^{-1} and 126 μmol P L^{-1} in their Al tolerance studies. Thus, the concentrations of Al and P used were different from the concentrations used in our inheritance studies (185 μmol Al L^{-1} and 45 μmol P L^{-1}). The methods Rhue and colleagues[20,21,22,25] used to assess Al tolerance were also different because they usually separated plants in the F_2 and backcross generations into classes as well as using root growth as the criterion for separation. Also, the seedlings were transplanted to treatments earlier (2- to 3-day old seedlings) compared to our study (7-day-old seedlings).

Silva[24] used techniques in which the seeds were germinated in sand and irrigated with nutrient solution containing 2780 μmol Al L^{-1}. Maize seedlings were stressed with Al at an early stage of germination or were germinated with Al in some experiments. After 7 days, the root length was measured and relative root lengths were determined by comparing measurements on plants grown with and without Al.

In a study with barley (*Hordeum vulgare* L.) seedlings, May *et al.*[18] concluded that the response of plants to variations in the environment decreased rapidly with the age of the plants. Thawornwong and Van

Diest[26] pointed out that young rice (*Oryza sativa* L.) seedlings were more susceptible to Al toxicity than older plants. Sartain and Kamprath[23] noted that short-term root elongation studies with soybean cultivars [*Glycine max* (L.) Merr.] only took into account the effects of Al on cell elongation and cell division. However, in another study with soybeans in which selection was made in a population, Hanson and Kamprath[12] concluded that Al tolerance based on growth in nutrient solutions apparently identified genetic differences for tolerance in established plants as well as tolerance that appeared unique in the seedling stage. This may account for some of the differences between the results reported in our studies compared to those of the other studies described.

Galvao and Silva[8] based their evaluations of Al tolerance in maize on shoot and root dry matter yields, which are not always related to Al tolerance[6,17,14]. Lopes *et al.*[14] and Naspolini *et al.*[19] found that the magnitude of general combining ability variances was higher than that of the specific combining ability variances. These results agree with those noted in our study.

It is evident that Al tolerance in maize is quantitatively inherited in the lines studies. However, the differences in level of Al tolerance of Brazilian maize inbred lines compared to USA inbred lines[16] do not eliminate the possibility of a major gene for Al tolerance as described by Silva[24]. Further investigation should be conducted using the more tolerant Brazilian lines in crosses with the less tolerant USA lines.

Several different mechanisms explaining plant Al tolerance have been described in the literature[4,5,6,13]. It is not clear how these mechanisms are related and which may be the most important in attempting to explain Al tolerance. Evidence does not support the concept that a single major gene controls Al tolerance; a more complex genetic system is more probable. Perhaps at specific stages of plant development, one mechanism could be more important than another and simple genetic control of Al tolerance might exist at specific growth stages.

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