Evaluation of inbred maize lines for aluminum tolerance in nutrient solution

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Summary Maize (*Zea mays* L.) inbred lines were grown in nutrient solution with different levels of Al and P to study their genetic variability for Al tolerance. Plant measurements for determining inbred line responses to Al were also evaluated. The best traits to assess maize for Al tolerance were seminal and adventitious root lengths.

Brazilian maize inbred lines were more tolerant to Al for the traits measured than USA inbred lines when grown in nutrient solution. Most inbred lines tested showed decreased root lengths, but a few Brazilian lines were not affected by the Al levels used. At higher Al levels most Brazilian lines were not affected as severely as the USA lines. Tolerance of the inbred lines to Al was increased by inclusion of P in nutrient solutions. The greatest Al-induced decrease in root length generally occurred at the lowest P level. The combination of 185 μmol Al L^{-1} and 45 μmol P L^{-1} in nutrient solutions was the best combination of Al and P to evaluate maize genotypes for Al tolerance in this study.

Introduction

Acid soils appear frequently in tropical areas. Oxisols which are strongly weathered soils and have low cation exchange capacities, occupy 8.1% of the world land area[8]. In tropical areas, Oxisols exhibit major mineral element deficiencies and toxicities; deficiencies of P, Ca, Mg, and Zn are common, toxic exchangeable Al is usually high, and the fixation of P by soil particles is extensive. Oxisols, Ultisols, and Inceptisols are estimated to occupy approximately 1000 million hectares in the tropics[24]. This corresponds to 33% of the total potentially arable land area of the world useful for crop production without irrigation.

Kamprath[17] indicated that the Al saturation in soils should be less than 45% for maximum growth of maize (*Zea mays* L.), but Olmos and Camargo[20] found that 25% Al saturation reduced maize yields. On a Brazilian acid Oxisol soil that had 55% Al saturation, 363 inbred maize lines were evaluated for their response to acid soil toxicity[1]. The soil had received no lime applications but had received relatively high amounts of N and P. Fifteen days after planting 19% of the inbred lines died and 45

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days later 70% of the inbred lines were dead. Decreases in maize yield due to Al toxicity have also been reported for Oxisols in Brazil[9,10], for ferrallitic and ferruginous soils in Madagascar[25]; for Oxisols and Ultisols of Puerto Rico[3]; for Andosols from northeastern Japan[23]; and for Ultisols of Pennsylvania in the USA[11].

Genetic variability in Al tolerance has been demonstrated among maize inbred lines, hybrids, and varieties for Al tolerance[1,2,6,10,16,22].In these studies, evaluations of maize germplasm for tolerance to Al were made in field experiments where plants were grown on acid soils, in greenhouse experiments where plants were grown in pots of acid soil, in germination studies where seeds were irrigated with Al-containing nutrient solutions in sand, and in studies where seedlings were grown in nutrient solutions with Al. The different approaches to assess Al tolerance have been responsible for many of the conflicting results that have been reported for genotypic differences in tolerance to Al[15]. Screening techniques used for the assessment of Al tolerance must consider the appropriate combination of factors like concentrations of Al, Ca, Mg, P, and K, the solution pH, source of N (ammonium or nitrate), and temperature. The traits used to measure Al genotypic differences also need to be considered[14].

The objectives of this research were to: (i) develop relatively easy and inexpensive techniques to evaluate seedlings of maize genotypes for Al tolerance; (ii) study genetic variation among homogeneous maize inbred lines for Al tolerance; and (iii) compare responses to tropical (Brazilian) and temperate (USA) maize inbred lines to Al.

Material and methods

Growth of plants

Seeds treated with captan [N-(trichloromethylthio)-4-cyclohexene-1,2-dicarboximide] were germinated seven days in rolled paper towels kept moist with aerated distilled water. The temperature was 27 ± 1°C for 16 h with fluorescent lights (Agro-Lite cool-white, F40)* at 150 $\mu E\,m^{-2}\,s^{-1}$ and 8 h of darkness at 19 ± 1°C. Seven-day-old uniform-sized seedlings without visual root injury were transferred to plastic plates containing either 126 (Experiment 1) or 42 (Experiment 2) plants per plate and grown in 6.5 L nutrient solution with treatments. Distilled water was added regularly to maintain volume. The initial pH of nutrient solutions was adjusted to 4.0, monitored daily, and adjusted to 4.0 if needed with 1 *N* HCl or NaOH. Plants were grown in treatment solutions 10 days before experiments were terminated.

The composition of nutrient solutions used for growth of maize was (μmol element L^{-1}): 10 900 NO_3-N; 3500 Ca; 2300 K; 1300 NH_4-N; 850 Mg; 590 S; 590 Cl; 25 B; 9.1 Mn; 2.29 Zn; 0.88 Mo; 0.63 Cu; 77 Fe as FeHEDTA (ferric hydroxethylethylenediaminetriacetate). Phosphorus and Al concentrations varied with the treatment. Aluminum was added to the nutrient solutions as $KAl(SO_4)_2$ and P as KH_2PO_4. Details of procedures used for growing plants in nutrient solution have been described[5,15].

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Growth conditions for Experiment 1 were 17 h light at 28 $\pm$ 1°C and 7 h darkness at 23 $\pm$ 1°C in a controlled environment chamber. Photosynthetic photon flux density (PPFD) was 350 $\mu E\, m^{-2} s^{-1}$ at plant level (60 cm below the lights). Lamps providing light were high pressure sodium (General Electric, Lucalux, LU4008)[3] and metal halide (General Electric, multivapor, MV400)[3].For Experiment 2, plants were grown in a controlled environment room with 16 h light at 27 $\times$ 1°C and 8 h darkness at 19 $\pm$ 1°C. Lamps providing light were fluorescent (Agro-Light cool-white, F40)[3] yielding 150 $\mu E\, m^{-2} s^{-1}$ PPFD at plant height (100 cm below the lamps).

Plant measurements to assess Al tolerance

In Experiment 1, only seminal roots were allowed to develop and the adventitious roots that had started to grow were removed. In Experiment 2, adventitious roots were allowed to develop. At the time seedlings in both experiments were put into treatment solutions, the initial seminal root lengths were measured for each plant. When experiments were terminated, the final seminal root length and the length of the longest adventitious root were measured on each plant. These and two other calculated root traits were used to assess plants for Al tolerance. Definition of each trait is:

Initial seminal root length (ISRL): The length of the primary seminal root when plants were transferred to treatment nutrient solutions;

Final seminal root length (FSRL): The length of the primary seminal root when experiments were terminated (plants grown 10 days in treatment solutions);

Relative seminal root length (RSRL): Calculated by dividing FSRL by ISRL;

Net seminal root length (NSRL): Calculated by subtracting ISRL from FSRL; and

Longest adventitious root length (LARL): The length of the longest adventitious (synonymous with crown) root when experiments were terminated (plants grown 10 days in treatment solutions).

Maize genotypes

The USA inbred lines used were obtained from the maize breeding program of the Department of Agronomy, University of Nebraska, Lincoln even though several of the lines were originally developed in other states. The inbred lines used were A554, A635, B37, B73, C103, CI64, H84, Mo17, N7A, N28, N132, N139, N152, N156, N168, N174, and W117.

The Brazilian inbred lines used were developed at and belong to the collection of the National Maize and Sorghum Research Center, Sete Lagoas, M.G., Brazil, and brought to Nebraska. Each of these lines had undergone at least six generations of selfing and are identified as L69, L153, L297, M1001, M1002, M1003, M1004, M1005, M1007, M1009, M1010.

Treatments, experimental design, and statistical analysis

Experiment 1. Treatments included four Al levels (0, 74, 148, and 222 $\mu mol\, L^{-1}$) and 21 maize inbred lines (B37, L69, L153, L297, M1001, M1002, M1003, M1004, M1005, M1007, M1009, M1010, Mo17, N7A, N28, N132, N139, N152, N156, N168, and N174). A split-plot design was used with Al levels as whole plots and inbred lines as subplots. Whole plots were arranged in a randomized complete block design with three replications and subplots consisted of six plants each. Each nutrient solution container, therefore, constituted a whole plot and included 21 subplots of six plants each. The P level in nutrient solutions was 64 $\mu mol\, L^{-1}$. Each plant of each subplot was evaluated for Al tolerance using ISRL, FSRL, NSRL, and RSRL, and subplot means were calculated. The analyses of variance were computed for each variable using subplot means of six plants.

Statistical analyses were performed using a fixed effects model. The Al levels sums of squares were partitioned into their linear and quadratic components. The Al level and genotype interactions sums of squares were likewise partitioned into genotype $\times$ Al levels linear and genotypes Al levels quadratic components.

To test for linear and quadratic effects of Al on each genotype, a different subdivision of degrees of freedom was allocated according to the following model:

$$Y_{ijn} = u + r_i + g_n + a_{jn} + e_{ijn},$$

where Y_{ijn} = the measurement of n^{th} genotype in the j^{th} Al level in the i^{th} replication, u = the overall mean effect, r_i = the effect of the i^{th} replication, g_n = the effect of the n^{th} genotype a_{jn} = the effect

Table 1. Mean relative seminal root length (RSRL), final seminal root length (FSRL), and net seminal root length (NSRL) of maize inbred lines grown in nutrient solution with Al (Experiment 1)

Inbred source	Inbred line	RSRL				FSRL (mm plant^{-1})				NSRL (mm plant^{-1})			
		0†	74	148	222	0	74	148	222	0	74	148	222
Brazil	L69	2.45	2.33	1.99	2.25	154	154	125	128	91	87	64	68
	L153	2.98	3.04	2.36	2.11	217	207	189	153	144	138	109	81
	L297	3.82	3.75	2.23	1.87	244	247	156	110	173	178	83	50
	M1001	3.44	3.23	2.33	1.80	297	242	198	163	210	164	111	71
	M1002	2.17	2.55	2.36	2.23	121	142	116	135	64	84	66	74
	M1003	2.54	2.76	2.40	1.88	191	198	177	147	116	125	105	69
	M1004	2.59	2.56	2.43	1.96	235	251	243	191	144	155	142	93
	M1005	3.89	3.79	3.16	2.88	239	241	213	165	177	175	144	106
	M1007	3.81	2.63	1.61	1.24	347	233	123	114	255	148	44	21
	M1009	3.45	2.62	1.58	1.32	247	187	136	107	174	113	49	27
	M1010	4.44	3.26	2.67	1.73	308	245	205	144	233	168	129	63
	Mean	3.23	2.96	2.28	1.93	236	213	171	142	162	140	95	66
USA	B73	1.97	1.65	1.35	1.32	194	175	131	121	95	69	33	29
	Mo17	2.99	2.59	1.99	1.64	167	143	103	96	108	85	51	37
	N7A	2.18	1.81	1.25	1.16	195	149	123	107	105	65	25	15
	N28	3.48	3.00	1.94	1.42	249	260	126	109	171	172	55	32
	N132	2.37	2.28	1.51	1.29	240	205	154	134	139	114	51	30
	N139	2.07	1.94	1.51	1.33	226	216	156	143	116	105	54	35
	N152	278	2.32	1.56	1.36	311	278	182	153	197	157	66	43
	N156	3.08	2.71	1.81	1.44	262	225	171	125	174	137	76	37
	N168	2.39	2.12	1.78	1.40	248	224	161	138	147	121	72	40
	N174	3.22	2.08	1.69	1.43	206	174	135	108	138	88	59	32
	Mean	2.65	2.25	1.64	1.38	230	205	144	123	139	111	54	33
Overall mean		2.96	2.62	1.98	1.67	233	209	158	133	151	126	74	50

† μmol Al L^{-1}.

of the jth Al level within the nth genotype, e_{ijn} = the random pooled component of error associated with the nth genotype at the jth Al level.

In this model, the pooled error mean squares provided only an approximated F-test for effects of Al levels within genotypes.

Experiment 2. Treatments included nine combinations of a 3^2 factorial for three Al levels (37, 111, and 185 μmol L^{-1})and three P levels (22.5, 45, and 67.5 μmol L^{-1}). Seven maize inbred lines (A554, A635, CI64, L69, L153, L297, and Mo17) were used. Traits measured were ISRL, FSRL, RSRL, NSRL, and LARL. The individual measurement analyzed was the mean value of six plants per plot. The experimental design was a split-plot with Al and P combinations in the whole plots and genotypes allotted to the subplots. Two replications of whole plots were arranged in a randomized complete block design.

The statistical analyses were performed using a fixed effects model and dividing Al and P levels sums of squares into linear and quadratic components. The Al × P level interaction sums of squares were also subdivided into interactions involving the linear and quadratic effects of Al and P.

Results and discussion

Experiment 1

The means for RSRL, FSRL, and NSRL and the analyses of variance

Table 2. Analysis of variance for relative seminal root length (RSRL), final seminal root length (FSRL), and net seminal root length (NSRL) on inbred maize lines grown in nutrient solution with Al (Experiment 1)

Source of variation	df	Mean squares		
		RSRL	FSRL (mm plant^{-1})	NSRL (mm plant^{-1})
Replications	2	0.2201	2714.77	2044.46
Al levels	3	21.7961**	133091.67**	133612.82**
Al linear	1	64.0803**	390368.00**	392624.26**
Al quadratic	1	0.0157	32.14	5.73
Deviation	1	1.2922	8874.87	8208.46
Error a	6	0.5145	2207.64	2392.30
Lines	20	2.5982**	12620.94**	9940.54**
Lines × Al levels	60	0.3760**	2369.23**	2228.05**
Lines × Al linear	20	0.9152**	5408.34**	5385.76**
Lines × Al quadratic	20	0.1317	987.02*	776.56*
Deviation	20	0.0812	712.34	521.83
Error b	160	0.0972	519.32	459.37
Total	251			
CV (%)		13.5	12.4	21.3

*, ** Statistical significance at $\alpha = 0.05$ and $\alpha = 0.01$.

for the USA and Brazilian inbred maize lines evaluated at four Al levels in Experiment 1 are presented in Tables 1 and 2. A consistency of results for the three traits was evident from the analyses of variance in Table 2. The linear responses to Al levels, differences among inbred lines, and the interaction of Al levels × lines were all statistically significant. Because of the significant Al levels × lines interactions, different analyses of variance were calculated and the linear and quadratic responses of Al levels were evaluated for each inbred line[18].

The Brazilian inbred lines L69 and M1002 were not affected by Al level (Table 1). Each of the other lines decreased in seminal root length with increasing Al level in the nutrient solution. However, at the highest Al level (222 μmol L^{-1}) the Brazilian lines L153, L297, M1001, M1003, M1004, M1005, and M1010 were affected less than the other inbred lines, especially when the RSRL and NSRL traits were used. Although differences at low levels of Al were noted, each of the USA and two of the Brazilian lines (M1007 and M1009) grew poorly at high levels of Al. In addition to the inbred lines L69 and M1002, the other inbred lines that grew relatively well under high Al stress should be desirable for production of hybrids to be grown on soils with high Al saturation.

The Brazilian inbred lines were generally more tolerant of Al than the USA inbred lines. The Brazilian lines were not developed from plants grown on soils with high levels of Al saturation, but the apparent random fixation of genes for tolerance to Al in inbred lines is an indication of the variability for tolerance in populations from which inbred

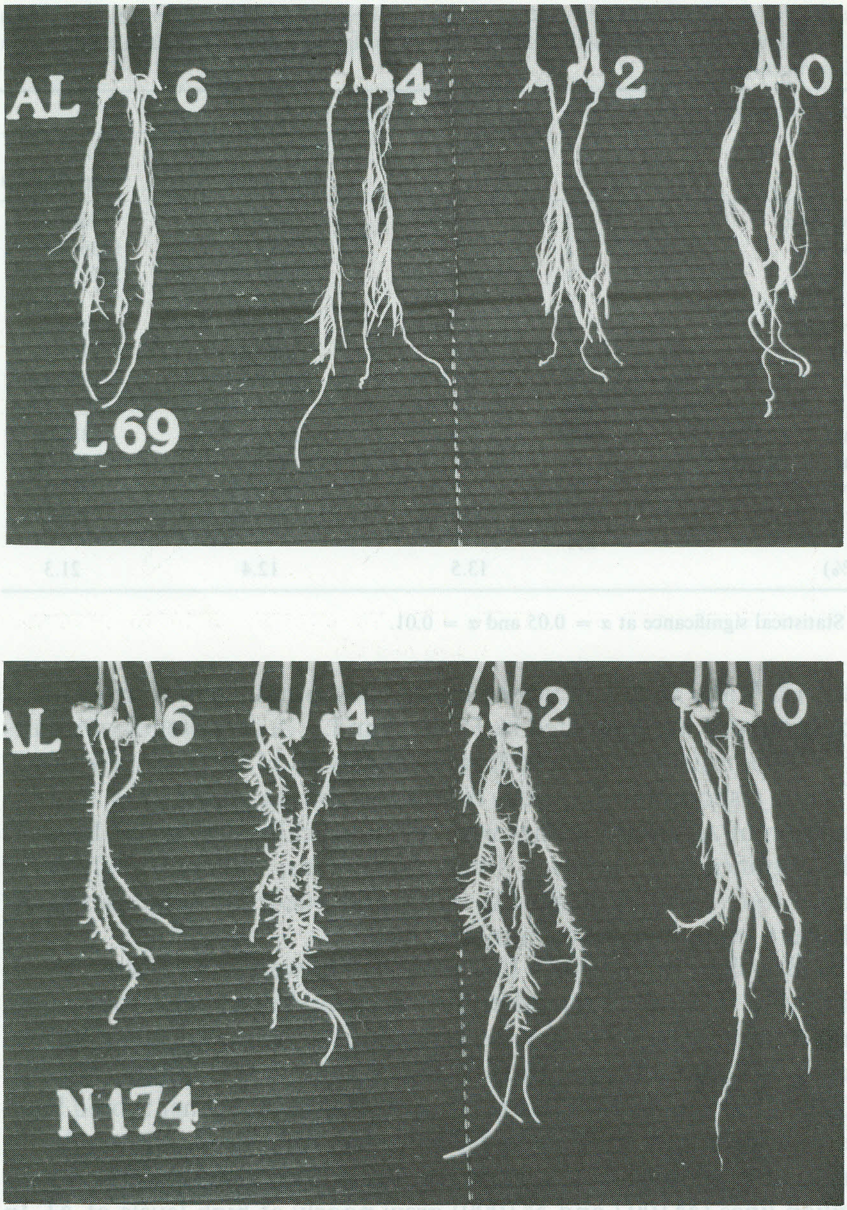

Fig. 1. Roots of the inbred maize lines L69 and N174 grown in nutrient solution at 222, 148, 74, and 0 μmol Al L^{-1} (6, 4, 2, and 0 mg Al L^{-1}) (left to right).

lines are developed. These lines had been tested for Al tolerance on acid soils in Brazil, and most of them showed high Al tolerance and grew well on the acid soils with high Al saturation[1].

The screening method used in this experiment showed considerable potential for large scale evaluations of inbred lines and progenies of

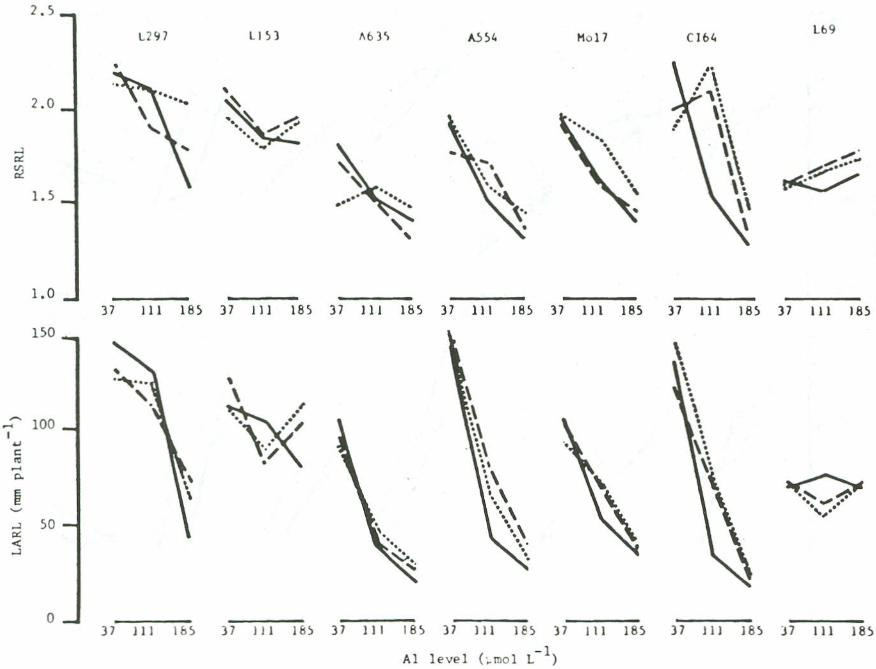

Fig. 2. Relative seminal root length (RSRL) and longest adventitious root length (LARL) of maize inbred lines grown at various levels of Al and P in nutrient solution (Experiment 2).

maize. By using six plants per plot, it was possible to evaluate 21 lines per container. Discrimination among inbred lines was relatively easy at 222 μmol Al L^{-1}, especially when using RSRL to assess Al tolerance. The utilization of the high Al level used overcame the necessity of calculating relative values from measurements of the same lines in solutions without Al. Thus, the size of the experiment could be decreased to half. Figure 1 shows visual symptoms of Al toxicity for the tolerant L69 and the non-tolerant N174 maize inbreds.

Experiment 2

Seven inbred maize lines were evaluated at different levels of Al and P in nutrient solutions; three Brazilian lines (L69, L153, and L297) and four USA lines (A554, A635, CI64, and Mo17) were tested. The means of four traits (RSRL, LARL, FSRL, and NSRL) for each inbred line grown at various levels of Al and P are presented as response curves (Figs. 2 and 3). The analyses of variance of these four traits are presented in Table 3. Even though results varied slightly among the traits, significant differences were consistent among main effects of Al levels, lines, and the triple interaction of Al × P × lines. Also the lack of significance of main effects of P and P × line interaction was consistent. Only for RSRL was the Al × P interaction significant.

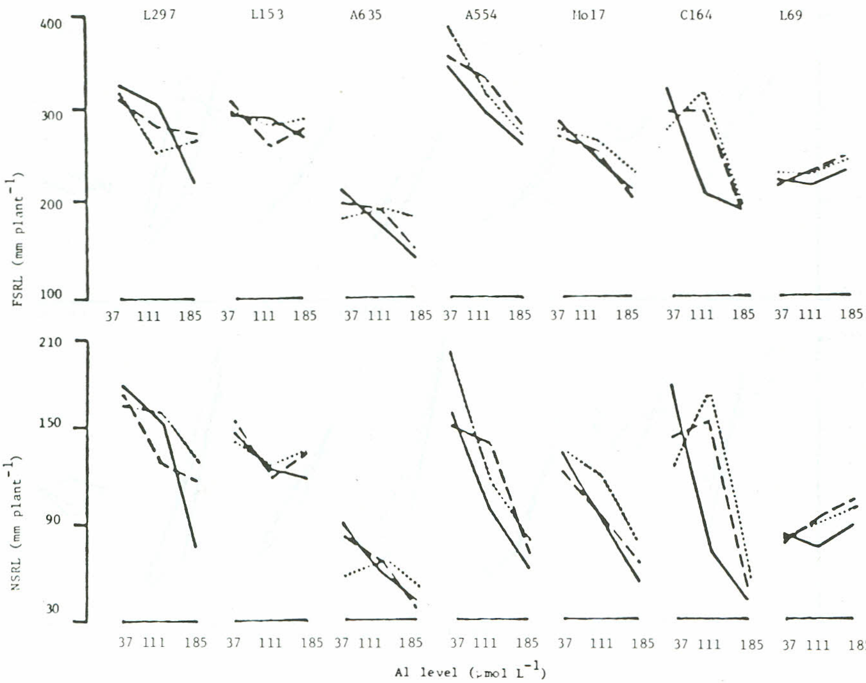

Fig. 3. Final seminal root length (FSRL) and net seminal root length (NSRL) of maize inbred lines grown at various levels of Al and P in nutrient solution (Experiment 2).

The inbred line L69 was not affected by Al level, and slight increases in root length at high levels of P were observed for each seminal root measurement. L69 was derived from a local Catete variety of the 'Cerrado' region in Brazil, and its response to Al level was similar in both Experiments 1 and 2.

The response of line L297 (derived from a cross of a tuxpeno line with the temperate single cross hybrid XL45) to Al levels depended on P level, especially for seminal root measurements. As the P level increased in the nutrient solution, the detrimental effects of Al decreased. The response of line L153, derived from a cross of a Catete population from Brazil and an Eto population from Colombia, for the four traits indicated some sensitivity to Al level, but somewhat independent of P level. However, L153 root lengths were greater than those of L69 at each Al and P level and greater than those of L297 at low P levels.

It was of interest to compare the results for these three Brazilian lines grown in nutrient solution with their grain yield response when grown in the field with three levels of Al saturation[10,19]. L69 was stable over each Al level in nutrient solution, but was intermediate in grain yield when grown in the field. L153 did not grow well at the high Al levels in nutrient solution, but two tons of lime ha^{-1} in the field was sufficient to promote

Table 3. Analysis of variance of relative seminal root length (RSRL), longest adventitious root length (LARL), final seminal root length (FSRL), and net seminal root length (NSRL) of maize inbred lines grown in nutrient solution with three levels each of Al and P (Experiment 2)

Source of variation	df	Mean squares			
		RSRL	LARL (mm plant^{-1})	FSRL (mm plant^{-1})	NSRL (mm plant^{-1})
Replications	1	0.0040	271.63	1225.78	257.14
Al levels	2	1.2314**	49749.11**	29056.89**	28618.88**
Al linear	1	2.4480**	96425.19**	57828.76**	56732.01**
Al quadratic	1	0.0149	3073.02**	285.02	505.75
P levels	2	0.0476	393.92	1230.05	1530.45
P linear	1	0.0953	624.30	2325.76	3012.01
P quadratic	1	0.0000	163.53	134.35	48.89
Al × P	4	0.0774*	185.08	856.26	1159.47
Al linear × P linear	1	0.2379**	565.79	2511.16	3001.78
Al linear × P quadratic	1	0.0012	172.02	190.72	172.02
Al quadratic × P linear	1	0.0668	1.17	323.15	1292.59
Al quadratic × P quadratic	1	0.0038	1.34	400.00	171.50
Error a	8	0.0182	254.81	1322.03	596.82
Lines	6	0.4775**	6518.90**	34879.68**	13590.75**
Al × lines	12	0.1396**	3703.32**	3382.19**	3349.94**
Al linear × lines	6	0.2231**	6176.50**	5972.96**	5753.90**
Al quadratic × lines	6	0.0561**	1230.15**	791.43	945.97**
P × lines	12	0.0171	136.16	241.08	246.09
P linear × lines	6	0.0199	213.55	305.96	335.37
P quadratic × lines	6	0.0142	58.78	176.21	156.81
Al × P × lines	24	0.0328**	232.83*	937.41*	680.98**
Al linear × P linear × lines	6	0.0201	193.99	627.74	426.28
Al quadratic × P linear × lines	6	0.0677**	313.96*	2370.95**	1434.57**
Al linear × P quadratic × lines	6	0.0139	90.34	330.11	205.80
Al quadratic × P quadratic × lines	6	0.0297	333.02*	420.83	657.25*
Error b	54	0.0152	126.47	514.38	280.34
Total	125				
CV (%)		7.03	13.98	8.77	15.07

*, ** Statistical significance at $\alpha = 0.05$ and $\alpha = 0.01$.

high grain yield. L297 responded adversely to Al levels in nutrient solution, but at high Al saturation in the field, grain yields were high. From these results, it was concluded that Al affected the high yielding L297 line by interfering with the uptake or utilization of P. This was not apparent for the other two Brazilian lines. At the highest level of Al, L29 and L153 were able to absorb and translocate P in a normal pattern. Relationships between P nutrition and Al tolerance have been reported[2,6,7,12,13,21].

The four USA inbred lines A554, A635, CI64, and Mo17 had decreased root lengths with increasing levels of Al. The largest decreases generally occurred at the lowest level of P. The inbred line CI64 was unique for seminal root measurements in that when grown with high levels of P, the addition of 111 μmol Al L^{-1} increased root length relative to the lowest level of Al. However, root development decreased sharply with the addition of the higher 185 μmol Al L^{-1}. Similar responses were reported for the inbred maize line B57[4]. Root growth may also be inhibited by high levels of P[5]. The addition of Al to the solution may have inactivated some of the P in solution. Because of the biological and statistical significance of the Al × P × line interaction, response curves for each trait of each line to the various levels of Al and P have been presented (Figs. 2 and 3).

Based on these results, 185 μmol Al L^{-1} and 45 μmol P L^{-1} in nutrient solutions were considered to be the best combination of Al and P to be used in genetic studies where 42 plants were grown per 6.5 L container for 10 days in treatment.

Although similarities among traits for assessing Al tolerance were noted in the maize inbreds, RSRL determined by the nutrient solution technique is recommended as the best of the traits to assess maize genotypes for Al tolerance. One concern was the effect of Al of root vigor during the seedling stage. RSRL was the only seminal root measurement that was corrected for ISRL. In Experiment 2, the correlations of ISRL with FSRL, NSRL, RSRL, and LARL were 0.68**, 0.31**, − 0.02, and 0.21*, respectively. The NSRL and LARL analyses showed higher coefficients of variation compared to RSRL. NSRL and LARL would be recommended as second choices to RSRL as traits for assessing Al tolerance in nutrient solution. The FSRL could not be recommended as a suitable trait to assess Al tolerance.

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