Revista Brasileira de Ciências Agrárias
ISSN: 1981-1160
agrarias.prppg@ufrpe.br
Universidade Federal Rural de Pernambuco
Brasil

Barbosa de Freitas, Lucas; Maximino Fernandes, Dirceu; Mendonça Maia, Suelen Cristina; Gallucci Mazziero, Beatriz
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Revista Brasileira de Ciências Agrárias, vol. 12, núm. 1, 2017, pp. 26-34
Universidade Federal Rural de Pernambuco
Pernambuco, Brasil

Agrária - Revista Brasileira de Ciências Agrárias
ISSN (on line) 1981-0997
v.12, n.1, p.26-34, 2017
Recife, PE, UFRPE. www.agraria.ufrpe.br
DOI:10.5039/agraria.v12i1a5414
Protocolo 5414 - 05/11/2015 • Aprovado em 03/02/2017

Aluminum in mineral nutrition of upland rice plants

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ABSTRACT

Although upland rice plants have been historically considered to be tolerant to aluminum, they may have their growth prevented or decreased when cultivated on aluminum soils, besides having their uptake of water and nutrients negatively influenced. Thus, the objective of this work was to evaluate the content and accumulation of macro and micronutrients in upland rice plants submitted to aluminum toxicity. The experimental design chosen was the randomized block design, with four replications; and the treatments were five doses of aluminum (0; 370; 740; 1100 and 1480 µmol L^{-1}). The evaluations conducted were on the content and accumulation of macro and micronutrients in the shoot and root of the plants. Due to the interaction between aluminum and calcium, the decrease in calcium content and accumulation are the most important effects caused by aluminum on the mineral nutrition of upland rice plants. Aluminum has a high negative influence on mineral nutrition of upland rice plants, especially at its roots.

Key words: accumulation; *Oryza sativa* L.; nutrient solution; toxicity

Alumínio na nutrição mineral de plantas de arroz de terras altas

RESUMO

Apesar de plantas de arroz de terras altas serem historicamente consideradas tolerantes ao alumínio, estas podem ter seu crescimento impedido ou diminuído no cultivo em solos com alumínio, além de influenciar negativamente sua absorção de água e nutrientes. Assim, o objetivo do trabalho foi avaliar o teor e acúmulo de macro e micronutrientes em plantas de arroz de terras altas submetidas a toxidez por alumínio. O delineamento experimental foi o de blocos casualizados, com quatro repetições; e os tratamentos foram cinco doses de alumínio (0; 370; 740; 1100 e 1480 µmol L^{-1}). As avaliações realizadas foram teor e acúmulo de macro e micronutrientes na parte aérea e raiz das plantas. Devido a interação entre alumínio e cálcio, o decréscimo no teor e acúmulo de cálcio são os efeitos mais importantes causados pelo alumínio na nutrição mineral das plantas de arroz de terras altas. O alumínio tem alta influência negativa na nutrição mineral de plantas de arroz de terras altas, especialmente em suas raízes.

Palavras-chave: acúmulo; *Oryza sativa* L.; solução nutritiva; toxidez

Introduction

Soils with aluminum (Al^{3+}) toxicity problem represent about 40% of the earth's surface and 50% of all potentially arable land in the world (Kochian et al., 2004), making toxicity caused to plants a major constraint on agricultural production. In Brazil, 60% of the soils are acidic and have Al^{3+} concentration that may be toxic to root growth. In general, the pH of most Brazilian soils varies between 3.7 and 5.5, and Al^{3+} is the predominant cation in more than one third of soils with a pH lower than 5.6 (Abreu Jr. et al., 2003).

Toxicity caused by Al^{3+} in plants has its primary effect on the roots, inhibiting their growth (Macêdo et al., 2009). The roots of plants under Al^{3+} stress become atrophied, brittle, thinly branched, have increased cell wall stiffness and thickness, and undergo changes in membrane transport proteins (Meriga et al., 2010; Motoda et al., 2010; Sun et al., 2010; Garzon et al., 2011; Guo et al., 2012). Consequently, the roots become inefficient in the uptake of water and nutrients (Mendonça et al., 2003; Freitas et al., 2006; Guo et al., 2007; Famoso et al., 2010).

Upland rice plants have been historically considered to be tolerant to soil acidity and to Al^{3+} (Famoso et al., 2010), being even used in open areas of cerrado, whose soils have acidic pH. However, they can have their growth prevented or diminished when cultivated in soils with Al^{3+} (Mendonça et al., 2003; Mendonça et al. 2005; Freitas et al., 2006; Guimarães et al., 2006; Macêdo & Jan, 2008), which may limit root growth (Kochian et al., 2004).

Evaluations are usually linked to plant growth and little information is available regarding mineral nutrition of upland rice plants grown in the presence of Al^{3+}. There are only few studies demonstrating the behavior of macronutrient uptake in rice plants cultivated under Al^{3+} toxicity (Mendonça et al., 2003; Freitas et al., 2006; Justino et al., 2006).

Thus, it is important to evaluate in detail mineral nutrition of upland rice plants under Al^{3+} toxicity, since macronutrient uptake is not fully elucidated and there are practically no studies addressing mineral nutrition with micronutrients. Therefore, the objective of this work was to evaluate the content and accumulation of macro and micronutrients in upland rice plants submitted to Al^{3+} toxicity.

Material and Methods

The experiment was carried out in a greenhouse belonging to the Department of Soils and Environmental Resources of the Faculty of Agronomic Sciences, São Paulo State University in Botucatu, São Paulo, Brazil.

The experimental design chosen was a randomized block design with four replications. The treatments were five doses of Al^{3+} (0; 370; 740; 1100 and 1480 µmol L^{-1}). Aluminum chloride was used to generate Al^{3+} toxicity in rice plants. The upland rice cultivar named Maravilha, which is susceptible to Al^{3+}, was used (Mendonça et al., 2003).

The composition of the nutrient solution used was 1.42 Ca, 1.51 K, 0.33 Mg, 0.95 N- NO_3, 0.41 N-NH_4, 0.01 P, 0.21 S, 0.21 Cl, 0.22 Fe, 0.009 Mn, 0.008 B, 0.00076 Zn and 0.00031 Cu mmol L^{-1}.

In order to obtain plants for the experiment, on April 17, 2012, upland rice seeds were treated with carboxin + thiram (400 mL per 100 kg of seeds) and later placed to germinate in a germination chamber at 25ºC.

After observing the beginning of radicle emergence, the paper rolls were placed vertically in plastic containers containing nutrient solution with 1/5 of the ionic strength, without Al^{3+}. The containers were transferred to the greenhouse, with an ambient temperature of 22 ° C to 27 ° C and controlled humidity.

After seven days, the plants were selected as for uniformity of shape and size (± 8 cm), and transferred to plastic pots, containing 4 L of nutrient solution at half ionic strength. The caps used to fix the plants were made from Styrofoam that were perforated to fit six plants per pot, trapped by pieces of foam, allowing the roots to come into contact with the nutrient solution.

At 7 days after transplant (DAT), the nutrient solution was replaced by full strength, and the plants kept growing until 21 DAT. The treatments were then added to the nutrient solution and the plants remained in growth under these conditions up to 56 DAT, and the experiment was then harvested.

During the whole period of the experiment, the nutrient solution was aerated and the pH was monitored daily, keeping it around 4.0 (± 0.1), using NaOH at 0.1 mol L^{-1} and HCl at 0.1 mol L^{-1} for its correction. The nutrient solution was renewed weekly by adding the respective treatments, and evapo-transpiration losses were manually replaced daily with demineralized water.

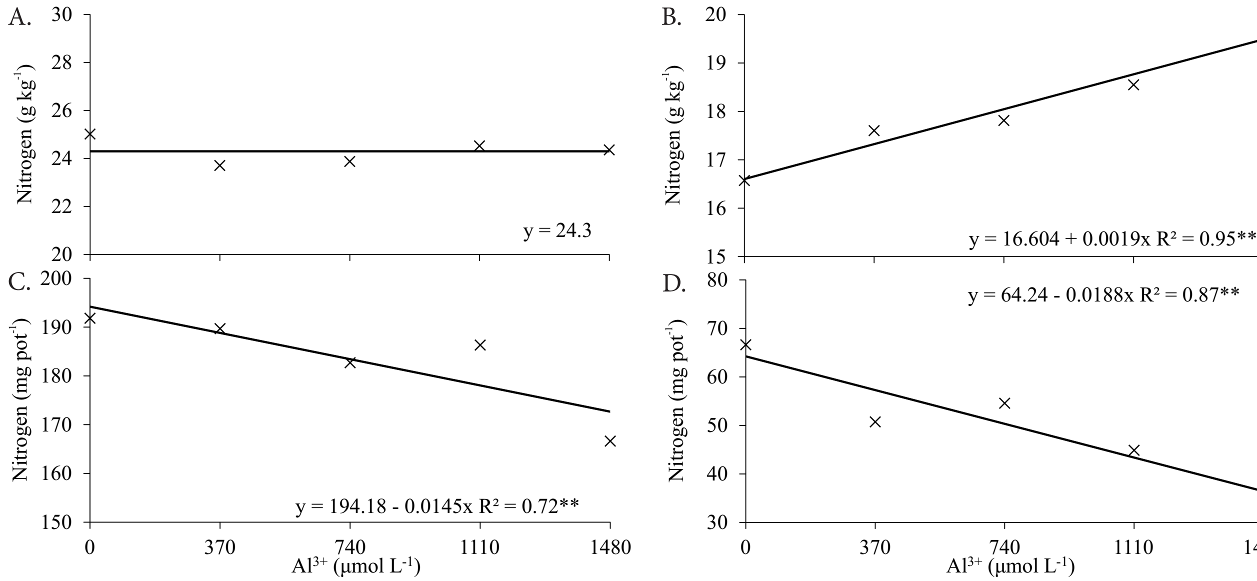
The evaluations were the content and accumulation of macronutrients – nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S) and micronutrients - boron (B), copper (Cu), iron (Fe), manganese (Mn) and zinc (Zn) in shoot and root.

The analysis of variance was performed by the F test and the effects of the Al^{3+} doses were evaluated by means of regression analysis, adopting the magnitude of the regression coefficients significant at 5% of probability by the test t as criterion to choose the model.

Results and Discussion

There was no difference between the Al^{3+} doses for N content in the shoot (Figure 1A). With the application of Al^{3+}, there was an increase in the N content in the roots (Figure 1B). This was due to the concentration effect, due to the toxic action of Al^{3+} on root growth (Macêdo et al., 2009); this can be confirmed by the accumulation of N in the root (Figure 1D), because as there was an increase in Al^{3+} doses, N accumulation was lower in the roots. There was also a decrease in N accumulation in the shoot (Figure 1C).

Al^{3+} reduces N uptake and nitrate reductase activity (Justino et al., 2006). Most of the N is uptake by plants in the form of nitrate and the enzyme nitrate reductase acts in the first phase of the reduction of nitric N to nitrite and then to ammonia, mediated by the enzyme nitrite reductase. Following the process, ammonia is fixed in amino acids, glutamine and glutamate, which in turn serve as a substrate for transamination



** p<0.01

Figure 1. Nitrogen content in shoot (A) and root (B) and accumulation in shoot (C) and root (D) of upland rice plants due to the application of aluminum doses.

reactions and for the production of amino acids necessary for the synthesis of proteins (Taiz & Zeiger, 2013).

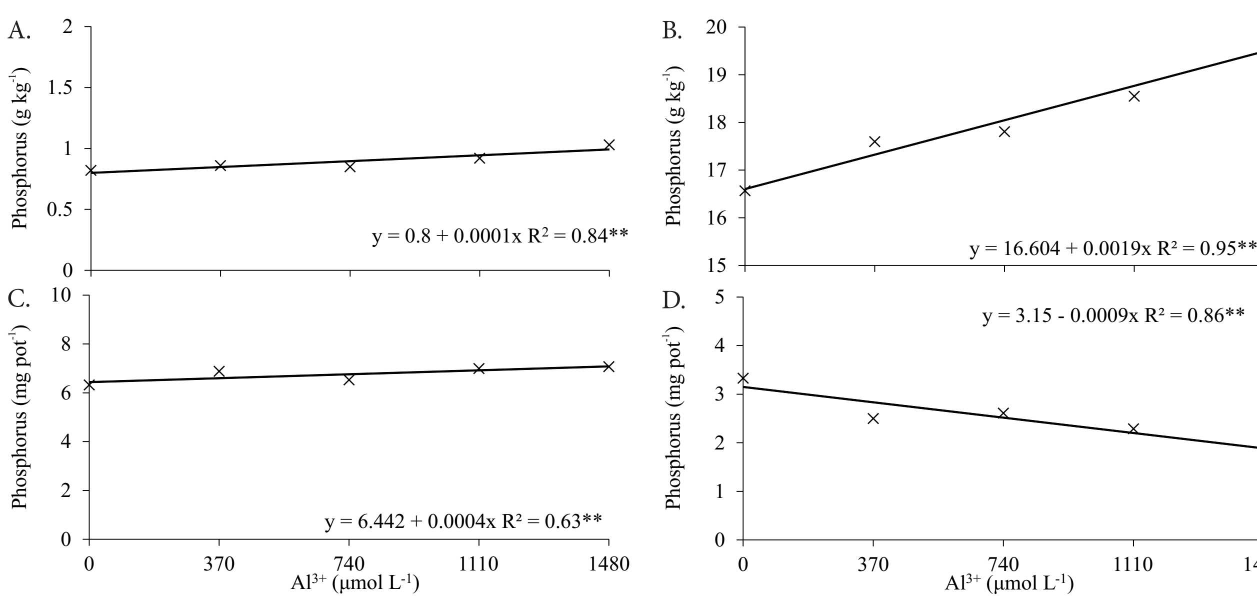
There was an increase in the content and accumulation of P in the shoot as the Al^{3+} doses increased (Figure 2A and C). There was also an increase in the content of P of the root (Figure 1B), which as occurred for the content of N in the root (Figure 1B), there was concentration effect (Figure 1B). This effect can also be verified by observing the accumulation of P in the root, which decreased with the application of Al^{3+} (Figure 2D), confirming the effect described. These results corroborate Macêdo & Jan (2008), who observed an increase in P content in the roots of four rice cultivars as the Al^{3+} doses increased in nutrient solution.

Also, Mendonça et al. (2003) and Freitas et al. (2006) observed a decrease in the P content of rice plants under to Al^{3+} stress. Justino et al. (2006), when evaluating P uptake and tolerance of rice cultivars submitted to Al^{3+} toxicity, observed a high variability between the cultivars tested regarding the uptake capacity of P.

Thus, a hypothesis can be raised that, although Al^{3+} decreases the accumulation of P in the roots of Maravilha cultivar (Figure 2D), the plants have an efficient mechanism of translocation of P to shoot.

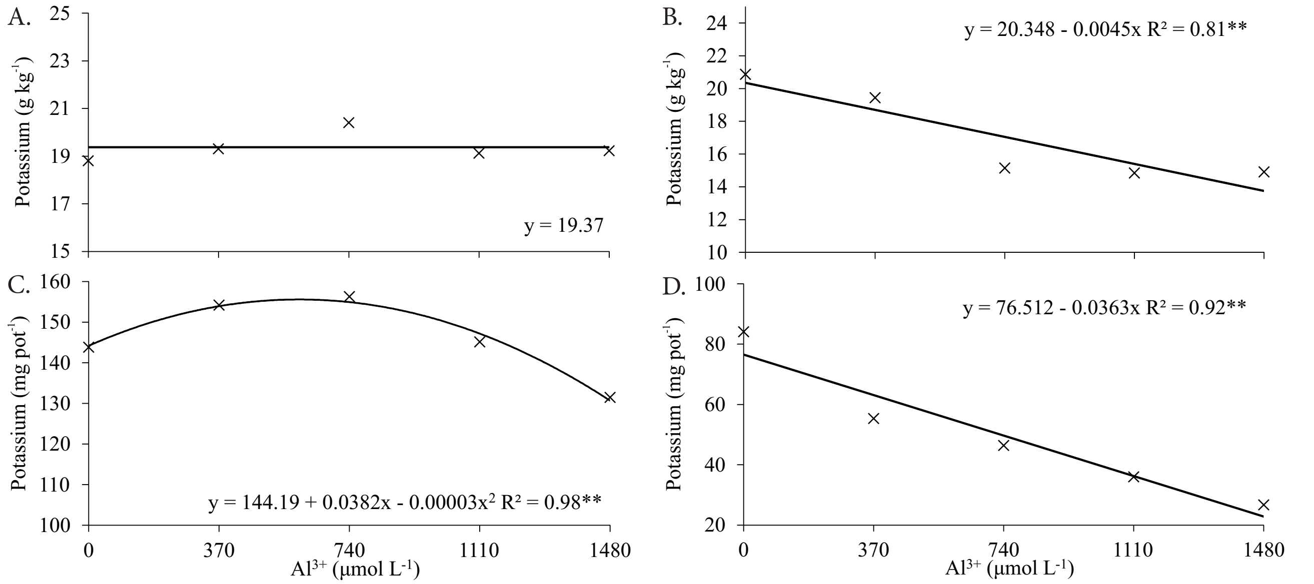
In addition to the effect of P in the interior of the plant, the existence of relationship between the availability of P and Al^{3+} in the soil solution is worth mentioning, in which, while increasing the concentration of Al^{3+}, the concentration of P is decreased by the formation of precipitates between the ions in question (Sousa et al., 2007).

The content of K in shoot was not affected by Al^{3+} in solution (Figure 3A). However, there was an initial increase in K accumulation in shoot and subsequent decrease when increasing doses of Al^{3+} (Figure 3C). Mendonça et al. (2003) reported that in low concentrations of Al^{3+} (370 µM), the K



** p<0.01

Figure 2. Phosphorus content in shoot (A) and root (B) and accumulation in shoot part (C) and root (D) of upland rice plants due to the application of aluminum doses.



** p<0.01

Figure 3. Potassium content in shoot (A) and root (B) and accumulation in shoot (C) and root (D) of upland rice plants due to the application of aluminum doses.

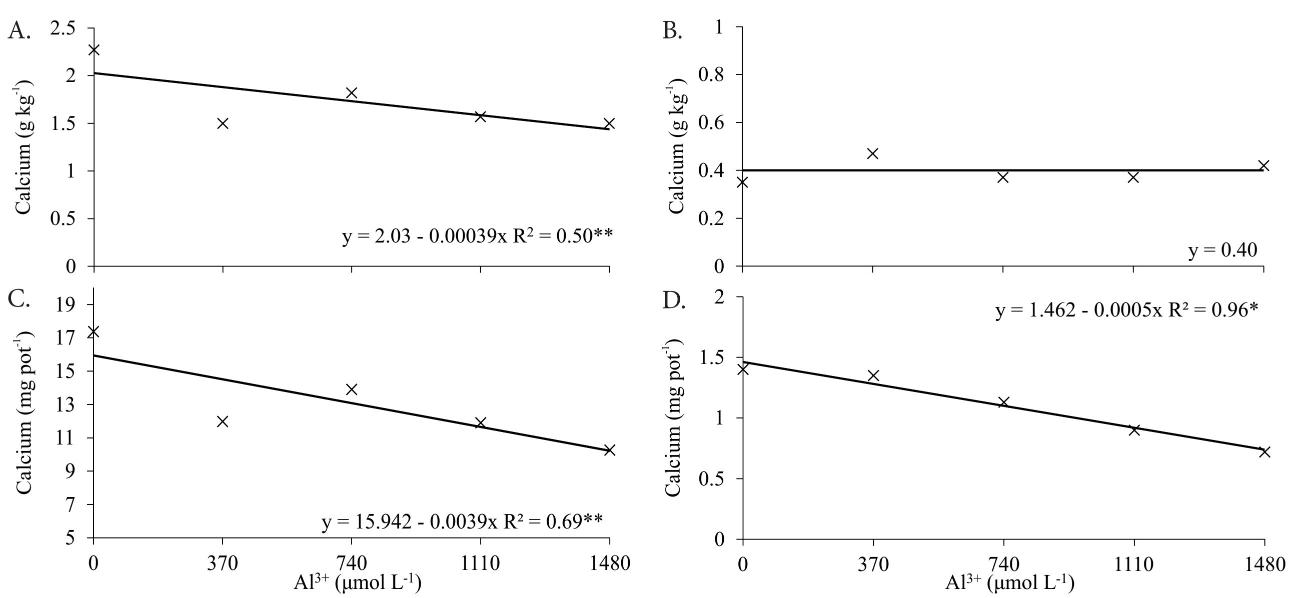
concentration in the rice plant may increase. However, as the doses at higher levels increase, there is a decrease in K concentration, as observed by Fageria & Carvalho (1982).

As Figure 3C shows, only at the dose of 1480 μmol L^{-1} of Al^{3+} there was a decrease in the accumulation of K in shoot compared to the other doses. It appears that, at 370 and 740 μmol L^{-1} doses of Al^{3+}, the plant was able to more efficiently translocate Al^{3+} to the shoot (Figure 3C), since the content and accumulation of K in the root decreased with increasing Al^{3+} doses (Figure 3B and D).

On the root the damaging effect of Al^{3+} doses is evident (Figure 3B and D), in which a decrease in the content and accumulation of K was observed. This result is in agreement with Mendonça et al. (2003), who observed a marked decrease in K content in the roots of Maravilha cultivar as the doses of Al^{3+} increased. Also, in the same work, the authors cite that K in the shoot was the macronutrient less affected by Al^{3+} toxicity. Noteworthy is that K and N are the most required nutrients by upland rice crop (Crusciol et al., 2003).

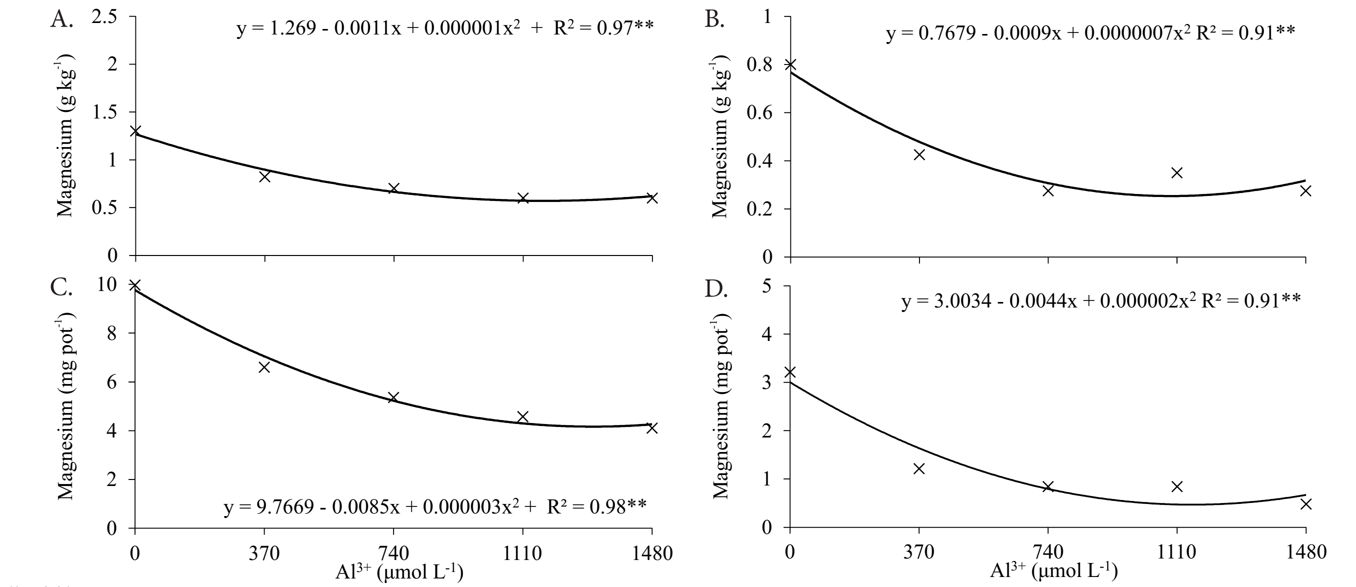
Macêdo & Jan (2008) observed an increase in K content in the shoot of IRAT112 rice cultivar when increasing doses of Al^{3+} in the solution. Also, Mendonça et al. (2003) did not observe decrease in K content in the shoot until the dose of 0.75 mM of Al^{3+}. On the other hand, Freitas et al. (2006) observed a decrease in K content while increasing doses of Al^{3+}.

The Ca content and accumulation in shoot and root decreased with the increase of the doses of Al^{3+} (Figure 4A, C and D), decreased with the increase of the doses of Al^{3+}. There was also a decrease in the content and accumulation of Mg in shoot and root (Figure 5A, B, C and D). Al^{3+} interferes negatively in the bases of the soil solution, especially Ca and Mg, decreasing their concentration and consequently their uptake by plants (Sousa et al., 2007).



* p<0.05 and ** p<0.01

Figure 4. Calcium content in shoot (A) and root (B) and accumulation in shoot (C) and root (D) of upland rice plants due to the application of aluminum doses.



** $p<0.01$

Figure 5. Magnesium content in shoot (A) and root (B) and accumulation in shoot (C) and root (D) of upland rice plants due to the application of aluminum doses.

In addition, Al^{3+} ion influences the alteration of calcium cellular homeostasis and the competition for calcium channels. Furthermore, Al^{3+} competes with Ca and Mg for uptake sites on the transporters and influx channels of mono and divalent cations. Consequently, it reduces the translocation of these elements to shoot (Kochian et al., 2004). Inhibition of calcium uptake due to Al^{3+} affects several cellular processes such as mitosis, cytokinesis, polar growth, cytoplasmic currents and cell signaling (Rengel & Zhang, 2003) and may interact and inhibit the enzyme phospholipase C associated with calcium transport pathways (Kochian et al., 2004).

Calcium is relatively immobile in the interior of the plant, not being redistributed. Moreover, it is involved in cell division and has structural function, integrating the cell wall, playing an important role in the maintenance of the spatial conformation of pectin networks; consequently, calcium deficiency negatively affects root growth by influencing its extensibility, stiffness and permeability (Rengel & Zhang, 2003).

Thus, it is necessary that Ca is available in the soil solution, especially in depth, so that the roots can grow in this direction. If there is little availability of Ca in the soil, the root will have its growth ceased because the plant is not able to redistribute Ca from other parts of the plant to the root growth zone. Besides, in the soil, Al^{3+} can also contribute to decrease the availability of Ca (Sousa et al., 2007). Combined to these features, Al^{3+} also has an influence on the reduction of root growth due to its direct toxicity to the plant tissue (Kochian et al., 2004).

Thus, there may be confusion on the symptoms of toxicity caused by Al^{3+} (Sousa et al., 2007), which may have occurred due to the toxic action of Al^{3+} itself or due to the decrease in the availability of Ca in the solution mediated by Al^{3+}, or even both occurring simultaneously. Therefore, further studies involving the interaction between Al^{3+} and Ca could elucidate this theme.

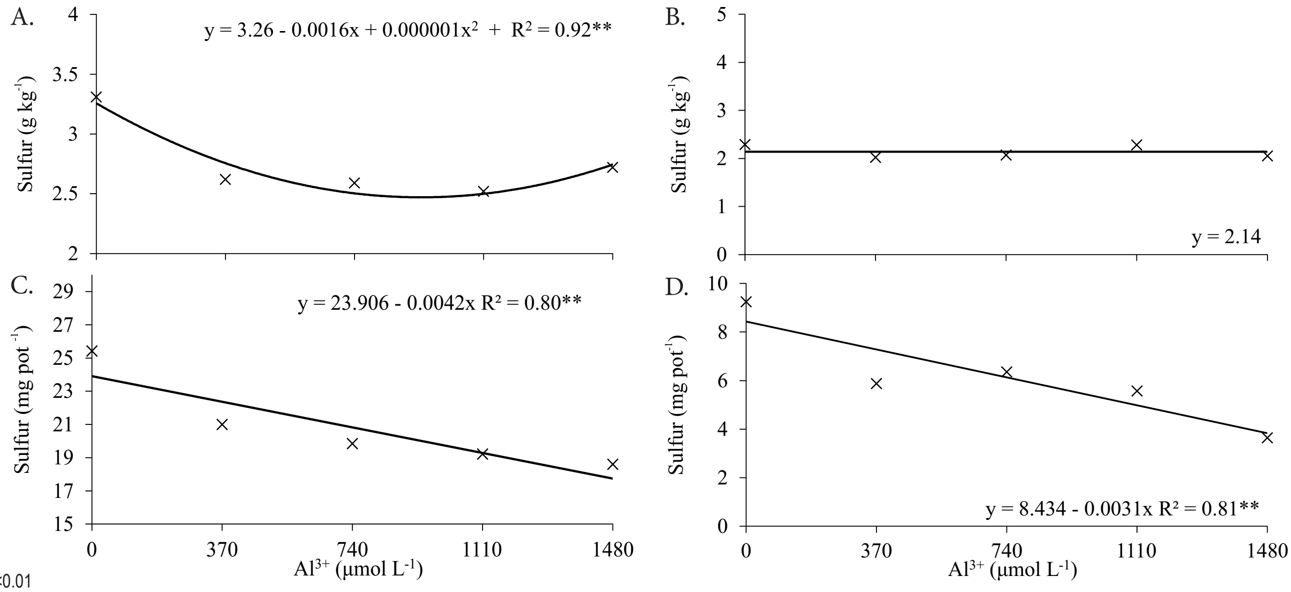
According to Fageria & Carvalho (1982), Mg and Ca, in that order, were the nutrients most affected by the toxicity caused by Al^{3+} in rice plants. Freitas et al. (2006) observed a reduction in Ca and Mg uptake by rice plants under Al^{3+} toxicity. On the other hand, Mendonça et al. (2003) observed a decrease in Ca content in roots of Maravilha cultivar only at a dose of 1.50 mM Al^{3+}, and the dose of 0.75 mM Al^{3+} was not enough to cause a decrease of Ca in the roots in relation to the control treatment. Also, in the same work, the authors mention that the efficiency of utilization of Ca by rice plants of Maravilha cultivar was not altered by Al^{3+}.

There was a decrease in the content and accumulation of S in the shoot (Figure 6A and C) and in the accumulation of S in the root (Figure 6D). There are few studies reporting the influence of Al^{3+} on the uptake of S by the roots of rice plants; however, Fageria & Carvalho (1982) observed a decrease in total S content in rice cultivars.

There was an initial decrease in B content of the shoot and, at the dose 1480 μmol L^{-1} of Al^{3+}, this content rise again, staying practically with the same concentration as dose 0 (Figure 7A). On the other hand, there was a decrease in the accumulation of B in shoot and root with the increase of Al^{3+} doses (Figure 10B).

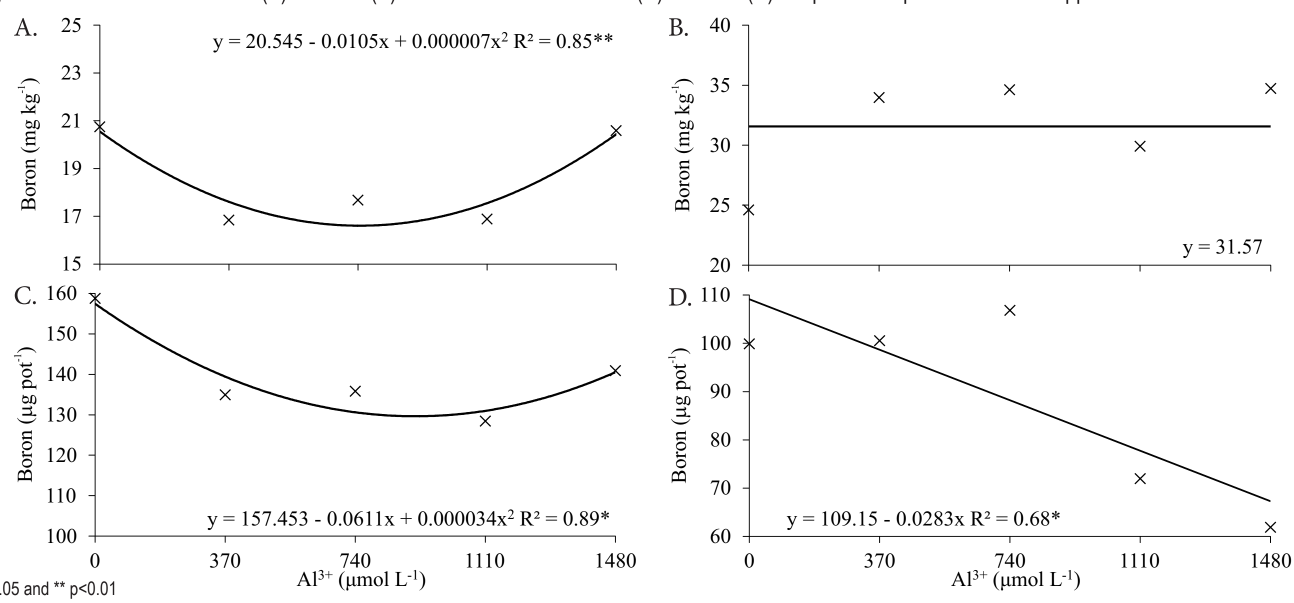
According to Lenoble et al. (1996), Al^{3+} induces B deficiency in plants and, consequently, accumulation of phenols in the tissues occurs. B is related to the synthesis of phenolic compounds, which may be important because of their ability to form compounds with Al^{3+}, contributing to decrease Al^{3+} toxicity in plant tissues (Barceló & Poschenrieder, 2002). Peixoto et al. (2007) observed that due to the interaction between Al^{3+} and B in sorghum plants, there was a greater accumulation of soluble phenols. Moreover, the same authors cite that the accumulation of phenols can result from both B deficiency and Al^{3+} toxicity, and there is need of further studies for complete elucidation of this issue.

For Cu accumulation in the shoot there was an initial increase and subsequent decrease with the application of Al^{3+} doses; however, at the highest dose of Al^{3+}, the Cu accumulation



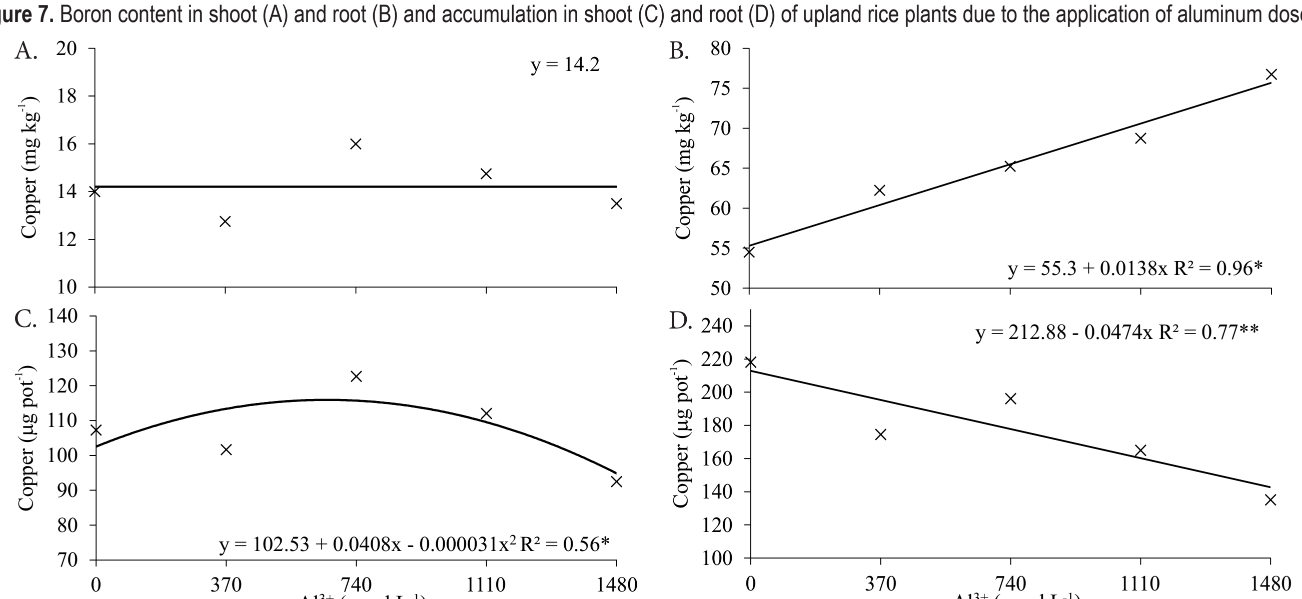
** p<0.01

Figure 6. Sulfur content in shoot (A) and root (B) and accumulation in shoot (C) and root (D) of upland rice plants due to the application of aluminum doses.



p<0.05 and ** p<0.01

Figure 7. Boron content in shoot (A) and root (B) and accumulation in shoot (C) and root (D) of upland rice plants due to the application of aluminum doses.



p<0.05 and ** p<0.01

Figure 8. Copper content in shoot (A) and root (B) and accumulation in shoot (C) and root (D) of upland rice plants due to the application of aluminum doses.

was lower than at the dose 0 of Al^{3+} (Figure 8C). On the other hand, Cu content in the root was increasing with the application of Al^{3+} (Figure 8B). This may have occurred due to the concentration effect, which can be confirmed by observing the results of Cu accumulation in the root, which were inverse in comparison to root content (Figure 8D). Sousa et al. (2007) report that the presence of Al^{3+} reduces the availability of Cu for uptake. This justifies the lower accumulation of Cu in the root of the rice plants.

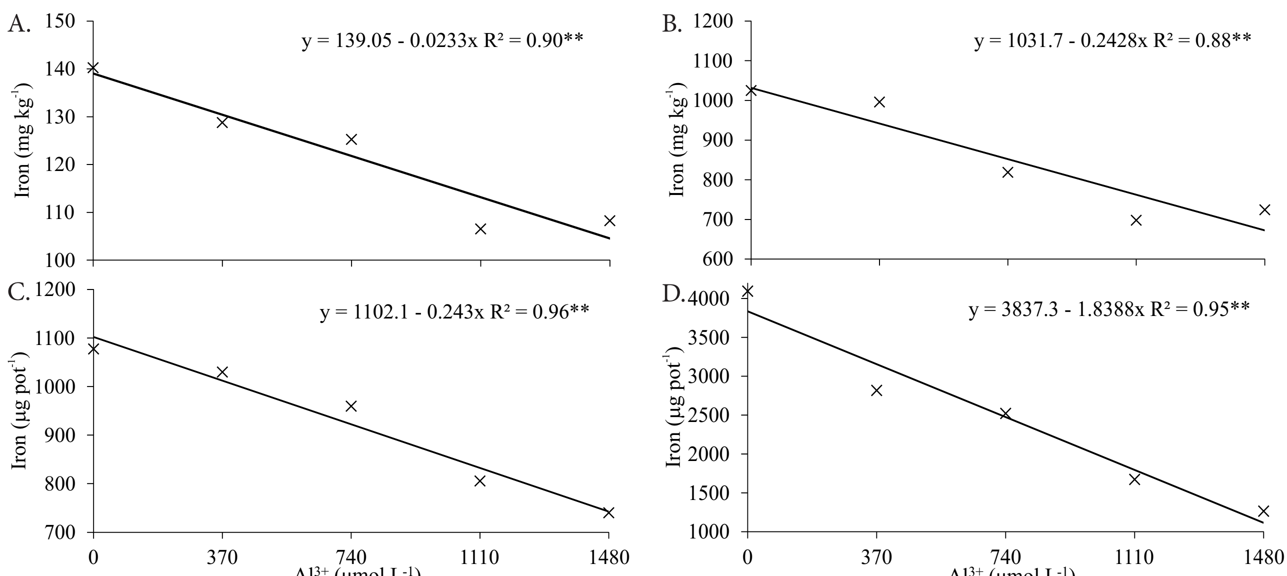
The content and accumulation of Fe, Mn and Zn in shoot and root (Figure 9, 10 and 11) decreased as the Al^{3+} doses increased. Thus, the negative influence of Al^{3+} on the uptake of these micronutrients becomes evident.

There was a high decrease in the content and accumulation of Fe and Mn in the higher doses of Al^{3+}. Therefore, greater attention should be given to these micronutrients when upland rice plants are cultivated in soil with high Al^{3+} concentration, as Fageria (2001) cites that these are the micronutrients accumulated in greater quantity by this culture.

The observed Mn content in shoot and root (Figure 10A and C) corroborate Macêdo & Jan (2008), who also observed decrease of Mn with the increase of doses of Al^{3+} when dealing with rice cultivars.

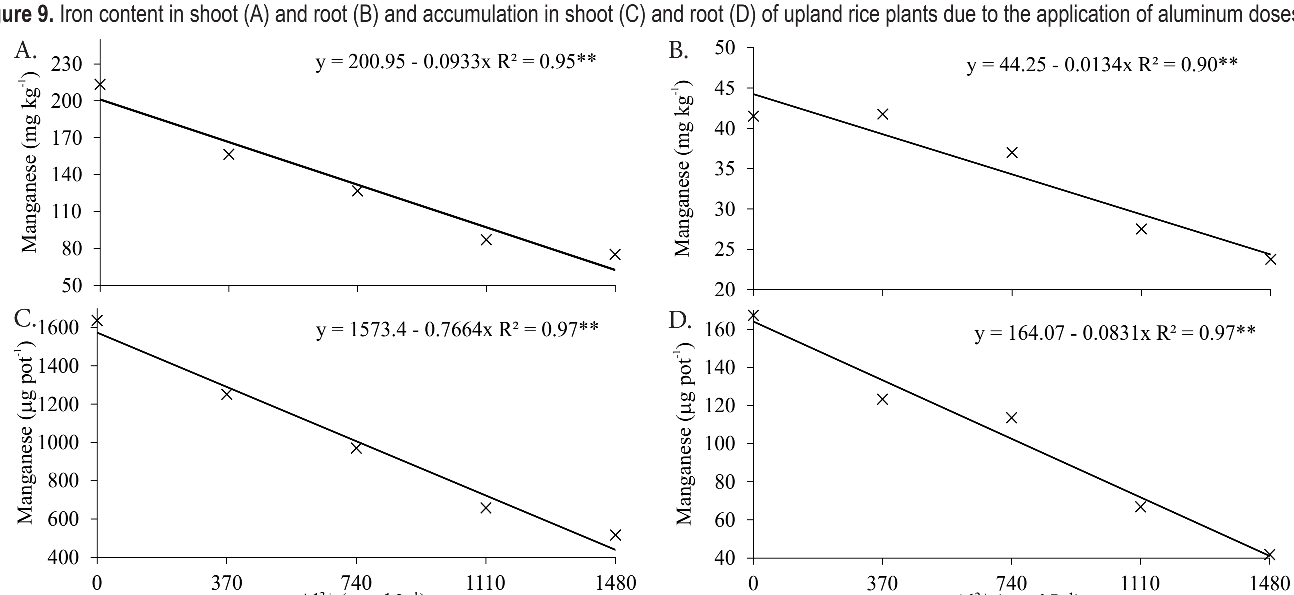
According to Sousa et al. (2007), interactions between Mn, Fe and Cu can occur. The uptake of these ions depends on balance between them. In this sense, when Al^{3+} influences some of these micronutrients, there may be consequent imbalance in their relations, which causes a decrease in uptake.

With regard to Zn, Epstein & Bloom (2006) state that plants with lower levels of this micronutrient have their development affected and do not reach their maximum genetic potential. Thus, as found in the present work (Figure 11), Al^{3+} decreases the uptake of Zn by the plant, which is an additional negative influence associated to Al^{3+}.



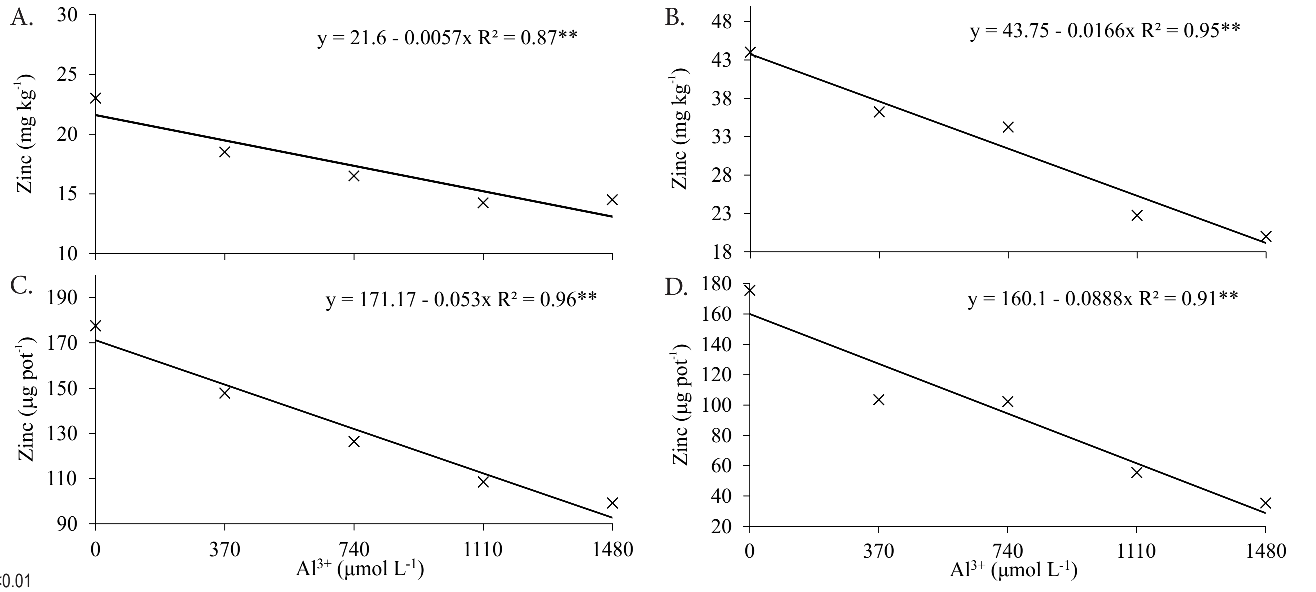
p<0.05 and ** p<0.01

Figure 9. Iron content in shoot (A) and root (B) and accumulation in shoot (C) and root (D) of upland rice plants due to the application of aluminum doses.



** p<0.01

Figure 10. Manganese content in shoot (A) and root (B) and accumulation in shoot (C) and root (D) of upland rice plants due to the application of aluminum doses.



** $p<0.01$

Figure 11. Zinc content in shoot (A) and root (B) and accumulation in shoot (C) and root (D) of upland rice plants due to the application of aluminum doses.

The toxic action caused by Al^{3+} on roots causes inhibition of root growth (Kochian et al., 2004) and, as a consequence, there is a negative influence on the uptake of macro and micronutrients in general.

Conclusions

Al^{3+} has a high negative influence on mineral nutrition of upland rice plants, especially in their roots.

Due to interaction between Al^{3+} and Ca, decrease in Ca contents and accumulation are the most important effects caused by Al^{3+} on mineral nutrition of upland rice plants.

Among the micronutrients, special influence of Al^{3+} occurs on Fe and Mn uptake.

Acknowledgements

To the São Paulo Research Foundation (FAPESP) for supporting this research (grant #2011/22182-8) and for providing a scholarship to the first author (grant #2011/09283-0) and to The National Council for Scientific and Technological Development (CNPq) for providing a research grant to the second author.

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