Comparisons of maize populations for aluminum tolerance in nutrient solution

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Key words Al effects on roots Al Ca Cl Cu Fe K Mg Mn P S Zn (*Zea mays*)

Summary The original Brazilian maize (*Zea mays* L.) base population 'Composto Amplo' and a fourth cycle of selection from 'Composto Amplo' were compared with the Hays Golden vareity, Nebraska B Synthetic, Corn Belt × Brazilian, and Corn Belt × Caribbean populations for Al tolerance when grown in nurtient solutions (241 μmol Al L^{-1}). Root lengths of the original 'Composto Amplo' population were slightly longer than those of the selected 'Composto Amplo' population when grown with Al, and these were considerably longer than the other populations. The selection of 'Composto Amplo' maize population for Al tolerance when grown in an acid Brazilian Oxisol soil, based on grain yield, decreased the frequency of the more Al tolerant plants in favor of intermediate Al tolerant plants. When both of the 'Composto Amplo' populations were compared with the temperate Corn Belt (Hays Golden and Nebraska B Synthetic) and Corn Belt × - tropical (Brazilian and Caribbean) populations, the 'Composto Amplo' populations had a higher frequency of genes for Al tolerance than the other populations. The population derived from the cross of Corn Belt × Brazilian materials consistently ranked high in Al tolerance relative to Hays Golden and Nebraska B Synthetic. The introgression of Brazilian germplasm into other populations increased the tolerance of these populations to Al toxicity.

The tropical populations had lower root Al concentrations, but similar Al contents as the temperate populations. Shoot concentrations of Cl and Fe were higher and P, S, and Zn were lower and shoot contents of Ca, K, Cl, Mn, and Cu were higher in the tropical compared to the temperate populations. Root concentrations of K, Cl, and Mn were higher and P, S, and Cu lower and root contents of Mg, Ca, K, Cl, Mn, and Zn were higher and S and Cu were lower in the tropical compared to the temperate populations. The tropical × temperate populations were intermediate to the tropical and temperate populations for element concentrations and contents.

Introduction

A major constraint to maize (*Zea mays* L.) production on tropical soils such as those found in Brazil is the problem created by excess acidity. Many mineral element deficiencies and toxicities occur in acid soils. Aluminum toxicity is one of the most serious problems[4]; hence, strategies to alleviate this disorder by adding lime or P or by developing more tolerant germplasm have been pursued. A promising strategy for overcoming Al toxicity has been to develop breeding procedures for the identification, selection, and improvement of Al-tolerant genotypes.

Maize population improvement for acid soil tolerance has received

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considerable attention in recent years. Bahia et al.[1] screened 195 populations in a Brazilian acid Oxisol soil and found considerable variation among populations for adaptation to such soils. Fewer populations were tested in subsequent years and CMS 14 and CMS 30 ('Composto Amplo') showed the greatest potential for population improvement by recurrent selection[10]. Beginning in 1975, the 'Composto Amplo' population was used to select for Al tolerance by measuring grain yield when grown on a Brazilian acid Oxisol with 45% Al saturation[11]. Each year, 500 half-sib families were tested, and the selected families were recombined at Sete Lagoas, Brazil, until four cycles of selection were completed.

The objectives of the study reported here were to (i) obtain information about changes in Al tolerance that occurred from selection for high grain yield in a population grown on acid soils of Brazil, (ii) compare non-tolerant and Al-tolerant populations for differences in mineral element uptake, (iii) examine the effect of tropical germplasm introgressed into Corn Belt populations on Al tolerance, and (iv) determine how this information might be used in breeding for Al tolerance in maize.

Materials and methods

Germplasm used

Six maize populations chosen for this study included (1) the original 'Composto Amplo', (2) a fourth cycle selection from 'Composto Amplo', (3) Hays Golden, (4) Nebraska B Synthetic, (5) Corn Belt × Brazilian Composite, and (6) Corn Belt × Caribbean Composite. The original 'Composite Amplo' is a composite with a broad genetic base developed at the Institute of Genetics, Luiz de Queiroz College of Agriculture, University of Sao Paulo, Piracicaba, S.P., Brazil. This population has been used extensively in the maize breeding program at the National Corn and Sorghum Research Center, Sete Lagoas, M.G., Brazil. Four cycles of selection between and within half-sib families of the original 'Composto Amplo' population were obtained by growing the plants of each cycle on a Brazilian acid Oxisol soil containing 45% Al saturation. The Hays Golden variety, developed at the Fort Hays (Kansas) Experiment Station, was collected in southwestern Nebraska and has been maintained at the Nebraska Agricultural Experiment Station. The Nebraska B Synthetic was developed from 32 inbred lines by Dr. J. H. Lonnquist at the Nebraska Agricultural Experiment Station where it has been maintained. A Corn Belt × Brazilian Composite was developed by Dr. J. H. Lonnquist by compositing two crosses: Corn Belt Composite × Brazilian #5 and Corn Belt Composite × Brazilian Composite 2 #1. The Corn Belt Composite consisted of the varieties Hays Golden, Barber Reid, Krug Yellow Dent, Lancaster Surecrop, and Golden Republic. A Corn Belt × Caribbean Composite was also developed by Dr. J. H. Lonnquist compositing R_{III} × Caribe #4, SSS_{III} × Caribe #4, $Krug_{III}$ × Caribe #4, and CBC × Colombian #6. R_{III}, SSS_{III}, and $Krug_{III}$ are improved synthetic varieties developed by three cycles of recurrent selection for general combining ability from Nubold Reid, Stiff Stalk Synthetic (Iowa), and Krug Yellow Dent, respectively[18].CBC is a Corn Belt Composite, and US342 is a double cross hybrid (C15 × KYS) × (WF9LH × 3811LH).

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 241 μmol Al L^{-1} as $KAl(SO_4)_2$. The nutrient solution and techniques used for growing plants have been described[3,14]. 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, 0.63 Cu, 0.83 Mo, and 77 Fe as FeHEDTA (ferrichydroxyethylethylenediaminetriacetate). The pH of nutrient solutions was adjusted initially to 4.0, monitored daily, and adjusted to 4.0 when necessary. Water was added to maintain solution volumes.

Plants were grown in a controlled environment room with 16 h light at 27 $\pm$ 1°C and 8 h darkness at 19 $\pm$ 1°C. The photosynthetic photon flux density was 150 $\mu E\, m^{-2} s^{-1}$ at plant height (40 cm below the lamps) provided by fluorescent lamps (Agro-Lite, cool white, F40)*. The experimental design was a randomized complete block with three replications. Each plot (plate) had 42 plants.

Handling of plants and traits measured to assess Al tolerance

When seedlings were initially transferred to treatment solutions, the lengths of seminal roots were measured, and adventitious roots that had started to grow were removed. Plants were grown in treatment solutions for 10 days. When experiments were terminated, the final seminal root length and length of the longest adventitious root were measured. Roots and lower leaves were thoroughly water rinsed, blotted dry, separated into shoots and roots (residual kernel pieces removed), dried in a forced-air oven at 70°C for a minimum of four days, weighed, and ground to pass a 0.5 mm screen.

The traits used to assess plants for tolerance to Al were (a) initial seminal root length, (b) final seminal root length, (c) longest adventitious root length, (d) relative seminal root length (the final seminal root length divided by the initial seminal root length), (e) net seminal root length (the final seminal root length minus the initial seminal root length), (f) shoot dry weight, and (g) root dry weight. Mineral element concentrations and contents were also determined to evaluate the populations for relationship of mineral elements to Al tolerance. Concentrations of Mg, Al, P, S, Cl, K, Ca, Mn, Fe, Cu, and Zn were determined in 13 mm diameter pellets (100 mg) of dried shoot and root tissue by energy-dispersive x-ray fluorescence spectrometry[17].

Results and discussions

Means for four of the traits measured in the six populations are presented in Table 1. The results were relatively consistent from one trait to another. The original and the selected (four cycles) 'Composto Amplo' populations both showed higher levels of Al tolerance than the other populations. A high frequency of favorable genes for Al tolerance existed in the original 'Composto Amplo' population as well as in the selected 'Composto Amplo'. The Corn Belt × Brazilian population which has been grown annually in Nebraska on non-acid soils for many years displayed more Al tolerance than either of the Corn Belt populations and the Corn Belt × Caribbean population. The latter three populations differed little from each other in Al tolerance. The introgression of Brazilian germplasm into a Corn Belt population apparently increased the Corn Belt population tolerance to Al toxicity. Root development of the six populations is illustrated in Figure 1.

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Table 1. Means for relative seminal root length (RSRL), longest adventitious root length (LARL), final seminal root length (FSRL), and net seminal root length (NSRL) of six maize populations grown in nutrient solution with Al (mm root^{-1})

Populations	RSRL	LARL	FSRL	NSRL
'Composto Amplo' original	2.09 a†	176 a	341 cd	178 a
'Composto Amplo' selected (4th cycle)	1.94 b	148 b	310 b	149 b
Corn Belt × Brazilian	1.27 c	115 c	158 c	33 c
Corn Belt × Caribe	1.08 d	97 d	150 cd	11 d
Hays Golden	1.12 d	71 e	167 c	18 cd
Nebraska B Synthetic	1.20 cd	81 de	135 d	22 cd

† Means followed by a common letter are not significantly different at $\alpha = 0.05$ according to Duncan's New Multiple Range Test.

Estimates of variability among individual plants within each population for four Al tolerance traits are reported in Table 2. The variance in the original 'Composto Amplo' population was higher than that of the selected 'Composto Amplo' for all measured traits, and both had greater plant-to-plant variances than the other populations. The Corn Belt × Brazilian population had more useful variability than the other three non-Brazilian populations. The Corn Belt × Caribbean and Hays Golden populations showed relatively little variability for Al tolerance.

The decrease in variability of the selected 'Composto Amplo' population compared to the original 'Composto Amplo' was best demonstrated

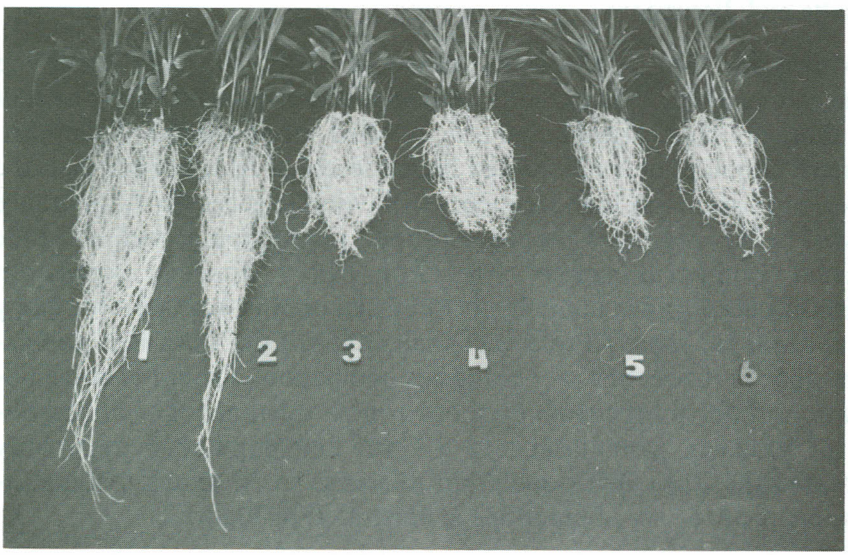

Fig. 1. Root development of maize populations grown in nutrient solutions with 241 μmol Al L^{-1}. Left to right: 1 = original 'Composto Amplo', 2 = selected 'Composto Amplo', 3 = Corn Belt × Brazilian, 4 = Corn Belt × Caribbean, 5 = Hays Golden, and 6 = Nebraska B Synthetic.

Table 2. Analyses of variance for relative seminal root length (RSRL), longest adventitious root length (LARL), final seminal root length (FSRL), and net seminal root length (NSRL) of six maize populations grown in nutrient solution with Al

Source of variation	df	Mean square values			
		RSRL	LARL	FSRL	NSRL
Replications	2	0.0005	264.89	30.11	35.65
Populations	5	0.5927**	4905.47**	24663.36**	16644.69**
Error	10	0.0051	90.82	136.77	90.98
CV (%)		4.9	8.3	5.6	13.9
Among plants	738	0.1055	2540.05	3213.06	2531.69
'Composto Amplo' original	123	0.2904	7513.12	9459.39	8219.02
'Composto Amplo' selected	123	0.2023	4112.17	5257.98	4840.76
Corn Belt × Brazilian	123	0.0752	1164.51	1900.91	1222.07
Corn Belt × Caribe	123	0.0046	984.95	606.13	88.97
Hays Golden	123	0.0105	697.96	827.21	235.47
Nebraska B Synthetic	123	0.0503	767.61	1226.72	583.84

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

using relative seminal root lengths (RSRL). Values above 1.0 represent greater tolerance to Al (Fig. 2). When frequency distributions of the two populations were compared, the frequency of the highly tolerant genotypes in the selected population decrease. The selection of germplasm grown in soils with relatively high Al saturation favoured the selection of germplasm with intermediate Al tolerance rather than germplasm with high Al tolerance. A possible explanation for the selection of intermediate types would be a negative correlation between a high level of Al tolerance and grain yield but information about this is limited. However, Martini *et al.*[19] and Silva[22] reported that Brazilian Al tolerant wheat (*Triticum aestivum* L.) varieties produced as well as other high yielding varieties when grown on soils without Al toxicity problems.

The use of nutrient solutions with Al could be an effective method to screen maize germplasm for Al tolerance. Large numbers of progenies could be evaluated for Al tolerance in nutrient solution, and the more tolerant progenies could than be evaluated for grain yield in the field on

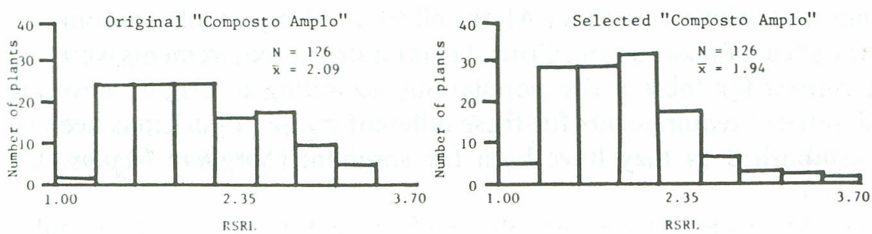

Fig. 2. Frequency distributions of relative seminal root length (RSRL) of plants from the original and 'Composto Amplo' populations grown in nutrient solution with 241 μmol Al L^{-1}.

soils with Al toxicity stresses. This two-stage selection program, which corresponds to the Hazel and Lush[15] use of independent culling levels for two traits, has promise for simultaneously improving both traits with minimum work. As Hazel and Lush[15] pointed out, the use of a selection index involving two traits is generally more efficient in animal breeding, but screening for Al tolerance among maize families could be accomplished on a large scale at minimum cost. Yield testing, on the other hand, is very expensive and should be limited to those families with relatively high Al tolerance. If any negative correlation between yield and Al tolerance is caused by linkage, genetic recombination should occur and simultaneous selection for two traits will be effective for both. To the extent that negative correlation is caused by pleiotropy, little can be done to improve both traits simultaneously. Additional information on the nature of the correlation is needed.

Because of the large differences among the six populations for Al tolerance, the roots and shoots of the plants were analyzed for mineral elements to determine if mineral elements could be related to genotype differences to Al tolerance. Dry matter yields and mineral element concentrations and contents in roots and shoots are presented in Tables 3 and 4.

Shoot and root dry matter yields (Table 3) followed trends similar to root length measurements for Al tolerance. That is, higher dry matter yields and longer roots were both associated with greater Al tolerance. Mineral element concentrations did not follow the same trend. Total dry matter yields of the populations were: original 'Composto Amplo' > selected 'Composto Amplo' ≥ Corn Belt × Caribbean = - Corn Belt × Brazilian > Hays Golden = Nebraska B Synthetic. The two temperate (Corn Belt) populations has the lowest dry matter yields. The Corn Belt × Caribbean population which was affected as badly as the temperate populations by Al had higher shoot and root dry matter yields.

Origin of the populations should be considered in the interpretation of the mineral element data (Tables 3 and 4). Since concentrations of mineral elements were not determined for these same populations grown in nutrient solutions without Al, the effect of Al is partially confounded by the effect of plant origin. Critical plant nutrient requirements were not determined for these maize populations according to origin, however, and nutrient requirements for these different maize populations need to be established as they have been for sorghum (*Sorghum bicolor* (L.) Moench)[9,13].

The Al concentrations in roots could be used to separate the populations by origin (Table 3); the tropical (Brazilian and Caribbean) populations had lower Al concentrations than the temperate populations (Table

Table 3. Dry matter yields and mineral element concentrations in shoots and roots of six maize populations grown in nutrient solution with Al

Population	Dry matter yield (mg 42 plants^{-1})	Mineral element concentration										
		Mg	Ca	K	P	S	Cl	Al†	Mn	Fe	Cu	Zn
		(mg g^{-1} dry wt.)							(μg g^{-1} dry wt.)			
Shoots												
'Composto Amplo' original	8670‡	2.9 d	7.3 a	65.4 b	2.6 c	3.2 c	8.8 a	–	47.5 a	103 b	9.2 ab	32.6 b
'Composto Amplo' selected	7000 b	3.0 cd	7.0 ab	70.7 a	3.0 c	3.5 c	9.2 a	–	47.3 a	108 b	9.0 ab	35.4 b
Corn Belt × Brazilian	6670 b	3.1 cd	6.4 c	62.2 bcd	4.6 ab	5.1 b	7.5 cd	–	39.1 ab	141 a	9.5 ab	53.2 a
Corn Belt × Caribbean	6800 b	3.4 bc	6.5 bc	60.5 cd	4.4 b	5.2 ab	7.9 bc	–	37.3 ab	129 a	7.7 b	50.6 a
Hays Golden	4930 c	3.5 ab	6.8 abc	59.3 d	4.9 ab	5.3 ab	7.1 d	–	41.9 ab	126 a	9.6 ab	48.2 a
Nebraska B Synthetic	4570 c	3.9 a	6.3 c	64.8 bc	5.2 a	5.5 a	8.0 b	–	34.9 b	132 a	10.6 a	51.7 a
Roots												
'Composto Amplo' original	3170 a	2.5 a	6.0 a	45.6 b	2.8 c	5.5 d	4.6 a	3.7 d	28.6 a	416 d	13.7 c	44.8 a
'Composto Amplo' selected	2430 b	2.4 a	4.8 bc	57.5 a	3.0 c	5.9 d	3.4 b	4.0 cd	24.3 a	496 cd	12.0 c	47.0 a
Corn Belt × Brazilian	2030 c	2.4 a	5.7 a	42.9 b	4.9 b	16.9 c	3.0 b	5.3 bc	14.2 b	554 bc	60.5 b	46.9 a
Corn Belt × Caribbean	2100 bc	2.2 ab	5.4 ab	38.1 c	4.8 b	18.1 bc	3.2 b	5.3 bc	15.9 b	571 bc	51.6 b	44.8 a
Hays Golden	1200 d	1.8 b	4.9 bc	33.1 d	5.6 a	22.2 a	2.4 c	8.8 a	12.3 b	705 a	83.1 a	45.2 a
Nebraska B Synthetic	1330 d	2.2 ab	4.6 c	38.2 c	5.2 ab	18.8 b	3.0 b	6.3 b	16.2 b	666 ab	78.1 a	42.8 a
Statistical significance of F test for treatment												
Shoots	**	**	*	**	**	**	**	–	ns	**	ns	**
Roots	**	*	**	**	**	**	**	**	**	**	**	ns

† The aluminum concentrations in shoots were below the minimum detectable limit of the instrument (< 100 g g^{-1}).
‡ Means followed by a common letter are not significantly different at $\alpha = 0.05$, according to Duncan's New Multiple Range Test.
*, ** Statistical significance at $\alpha = 0.05$ and $\alpha = 0.01$, respectively; ns = nonsignificant.

3). These differences were not significant for Al content (total amount in plant parts), which would indicate a possible dilution effect from larger roots (Table 4). Since Al in the shoots was very low, Al apparently was not translocated from roots to shoots, which has also been noted in other studies with maize[2,20]. The Al may have become bound to the root surfaces[20] and root cell walls[7,16].

Concentrations of Mg, Ca, and K in the plants were dependent on the element and the plant part (Table 3). Concentrations of Mg in shoots were higher for both of the temperate populations, but these populations differed only slightly in root Mg concentration. The discrimination among populations for Ca in the shoots and roots did not appear to be related to plant origin. Both of the 'Composto Amplo' populations had higher K concentrations in shoots and roots than the other populations. The contents of Mg, Ca, and K followed approximately the same trend as the dry matter yield differences (Table 4). Detrimental effects of Al on Mg, Ca, and K uptake and translocation, as well as differences in critical levels of these elements in each population, may help to explain the results obtained. Effects of Al on element uptake have been reported for maize[2,21].

Concentrations of P and S were different from those of Mg, Ca, and K (Table 3). The two Al tolerant 'Composto Amplo' populations had lower P and S concentrations in both the shoots and roots than did the non-tolerant populations. The temperate × tropical populations consistently had higher P and S contents in both shoots and roots than the other populations (Table 4). The tropical and temperate populations did not differ in P and S in shoots, but the temperate populations had lower contents of P and higher contents of S in roots. Mineral element uptake and distribution were not related to root length measurements not to dry matter yields of the different populations. Origin of population may be important for element concentration and content. Chlorine concentrations and contents were similar to Mg, Ca, and K.

The P concentrations and contents noted in the Al tolerant and non-tolerant populations used in this study did not agree with results reported by others. The contents of P noted (Table 4) did not indicate that Al interfered with P absorption and translocation.The lower P concentrations in the Al tolerant populations may have been due to plant growth dilution. A relationship between P nutrition and Al tolerance in maize plants has been reported[5,6,12,20].

Although mineral element data obtained in most studies have been experiments involving homogeneous maize genotypes, the data obtained in this study were obtained from heterogenous populations. A higher level of Al in nutrient solutions would probably be required for Al to cause detrimental effects on P uptake. Although Al decreased root length

Table 4. Mineral element contents in shoots and roots of six maize populations grown in nutrient solution with Al

Genotype	Mineral element content										
	Mg	Ca	K	P	S	Cl	Al[†]	Mn	Fe	Cu	Zn
	(mg 42 plants^{-1})							(μg 42 plants^{-1})			
Shoots											
'Composto Amplo' original	25.1 a[‡]	63.7 a	565 a	22.7 b	28.0 b	76.2 a	–	413 a	896 ab	80.3 a	283 b
'Composto Amplo' selected	20.8 bc	48.9 b	495 b	21.0 b	24.8 c	64.1 b	–	332 ab	759 bc	63.1 b	247 c
Corn Belt × Brazilian	20.9 bc	42.7 b	415 c	30.9 a	34.0 a	49.8 d	–	260 bc	940 a	63.5 b	354 a
Corn Belt × Caribbean	22.9 ab	44.2 b	411 c	30.2 a	35.0 a	53.9 c	–	254 d	880 ab	52.4 b	344 a
Nebraska Hays Golden	17.2 d	33.7 c	293 d	24.3 b	26.1 bc	35.0 e	–	207 cd	623 c	43.4 b	238 c
Nebraska B Synthetic	17.7 cd	28.9 c	296 d	23.5 b	25.3 c	36.4 e	–	160 d	603 c	48.0 b	235 c
Roots											
'Composto Amplo' original	8.00 a	19.1 a	144 a	8.8 ab	17.2 c	14.5 a	11.7 a	91 a	1307 a	43.5 c	142 a
'Composto Amplo' selected	5.80 b	11.8 b	139 a	7.3 bc	14.5 c	8.2 b	9.7 ab	60 b	1227 ab	29.6 c	115 b
Corn Belt × Brazilian	4.90 b	11.6 b	87 b	10.0 a	34.4 a	6.2 c	10.7 ab	29 c	1128 ab	122.8 a	95 c
Corn Belt × Caribbean	4.50 b	11.3 h	80 b	10.1 a	38.1 a	6.6 bc	11.1 ab	33 c	1199 ab	108.5 ab	94 c
Nebraska Hays Golden	2.20 c	5.9 c	40 c	6.8 c	26.7 b	2.9 d	10.5 ab	15 c	846 b	99.8 b	54 d
Nebraska B Synthetic	3.00 c	6.1 c	50 c	6.9 c	25.0 b	4.0 d	8.4 b	21 c	885 b	102.3 b	57 d
Statistical significance of F test for treatment											
Shoots	**	**	**	**	**	**	–	**	**	**	**
Roots	**	**	**	**	**	**	ns	**	ns	**	**

[†] It was not possible to estimate the content of Al in shoots since the concentrations were usually below the minimum detectable limit of the instrument (< 100 μg g^{-1}).
[‡] Means followed by a common letter are not significantly different at $\alpha = 0.05$, according to Duncan's New Multiple Range Test.
*, ** Statistical significance at $\alpha = 0.05$ and $\alpha = 0.01$, respectively, ns — nonsignificant.

dramatically, no P deficiency symptoms were noted on any of the plants in the populations.

The results for Mn, Fe, Cu, and Zn indicated different responses for each element. The more Al tolerant tropical populations did not show differences for Mn and Cu in shoots compared to the non-tolerant populations (Table 3). Iron and Zn concentrations were lower in the tolerant populations than in the non-tolerant populations. Aluminum tolerant populations had root concentrations of Zn similar to non-tolerant populations, but had lower root Fe and Cu and higher root Mn.

Distinctions between tolerant and non-tolerant populations were noted for Mn contents in the shoots which were higher in the Al tolerant populations than in the non-tolerant populations (Table 4). No differences among populations were noted for Fe contents in the roots, but tolerant populations had higher Mn and Zn contents and lower Cu contents. These results agree with comparisons made between Al tolerant and non-tolerant inbred maize lines for Mn, but not for Fe, Zn and Cu[2]. The concentrations and contents of Cu in roots were extremely low in the Al tolerant populations compared with the non-tolerant populations. Duncan[8] and Furlani[13] reported that differences in concentrations of Fe, Mn, and Cu might be used to distinguish Al tolerant and non-tolerant genotypes of sorghum.

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