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Genetic analysis of means and variances of aluminum tolerance in maize

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ABSTRACT. In acid soils, aluminum constraints productivity of nonadapted plants. Aluminum most evident phytotoxic effect is the decrease in root growth. Joint use of liming and tolerant genotypes would make good use of acid soils. However, there are conflicting results from studies on tolerance inheritance in maize (*Zea mays* L.). The aim of this research was to estimate genetic parameters of tolerance in a family of tolerant and nontolerant inbred lines and their derived generations F_1 and F_2 and backcrosses. Net length of seminal roots of seedlings, developed in a nutrient solution with 4.5 mg/L aluminum, was analyzed. Additive and dominant standard proved sufficient and showed the additive gene effect as the chief generating factor of variability. Narrow-sense heritability was close to one and the number of *loci* was estimated as between two and three. Quick gains in selection cycles may be foreseen for net length of seminal roots.

Key words: maize, aluminum tolerance, tolerance inheritance.

RESUMO. Análise genética de médias e variâncias da expressão da tolerância ao alumínio em milho. Nos solos ácidos, o alumínio limita a produtividade de plantas não adaptadas e seu efeito fitotóxico mais evidente é a redução do crescimento das raízes. O uso combinado de calagem e genótipos tolerantes permitiria o aproveitamento dos solos ácidos. Os resultados de estudos sobre a herança da tolerância em milho (*Zea mays* L.) são conflitantes. O objetivo deste trabalho foi estimar parâmetros genéticos da tolerância em uma família de uma linhagem tolerante e uma sensível e suas gerações derivadas F_1, F_2 e retrocruzamentos. Foi analisado o comprimento líquido da radícula de plântulas desenvolvidas em solução nutritiva com 4,5 mg/L de alumínio. O modelo aditivo-dominante foi suficiente e mostrou o efeito gênico aditivo como o principal fator gerador de variabilidade. A herdabilidade restrita situou-se próxima da unidade e o número de *loci* foi estimado entre dois e três. Podem ser previstos ganhos rápidos em ciclos de seleção para o comprimento líquido da radícula.

Palavras-chave: milho, tolerância ao alumínio, herança da tolerância.

Aluminum has been identified as a decreasing factor in the potential productivity of plants not adapted to acid soils (Foy *et al.*, 1978; Ziegler *et al.*, 1995). In Brazil, aluminum is a decisive factor in agriculture since there are approximately 1.8 million km^2 of open land, called *cerrado*, with acid soil (Lopes, 1984; Silva, 1976).

Many phytotoxic effects of aluminum are well known in nontolerant plants, but the mechanism involved has not yet been determined. Nevertheless, many attempts have been made to explain aluminum toxicity (Bennet and Breen, 1991; Delhaize and Ryan, 1995; Kochian, 1995; Matsumoto, 1991, 2000). The most plausible explanation has been the decrease of mitotic activity in root meristems (Sivaguru and Horst, 1998). Due to deficient development of the root system, plants produce only surface roots, and thus the ability of using soil nutrients is impaired. Besides, the susceptibility to occasional water deficiency increases (Foy *et al.*, 1978).

In acid soils, other adverse factors may be present due to complex interactions in low pH. While essential nutrients are made unavailable, other toxic elements, such as manganese, become available (Foy *et al.*, 1978). One alternative to reverse the disadvantage of acid soils is liming. This results in a higher pH in soil, makes aluminum insoluble and precipitates it, since it turns up to be unavailable to plants (Marion *et al.*, 1976). On the other hand, there are economic and technical difficulties in solving the aluminum problem exclusively by liming (Pandey *et al.*, 1994; Zeigler *et al.*, 1995). Perhaps the best approach for a better use of acid soils includes pH neutralization by liming and the simultaneous use of aluminum-tolerant plants.

A genetic variability decreasing aluminum toxicity has been found in almost all cultivated species and this has motivated selections of tolerant genotypes. The use of aluminum tolerant plants may greatly contribute towards the agricultural bettering of large extensions of land with acid soils (Spehar and Souza, 1999). The subject matter has already been extensively discussed (Foy *et al.*, 1978; Khan and McNeilly, 1998; Matsumoto, 1991; Rhue, 1979; Zeigler *et al.*, 1995). In Brazil, maize (*Zea mays* L.) cultivation has its own limitations in the *cerrado*. As a general rule, productive germoplasms are nontolerant to aluminum, but some indigenous cultivars of the Atlantic coast of South America are tolerant, although with low productivity (Prioli, 1987). These populations are sources of aluminum tolerance and may be used to obtain tolerant and, at the same time, productive genotypes.

Attempts to determine inheritance of aluminum tolerance in maize produced conflicting and nonconclusive results. While the conclusions derived from a few studies indicate monogenic inheritance (Rhue *et al.*, 1978; Garcia and Silva, 1979; Jorge and Arruda, 1997), other studies indicate quantitative inheritance with high heritability and few *loci* involved (Magnavaca, 1982; Magnavaca *et al.*, 1987; Prioli, 1987; Sawazaki and Furlani, 1987).

Additional information that contributes towards the explanation of mechanisms of inheritance of aluminum tolerance in maize is necessary. The main aim of the present work was to estimate genetic parameters of aluminum tolerance in maize through generation analysis.

Material and methods

The methodology of genetic analysis of means and variances of generations, also known as scale (Mather and Jinks, 1971; Cruz and Regazzi, 1994), has favored the investigation on inheritance of aluminum tolerance in maize. Populations analyzed consisted of two parent inbred lines, derived generations F_1, F_2 and backcrosses of F_1 with the two parental inbreds. The model required that parental inbred lines must be divergent with regard to the characteristic under analysis.

Inbred lines, F_1, F_2 and backcrosses. Two inbred lines L922 and Ast214, developed at the State University of Campinas, Campinas, SP, Brazil, were used. Both inbred lines have contrasting phenotypes with regard to aluminum tolerance (Prioli, 1987). Inbed line L922 (also called Cat100-6), derived from *Cateto* race, has orange *flint* endosperm and is highly tolerant to aluminum toxicity. Inbred line Ast214, derived from *Tuxpeño* germoplasm, has a yellowish dent endosperm and is highly nontolerant to aluminum. The inbred lines were maintained by controlled self-pollination. They were also crossed among themselves to produce the hybrid F_1(L922 x Ast214). In the seeding of the following year the two inbred lines were selfed once more and crossed for the production of new F_1 seeds. Besides, F_1 plants were self-pollinated for the production of F_2, whilst other F_1 plants were pollinated by inbred line L922 or by Ast214 for two backcrosses. By this procedure, seeds of a same age were obtained for the two inbred lines, generations F_1, $F_{2,}$ and the backcrosses BC(F_1 x L 922) and BC(F_1 x Ast214). In this work, the use of seeds of a same age for all populations was important in order to avoid aging effects, mainly loss of vigor. Aging effects would represent an error source in the experiment that could lead to misinterpretation of results.

Nutrient solution and aluminum level. A modified nutrient solution suggested by Clark (1975) was used, consisting of 3.43 mM $Ca(NO_3)_2.4H_2O$, 1.27 mM NH_4NO_3, 0.55 Mm KCl, 0.56 mM K_2SO_4, 0.83 mM $Mg(NO_3)_2.6H_2O$, 32.33 μM KH_2PO_4, 61.51 μM $FeSO_4$, 47.29 μM EDTA, 8.28 μM $MnCl_2.4H_2O$, 23.1 μM H_3BO_3, 2.14 μM $ZnSO_4.7H_2O$, 0.56 μM $CuSO_4.5H_2O$, 0.75 μM $Na_2MoO_4.2H_2O$. The nutrient solution was prepared with distilled and deionized water immediately before starting the experiment. Double salt $KAl(SO_4)_2.12H_2O$ was added to the nutrient solution, to a final concentration of 4.5 μg/mL of aluminum ion. This aluminum concentration is appropriate for the discrimination of tolerant and nontolerant maize genotypes (Prioli, 1987). This nutrient solution containing aluminum reaches pH 4.0. The nitrate/ammonia balance in this solution is such that the pH remains stable throughout the experiment period, maintaining the aluminum solubility.

Seed germination and growth room. Seeds were germinated on filter paper wetted with distilled water, which were vertically conditioned in plastic pots containing approximately 3 cm of water. Sealed pots were placed in a dark room with controlled temperature at 26 ±1°C, and kept for 2-3 days till seminal roots reached approximately 2 cm. Seedlings were transferred to holes in floating polystyrene (Styrofoam) plates, so that the seminal roots remained immersed in the nutrient solution. Distilled and deionized water was added daily to maintain the nutrient solution volume, avoiding changes in concentration of nutrients and aluminum. The pH was monitored daily. Due to the nitrate/ammonia balance there was no need of any corrections with acids or bases. During the whole period of the experiment the nutrient solution was oxygenated by forced aeration. Temperature of growth room was maintained at 26 ±1°C and photoperiod monitored to 14/10 hours of light/dark. Artificial illumination was provided at a light intensity of approximately 350 $\mu E.m^{-2}.s^{-1}$ at seedling level.

Plant measurements and calculated variable. Prior to the transfer of seedlings to nutrient solution, the initial seminal root length (ISRL) was measured. Roots were again measured after ten days of growth in the nutrient solution with aluminum. The final seminal root length (FSRL) was thus obtained. The net seminal root length (NSRL), or rather the difference between FSRL and ISRL, was used as the indicative factor of tolerance.

Generation means and variance analyses. A family comprising six populations was studied: two inbred lines, generations F_1, F_2 and backcrosses of F_1 with the two parental lines. Analyses of means and variances of populations followed the method described by Mather and Jinks (1971, 1984). Completely random design was adopted and each plant was taken as an experimental unit (Snedecor and Cochran, 1974). Replications were equal to the number of evaluated individuals in each population. Complete and reduced models of genetic parameters underwent null significance tests by *t*-test (Cruz and Regazzi, 1994; Snedecor and Cochran, 1974).

Parental inbred lines and F_1 are genetically uniform populations, so they could be evaluated with fewer seedlings than the segregating populations. In this experiment, 93 seedlings of inbred line L922, 95 seedlings of inbred line Ast214 and 101 seedlings of F_1 were evaluated. Because generation F_2 and backcrosses had genotypic differences, in each of these populations the number of seedlings in the experiment was higher, as recommended by Ramalho *et al.* (1993). Consequently, 186 seedlings of backcross BC(F_1 x L922), 185 seedlings of backcross BC(F_1 x Ast214) and 311 seedlings of generation F_2 were used. Genetic and statistical analyses of data were performed by GENES software (Cruz, 1997).

Results and discussion

Characteristics related to seminal roots of seedlings in nutrient solution with aluminum are efficient for the discrimination of genotypes of aluminum tolerant and nontolerant maize seedlings (Garcia *et al.*,. 1979; Magnavaca, 1982; Magnavaca *et al.*, 1987; Prioli, 1987; Rhue and Grogan, 1976, 1977; Rhue *et al.*, 1978; Ryan *et al.*, 1993; Silva and Furlani, 1976; Urrea-Gomez *et al.*, 1996). Among the most frequently mentioned traits in literature the net seminal root length (NSRL) notoriously indicates aluminum tolerance or nontolerance in seedlings. The diallel analysis made by Prioli (1987) showed that, with logarithmic transformation, the additive-dominant model would be enough to explain the genetic variability of aluminum tolerance in maize. Therefore, in the present work, the logarithmic transformation was applied with the purpose of minimizing influence of epistatic effects on the expression of aluminum tolerance. Means, variances and coefficients of variation of NSRL in scales of direct and logarithmic measurements are given in Table 1. Logarithmic transformation was efficient as shown by the substantial decrease of variation coefficients of all populations. The only exception was inbred line Ast214 with proportionally higher variance.

Comparison measurements by *t*-test showed that the two lines differed not only in the direct scale (t = 39.7**) but also in log transformation (t = 22.8**). In Table 1 it is shown that means of F_1 population was close to that of tolerant inbred line L922. Dominance of tolerance over aluminum susceptibility is indicated. Dominance of aluminum tolerance found at this point level has already been shown in other studies (Rhue *et al.*, 1978; Garcia and Silva, 1979; Jorge and Arruda, 1997; Prioli, 1987), but studies of Magnavaca (1982) and Magnavaca *et al.* (1987) have given contrary results.

Table 1. Total seedlings, means, variances, coefficient of variation and variance of means of net seminal root length, in direct (cm) and logarithmic scales, of seedlings of inbred lines of maize, tolerant and nontolerant to aluminum, respectively L922 and Ast214, of generations F_1, F_2 and of backcrosses, after 10 days of growth in nutrient solution with 4.5 mg/L of aluminum

Population	Number of	Direct scale (cm)				Log scale			
	seedlings	Mean	Variance	CV (%)	Variance of mean	Mean	Variance	CV (%)	Variance of mean
L922	93	18,19	6,68	14,2	0,072	1,255	0,0045	5,1	0,00005
Ast 214	95	4,91	3,89	40,2	0,041	0,641	0,0635	39,3	0,00067
F_1	101	20,09	6,99	13,2	0,069	1,298	0,0043	5,0	0,00004
F_2	311	15,44	45,74	43,8	0,147	1,129	0,0633	22,3	0,00020
BC(F_1 x L922)	186	20,47	6,97	12,9	0,037	1,307	0,00372	4,7	0,00002
BC(F_1 x Ast214)	185	11,98	36,31	50,3	0,196	1,016	0,0605	24,2	0,00033

Table 2 lists, in two scales, the estimates of genetic parameters associated with NSRL. Although there were negative estimates of variance caused by dominance in the direct scale, estimates were near zero by logarithmic transformation. As a general rule, concordance exists in results obtained in diallel cross analysis by Prioli (1987). Estimates for narrow sense heritability were slightly higher than 1 and higher than the estimates of heritability in a broad sense. Furthermore, there is a similarity in estimated number of *loci* (between 2 or 3) involved in NSRL. In this case, however, estimates of middle level of dominance, based on means, were calculated for tolerance higher than 1. Prioli (1987) showed only partial dominance. This difference may be interpreted as a consequence of the inclusion of moderately tolerant and nontolerant inbred lines of maize in the diallel cross, and may mask expressions of higher dominance in inbred line crosses by means of extreme and opposing responses. Nevertheless, in this research the two most discrepant available inbred lines were used, allowing the detection of the highest dominance level.

Table 2. Estimates of genetic parameters, in direct and logarithmic scales, of net seminal root length (NSRL) of maize seedlings developed for 10 days in nutrient solution with 4.5 mg/L aluminum

Genetic	NSRL	
Parameters	Direct scale (cm)	Log scale
Phenotypic variance	45.74	0.0633
Environmental variance	6.14	0.0191
Genotypic variance	39.60	0.0442
Additive variance	48.20	0.0624
Dominance variance	–8.60	–0.0182
Broad-sense heritability (%)	86.6	69.9
Narrow-sense heritability (%)	105.4	98.6
Average degree of dominance (based on means)	1.29	1.14
Maximum value in F_2	31.5	1.50
Minimum value in F_2	2.4	0.38
Number of genes (based on variances)	2.2	2.5

It should be emphasized, however, that although in this research parents are divergent, the genetic and statistical model used for the calculation of the number of *loci* allows equal effects (Cruz and Regazzi, 1994). If this presupposition were not true, estimates would give an approximate number of *loci* but would not necessarily correspond to the parameter values.

High estimates of narrow sense heritability foresee without any doubt that selection will cause pronounced gains. Gains over 50% in the direct scale are foreseen with a selection of 20% of the most aluminum-tolerant F_2 individuals, or rather, with higher NSRL. In the logarithmic scale gains are lower and amount to approximately 20% (Table 3).

Table 3. Prediction of gains by selection of net seminal root length (NSRL), in direct and logarithmic scales, of maize seedlings developed for 10 days in nutrient solution with 4.5 mg/L aluminum

Genetic	NSRL	
Parameters	Direct scale (cm)	Log scale
Number of selected individuals	62	62
Original mean of F2	15.44	1.129
Means of the selected individuals	23.57	1.37
Selection differential	8.13	0.24
Selection gain	8.57	0.238
Selection gain (%)	55.48	21.07
Predicted mean to first cycle selection	24.01	1.37

The complete model of the mean genetic analysis of the six populations includes genetic parameters: means, additive effect, dominance deviations and three types of nonallelic interactions or epistasis. By means of this model the gene effect (with the highest estimates) caused by dominance was identified, to which corresponds the highest variance (Table 4). There were nonsignificant epistasis effects, although without any consistency between direct and logarithmic scales. When analysis was undertaken with direct measurements, the interactions additive x additive and dominant x dominant were not significant at 5% probability level by *t*-test. On the other hand, interaction additive x additive was significant at 1% level. Logarithmic transformation caused opposite results: additive x dominant type of epistasis was not significant, whilst interactions additive x additive and dominant x dominant were significant at 1% probability level (Table 4).

Table 4. Null significance test of entire models of genetic parameters obtained from means of net seminal root length, in direct (cm) and logarithmic scales, of seedlings of inbred lines of maize, aluminum tolerant and nontolerant respectively, L922 and Ast214, derived generations F_1, F_2 and backcrosses, after 10 days of growth in a nutrient solution with 4.5 mg/L aluminum

Genetic	Direct scale (cm)				Log scale			
Parameter	Estimate	Variance	DF	*t*	Estimate	Variance	DF	*t*
m	8.41	3.32	865	4.62★★	7.1879	0.606	865	9.22★★
a	6.64	0.03	186	39.54★★	2.0479	0.004	186	32.40★★
d	16.45	18.15	965	3.86★★	–2.920	3.172	965	1.64ns
aa	3.14	3.29	682	1.73ns	–2.164	0.602	679	–2.79★★
ad	3.69	1.05	555	3.61★★	0.497	0.155	555	1.26ns
dd	–4.77	6.48	965	–1.87ns	4.837	1.169	965	4.47★★

1/ m = mean of inbred lines derived from F_2; a = measurement of additive effect; d = measurement of dominance deviation; aa = measurement of interactions additive x additive; ad = measurement of interactions additive x dominant; dd = measurement of interactions dominant x dominant; ns Not significant at 5% probability level, by *t*-test; ★★ Significant at 1% probability level, by *t*-test

With the nonorthogonal decomposition of the parameters sum of squares, R^2 may be employed as an indicator of the contribution of each genetic effect towards the variability of the characteristics under analysis (Cruz and Regazzi, 1984). Results obtained by genetic analysis with complete model showed that the participation of effects of epistasis effects on variability would be irrelevant, although they might be significant in some cases. The additive effect produced more than 90% variability of the net seminal root length (Table 5). Change to the logarithmic scale did not alter results. This means that the additive effect remained the most important genetic component in NSRL variability as a response of maize seedlings to stress caused by aluminum in the nutrient solution. Epistasis was also detected by Magnavaca (1982) in NSRL determination in two out of six families studied. There was a significant effect on the diallel cross studied by Prioli (1987).

Table 5. Nonorthogonal decomposition of the parameters sum of squares (m, a, d, aa, ad, dd), by Gauss's elimination method, net length of seminal roots in direct (cm) and logarithmic scales, of seedlings of inbred lines of maize, tolerant and nontolerant to aluminum respectively, L922 and Ast214, derived generations F_1, F_2 and backcrosses, after 10 days of growth in nutrition solution with 4.5 mg/L aluminum

Source of Variation1/	Direct scale (cm)		Log scale	
	SS	R^2 (%)	SS	R^2 (%)
m/a,d,aa,ad,dd	2.88	3.03	0.027	12.31
a/m,d,aa,ad,dd	88.29	92.65	0.189	84.83
d/m,a,aa,ad,dd	1.91	2.01	0.004	1.85
aa/m,a,d,ad,dd	0.41	0.43	0.001	0.32
ad/m,a,d,aa,dd	1.36	1.43	0.000	0.05
dd/m,a,d,aa,ad	0.42	0.44	0.002	0.66

1/ m = mean of inbred lines derived from F_2; a = measurement of additive effect; d = measurement of dominance deviation; aa = measurement of interactions additive x additive; ad = measurement of interactions additive x dominant; dd = measurement of interactions dominant x dominant

Minimum influence of non-allelic interactions suggests that there is no need for the complete model. The greatness of the additive effect would guarantee the use of a simpler or more reduced genetic model, or additive-dominant model, to explain and describe the inheritance of aluminum tolerance evaluated by NSRL. The use of the additive-dominant model generated estimates of genetic parameters with their respective test of significance (Table 6). Scales apart, means was the parameter with the highest estimates.

Table 6. Null significance test of genetic parameters of additive-dominant model, obtained from means of net seminal root length in direct (cm) and logarithmic scales, of seedlings of inbred lines of maize, aluminum tolerant and nontolerant respectively, L922 and Ast214, derived generations F_1, F_2 and backcrosses, after 10 days of growth in nutrition solution with 4.5 mg/L aluminum

Genetic	Direct scale (cm)				Log scale			
Parameter	Estimates	Variance	DF	*t*	Estimates	Variance	DF	*t*
m	11.82	0.02	865	77.4★★	0.966	0.0001	865	92.7★★
a	7.03	0.02	186	46.6★★	0.305	0.0001	186	29.6★★
d	8.71	0.09	965	28.9ns	0.348	0.0002	965	27.1★★

1/ m = mean of inbred lines derived from F_2; a = measurement of additive effect; d = measurement of dominance deviation; ★★ Significant at 1% probability level by *t*-test

According to Cruz and Regazzi (1994), a way of evaluating the acceptability of a model is the correlation measurement between means of populations analyzed and estimated means by equation inherent to the model $Y_e = X\beta$. The means analyzed, the means estimated by the model and the correlations between them are shown in Table 7. Correlations and determination coefficients (R^2), always with magnitudes over 0.95, prove the suitability of the additive-dominant model. In other words, the additive-dominant model produces estimates of population means closely equal to those found in the experiment with or without logarithmic transformation.

Table 7. Means observed and estimated by additive-dominant model of net seminal root length (NSRL), in direct and logarithmic scales, of seedlings of inbred lines of maize, aluminum tolerant and nontolerant respectively, L922 and Ast214, derived generations F_1, F_2 and backcrosses, after 10 days of growth in nutrition solution with 4.5 mg/L aluminum

Population	NSRL (cm)		NSRL (log scale)	
	Observed	Estimated	Observed	Estimated
L922	18.19	18.85	1.26	1.27
Ast 214	4.91	4.79	0.64	0.66
F1	20.09	20.53	1.30	1.32
F2	15.44	16.17	1.13	1.14
BC(F1 x L922)	20.47	19.69	1.31	1.293
BC(F1 x Ast 214)	11.98	12.66	1.02	0.99
$R(Y_{obs}, Y_{est})$	0.9949		0.9970	
R^2	0.9898		0.9940	

Table 8 lists the nonorthogonal decompositions of the sum of squares. They were obtained by the additive-dominant model. R^2 shows that means was the parameter that best contributed towards variability. In a lesser proportion, the second parameter that produced variability was the additive effect; the least influential was the gene effect caused by dominance.

Table 8. Nonorthogonal decomposition of the parameters (m, a, d) sum of the squares by Gauss's elimination method, net seminal root length, in direct (cm) and logarithmic scales, of seedlings of inbred lines of maize, aluminum tolerant and nontolerant respectively, L922 and Ast214, and derived generations F_1, F_2 and backcrosses, after 10 days of growth in nutrition solution with 4.5 mg/L aluminum

Source of	Direct scale (cm)		Log scale	
variation[1/]	SS	R^2 (%)	SS	R^2 (%)
m/a,d	5995.67	66.61	8590.99	84.24
a/m,d	2169.17	24.10	873.94	8.57
d/m,a	836.45	9.29	733.67	7.19

[1/] m = mean of inbred lines derived from F_2; a = measurement of additive effect; d = measurement of dominance deviation.

There are indications that aluminum tolerance in maize has high heritability and is determined by a few *loci*. The complete and reduced models of genetic analysis of generation means consistently expressed the best performance of the additive effect as a variability source. Results seem to infer that it is possible to obtain inbred lines with higher elite genotypes. Further, quick gains may be foreseen in tolerance selection cycles based on NSRL in segreganting populations.

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