Australian Journal of Crop Science AJCS

AJCS 10(1): 42-49 (2016) ISSN:1835-2707

Brazilian maize landraces: source of aluminum tolerance

Caroline de Jesus Coelho[1], Dayane Molin[2], Guilherme de Jong[3], José Raulindo Gardingo[1], Eduardo Fávero Caires[1], Rodrigo Rodrigues Matiello[1,2,4]*

[1]Postgraduate Program in Agronomy, State University of Ponta Grossa, Ponta Grossa, Brazil; CEP: 84030-900.
[2]Postgraduate Program in Evolutionary Biology, State University of Ponta Grossa, Ponta Grossa, Brazil; CEP: 84030-900.
[3]Postgraduate Program in Genetic and Plant Breeding, Federal University of Lavras, Lavras, Brazil; CEP: 37200-000.

[*]Corresponding author: rrmatiel@uepg.br

Abstract

The aim of this study was to prospect alleles for aluminum (Al) tolerance in different maize germplasms and to estimate the genetic parameters associated with that tolerance. Fifty-two hybrids from 4 seeds companies and 50 maize landraces were evaluated after 48 h of exposure to Al. The difference in root growth (DIF) was used to estimate the relative aluminum tolerance index (RATI). The results showed for both maize germplasms (hybrids or landraces) differences in root growth of genotypes when exposed to Al. The comparison between different germplasms clearly demonstrated the superiority of maize landraces for tolerance to Al in relation to hybrid genotypes were 17 of 50 landraces evaluated was classified as Al tolerant. Estimates of genetic parameters in both germplasms indicated, to this random sample of genotypes, the possibility of success for the development and selection of improved populations and an increase in the frequency of alleles for Al tolerance.

Keywords: *Zea mays*; minimum solution; genetic variability; aluminum toxicity; germplasms.

Introduction

World estimates indicate that approximately 50% of available soils for agricultural production are acidic (Kochian et al., 2002). In Brazil, almost 60% of soils destined for agriculture are acidic. Aluminum (Al) toxicity is one of the most limiting factors for crop cultivation in acidic soils because at pH < 5.0, the element is solubilized in Al^{3+} toxic form in the soil solution, resulting in significant losses in crop yields (Ezaki et al., 2013). The most noticeable symptom of Al toxicity is root growth inhibition and the primary target of toxicity is the root apex. The accumulation of Al in the cell walls occurs in this region, which results in the inhibition of the division and elongation of the root cells (Doncheva et al., 2005). In conventional tillage systems the incorporation of lime into the soil results in Al insolubilization (Caires et al., 2006). Changes in current farming systems, such as the adoption of no-till, seek to reduce soil losses through the maintenance of permanent soil cover, with continuous replenishment of vegetation or crop residues, thereby avoiding soil disturbance (Cassol et al., 2007). In these cropping systems, the surface-applied lime does not generally reduces the soil acidity beyond the point where it was applied and this restricts the Al neutralization in the soil surface layers (Caires et al., 2008). Since the Al toxicity in the layers below the soil surface can compromise crop root growth and yield, the use of minimum levels of soil remediation should be always associated with the choice of genotypes adapted to soil acidity for a more efficient use of nutrients (Boni et al., 2009).

The understanding about the inheritance of Al tolerance is of extreme importance in the development of procedures that are more suitable for the selection of genotypes with increased tolerance. Due to the large number of biochemical pathways involved in tolerance stress, it is considered that different genes may be involved in tolerance (Ferreira et al,. 2006). In maize, it has been observed that aluminum tolerance is a complex phenomenon that involves multiple genes and probably numerous physiological mechanisms (Ninamango-Cárdenas et al., 2003). One such mechanism is citrate exudation from the roots; however, other mechanisms may also be involved in tolerance (Piñeros et al., 2005). Despite the fact that Al tolerance is a quantitative inheritance, few candidate genes have been described in the literature. Members of the MATE (multidrug and toxic compound extrusion) family have been associated with Al tolerance. The *ZmMATE1* (*SbMATE* homologous gene in sorghum) and *ZmMATE2* genes represent strong candidates for genes of higher Al tolerance in maize (Maron et al., 2010). Studies in rice have shown that the Nramp aluminum transporter 1 (*Nrat1*) was found to be associated with Al tolerance (Simões et al., 2012). Recently, a homologue of this gene was identified in maize inbred lines. That particular research encouraged further investigation of the involvement of *ZmNrat1* in maize Al tolerance (Guimarães et al., 2014).

The present study aimed to prospect alleles for Al tolerance in different maize germplasms (hybrid and landraces) and to also estimate the genetic parameters associated with Al tolerance in these germplasms.

Results

Aluminum tolerance characterization

The variance analysis showed significant differences (P < 0.01) between the genotypes for DIF in hybrids and maize landraces (Table 1).

Table 1. Analysis of variance for the difference in root growth (DIF) to hybrids and maize landraces germplasms after 48 h of Al exposure

		Mean Squares (MS)	
Source of Variation	D.F.	DIF (Hybrids)	DIF (Landraces)
Blocks	2	0.27	0.82
Genotypes	51	0.69 **	0.57**
Error	102	0.04	0.057
CV (%)		10.9	10.7

** significant at 1% of probability

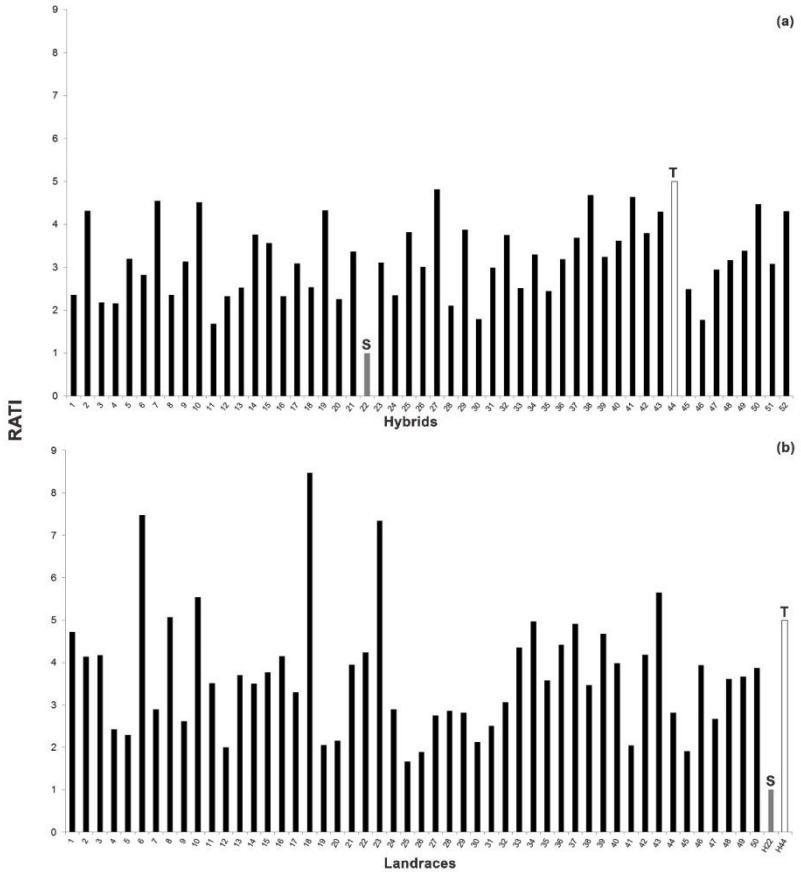

Fig 1. Relative Aluminum Tolerance Index (RATI) for: **a-** 52 maize hybrids; **b-** 50 maize landraces after 48 h of Al exposure (T: tolerant and S: sensitive).

The DIF means for the hybrid germplasm ranged from 0.60 (H 22) to 2.65 cm (H 44). On the other hand, for the maize landraces the DIF amplitude varied from 1.66 (V25) to 3.66 cm (V 18). On this set of genotypes greater Al tolerance was showed to the varieties: Crioulo Rosa (V 18), Dente de Ouro 2 (V 6) and Crioulo Sabugo Fino (V 23), as demonstrated by the DIF average, which was more than 3.30 cm (data not shown). For the relative aluminum tolerance index (RATI) the hybrids H 22 and H 44 were used as sensitive (H 22) and tolerant (H 44) controls, assuming indexes of 1 and 5, respectively. The hybrids with greatest Al tolerance after 48 h of exposure (RATI > 4.0) were: H 2 (4.3); H 7 (4.6); H 10 (4.5); H 19 (4.3); H 27 (4.8); H 38 (4.7); H 41 (4.6); H 43 (4.3); H 50 (4.5) and H 52 (4.3). Most of the hybrids (37) showed intermediate RATI, with indices ranging from 2.1 (H 28) to 3.9 (H 29). The highest level of Al sensitivity was observed for the hybrids H 11 (1.7), H 30 (1.8) and H 46 (1.8) (Fig 1a). For the landrace maize germplasm, it was found that the varieties V 18 (8.5), V 6 (7.5), V 23 (7.3), V 43 (5.7), V 10 (5.5) and V 8 (5.1) stood out due to greater Al tolerance index. The RATI identified 17 of the 50 landraces as being Al tolerant, with an index ≥ 4.0. Only 5 landraces presented RATI < 2, with the lowest index (1.66) being for RS-22 (V 25) (Fig 1b). The distribution of maize genotypes into RATI classes made it possible to view the greater tolerance of the landrace germplasm in compare to hybrids, because the genotype's greater frequency in classes 4 and 5 (Fig 2a, b). The grouping analysis by the UPGMA enabled the formation of groups of genotypes according to the dissimilarity index (Fig 3). The number of groups was determined according to Mojena's (1977) method, which is based on the relative size of fusion levels or distances in the dendrogram. Using a constant K = 1.6, the dendrogram cut point was determined at a distance of 1.19, which corresponded to 25.4% of the maximum distance observed in the group's levels of fusion (Fig 3). The 102 maize genotypes (hybrids and landraces) were distributed into the following 5 groups based on genetic dissimilarity (Fig 3). GI comprised 48 genotypes, of which 25 were landraces and 23 hybrids. These genotypes showed an intermediate tolerance to Al, with a DIF of 1.96 cm and RATI of 3.26 (Table 2). GII grouped together 25 genotypes, of which 17 were hybrids and 8 landraces. This group showed greater Al sensitivity, with an average of 1.4 cm and 2.17 for DIF and RATI, respectively.

Table 2. Average of DIF and RATI for each group of genotypes by UPGMA method.

Groups	N[a]	DIF (cm)	RATI
I	48	1.96	3.26
II	25	1.40	2.16
III	25	2.48	4.60
IV	1	0.60	1.00
V	3	3.45	7.77

[a]N: number of genotypes in groups.

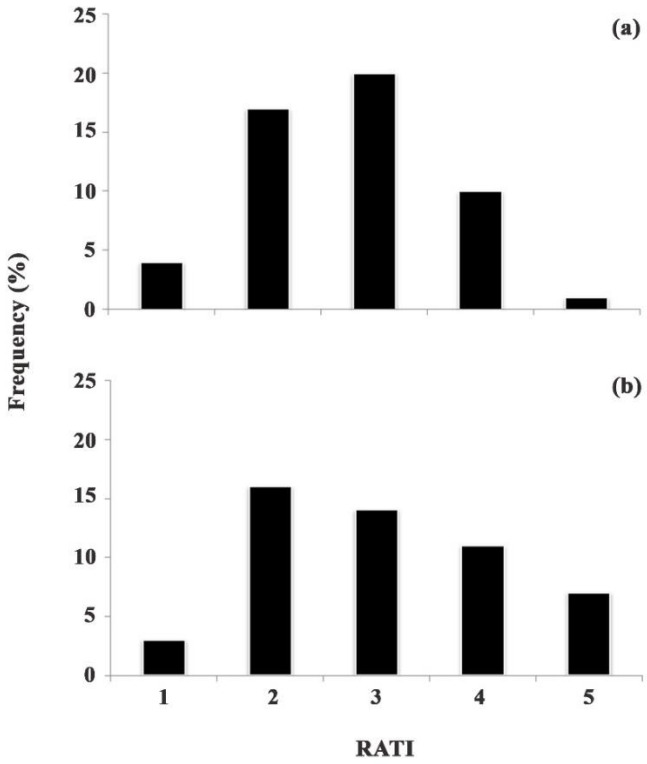

Fig 2. Frequency distribution of maize genotypes in classes of the Relative Aluminum Tolerance Index (RATI). **a-** hybrids germplasm; **b-** landraces germplasm.

GIII was made up of 14 landraces and 11 hybrids (including tolerant control H 44). In this group it was possible to observe higher Al tolerance; on average, the 25 genotypes showed a DIF of 2.38 cm and RATI of 4.60 (Table 2). GIV was made up of only hybrid H 22 (sensitive control), which showed a great dissimilarity in comparison with the other genotypes because it had a lower DIF and RATI (Table 2). On the other hand, GV, which comprised 3 varieties (V 6, V 23 and V 18), showed the highest Al tolerance and was the most dissimilar of the grouping analyses. This group of maize landraces demonstrated an average DIF and RATI of 3.45 cm and 7.77, respectively (Table 2). The cophenetic correlation coefficient was 0.84, and significant by the Mantel test ($P \leq 0.01$).

Genetic parameters for Al tolerance

The estimative of genetic parameters associated with Al tolerance, in both germplasms (hybrids and landraces), showed the genetic component ($\hat{\sigma}^2_g$) to be bigger in relation to the environment compound ($\hat{\sigma}^2_e$). The broad sense heritability ($\hat{h}^2_a$) was of a large magnitude, being 95% (hybrids) and 89% (landraces). The $\hat{b}$ quotient (CV_g/CV_e) was higher than 1 for the two germplasms (Table 3).

Discussion

Through the variable DIF it was possible to identify contrasting groups of genotypes in terms of Al tolerance. In relation to the hybrids, most of the evaluated genotypes were found in the intermediary tolerance group. These results are in accordance with Mazzocato et al. (2002), who verified the formation of distinct groups (Al tolerant and sensitive) after measuring the DIF of 22 maize genotypes. Paterniani and Furlani (2002) evaluated 45 single-cross hybrids and 10 inbred lines in complete nutritive solution with Al. They observed that 13 hybrids and 3 inbred lines stood out with the largest DIF. For the landraces, it was also possible to observe the formation of contrasting groups of genotypes. Similar results were found by Machado et al. (1998), who evaluated 36 landraces in nutrient solution with Al, of which 8 stood out due to large root length.

The best phenotypic index used to characterize genotype tolerance/ sensitivity has been differences in root length,

Table 3. Estimates of genetic parameters: environmental variance ($\hat{\sigma}^2_e$), genetic variance ($\hat{\sigma}^2_g$), heritability in the broad sense ($\hat{h}^2_a$), genetic variation coefficient (CV_g), environmental variation coefficient (CV_e) and $\hat{b}$ quotient for DIF in hybrids and maize landraces germplasms after 48 h of Al exposure.

Parameters	DIF	
	Hybrids	Landraces
$\hat{\sigma}^2_e$	0.04	0.06
$\hat{\sigma}^2_g$	0.22	0.17
$\hat{h}^2_a$	0.95	0.89
CV_g (%)	27.11	18.31
CV_e (%)	11.56	10.68
Quotient $\hat{b}$	2.35	1.71

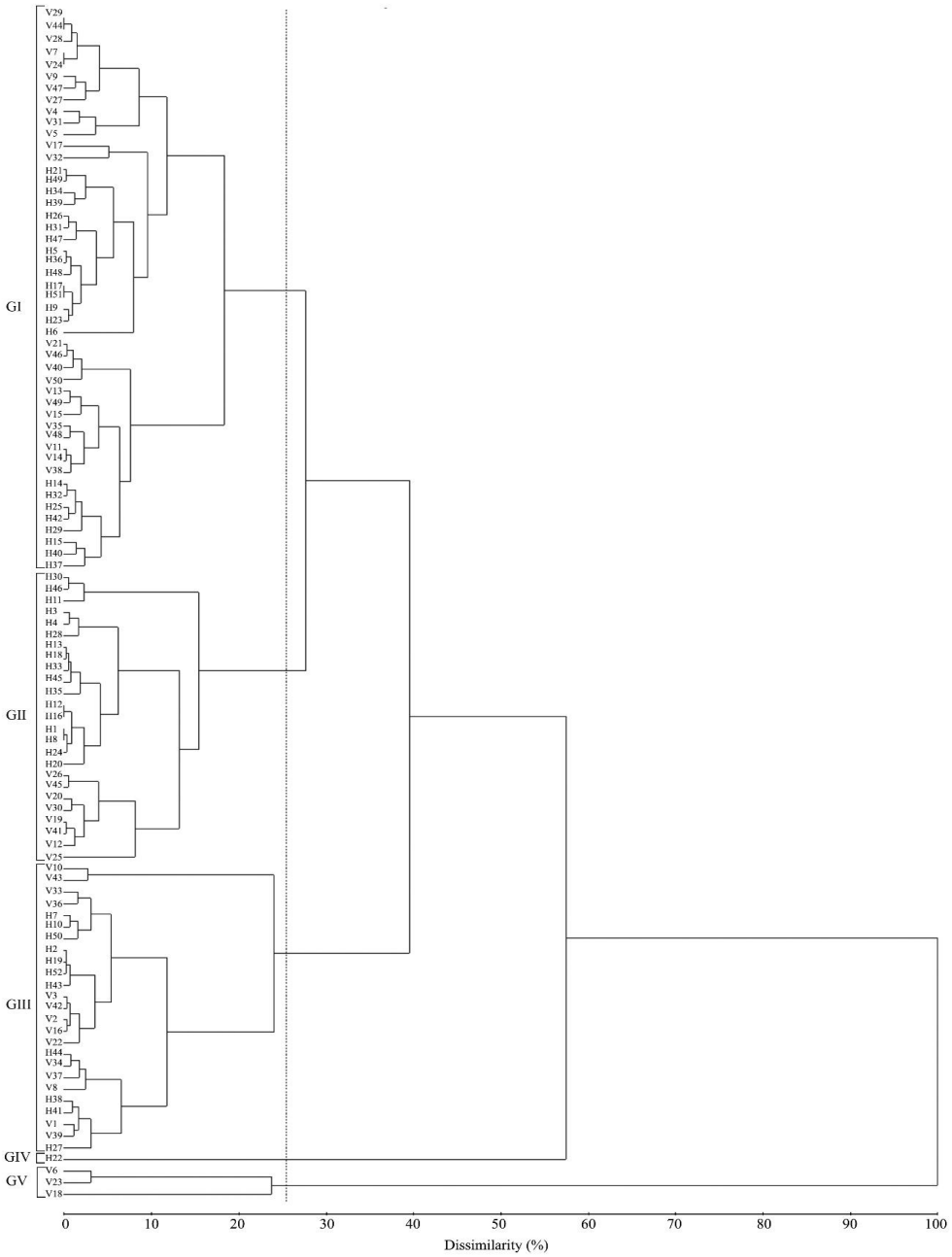

Fig 3. Grouping of 102 maize genotypes (hybrids and landraces) through the UPGMA method from the generalized Mahalanobis square distance (D^2). Dotted line representing the dendrogram cut point (Mojena 1977), determined at a distance of 1.19, which corresponded to 25.4% of the maximum distance observed in the group's levels of fusion.

Table 4. List of commercial / pre-commercial hybrids of different seed companies and maize landraces germplasm with their places of origin

Hybrids	Origin	Landraces	Origin
H 1 – HD[a]		V 1 – Caiano FE 121	Tenente Portela – RS[b]
H 2 – HT		V 2 – Pintadinho FE 109	Canela – RS
H 3 – SH		V 3 – Catete Amarelo	Canguçú – RS
H 4 – SH	Monsanto	V 4 – Cunha	Ibarama – RS
H 5 – SH		V 5 – Roxo Índio I	Canguçú – RS
H 6 – SH		V 6 – Dente de Ouro 2	Pelotas – RS
H 7 – DH		V 7 – Branco Dentado	Canguçú – RS
H 8 – SH		V 8 – Argentino FE128	Alto União – RS
H 9 – TH		V 9 – Cinquentinha	Ibarama – RS
H 10 – SH		V 10 – Roxo Índio II	Canguçú – RS
H 11 – TH		V 11 – Caiano Rajado	Canguçú – RS
H 12 – SH		V 12 – BR 451	Pelotas – RS
H 13 – SH		V 13 – Argentino Flint	Canguçú – RS
H 14 – SH	Pioneer	V 14 – Pop.5 (CNMS 5)	Pelotas – RS
H 15 – SH		V 15 – Dente de Ouro	Canguçú – RS
H 16 – SH		V 16 – Branco Duro Canguçú	Pelotas – RS
H 17 – SH		V 17– Colonial	Pelotas – RS
H 18 – SH		V 18 – Crioulo Rosa	Veranópolis – RS
H 19 – TH		V 19 – Crioulo Rajado	Veranópolis – RS
H 20 – TH		V 20 – Branco Oito Carreiras	Veranópolis – RS
H 21 – SH		V 21 – Crioulo	Veranópolis – RS
H 22 – SH /Pre		V 22 – Crioulo Riscado	Veranópolis – RS
H 23 – SH /Pre		V 23 – Crioulo Sabugo Fino	Veranópolis – RS
H 24 – SH /Pre		V 24 – Sabuguinho Cabo Roxo	Veranópolis – RS
H 25 – SH		V 25 – RS-22	Veranópolis – RS
H 26 – SH /Pre		V 26 – Crioulo Veranópolis	Veranópolis – RS
H 27 – SH		V 27 – Crioulo Palha Roxa	Veranópolis – RS
H 28 – SH /Pre	Syngenta	V 28 – Crioulo Asteca	Veranópolis – RS
H 29 – SH /Pre		V 29 – Crioulo Cunha Roxo	Veranópolis – RS
H 30 – SH /Pre		V 30 – IPR-119	Londrina – PR
H 31 – SH		V 31 – Milho Caiano	Ponta Grossa – PR
H 32 – SH /Pre		V 32 – Milho Branco	Ponta Grossa – PR
H 33 – SH /Pre		V 33 – Cravinho	Rio Azul – PR
H 34 – SH /Pre		V 34 – Milho Paiol	Ponta Grossa – PR
H 35 – SH		V 35 – Milho Carioca	Rio Azul – PR
H 36 – SH		V 36 – Milho Amarelo Antigo	Rio Azul – PR
H 37 – SH		V 37 – Milho Encantilado	Rio Azul – PR
H 38 – SH		V 38 – Asteca	Rio Azul – PR
H 39 – TH		V 39 – Nutricional	Rio Azul – PR
H 40 – TH		V 40 – Milho Branco	Rio Azul – PR
H 41 – SH		V 41 – Caiano	Rio Azul – PR
H 42 – SH		V 42 – Milho Palha Roxa	Rio Azul – PR
H 43 – SH		V 43 – Milho Pérola	Rio Azul – PR
H 44 – SHM	Dow AgroSciences	V 44 – Milho Mistura	Rio Azul – PR
H 45 – SH		V 45 – Carioca	Rio Azul – PR
H 46 – SH		V 46 – Milho Branco para Palha	Rio Azul – PR
H 47 – SHM		V 47 – Milho Amarelo Antigo	Rio Azul – PR
H 48 – TH		V 48 – Milho Palha Roxa	Rio Azul – PR
H 49 – SH		V 49 – Eldorado	Muqui – ES
H 50 – TH		V 50 – Fortaleza	Muqui – ES
H 51 – SH			
H 52 – SH			

[a] SH: Single-cross hybrid; DH: Double-cross hybrid; TH: Triple-cross hybrid; SHM: Single-cross modified hybrid; Pre: Pre-comercial
[b] RS state of Rio Grande do Sul; PR state of Paraná; ES state of Espírito Santo

mainly when the average of many individuals has been used (Martins et al. 1999). Taking this into account, in order to classify the tolerance levels of different genotypes, the relative aluminum tolerance index (RATI) proposed by Camargo et al. (1991), has proved to be efficient (Machado et al. 1998). Paterniani and Furlani (2002) analyzed a sample of 45 single-cross hybrids and 10 maize inbred lines and reported that 13 hybrids and 2 inbred lines showed RATI > 4.0. The number of maize landraces (17) classified as Al tolerant in the present study was much higher than the 3 out of 36 varieties with RATI > 4.0 related by Machado et al. (1998). The aforementioned authors found that greater tolerance of landraces may be related to the place of origin, which may have Al toxicity problems. The comparison of germplasms confirmed the superiority of the maize landrace germplasm in terms of Al tolerance. The differences observed in Al tolerance may reflect the continued cycles of natural and artificial selection that these varieties have undergone in

their respective origin/growth environments. Over time, hybrid maize germplasm has undergone numerous cycles of artificial selection that has mainly been aimed at increasing productive potential and agronomic adequacy for the ideotype of the plant such as: cycle, plant height, lodging and architecture in order to achieve more responsive growth environments. The experimental results showed genotypes with high levels of root growth, even when exposed to a minimum solution containing 4 mg L^{-1} of Al. These results are possibly associated with genes such as the MATE gene family, which are represented by *ZmMATE1* and *ZmMATE2*. These have been indicated in the current literature as the main genes responsible for Al tolerance in maize. Although recently, Guimarães et al. (2014) reported the *ZmNrat1* gene is also strongly associated with Al tolerance in maize.

In the present study, the estimated magnitudes of genetic variance and heritability coefficient indicate the possibility of success in improved maize populations regarding Al tolerance. The high proportion of genetic compounds in relation to environmental variance in both maize germplasms confirmed the genetic variability to tolerance that exists among hybrids and maize landraces. It is possible that the genetic control of this trait in these genotype samples might be correlated to a few genes with a great effect of the alleles on tolerance/sensibility to Al. Similar results were observed by Priolli et al. (2000), who evaluated the liquid main root length of maize in complete nutritive solution. These authors found that Al tolerance in this germplasm was associated with the action of 2 or 3 genes.

The genetic control of Al tolerance in maize seems to quite diverse when one compares the studies involving the evaluation of different maize germplasms, as well as different characterization techniques (field and greenhouse). Some studies have reported on the qualitative inheritance involved in tolerance, which varies from dominant gene action (Rhue et al., 1978; Garcia Júnior and Silva 1979; Miranda et al. 1984) to additive action (Sawazaki and Furlani 1987). However, a more complex genetic control of tolerance, quantitative tolerance, has been proposed by several authors (Magnavaca 1982; Pandey and Gardner 1992; Sibov et al., 1999; Welcker et al., 2005; Pandey et al. 2007; Conceição et al., 2009).

Materials and Methods

Germplasm characterization for Al tolerance

Fifty-two hybrids (commercial and pre-commercial) from different seeds companies was used. These included: 7 from Monsanto (Saint Louis, MO, USA), 14 from Pioneer Hi-Bred International (Johnston, IA, USA), 14 from Syngenta (Basel, Switzerland) and 17 from Dow AgroSciences (Indianapolis, IN, USA) (Table 4). For the landrace germplasm, a random sample of 50 maize landraces was evaluated, which was collected from different regions in Brazil (Table 4).

During the first experiment, 52 hybrids were evaluated after 48 hours exposure to Al. At the second experiment, 50 maize landraces plus 2 control hybrids (H 44 tolerant and H 22 sensitive) were subjected to Al stress for 48 hours. The time exposure was defined according Coelho et al. (2015) . The seeds (hybrids and landraces) were packed in sterilized germination paper (Germitest®) and placed in a germination chamber for 3 days at 24 °C and 100% RH, until they reached 4.0 cm root length.

The experiments were conducted in randomized blocks with three replications. The treatments consisted of 52 hybrids (1st experiment) and 50 maize landraces + 2 control hybrids (2nd experiment). Firstly, the root length was measured (IL – initial length) and then immediately transferred to the minimum solution with Al. The seedlings were placed on polystyrene trays with 288 cells (12 x 24). Twelve seedlings of each genotype were evaluated per replication. The trays were arranged in a fiberglass tank with 280 L of treatment solution, which was composed of 4 mg L^{-1} of Al ($AlCl_3.6H_2O$) and 40 mg L^{-1} of Ca ($CaCl_2$) (Coelho et al., 2015). The root remained submerged in solution for 48 hours with constant aeration. The pH solution was adjusted in the range of 4.2 to 4.6. After the exposure period, the root length was evaluated again (FL – final length). The difference between the variables IL and FL (FL-IL) was named as DIF (cm) (Mazzocato et al., 2002). Using the DIF data, the relative aluminum tolerance index (RATI) was estimated according to the equation adapted from Camargo et al. (1991). The sensitive and tolerant hybrids controls received RATI values of 1.0 and 5.0, respectively.

$$RATI = \left[\frac{DIF_x - DIF_s}{DIF_T - DIF_s} \times 4.0\right] + 1.0$$

DIF_x = DIF for each genotype;
DIF_s = DIF for sensitive control;
DIF_T = DIF for tolerant control.

Statistical analysis

The DIF data were submitted to individual variance analysis for each experiment. For genetic divergence the genetic distance was calculated between pairs of genotypes, applying the generalized Mahalanobis distance (D_{ij}^2). From the dissimilarity matrix, cluster genotypes were constructed using the UPGMA method. The dendrogram was established from the lowest dissimilarity between the pairs of genotypes. To confirm the dendrogram's ability to reproduce the dissimilarity matrix the cophenetic correlation coefficient (CCC) was calculated. All analyses were performed using GENES software (Cruz, 2013).

Estimates of genetic parameters for Al tolerance

The genetic parameters were estimated from the DIF variable using the mathematical expectation of the analysis of variance means squares, according to Vencovsky and Barriga (1992).

The estimation of genetic variance was obtained by: $\hat{\sigma}_g^2 = 1/r(QMt - QMe)$, where (r) is the number of replications, (QMt) the mean square of hybrid or landraces and (QMe) the error mean square of the analysis of variance. The environmental variance was estimated by: $\hat{\sigma}_e^2 = QMe$. The heritability in the broad sense was estimated through: $\hat{h}_a^2 = \frac{\hat{\sigma}_g^2}{\left[\hat{\sigma}_g^2 + \left(\hat{\sigma}_e^2/r\right)\right]}$. Furthermore, the genetic variation coefficient was estimated by $CV_g = \frac{\sqrt{\hat{\sigma}_g^2}}{Y_0}.100$ and the coefficient of variation of the experimental error: $CV_e = \frac{\sqrt{\hat{\sigma}_e^2}}{Y_0}.100$, where Y_0 was the overall DIF average and the quotient $\hat{b}$ estimated by $\hat{b} = \frac{CV_g}{CV_e}$.

Conclusion

The characterization of hybrids and maize landraces germplasms to Al tolerance in minimal solution made it possible to confirm the large contribution of genetic compounds in this sample of maize genotypes. The Dente de

Ouro 2 (V 6), Crioulo Rosa (V 18) and Crioulo Sabugo fino (V 23) varieties could be explored in breeding programs as a source of Al tolerance because these landraces demonstrated the greatest Al tolerance. The utilization of these genotypes as base germplasm could provide the introgression of alleles of interest in elite germplasms, making possible the development of commercial genotypes with more Al tolerance.

Acknowledgements

We thank the maize seeds companies Monsanto, Pioneer Hi-Bred International, Syngenta and Dow AgroSciences for hybrids seeds. This research was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES. Matiello, R.R. is supported by a fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq.

References

Boni TA, Prioli AJ, Prioli SMAP, Lucio LC (2009) Inheritance of aluminum tolerance in maize. Crop Breed Appli Biotech. 9: 153.

Caires EF, Barth G, Garbuio FJ (2006) Lime application in the establishment of a no-till system for grain crop production in Southern Brazil. Soil Till Res. 89: 3-12.

Caires EF, Pereira Filho PRS, Zardo Filho R, Feldhaus IC (2008) Soil acidity and aluminium toxicity as affected by surface liming and cover oat residues under a no-till system. Soil Use Manag. 24: 302-309.

Camargo CEO, Felício JC, Ferreira Filho AWP (1991) Triticale: tolerância ao alumínio em solução nutritiva. Bragantia. 50: 323-330.

Cassol AE, Denardin JE, Cochhann RA (2007) Sistema plantio direto: evolução e implicações sobre a conservação do solo e da água. In: da Silva LS, Reichert JM, Tópico em Ciência do Solo. Edited by Ceretta CA, Viçosa, Sociedade Brasileira de Ciência do Solo, pp 333–370.

Coelho CJ, Molin D, Wood Joris HA, Caires EF, Gardingo JR, Matiello RR (2015) Selection of maize hybrids for tolerance to aluminum in minimal solution. Genet Mol Res. 14: 134-144.

Conceição LDHCS, Tessele C, Barbosa Neto JF (2009) Diallel analysis and mapping of aluminum tolerance in corn inbred lines. Maydica. 54: 55-61.

Cruz CD (2013) GENES: a software package for analysis in experimental statistics and quantitative genetics. Acta Sci. 35: 271–276.

Doncheva S, Amenós M, Poschenrieder C, Barceló J (2005) Root cell patterning: a primary target for aluminium toxicity in maize. J Exp Bot. 56: 1213-1220.

Ezaki B, Jayaram K, Higashi A, Takahashi K (2013) A combination of five mechanisms confers a high tolerance for aluminum to a wild species of Poaceae, *Andropogon virginicus* L. Environ Experim Bot. 93: 35-44.

Ferreira RP, Moreira A, Rassini JB (2006) Toxidez de alumínio em culturas anuais. São Carlos, SP: Embrapa Pecuária Sudeste, 34 p. (Documentos, 63).

Garcia Júnior O, Silva WJ (1979) Herança da tolerância ao alumínio na variedade de milho Piranão. Rev Ceres. 25: 71-78.

Guimarães CT, Simões CC, Pastina MM, Maron LG, Vasconcellos RCC, Guimarães LJM, Lana UGP, Tinoco UGP, Noda RW, Jardim-Belicuas SN, Kochian LV, Alves VMC, Parentoni SN (2014) Genetic dissection of Al tolerance QTLs in the maize genome by high density SNP scan. BMC Genomics. 15: 153.

Kochian LV, Pence NS, Letham LD, Piñeros MA, Magalhães JV, Hoekenga OA, Garvin DF (2002) Mechanisms of metal resistance in plants: aluminum and heavy metals. Plant Soil. 247: 109-119.

Machado AT, Machado CTT, Furlani PR (1998) Avaliação e caracterização de variedades locais de milho para condições adversas de ambiente. In: Soares AC, Machado AT, Silva BM, Weid JM (Orgs.) Milho Crioulo: Conservação e uso da biodiversidade. AS-PTA – Assessoria e serviços a projetos em agricultura alternativa, Rio de Janeiro, pp.151-185.

Magnavaca R (1982) Genetic variability and the inheritance of aluminum tolerance in maize (Zea mays L.). Thesis, University of Nebraska

Maron LG, Piñeros MA, Guimarães CT, Magalhães JV, Pleiman JK, Mao C, Shaff J, Belicuas SN, Kochian LV (2010) Two functionally distinct members of the MATE (multi-drug and toxic compound extrusion) family of transporters potencially underlie two major aluminum tolerance QTLs in maize. Plant J. 61: 728-740.

Martins PR, Parentoni SN, Lopes MA, Paiva E (1999) Eficiência dos índices fenotípicos de comprimento de raiz seminal na avaliação de plantas individuais de milho quanto à tolerância ao alumínio. Pesqui Agropecu Bras. 34: 1897-1904.

Mazzocato AC, Rocha PSG, Sereno MJCM, Bohnem H, Grongo V, Barbosa Neto JF (2002) Tolerância ao alumínio em plântulas de milho. Cienc Rural. 32: 19-24.

Miranda LT, Furlani PR, Miranda LEC, Sawazaki E (1984) Genetics of enviromental resistance and super genes: latente aluminum tolerance. Maize Genet Coop News Letter. 58: 46-48.

Mojena R (1977) Hierarchical grouping methods and stopping rules - An evaluation. Comput J. 20: 359-363.

Ninamango-Cárdenas F, Guimarães CT, Martins PR, Parentoni SN, Carneiro NP, Lopes MA, Moro JR, Paiva E (2003) Mapping QTLs for aluminum tolerance in maize. Euphytica 130:230-232. doi: 10.1023/A:1022867416513

Pandey S, Alberto L, Leon N, Keith D, Stephen F (2007) Breeding maize for tolerance to soil acidity. Plant Breed Rev. 28: 59-100.

Pandey S, Gardner CO (1992) Recurrent selection for population, variety, and hybrid improvement in tropical maize. Adv Agron. 48: 1-87.

Paterniani MEAGZ, Furlani PR (2002) Tolerância à toxicidade de alumínio de linhagens e híbridos de milho em solução nutritiva. Bragantia. 61: 11-16.

Piñeros MA, Shaff JE, Manslank HS, Alves VMC, Kochian LV (2005) Aluminum resistance in maize cannot be solely explained by root organic acid exudation. A comparative physiological study. Plant Physiol. 137: 231-241.

Prioli AJ, Scapim CA, Prati RM, Priolli SMAP, Bravo JP, Hoshino AA, Boni TA, Munhoz REF (2000) Genetic analysis of means and variances of aluminum tolerance in maize. Acta Scient. 22: 869-875.

Rhue RD, Grogan CO, Stockmeyer EW, Everett HL (1978) Genetic control of aluminum tolerance in corn. Crop Sci. 18: 1063-1067.

Sawazaki E, Furlani PR (1987) Genética da tolerância ao alumínio em milho cateto. Bragantia. 46: 269-278.

Sibov ST, Gaspar MJ, Ottoboni LMM, Arruda P, Souza AP (1999) Two genes controlling aluminum tolerance in maize: genetic and molecular mapping analyses. Genome. 42: 475–482.

Simões CC, Melo JO, Magalhães JV, Gumarães CT (2012) Genetic and molecular mechanisms on aluminum tolerance in plants. Genet Mol Res. 11: 1949-1957.

Vencovsky R, Barriga P (1992) Genética biométrica no fitomelhoramento. Ribeirão Preto: Sociedade Brasileira de Genética.

Welcker C, The C, Andreau B, De Leon C, Parentoni SN (2005) Heterosis and combining ability for maize adaptation to tropical acid soils: implications for future breeding strategies. Crop Sci. 45: 2405-2413.