

## BORON ALTERS CATION EXCHANGE PROPERTIES OF CORN ROOTS BUT DOES NOT DECREASE ALUMINUM TOXICITY

### *BORO ALTERA AS PROPRIEDADES DE TROCA CATIONICA DA RAIZ DE MILHO, MAS NÃO DIMINUI A TOXIDEZ POR ALUMÍNIO*

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**ABSTRACT:** Most studies that have registered amelioration of Al toxicity due to root cation exchange capacity (CEC) decrease with B application were conducted using eudicotyledonous species (high root CEC). However, the effect of B/Al interaction on the root CEC values in species with low root CEC such as corn (*Zea mays* L.) has been understudied. Thus, this study aimed to: (1) verify if B decreases root CEC and if it benefits the growth and nutrient uptake in corn plants under Al toxicity; and (2) verify which method of root CEC analysis better differentiates the effects of B and Al. Corn seedlings were grown in complete nutrient solution with the following treatments: 0, 50, and 200  $\mu\text{M}$  of B versus 0 and 300  $\mu\text{M}$  of Al. Root attributes showed correlations with nutrient depletion from the nutrient solution, but nutrient depletion generally varied with transpiration in two depletion tests. The addition of B or Al in nutrient solution decreased root CEC; however, B failed to decrease Al toxicity in corn plants. The four methods used to determine CEC of corn roots had contrasting results, particularly with respect to the effect of B in the presence of Al.

**KEYWORDS:** Metal sorption. Ionic stress. Root traits. Plant methods.

### INTRODUCTION

In acid soils, Al toxicity is first detected in root system of sensitive species, usually with a growth decrease. Due to rhizotoxicity, absorption of nutrients and water is limited, impairing plant growth (KOCHIAN et al., 2015). Although Al is strongly retained in root tissue, toxic levels can reach the shoot in some crops (HORST et al., 2010). On the other hand, B deficiency induces a negative impact on meristematic tissues, which impairs growth of underground and aerial tissues due to thickening and weakening of cell walls. In general, the largest fraction of B in plants is associated with cell walls (GOLDBACH; WIMMER, 2007); however, B toxicity can affect roots and shoots (BARBOSA et al., 2013; ÇATAV et al., 2018).

Symptoms of Al toxicity and B deficiency have aroused interest concerning B/Al interactions in plants. LeNoble et al. (1996) reported decreased Al toxicity when B was added at levels above the normal range. Subsequently, different mechanisms have been associated with the amelioration of Al toxicity, such as B effects on ascorbate metabolism (LUBASZEWSKI; BLEVIS, 1996), synthesis of antioxidants (RIAZ et al., 2018), and reducing root cation exchange capacity (CEC) (HORST et al., 2010).

Root CEC occurs due to the presence of negative charges in cell walls and plasma

membranes, the two main sources of negative electrical charge of roots (WHITE, 2012; GUIGUES et al., 2014). Root cation binding properties have been assessed in terms of acquisition of nutrients and toxic elements (CEZAR et al., 2015; BARBOSA et al., 2017). In these studies, different analytical methods have been used in root CEC determinations.

Studies investigating the amelioration of Al toxicity due to root CEC decreases by B application have used eudicotyledonous species (high root CEC) (STASS et al., 2007; YU et al., 2008; HORST et al., 2010). However, the effect of B/Al interaction on root CEC values in species with low root CEC such as monocotyledonous corn is not well known. Thus, this study aimed to: (1) verify if B decreases root CEC and benefits growth and nutrient uptake in corn plants under Al toxicity; and (2) verify which method for root CEC analysis better differentiates the effects of B and Al.

### MATERIAL AND METHODS

The experiment was conducted in a plastic greenhouse (ambient light and partial temperature control) in Curitiba, Paraná State, Brazil. Due to lack of light control, it is important to state that the experiment was conducted during a period (November 2012) when cultivation of corn is recommended in this region. Greenhouse

temperature control consisted of air extractors and an air humidifying system that automatically activates when temperature reach 28°C, and remaining operating until the temperature drops below 28°C.

Corn seeds (single-cross hybrid DKB 350) were germinated in washed sand moistened with deionized water. Seedlings (4 seedlings) at three days of emergence were fixed in expanded polystyrene and transferred to plastic pots containing 1.5 L Hoagland solution (continuously aerated and without addition of B) with up to 1/5 of the solution at pH 4.5. One day after transplanting (DAT), 0, 50, and 200 µM B (H<sub>3</sub>BO<sub>3</sub>) x 0 and 300 µM Al (AlCl<sub>3</sub>) were added to treatment nutrient solutions in a factorial design with four replicates per treatment. The average experimental temperature in the greenhouse was 26°C.

After 12 DAT, two pots without plants were added. The pots were weighed with and without nutrient solution. Aliquots of 30 mL of solution (which reflected additions of B and Al) were collected at time zero and after 24 hours (Test I); these aliquots were filtered on filter paper and packaged in plastic bottles for storage at 4°C. After the initial 24 hour test, pots were weighed again. Subsequently, the nutrient solution was replaced in the absence of B and Al treatments (Test II); aliquot collections were conducted as described above. By difference in mass of liquid in the pots containing plants (evapotranspiration) and those without plants (evaporation), transpiration data were obtained for

each test. For the nutrient solution we determined: NH<sub>4</sub><sup>+</sup> - spectrometry UV/VIS (phenate) (Bel Photonics, SP2000); K - flame emission spectrometry (Digimed, MD-62); and Ca, Mg, Fe, Mn, Cu, and Zn - atomic emission spectrometry (Varian, AA240FS). Based on the difference between the initial nutrient content and the final content, nutrient depletion over a 24 hour period was determined.

At 14 DAT, corn plants were removed from the nutrient solution, and plants were then separated into roots and shoots. The roots were rinsed in deionized water (15 second immersion), dried on paper towels, and mass determined. The root system from one plant per experimental unit was stored in 60% ethanol. The roots stored in ethanol were analyzed using 2-D WinRHIZO® equipment and values attributes of length, surface area, and volume were determined. The other roots and shoots of plants were subjected to drying in a forced ventilation oven at 65°C for 72 h. The dry matter of corn roots and shoots was then determined.

Dry roots were ground in a porcelain mortar and analyzed for CEC by different methodologies (Table 1). The remaining root and shoot tissues were ground with a Wiley mill, passed through a 1 mm sieve, and subjected to dry digestion (MARTINS; REISSMANN, 2007). The B and Al concentrations were determined by optical emission spectrometry with inductively coupled plasma (Varian 720-ES).

**Table 1.** Description of sequential steps for analysis of root cation exchange capacity (CEC).

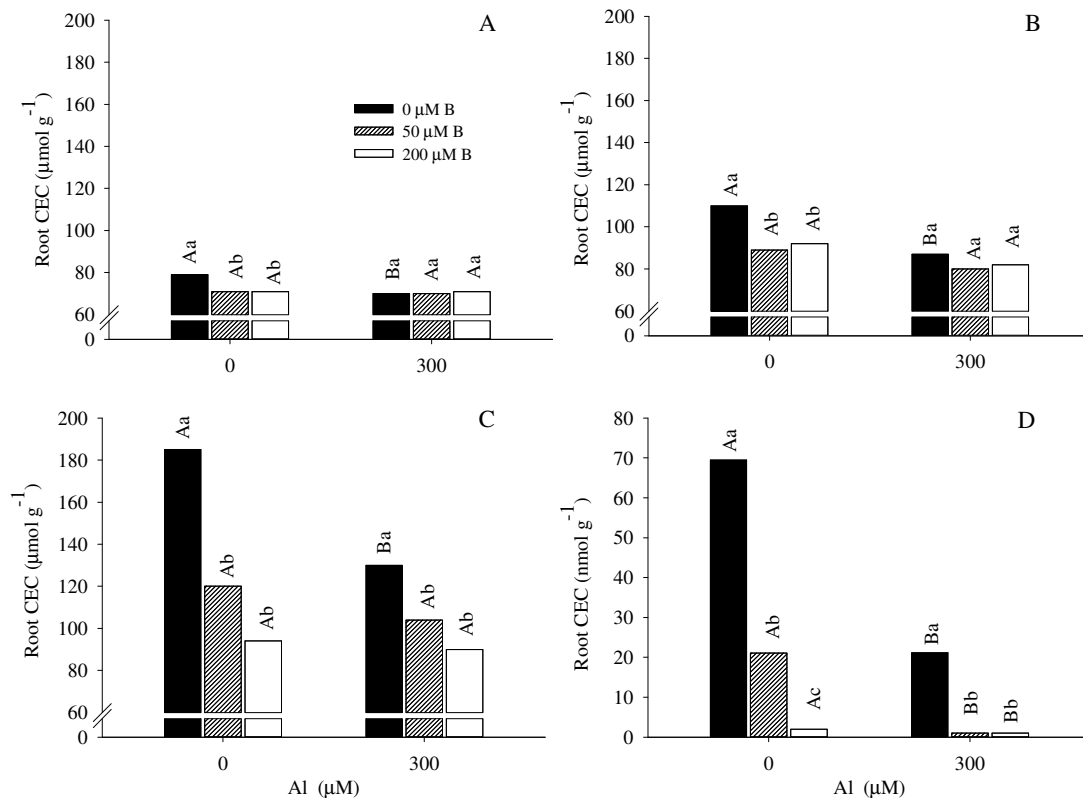
M <sup>a</sup>	1 <sup>st</sup> step <sup>b</sup>	2 <sup>st</sup> step	3 <sup>st</sup> step	Root CEC
1	Stirring for 5 minutes with 100 mL of HCl 0.01 mol L <sup>-1</sup>	Stirring for 5 minutes with 100 mL of KCl 1 mol L <sup>-1</sup> (pH 7.0)	Addition of KOH 0.01 mol L <sup>-1</sup> in extract of 2 <sup>nd</sup> step until pH returns to 7.0	Base amount added until the pH returns to 7.0
2 <sup>c</sup>	Stirring for 2 hours with 20 mL of HCl 0.05 mol L <sup>-1</sup>	Determination of Ca, Mg, Fe, Mn, Cu, and Zn in the extract of 1 <sup>st</sup> step	-----	Extraction sum of Ca, Mg, Fe, Mn, Cu, and Zn
3	Stirring for 2 hours with 20 mL of HCl 0.05 mol L <sup>-1</sup>	Stirring for 2 hours with 20 mL with 1.0; 1.0; 0.2; 0.2; 0.2 and 0.2 mg L <sup>-1</sup> of Ca, Mg, Fe, Mn, Cu, and Zn	Determination of Ca, Mg, Fe, Mn, Cu, and Zn in extract of 2 <sup>nd</sup> step	Total amount of cation adsorbed by root tissue
4	Stirring for 2 hours with 20 mL of HCl 0.05 mol L <sup>-1</sup>	Stirring for 2 hours with 20 mL of KOH solution with pH 11	Determination of pH in extract of 2 <sup>nd</sup> step	Difference between H <sup>+</sup> concentration in equilibrium solution and initial solution of KOH

(a) M = method; M1 - pH 7 method (CROOKE, 1964); M2 (cationic extraction), M3 (cationic adsorption) and M4 (Delta pH 11) were adapted from Wu and Hendershot (2009). (b) All methods used 50 mg of dried root for analysis. Between each step, extracts were filtered and after the first stage (except M2) acid excess was withdrawn from root tissue with deionized water. Cation concentrations in M2 and M3 were determined by atomic absorption spectrometry (Varian, AA240FS). (c) In addition, K were determined (flame emission spectrometry - Digimed, MD-62) in extraction by HCl.

Data were submitted to analysis of variance following a completely randomized design with a 3x2 factorial arrangement (3 levels of B x 2 levels of Al) with four replications. For data analysis, Tukey's test and Pearson correlations were used. All tests were performed at the 5% significance level.

## RESULTS

Application of B and Al in nutrient solution caused decreases in corn root CEC. However, among the four methods tested some differences were noted (Figure 1).



**Figure 1.** Root cation exchange capacity (CEC) in corn grown in nutrient solution with different B and Al levels. A, B, C and D represent Methods 1, 2, 3, and 4, respectively. For each B level (Al effect), averages followed by different uppercase letters and for each Al level (B effect), averages followed by the different lowercase letters represent differences by the Tukey test ( $p < 0.05$ ).

In treatments without addition of Al, Ca, and Mg, macronutrients were extracted in greater quantity from root tissue when B was not applied in solution, whereas this behavior did not occur in the presence of Al (Table 2). These results are due to reduced root CEC in the presence of Al, thus, the effect of B on the amount of Ca and Mg extracted by roots had probably been minimized. The amount of Fe extracted from roots increased with B addition, however, extracted amounts of other micronutrients (Mn, Cu, Zn) had no impact on B (Table 2). In the absence of Al, the adsorption of Ca, Mg, Fe, Mn, Zn, and Cu decreased with B addition to the nutrient solution. However, in the presence of Al, the discrimination of B levels was repeated only for the adsorption of Fe and Cu (Table 2).

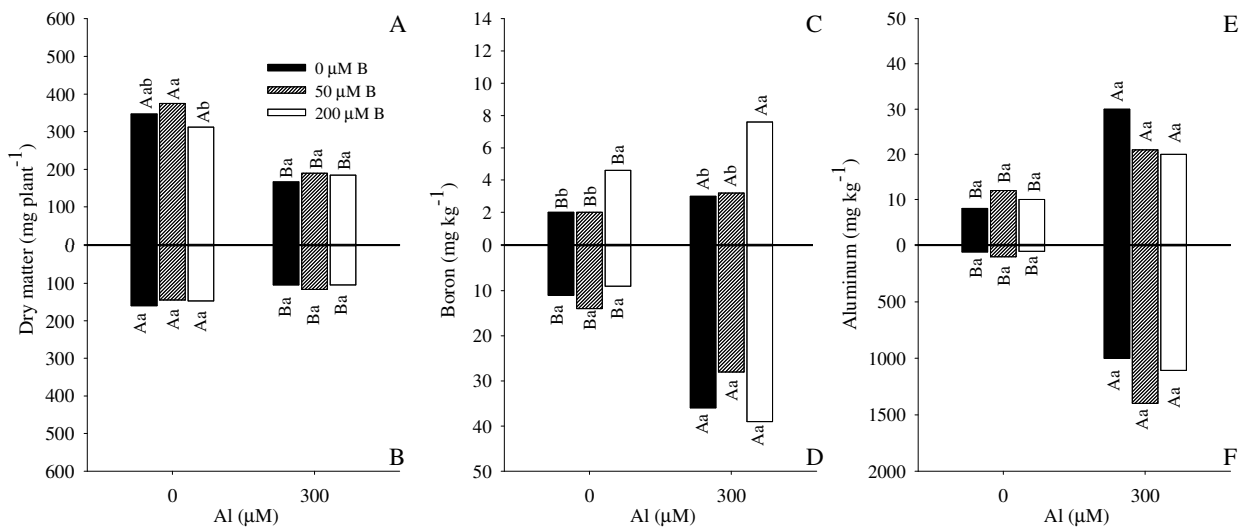
The corn shoot and root dry matter (DM) decreased with Al addition, however, B failed to decrease this toxicity. On the other hand, when B (50 μM) was added in the absence of Al, the shoot DM presented higher accumulation (Figure 2A-B). The B concentration in shoots increased only at a level of 200 μM, regardless of the presence (or not) of Al in nutrient solution, whereas the concentrations in roots were unaffected. However, for plants under Al toxicity the B concentration was higher in shoots and roots (Figure 2C-D). Plants under Al toxicity showed high concentrations, especially in root tissue (Figure 2E-F).

The Al toxicity was detrimental to root length, surface area and volume. However in all cases, B failed to decrease Al toxicity (Table 3).

**Table 2.** Extraction and adsorption of nutrients in root of corn grown in nutrient solution with B and Al levels.

Nutrient	Al ( $\mu\text{M}$ )			300			
	B ( $\mu\text{M}$ )	0	50	200	0	50	200
----- g kg <sup>-1</sup> -----							
Extraction							
K		17.8 Ab	21.5 Aa	19.0 Aab	8.81 Ba	8.65 Ba	8.02 Ba
Ca		2.32 Aa	1.62 Ab	1.81 Ab	1.86 Ba	1.72 Aa	1.77 Aa
Mg		0.97 Aa	0.82 Aab	0.77 Ab	0.68 Ba	0.60 Ba	0.62 Ba
Fe		0.23 Bb	0.26 Bab	0.31 Aa	0.33 Aa	0.34 Aa	0.35 Aa
Mn		0.23 A	0.27 A	0.23 A	0.15 B	0.16 B	0.17 B
Cu		0.13 A	0.16 A	0.15 A	0.11 B	0.10 B	0.11 B
Zn		0.15 A	0.16 A	0.16 A	0.12 B	0.13 B	0.11 B
Adsorption							
Ca		1.91 Aa	1.05 Ab	1.07 Ab	1.01 Ba	1.05 Aa	1.04 Aa
Mg		1.29 Aa	0.71 Ab	0.98 Aab	0.74 Ba	0.84 Aa	1.04 Aa
Fe		2.78 Aa	2.05 Ab	0.58 Ac	2.30 Ba	1.12 Bb	0.63 Ab
Mn		0.79 a	0.68 a	0.31 b	0.67 a	0.52 a	0.18 b
Cu		1.18 Aa	0.81 Ab	0.40 Ac	0.93 Ba	0.57 Ab	0.31 Ab
Zn		0.47 Aa	0.45 Aa	0.27 Ab	0.40 Aa	0.31 Aa	0.27 Aa

For each B level (Al effect), averages followed by the different uppercase letters and, for each Al level (B effect), averages followed by the different lowercase letters present difference by Tukey test ( $p < 0.05$ ).



**Figure 2.** Dry matter, concentration of B and Al in corn grown in nutrient solution with B and Al levels. Shoots (A, C, E) and roots (B, D, F). For each B level (Al effect), averages followed by the different uppercase letters and, for each Al level (B effect), averages followed by the different lowercase letters present differences by Tukey test ( $p < 0.05$ ).

**Table 3.** Root length, surface area, and volume of corn grown in nutrient solution with B and Al levels.

Root attributes	Al ( $\mu\text{M}$ )			300			
	B ( $\mu\text{M}$ )	0	50	200	0	50	200
Length		204 A	190 A	206 A	98 B	112 B	97 B
Surface area		54 A	52 A	60 A	30 B	36 B	30 B
Volume		16 A	18 A	21 A	10 B	13 B	10 B

For each B level (Al effect), averages followed by the different uppercase letters present difference by Tukey test ( $p < 0.05$ ). B levels did not present differences by Tukey test. Length, cm. Surface area, cm<sup>2</sup>; Volume, mm<sup>3</sup>.

In Test I, there was a decrease in  $\text{NH}_4^+$ , K, and Zn depletion from the nutrient solution and in corn transpiration under Al toxicity. In Test II, lower  $\text{NH}_4^+$  and K depletion from nutrient solution for corn under Al toxicity was recorded, while there was a greater depletion of Cu from nutrient solution in plants grown without Al and with B presence (50  $\mu\text{M}$ ). For transpiration in Test II, the Al toxicity decreased values only in the absence and addition of

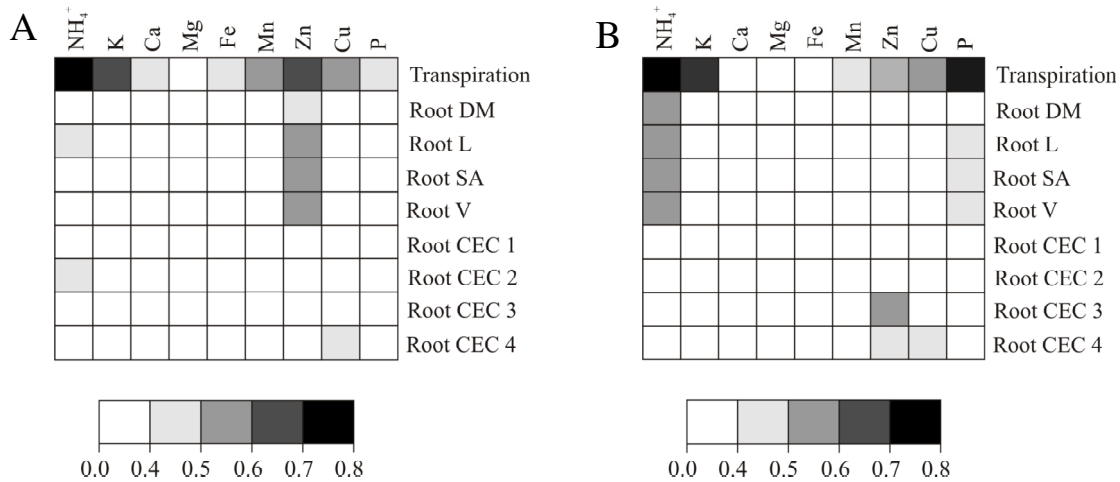
B (50  $\mu\text{M}$ ) (Table 4). Correlations among nutrient depletion and corn plant attributes indicated variations considering the two depletion tests (Figure 3).

In general, depletion of  $\text{NH}_4^+$ , K, Ca, Fe, Mn, Zn, and Cu (Test I), and  $\text{NH}_4^+$ , K, Mn, Zn, and Cu (Test II) from nutrient solution, correlated (positive) mainly with transpiration.

**Table 4.** Nutrient depletion and transpiration (T) of corn grown in nutrient solution with B (0, 50, and 200  $\mu\text{M}$ ) and Al (0 and 300  $\mu\text{M}$ ) levels<sup>a</sup>.

Variables <sup>b</sup>	Al ( $\mu\text{M}$ )	0			300		
	B ( $\mu\text{M}$ )	0	50	200	0	50	200
Test I <sup>c</sup>							
----- $\mu\text{mol g}^{-1}$ root fresh matter -----							
K		49.1 A	53.7 A	51.4 A	39.5 B	39.8 B	42.6 B
$\text{NH}_4^+$		18.4 A	18.8 A	18.4 A	17.3 B	17.2 B	17.4 B
Ca		15.8	17.2	16.0	15.1	17.4	16.1
Mg		11.3	13.4	13.0	12.0	12.2	12.6
Fe		7.35	7.38	7.28	7.02	7.16	6.92
Mn		7.60	7.25	7.10	6.65	7.57	7.13
Cu		2.02	2.02	1.86	1.93	1.61	1.11
Zn		1.70 A	1.73 A	1.66 A	1.28 B	1.47 B	1.36 B
----- $\text{mL plant}^{-1}$ -----							
Transpiration		28.7 Ab	39.3 Aa	19.8 Ab	18.7 Ba	16.7 Ba	13.7 Ba
Test II							
----- $\mu\text{mol g}^{-1}$ root fresh matter -----							
K		40.2	53.6	49.1	49.3	48.9	51.6
$\text{NH}_4^+$		17.8 Aa	18.1 Aa	18.2 Aa	16.3 Ba	16.7 Ba	17.5 Aa
Ca		13.9	13.0	13.5	12.8	13.5	13.0
Mg		12.6	13.3	11.8	12.9	14.0	12.2
Fe		7.73	7.30	7.44	6.25	6.04	6.50
Mn		6.20	6.79	5.90	5.90	6.29	5.62
Cu		2.66 Ab	2.95 Aa	2.51 Ab	2.64 Aa	2.70 Aa	2.59 Aa
Zn		1.77	1.77	1.54	1.67	1.58	1.58
----- $\text{mL plant}^{-1}$ -----							
Transpiration		20.6 Aa	22.6 Aa	15.6 Aa	7.5 Ba	8.0 Ba	12.9 Aa

(a) For each B level (Al effect), averages followed by the different uppercase letters and, for each Al level (B effect), averages followed by the different lowercase letters present difference by Tukey test ( $p < 0.05$ ). (b) Variables. (c) Test I: nutrient solution with B and Al; Test II: nutrient solution without B and Al.



**Figure 3.** Pearson correlations ( $p < 0.05$ ) between nutrient depletion and attributes of corn grown in nutrient solution with B and Al levels (A: Test I; B: Test II). CEC of roots 1, 2, 3, and 4 correspond to the methods KCl pH 7, cationic extraction, cationic adsorption, and Delta pH 11, respectively. Scales indicate the value of the correlation coefficient.

## DISCUSSION

Decreases in root CEC by adding B (Figure 1) corroborates the results observed by Stass et al. (2007) for cell walls in root tips of bean. The authors found that addition of 50  $\mu\text{M}$  B in nutrient solution reduced the total amount of pectin in cell walls and reduced carboxyl groups ( $\text{COO}^-$ ) in the cell walls by 25 nmol per tip. This reduction of negative charges occurs simultaneously with cell wall structural changes, keeping in mind that the formation of the rhamnogalacturonan-II dimer (RG-II) from a bridge between B and two rhamnogalacturonan-II monomers (RG-II) decreases the pore size of the cell wall (HORST et al., 2010). However, Guigues et al. (2014) report that the negative charges on the plasma membrane also contributes to root CEC. Tanada (1995) note that B binds with components of the plasma membrane which can increase the membrane negative charge. However, this effect was probably unimportant in determining the CEC of corn roots, since our results corroborate those of Stass et al. (2007) who studied cell walls. Thus, whereas the majority of B is associated with plant cell walls, it is likely that the reduction of root CEC had been affected by changes in cell walls. On the other hand, decreases in root CEC with Al addition to nutrient solution (Figure 1) was due to the high adsorption strength of this element to root tissue components (HORST et al., 2010).

Differential sensitivity of methods (Figure 1) may have occurred, in part, by the acid pre-treatment. In the KCl pH 7 method (CROOKE, 1964), the acid solution is 0.01 mol  $\text{L}^{-1}$  (stirring for 5 minutes), whereas the cationic adsorption and

Delta pH 11 methods had acid solutions of 0.05 mol  $\text{L}^{-1}$  (stirring for 2 hours), both with HCl. Therefore, use of pre-treatment with the highest HCl concentration and longer extraction time, probably promoted greater release of cation exchange sites in root tissue that allowed subsequent tests to better express the effects of B and Al on CEC of roots. On the other hand, using the sum of cationic nutrients extracted by HCl solution 0.05 mol  $\text{L}^{-1}$  provided results similar to the pH 7 method. Besides the effect of pre-treatment, the higher expression of differences in Delta pH 11 was related to the method of calculating root CEC. This calculation considers the concentrations of  $\text{H}^+$  obtained from the pH value of the solution that varies on a logarithmic scale. However, Meychik and Yermakov (2001) found that three main exchange groups of cations in cell walls (galacturonic acid, carboxylic acids, and phenols) have a dissociation constant ( $pK_a$ ) in pH less than 10. Thus, when roots charged with  $\text{H}^+$  are placed in solution with pH 11, deprotonation of these groups can be expected along with acidification of the final solution, which may have contributed to increased differentiation of B and Al treatments.

The higher amount of Fe extracted in roots with low CEC (Table 2) indicates that a reduction in bond strength of this metal. Similarly, Ye et al. (2015) with tomato roots with different degrees of cell wall methylation ( $>$  methylation corresponds to  $<$  root CEC), found that Fe was extracted in greater quantities when the level of methylation was high. Overall, the contribution of different cations to the CEC values (cationic extraction method) is

consistent with concentrations in the nutrient solution. Thus, Ca showed higher concentration compared to other nutrients (except K), consequently, there was a higher concentration extracted from roots that corroborate findings of Wu and Hendershot (2009). In addition, K showed higher extraction of roots in the absence of Al and the presence of 50  $\mu\text{M}$  B, which did not occur in the presence of Al (Table 2). Thus, the extraction of K did not vary with root CEC.

The contents of Fe and Cu adsorbed in roots showed greater sensitivity to variations of root CEC than other cations since the decrease in root CEC with addition of B provide less adsorption in root tissue in the absence or presence of Al (Table 2). Araújo et al. (2007) also found high Fe adsorption in roots of *Paspalum notatum*. This result occurs because Fe is in the trivalent form ( $\text{Fe}^{3+}$ ) in solution, however, these authors reported that results varied depending on solutions used and root pre-treatment, and under some conditions Cu adsorption exceeded that of Fe. However, the amount of cations adsorbed to root tissue suggests that adsorption is preferably different between high and low root CEC values, although concentrations used in the adsorption solution are not the same for Ca and Mg, Fe, Zn, Cu, and Mn. In the treatment without B and without Al (higher root CEC) and the treatment with the addition of 200  $\mu\text{M}$  of B and 300  $\mu\text{M}$  of Al (lower root CEC) the adsorption order was  $\text{Fe} > \text{Ca} > \text{Mg} > \text{Cu} > \text{Mn} > \text{Zn}$  and  $\text{Ca} = \text{Mg} > \text{Fe} > \text{Cu} > \text{Zn} > \text{Mn}$ , respectively. These results are probably related to factors such as affinity for cations by exchange sites (WU; HENDERSHOT, 2009), cell wall composition (STASS et al., 2007), and CEC variations in the plasma membrane (GUIGUES et al., 2014).

The corn DM decrease with the addition of Al and the B failed to decrease this toxicity (Figure 2). Studies have found amelioration of Al toxicity with B application generally occurs using species with a high B demand, like squash (LUBASZEWSKI; BLEVIS, 1996), clover (FAVARETTO et al., 2007), and pea (YU et al., 2009). However, in one of the few studies with grasses, Hossain et al. (2004) reported amelioration of Al toxicity with the addition of B in nutrient solution for seedlings of wheat, a species with low B requirements.

The B increase in plants under Al toxicity is related to DM reduction that may have concentrated the B (Figure 2C-D). However, Wang (2004) reported that corn plants grown under Al toxicity did not present B concentration alterations. On the other hand, plants under Al toxicity showed high

concentrations of the element, especially in root tissue (Figure 2E-F), due to the strong interaction of Al with root tissue (HORST et al., 2010; DOMINGUES et al., 2016). However, the addition of B did not change Al concentration in corn. Similarly, Wang (2004) found no change in Al concentrations with addition of B in corn. In contrast, some studies have found a decrease in Al concentrations by adding B (YU et al., 2009), indicating variation between species. Studying bean plants, Stass et al. (2007) found that in cell walls of roots with low CEC, the Al concentration was lower in roots. However, while in our study B reduced root CEC, there was no change in the Al concentration in roots. These results indicate that, in our study, the affinity of Al biomolecules in roots was more important than the change in electrical charges.

Pereira et al. (2008) reported similar effects of Al on sorghum root systems grown in nutrient solution. The amelioration of Al toxicity in the root system in response to B addition has been recorded in leguminous plants, particularly for root-growth related attributes (LENOBLE et al., 1996; FAVARETTO et al., 2007). Studying corn plants, Wang (2004) found no amelioration of Al rhizotoxicity with the addition of B to the nutrient solution. Hossain et al. (2004) observed that in Al-sensitive wheat genotypes, the effect of B on root growth was higher than in tolerant genotypes.

The decrease in absorption of nutrients by Al toxicity (Table 4) was mainly due to the negative effects of Al on the root system and metabolism (HORST et al., 2010; PEREIRA et al., 2008), including transpiration (RUFYIKIRI et al., 2001; BARBOSA et al., 2017). Furthermore, the high concentration of Al in nutrient solution may also reduced the absorption of nutrients due to competition for cationic sites exchange, absorption to the root cell plasma membranes, and decrease of nutrient activity in solution (WHITE, 2012). On the other hand, the positive B effect at 50  $\mu\text{M}$  on the depletion of Cu may be related to increased demand by plants of this treatment, which also had higher shoot dry matter (Figure 2A).

The correlation between  $\text{NH}_4^+$  depletion and transpiration (Figure 3) probably occur because the main ion-root contact mechanism for  $\text{NH}_4^+$  (mass flow) was directly affected by transpiration. Other nutrients can also be affected by this mechanism; however, the participation of the diffusion mechanism becomes important, especially for K and P (MARSCHNER; RENGEL, 2012). However, our study used cultivation with aerated nutrient solutions, thus mass flow mechanism likely gained

more importance in contributing to the acquisition of nutrients.

York et al. (2015) reported that the higher acquisition capabilities of N in modern corn hybrids are related to anatomical and architectural attributes of the root system, which may likely affect the absorption of other nutrients (Figure 3). On the other hand, nutrients have different affinities for cationic exchange sites (Table 2) and charged ionic species near the surface are affected by cation distributions (WHITE, 2012). In our study, root CEC had a positive correlation to Zn, Cu, and  $\text{NH}_4^+$  (especially Zn), as correlation occurred in two methods, and Cu as there was correlation in both tests (Figure 3). Riseman et al. (2005) found increased Zn, Cu, and Mg absorption in a Persian Violet genotype with high root CEC, while Cezar et al. (2015) reported correlations between the CEC of roots in oat and K and Cu depletion from the nutrient solution.

## CONCLUSIONS

The addition of B in nutrient solution decreased root CEC, which also occurred when Al

was added. However, B failed to decrease Al toxicity in relation to corn growth, Al concentration, nutrient uptake, and transpiration.

The methods used to determine CEC of corn roots had contrasting results, particularly with respect to the effect of B in the presence of Al. The Delta pH 11 method allows greater differentiation between treatments with the addition of B and Al and, in sequence, the cationic adsorption method has the advantage of allowing for the study of the adsorption preference of cations by the roots.

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**RESUMO:** A maioria dos estudos que registraram amenização da toxidez de Al devido ao decréscimo da capacidade de troca de cátions (CTC) radicular com a aplicação de B foram realizados com espécies eudicotiledôneas (alta CTC radicular). Contudo, o efeito da interação B/Al nos valores de CTC radicular em espécies de baixa CTC radicular, como no milho (*Zea mays* L.), é pouco conhecido. Assim, os objetivos desse estudo foram: (1) verificar se o B reduz a CTC radicular e se isso beneficia o crescimento e a absorção de nutrientes em plantas de milho sob toxidez por Al; (2) verificar qual método para análise de CTC radicular diferencia melhor o efeito do B e Al. Plântulas de milho foram cultivadas em solução nutritiva completa com os seguintes tratamentos: 0, 50 e 200  $\mu\text{M}$  de B versus 0 e 300  $\mu\text{M}$  de Al. Os atributos radiculares apresentaram correlações com a depleção de nutrientes da solução nutritiva, mas, em geral, a depleção de nutrientes variou principalmente com a transpiração em dois testes de depleção. A adição de B na solução nutritiva reduziu a CTC radicular, o que também ocorreu quando o Al foi adicionado, contudo, o B não aliviou a toxidez por Al nas plantas de milho. Os quatro métodos usados para determinar a CTC radicular do milho tiveram resultados contrastantes, particularmente com relação ao efeito do B na presença de Al.

**PALAVRAS-CHAVE:** Sorção de metais. Estresse iônico. Atributos radiculares. Métodos de plantas.

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