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Evaluation of maternal effect on inheritance of aluminum-tolerance in maize

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ABSTRACT. Open land, called *cerrado*, almost occupies one fourth of Brazilian territory and is characterized by acid soils with high aluminum saturation. The productivity of non-naturalized plants is reduced since growth of roots is greatly restrained. The use of aluminum-tolerant genotypes together with liming is a very promising strategy for the agricultural use of open land. Knowledge of inheritance mechanisms of aluminum-tolerance contributes towards obtaining of tolerant and productive genotypes. The aim of this research was to investigate the hypothesis of maternal effect on aluminum tolerance of maize inbred lines. Seedlings from six pairs of reciprocal crosses, produced by two tolerant and three non-tolerant inbred lines, were evaluated. Seminal root growth rates in presence of aluminum were similar among all progenies derived by reciprocal crosses. The results demonstrated the control of aluminum tolerance by dominant nuclear alleles in maize, without any detectable effect of extranuclear genes.

Key words: aluminum-tolerance, maize, maternal effect.

RESUMO. Avaliação do efeito materno na herança da tolerância ao alumínio em milho. Os cerrados ocupam quase um quarto do território brasileiro e têm solos ácidos com alta saturação de alumínio, que reduz a produtividade de plantas não adaptadas, pois limita o crescimento das raízes. O uso de genótipos tolerantes ao alumínio, em combinação com calagem, é uma estratégia promissora para a exploração agrícola dos cerrados. O conhecimento dos mecanismos de herança da tolerância ao alumínio contribuirá para a obtenção de genótipos tolerantes e produtivos. O objetivo deste trabalho foi determinar se há efeito materno na resposta ao alumínio em cruzamentos recíprocos de linhagens endogâmicas de milho. Foram utilizados seis pares de cruzamentos recíprocos entre duas linhagens tolerantes e três sensíveis. Os cruzamentos recíprocos mostraram taxas de crescimento similares na presença de alumínio, evidenciando o envolvimento de alelos dominantes de *loci* nucleares na determinação da tolerância, sem influência detectável de genes extranucleares.

Palavras-chave: tolerância ao alumínio, milho, efeito materno.

The open land called *cerrado* in Brazil occupies an area of 1.8 million km^2. Its soil is acid and contains high concentrations of soluble aluminum. Soil acidity causes the non-availability of essential nutrients, whereas soluble aluminum impairs cell division in the root meristems. Because length and thickness of root tips decrease, roots become brownish and brittle. Soil is thus explored only at the surface and in small volumes. This fact enhances the soil susceptibility to droughts and the decrease of productivity of many cultures (Borgonovi *et al.*, 1987; Foy *et al.*, 1978; Lopes, 1984; Silva, 1976).

Liming of acid soils raises their pH and precipitates aluminum. The latter becomes unavailable to plants (Marion *et al.*, 1976). However, this is a partial solution to the problem since lime application is technically impossible in great extensions of land beyond the soil arable layer. Aluminum non-tolerant plant roots grow on the corrected soil surface without affecting the deeper layers. Consequently, the improvement of the soil entire nutritional potentiality is impaired and the plants remain susceptible to occasional water deficiencies (Matzenbacher, 1986; Pandey *et al.*, 1994; Rao *et al.*, 1993; Zeigler *et al.*, 1995).

The existence of genetic variability for aluminum tolerance has been found in various plants. This amounts to intra-species differences in their capacity to obtain nutrients and develop in the presence of aluminum. The existence of genetic variability indicates the possibility of obtaining genotypes or productive variables in acid soils. Thus, a promising strategy for agricultural exploitation of *cerrado* soils lies in the combination of liming with the employment of aluminum-tolerant genotypes (Foy *et al.*, 1978; Matzenbacher, 1986; Pandey *et al.*, 1994; Rao *et al.*, 1993; Spehar and Souza, 1999; Zeigler *et al.*, 1995).

The most efficient aluminum-response characteristics in grass are related to roots and, in a special manner, to their length (Foy *et al.*, 1978). Studies on the inheritance of tolerance in maize have focussed on the seminal root length. Nevertheless, results were inconclusive and produced conflicting interpretations on the inheritance issue. While some authors record monogenic inheritance (Rhue *et al.*, 1978; Garcia and Silva, 1979), others insist on unequivocal evidence of quantitative inheritance (Magnavaca, 1982; Magnavaca *et al.*, 1987; Prioli, 1987).

There is scanty information on the participation of extranuclear genes in tolerance. While trying to analyze the maternal effect on inheritance of tolerance, the aim of this research was to determine whether reciprocal crosses of maize inbred lines respond differently to aluminum.

Materials and methods

Plant materials. Aluminum tolerant and non-tolerant inbred lines of maize (*Zea mays* L.), developed at the State University of Campinas, Campinas, Brazil, were used. The aluminum-tolerant inbred lines, L922 (also called Cat100-6) and L902, have orange-colored flint endosperm and they were derived from *Cateto*, an autochthonous race adapted to the Southern Atlantic Coast of South America. The non-tolerant inbred lines (Ast86-4, Ast214 and L477) were derived from Tuxpeño, a dent race with yellow endosperm adapted to the coastal region of the Gulf of Mexico. Inbred lines were multiplied by self-pollination. Through controlled pollination, six pairs of reciprocal F_1 hybrids were produced by two-way crosses between plants of the two tolerant and the three non-tolerant inbred lines.

Nutrient solution and aluminum level. Clark's saline nutrient solution (Clark, 1977) was prepared with distilled and deionized water, with a few modifications. Solution contained 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 $Na_2MoO_4.2H_20$.

Aluminum in the salt $KAl(SO_4)_2.12H_2O$ was added to the solution to a final concentration of 4.5 μg/mL of Al^{3+}. According to Prioli (1987), this aluminum dose is adequate for discrimination of tolerant and non-tolerant maize genotypes. The pH was adjusted to 4.0 to avoid aluminum precipitation.

Seed germination and seedling growth. Seeds were germinated on paper, in a dark room at controlled temperature of 26 ±1 ºC, until the seminal roots were approximately 2 cm long. Seedlings were transferred to plastic tanks with aluminum nutrient solution in growth room. Seedlings were then placed on floating polystyrene plates (styrofoam) so that the seminal roots remained immersed in the nutrient solution.

Nutrient solution was constantly aired to ensure oxygenation, while distilled and deionized water was added daily to maintain constant volume and to avoid concentration changes of nutrients and aluminum. pH was monitored and corrections were unnecessary. Room temperature was maintained at 26 ±1 ºC with a 14/10 h light/dark photoperiod and light intensity of approximately 350 $\mu E.m^{-2}.s^{-1}$ at the plant level.

Plant measurements and calculated variables. *Initial Seminal Root Length* (ISRL) was measured immediately before transferring seedlings to the aluminum solution. After seven days of growth, the individual *Final Seminal Root Length* (FSRL) was measured. The *Net Seminal Root Length* (NSRL), or rather, the difference between the FSRL and ISRL, was the indicating characteristic of aluminum-tolerance rate.

Experimental design, statistical and genetic analysis of experiments. NSRL averages of reciprocal crosses were compared by *t*-test (Snedecor and Cochran, 1974; Steel and Torrie, 1980). Moreover, correlation analysis was undertaken with the NSRL of cross with tolerant mother and the NSRL of reciprocal cross (non-tolerant mother) as interdependent variables. It was expected that coefficient *r* would be equal to one if there were no differences between reciprocal crosses. Estimated value of *r* underwent significance tests for hypothesis Ho: $r = 1$ (Snedecor and Cochran, 1974; Steel and Torrie, 1980).

Results and discussion

In Table 1, the effect of aluminum on the growth of seminal roots of non-tolerant and tolerant inbred lines of maize and their F_1 hybrids is shown. Tolerant lines L922 and L902 showed similar seminal root growth with approximately 14 cm of NSRL. Although inbred line L477 was considered non-tolerant, its NSRL amounting to 13.16 cm did not differ greatly from NSRL values of tolerant inbred lines. This is due to the fact that inbred line L477 develops a very long seminal root in the absence of aluminum. In L477, the NSRL value of 13.16 cm represents nearly 50% of the growth that would be obtained in the nutrient solution without aluminum. On the other hand, non-tolerant inbred lines Ast86-4 and Ast214 had low NSRL values, namely, 8.41 and 3.90 cm respectively.

Averages of reciprocal crosses between tolerant and non-tolerant inbred lines are shown in Table 1. Hybrid vigor was observed in crosses between non-tolerant line L477 and tolerant inbred lines L922 and L902. Independently of direction, results of crosses were always close to or higher than values of tolerant inbred lines, perhaps due to aluminum-tolerant dominance. Pattern of expression in descendants confirms reports of many authors. With the exception of Magnavaca (1982) and Magnavaca *et al.* (1987) suggesting the aluminum non-tolerant trend to be dominant, all reports indicated tolerance to be a phenotype determined by dominant alleles of one or more *loci* (Garcia and Silva, 1979; Prioli, 1987; Jorge and Arruda, 1997).

Since offspring F_1 systematically presents the phenotype of tolerant parent inbred line, this at least proves the preponderance of nuclear genes in tolerance conditioning. If important participation of extranuclear factors existed, descendants with a phenotype similar to that of the female parent would have been produced. This is due to the maternal uniparental inheritance of mitochondria and chloroplasts in maize.

Average NSRL of reciprocal crosses was compared by *t*-test (Table 1). Although not all reciprocal crosses may be considered similar, as a general rule they have similar response to aluminum. Significant differences were detected between reciprocal crosses of inbred lines L922 and Ast86-4 and between reciprocal crosses of inbred lines L902 and L477. These differences were not apparently related with possible discrepant responses to aluminum between the two directions of the cross. This fact may be inferred from F_1 values. Although slightly different, they were close to dominant parent line. If significance resulted from aluminum-tolerance, contrary trends within the cross pair would be found.

The two pairs of reciprocal crosses with significant differences share females with a more voluminous endosperm in cross and with greater growth. Inbred line L922 has a small flint endosperm, whereas inbred line Ast86-4 has a great dented endosperm. The same happens in the other cross pair, or rather, the endosperm of inbred line L902 is of the small flint type, while line L477 has a voluminous dented endosperm. It may be expected that the nutrient reserve quantity mobilized during the first days of development of seedling would be greater in dented inbred lines. This would allow a better performance in the seminal root growth. However, this would not be a full explanation to the data. Since it is female, inbred line Ast86-4 would cause greater growth when crossed with L922, but not with L902. Similarly, inbred line L477 will only increase the size of the seminal root when it functions as a female for L902. Thus other variables interfere in the development of seedlings. Besides nutritional differences in the seedling phase, specific interactions among crossed genotypes would contribute towards the production of differential growth.

Table 1. Averages (cm) and significance test for *Net Seminal Root Length* (NSRL) in reciprocal crosses between tolerant (T) and non-tolerant (N) maize inbred lines developed during seven days in a nutrient solution with 4.5 µg/mL of Al^{3+}

NSRL Averages of Inbred Lines				NSRL Averages of Reciprocal Crosses		GL	*t*	p
T		N						
Inbred	NSRL	Inbred	NSRL	F_1(T x N)	F_1(N x T)			
L922	13.50	Ast214	3.90	14.09 ±2.24	14.37 ±2.18	69	–0.53	0.60ns
		Ast86-4	8.41	15.83 ±1.41	17.19 ±1.64	78	–3.99	0.00**
		L477	13.16	19.23 ±1.41	18.76 ±1.42	78	1.47	0.15ns
L902	14.35	Ast214	3.90	12.91 ±2.01	12.89 ±1.72	78	0.03	0.98ns
		Ast86-4	8.41	14.76 ±1.21	14.79 ±1.66	78	–0.11	0.91ns
		L477	13.16	16.44 ±1.39	18.20 ±1.74	77	–4.76	0.00**

ns Non-significant at 5% probability level by *t*-test; ** Significant at 1% probability level by *t*-test

Another approach that confirms the interpretation of nuclear inheritance for tolerance is the simple linear correlation analysis between NSRL in both directions of the cross (Figure 1). If reciprocal crosses were equal with regard to the growth of seminal roots, it would be expected that coefficient *r* would not be different from one. In other words, the growth of the seminal root in a cross would be of the same size and proportional to the growth of the seminal root of the reciprocal cross. The correlation coefficient of reciprocal crosses sampled was r = 0.93. This value was not significantly different from one, by *t* test. Therefore, the correlation coefficient shows that results are consistent and indicates that tolerance transmission is independent of the cross direction.

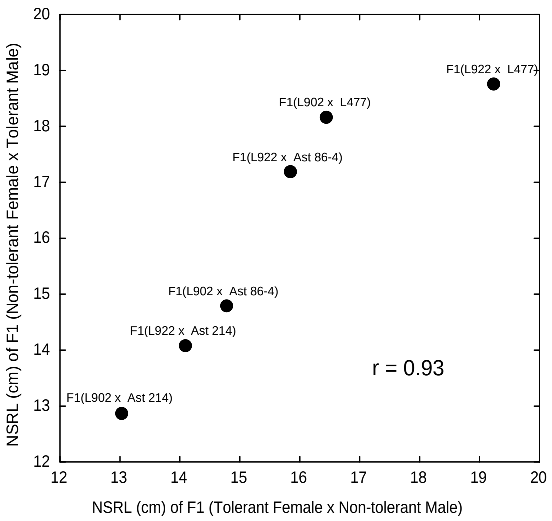

Figure 1. Dispersion diagram associated with correlation coefficient (*r* = 0.93) of *Net Seminal Root Length* (NSRL) of maize seedlings in reciprocal crosses between aluminum-tolerant (L902 and L922) and non-tolerant (Ast86-4, Ast214 and L477) inbred lines, developed in nutrient solution with 4.5 μg/mL of Al^{3+}. The correlation coefficient was not significantly different from one, by *t* test

The results demonstrated absence of any detectable effect of extranuclear genes controlling aluminum tolerance in maize, and confirmed that the tolerance is conditioned by dominant nuclear alleles in this species. The genetic control of response to aluminum toxicity in maize suggests that there is a possibility of manipulation and exploitation of tolerance in breeding programs. Aluminum tolerance may be selected in genetically variable populations and possibly transferred to lines with an excellent combinatory capacity in hybrid production.

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