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Aluminum toxicity reduces the nutritional efficiency of macronutrients and micronutrients in sugarcane seedlings

Toxidez de alumínio reduz eficiência nutricional de macronutrientes e micronutrientes em mudas de cana-de-açúcar

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ABSTRACT

Although the effects of aluminum on the content and accumulation of mineral nutrients in crops have been studied, but nothing is known about its effect on the nutritional efficiency of sugarcane. Therefore, this study aimed to evaluate the effect of aluminum toxicity on nutritional efficiency, nutrient accumulation, and growth of sugarcane seedling. Sugarcane seedlings of the genotype IACSP95-5000, obtained from one-bud mini-cuttings (3 cm), were used in the test. Seedlings were subjected to treatments in a completely randomized design, with eight Al concentrations in the nutrient solution (0, 10, 20, 30, 40, 50, 60, and 70 mg L^{-1}) and three replicates, totaling 24 experimental units. Analyses determined the contents, accumulation, and absorption, transport, and use efficiency of macronutrients, micronutrients, and aluminum, in addition to dry matter production. The results show that Al affected all variables analyzed, with a decrease in the nutritional efficiency of macronutrients and micronutrients and a drastic decrease in the accumulation of macronutrients in the aerial part, which reflected in the decrease in the dry matter of the plants. The root system was the most affected, with a decrease in growth of up to 60%. Aluminum reduced the use efficiency of nutrient in decreasing order: Ca (69%)> N (60%)> K (59%)> Mg (50%)> S (49%)> P (40%). As for micronutrients, the following decreasing order was observed: Fe (73%)> Zn (59%) = Cu (59%)> Mn (25%).

Index terms: Use efficiency; acidity; accumulation; abiotic stress; *Saccharum* spp.

RESUMO

Embora os efeitos do alumínio sobre o teor e acúmulo de nutrientes minerais nas culturas sejam tenham sido estudados, mas nada se sabe sobre seu efeito na eficiência nutricional da cana-de-açúcar. Diante disso, o objetivo deste trabalho foi avaliar o efeito da toxidez de alumínio nas eficiências nutricionais, teor e acúmulo de nutrientes e crescimento de mudas de cana-de-açúcar. Para o ensaio foram utilizadas mudas de cana do genótipo IACSP95-5000 as quais foram obtidas a partir de minitoletes (3 cm) contendo uma gema cada um. As mudas foram submetidas aos tratamentos em delineamento inteiramente casualizado com 8 concentrações de Al^{+3} (0, 10, 20, 30, 40, 50, 60, 70 mg L^{-1}) em solução nutritiva com 3 repetições, perfazendo 24 unidades experimentais. As análises determinaram o conteúdo, acúmulo e absorção, transporte e eficiência de uso de macronutrientes, micronutrientes e alumínio, além da produção de matéria seca. Os resultados mostram que o Al afetou todas as variáveis analisadas, com diminuição na eficiência nutricional dos macronutrientes e micronutrientes e diminuição drástica no acúmulo de macronutrientes na parte aérea, o que refletiu na diminuição da matéria seca das plantas. O sistema radicular foi o mais afetado, com uma diminuição no crescimento de até 60%. O alumínio reduziu a eficiência de uso de nutrientes em ordem decrescente: Ca (69%)> N (60%)> K (59%)> Mg (50%)> S (49%)> P (40%). Quanto aos micronutrientes, observou-se a seguinte ordem decrescente: Fe (73%)> Zn (59%) = Cu (59%)> Mn (25%).

Termos para indexação: Eficiência de utilização; acidez; acúmulo; estresse abiótico; *Saccharum* spp.

INTRODUCTION

Brazil is the world's largest sugarcane producer, showing its great importance for Brazilian agribusiness (Unica, 2020). The increasing global demand for ethanol made from renewable sources, associated with abundant arable land and favorable edaphoclimatic conditions for sugarcane, makes Brazil promising in exports of this commodity (Companhia Nacional de Abastecimento - CONAB, 2017).

Although sugarcane can be produced under different soil types (Sanches et al., 2019; Schossler et al., 2019), it requires corrected and balanced soils to reach high productivities (Vieira-Junior et al., 2008), showing a decrease in yield as soil characteristics move away from ideal conditions (Maia et al., 2018; Souri; Hatamian, 2019). Sugarcane cultivation areas have been increasing in Brazil in recent years due to its importance (Caldarelli; Gilio, 2018). Regions to which sugarcane has migrated are characterized by acid soils, generalized nutrient deficiency, and high contents of toxic elements, such as Al (Schultz et al., 2017; Sousa; Cazetta; Nascimento, 2018). About 70% of the areas cultivated with sugarcane have acid soils (Nogueirol et al., 2015; Schultz et al., 2017).

Aluminum toxicity in plants is considered one of the main factors that limit plant productivity in agricultural soils (Zhou et al., 2015; Maia et al., 2018; Yan et al., 2019). Worldwide, approximately 30% of the total area and more than 50% of potentially arable land are acids (Guo; Chen; Yang, 2018; Riaz et al., 2018). Tropical South America has about 85% acid soils, being 24% located in central Brazil (Fageria; Nascente, 2014). In Brazil, the occurrence of soils with the potential for agricultural activity affected by problems of Al toxicity reaches about 60% (Nogueirol et al., 2015; Maia et al., 2018). Nevertheless, taking some strategies including soil and cropping management programs and cultivation of more resistant crops are necessary in this regard (Souri, 2016; Souri; Neumann, 2018).

Toxicity occurs through a series of symptoms that demonstrate the continuous Al effect on the root system and shoot growth, probably due to the limited absorption and use of nutrients (Guo; Chen; Yang, 2018; Sousa; Cazetta; Nascimento, 2018). Root ends are most affected by aluminum toxicity (Sousa; Cazetta; Nascimento, 2018; Maia et al., 2018), which reduces root system volume and increases plasma membrane permeability (Yu et al., 2011), consequently hindering the water and nutrient absorption mechanism (Maia et al., 2018; Riaz et al., 2018). In this context, the harmful effect of aluminum on plants has deserved the attention of the scientific community (Ecco; Santiago; Lima, 2014; Barbosa et al., 2017; Zhu et al., 2019).

The effects of aluminum toxicity on contents and accumulations of macronutrients and micronutrients in crops have been known for some time. However, nothing is known about the toxicity effect on the nutritional efficiency of sugarcane, and it may be one of the essential characteristics to respond to drastic reductions in plant growth and development and even to be used as a tool for choosing tolerant cultivars. Soil acidity negatively affects nutrient use efficiency and thereby reduces dry matter and crop productivity (Fageria; Baligar; Li, 2008).

Nutritional efficiency is defined as the ability of a genotype or cultivar to acquire nutrients from the cultivation medium and/or incorporate or use them for the production of the shoot and root biomass or other usable plant material such as seeds, grains, fruits, and forage (Blair, 1993; Souri; Hatamian, 2019). Therefore, inter- and intra-specific variations in plant growth and nutrient use efficiency are mediated by genetic and physiological control and can be modified by the interaction between environmental conditions and cultivation management strategies (Baligar; Fageria; He, 2001; Aghaye Noroozlo; Souri; Delshad, 2019; Hatamian et al., 2020a). Accordingly, to these authors acidity and element toxicity, such as Al, can decrease the nutritional efficiency of plants.

Nutrient use efficiency is one of the tools used to point out flaws in the process of absorption, transport, and nutrient use, assisting in understanding the effects of Al on cultivated plants. Plants with better performance under certain stressful conditions may be the result of improved nutritional efficiency (Prado, 2020). Despite this important tool, no studies can be found in the literature evaluating the effect of aluminum toxicity on the nutritional efficiency of sugarcane, which could help to understand the intrinsic mechanisms that determine varied responses in plants more or less tolerant to toxicity.

Therefore, the hypothesis is raised that aluminum toxicity affects not only the content and accumulation of nutrients, but also the nutritional efficiency of sugarcane seedlings. Thus, this study aimed to evaluate the effects of aluminum toxicity on nutritional efficiency, nutrient accumulation, and growth of sugarcane seedlings.

MATERIAL AND METHODS

The experiment was developed at the School of Agricultural and Veterinary Studies of the São Paulo State University (Unesp), located in Jaboticabal, SP, Brazil (21°15′22″ S and 48°18′58″ WG, with an altitude of 575 m). Sugarcane seedlings of the genotype IACSP95-5000, which is indicated for favorable environments, i.e., it is sensitive to acid and poor soils (Chaves et al., 2015), were used in the experiment. Seedlings were obtained from one-bud mini-cuttings (3 cm), following the methodology described by Sousa, Cazetta and Nascimento, (2018). These mini-cuttings were planted in 0.50-dm^3 plastic containers filled with washed and sieved sand. Seedlings originated from bud sprouting were grown in the sand for 20 days without any water restriction.

The most uniform seedlings were selected and submitted to a completely randomized experiment, with eight concentrations of Al in the nutrient solution (0, 10, 20, 30, 40, 50, 60, and 70 mg L^{-1}) and three replicates, totaling 24 experimental units. Each experimental unit consisted of a 0.5-dm^3 plastic pot filled with washed sand. The aluminum source was $AlCl_{3,}$ and the pH of the nutrient solution was adjusted to 4.0 ± 0.1 using HCl or NaOH solution. Macronutrients and micronutrients were supplied provided through a Hoagland and Arnon (1950) nutrient solution. The nutrient solution was provided by an alternative hydroponic system adapted for sugarcane (Sousa; Cazetta; Nascimento, 2018). The experiment was conducted for 30 days. During this period, the nutrient solution with its respective treatments was replaced weekly. Solution volume was filled up daily with distilled water between changes. Plants remained under treatment conditions for 30 days, and possible changes due to aluminum toxicity were observed. Subsequently, the length, width, and height of the leaf +1 (First fully expanded leaf) were measured using a ruler, and the plant was then cut close to the surface. A caliper was used to measure the stem diameter.

After harvesting, all plants were divided into shoot, roots, and cuttings. The roots were washed with running water, and then the fresh weight and root volume were measured. The root system volume was measured by the method of Carrigan and Frey (1980), using a 100-mL graduated cylinder filled with 50 mL of distilled water, where the root was inserted. The root volume corresponded to the difference between the water volume with the introduced root and the initial water volume.

Then, all samples were placed in identified paper bags, weighed to determine the fresh weight, and placed in a forced-air circulation oven set at 65±5 °C until constant weight to determine the dry matter using an analytical balance. After determining the dry matter, these samples were ground, sieved with a 0.5-mm mesh-opening sieve, and subjected to macronutrient and micronutrient determination, following the methodology described by Bataglia et al. (1983). Nutrient accumulation was determined based on the product of the nutrient content by plant dry matter. The determination of Al content was carried out using 0.5 g of each sample digested with 6 mL of a mixture of nitric and perchloric acid (2:1, v/v), with extract diluted to 50 mL. Then, Al content in this extract was determined by atomic absorption spectrophotometry in an acetylene/nitrous oxide flame.

Nutritional efficiency was determined based on the accumulation of nutrients and Al. Uptake efficiency was determined by the ratio of the nutrient accumulated in the entire plant to the dry root mass (Swiader; Chyan; Freiji, 1994). The translocation efficiency was calculated by the ratio of the nutrient accumulated in the shoot to the nutrient accumulated in the entire plant (Li; Mckeand; Allen, 1991). The efficiency of use was obtained by the ratio of the square of the dry mass of the whole plant to the nutrient accumulated in the whole plant (Siddiqi; Glass, 1981).

The results were subjected to analysis of variance by the F-test and, when a significant effect was detected, a polynomial regression analysis was applied. The statistical analysis was carried out using the software Agroestat (Barbosa; Maldonado Junior, 2015).

RESULTS AND DISCUSSION

Aluminum content had significant increasing variation ($P<0.05$) in the root, with values three times higher at the maximum dose (70 mg L^{-1} Al) relative to the minimum dose, but remaining constant for cuttings and shoot (Figure 1A). On the other hand, accumulation showed no significant variation for the analyzed plant parts (Figure 1B).

The fact that aluminum content increased only in the root confirms the observations that this element has preferential accumulation in the root system, with a small amount translocated to the shoot, thus showing its low mobility in the plant (Yan et al., 2018; Li et al., 2018). Thus, symptoms of Al toxicity in the aerial part are not always easily identifiable (Souza et al., 2016; Sousa; Cazetta; Nascimento, 2018) and, unlike the root system, it has little direct effect on that part of the plant, mainly in a relatively short period of time (Rossiello; Jacob-Netto, 2006). The high availability of Al in the growing environment can also induce nutrient deficiency due to its interference in the solubilization/precipitation processes in the solution, uptake by roots, transport, and use of nutrients in the plant.

Nitrogen content had a linear behavior, increasing in the root and culm billet and decreasing in the shoot as Al^{3+} concentrations increased (Figure 2A). Accumulation had a quadratic decrease for the shoot, a linear decrease for root, and a slight increase in the cuttings as Al concentrations increased (Figure 2B).

Nutrients P, K, and S showed similar behaviors regarding their contents in the cuttings and root, with no significant effect ($P>0.05$). P, K, and S contents in the shoot (Figure 2C, E, and G) decreased as Al concentration increased in the solution, with a linear decrease for S. The behavior of accumulation was similar for these nutrients in all plant parts, with a quadratic decrease for shoot and a linear decrease for root, while no significant variation was observed I the culm billet (Figure 2D, F, and H).

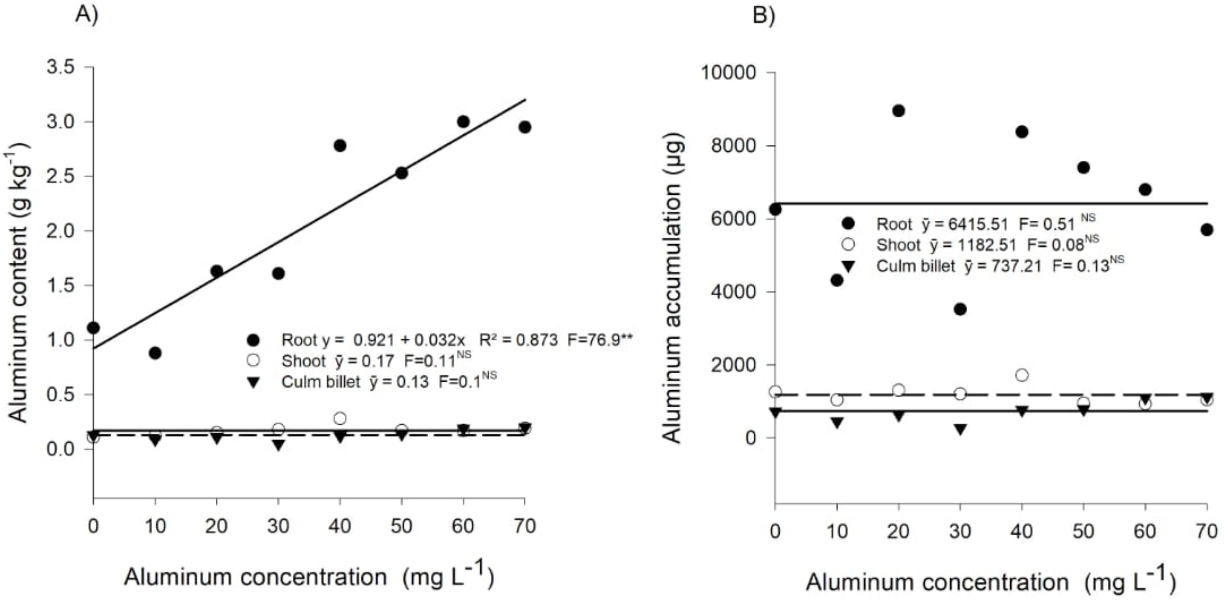

Figure 1: Content (A) and accumulation (B) of Al in sugarcane seedlings submitted to eight Al concentrations in the nutrient solution.

Unchanged phosphorus contents in the root may be more related to the transport and redistribution than to its absorption, with even an increase in P contents in some cases (Salvador et al., 2000). According to other authors, it is likely that part of the aluminum contained in the root tissues may precipitate part of the absorbed phosphorus, thus reducing its translocation to the shoot (Jiang et al., 2009; Sade et al., 2016). Moreover, Al toxicity usually reduces P concentration in the shoot, but the degree of interference varies according to the species and plant genotype (Foy, 1988).

Nutrients Ca and Mg showed similar behavior in terms of content, with a linear decrease in the root and no significant variation in the culm billet (Figure 3A and C). A quadratic increase was observed for Ca content as Al concentrations increased, while Mg content had a quadratic decrease. The behavior of accumulation was similar for both nutrients in the root and culm billet, with a linear decrease in the root and no significant variation in the culm billet. Ca accumulation in the shoot presented a slight increase, while Mg accumulation had a decrease with Al addition in the solution (Figure 3B and D).

A reduction in nutrient contents under conditions of high Al concentrations, as found for Ca and Mg in the root and shoot for N, P, K, Mg, and S in this study, is common. In addition to the abnormal root formation, the reduction of these elements in different plant parts may be related with the interference in higher Al ions in enzymatic reactions and arrangement of polysaccharides in the cell walls (Bojórquez-Quintal et al., 2017), thus damaging different processes, such as absorption, transport, and the use of several nutrients.

According to Faquin, Vale and Furtini Neto (1997) and Malavolta, Vitti and Oliveira (1997), soluble aluminum, besides causing phytotoxicity in plants, competes with other cations, mainly Ca and Mg, for the same absorption sites in the exchange complex. Likewise, the reduction of K content in the shoot with increased aluminum levels occurs due to the competition of cations (Al and K^+) for absorption sites in the transporters or influx channels of monovalent and divalent cations, reducing both its translocation to the shoot or its energy supply for energy-dependent transportation systems (Kochian, 1995). It has been shown that heavy metals can significantly damage conducting vessels of plants including the transportation pathways from the roots to the stems and shoots (Hatamian, et al., 2020b; Souri; Hatamian; Tesfamariam, 2019), that probably Al with a similar effect can damper transportation vessels of plants.

Calcium was the only macronutrient that had its content increased in the shoot with an increase in Al contents. On the contrary, Salvador et al. (2000) observed that Ca contents at doses of 0.0 and 5.0 mg L^{-1} of aluminum were similar, from which decreases in the leaves and stem occurred, reaching higher proportions according to an increase in Al additions. Veloso et al. (1995) also found a decrease in Ca content studying black pepper.

The behavior regarding Zn and Cu content was similar, with no significant effect ($P>0.05$) in the analyzed plant parts (Figure 4A and C). Zn accumulation was constant in the root and culm billet, with a linear decrease in the shoot as Al concentrations increased (Figure 4B). A significant effect ($P<0.05$) was observed regarding Cu accumulation (Figure 4D) in the three plant parts, with a marked linear decrease in the root and shoot and a slight increase in the culm billet.

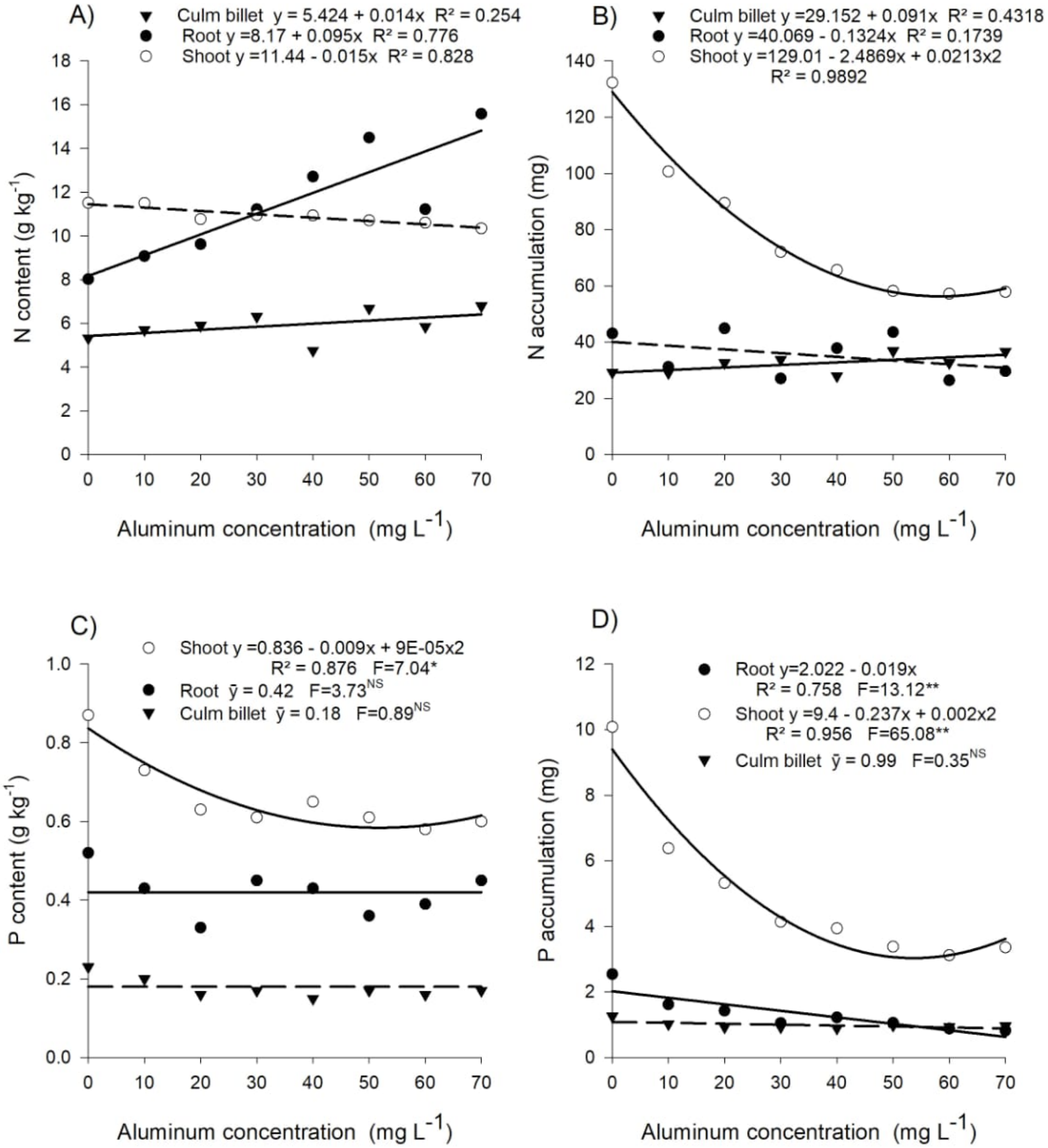

Figure 2: Content (A, C, E, and G) and accumulation (B, D, F, and H) of macronutrients (N, P, K, and S) respectively, in sugarcane seedlings submitted to eight Al concentrations.

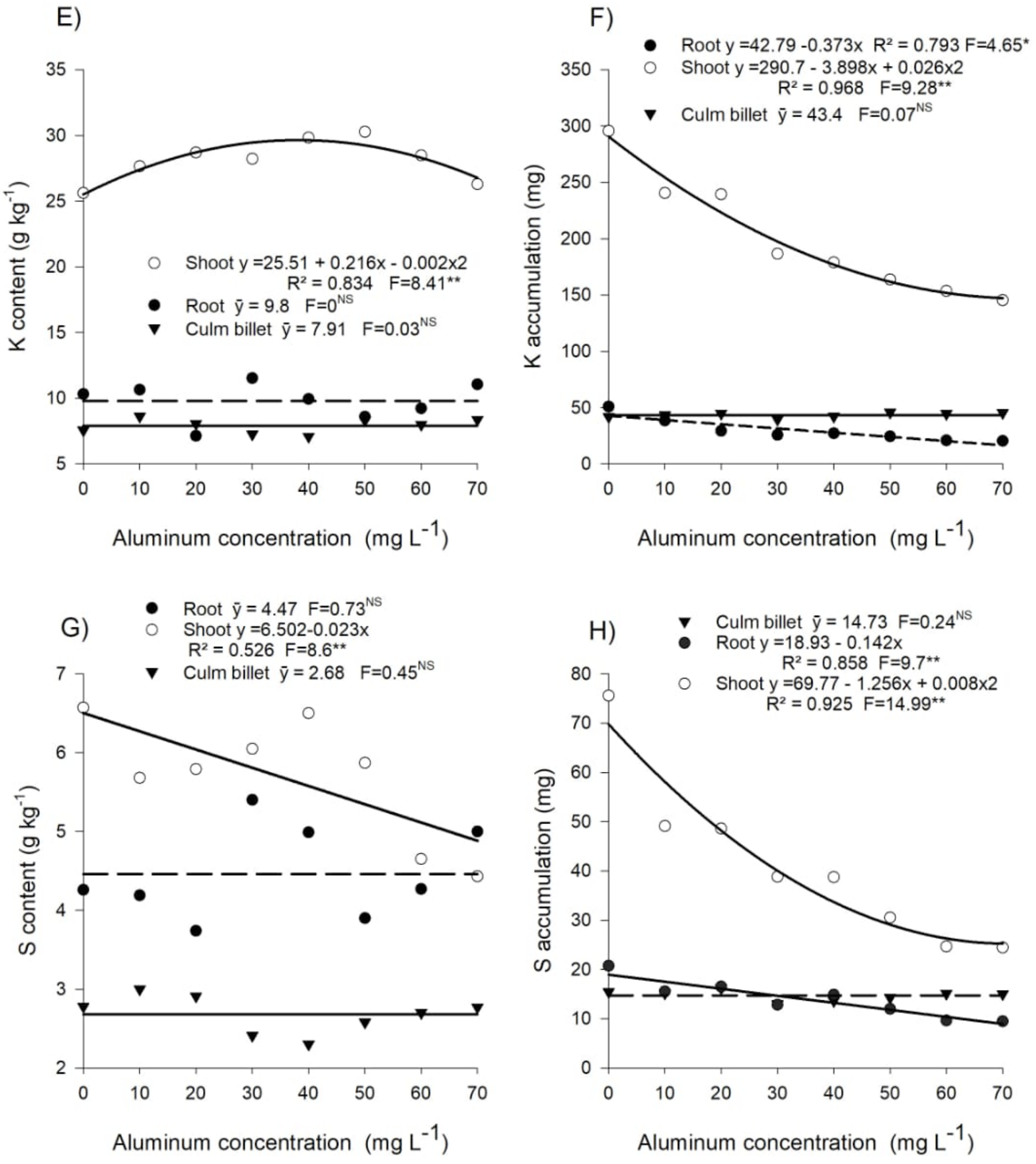

Figure 2: Continuation.

Iron and manganese content remained constant in the culm billet and shoot, showing a difference only in the root, with an increase for Fe and a decrease for Mn as Al concentrations increased (Figure 5A and C). However, Fe accumulation showed no variation in the analyzed plant parts (Figure 5B). On the other hand, Mn showed a decrease in the root and shoot as Al increased in the solution (Figure 5D).

The results of Zn, Cu and Mn corroborate with Salvador et al. (2000), who worked with guava seedlings submitted to Al toxicity. Cu and Zn mobility in plants are limited (Kirkby; Romheld, 2007), which could explain the contents of these elements without significant variation in the plant parts. The increased Fe content in the root may be related to the Al toxicity and its low redistribution. Iron is accumulated in the roots of plants that grow under Al concentrations without a significant increase in translocation to their shoots, confirming the results found by Salvador et al. (2000) who worked with guava, under Al concentrations. Despite the decreasing linear effect observed for Mn as Al concentrations increased, manganese and iron under acid conditions are more available to plants (Benett et al., 2013) and, therefore, can be more accumulated compared to other elements depending on other factors.

Nitrogen transport efficiency presented no significant effect (Figure 6B). However, Al concentrations significantly affected N uptake and use efficiency (Figure 6A and C). Absorption efficiency showed a linear increase as Al concentrations increased. Nitrogen use efficiency decreased linearly with an increase in Al concentrations, with a 60% reduction in concentration of 70 mg L^{-1} of aluminum compared to the control.

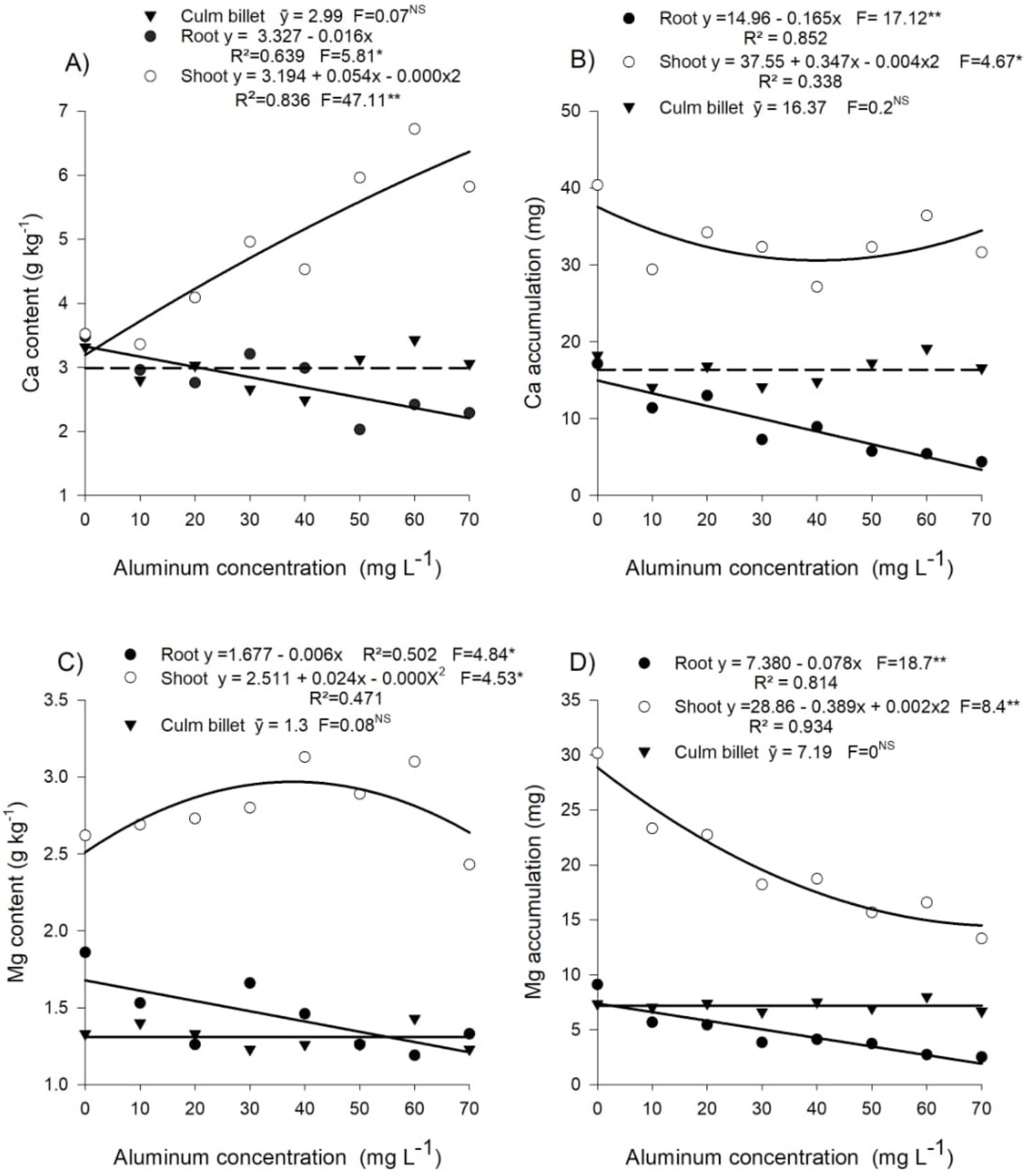

Figure 3: Content (A and C) and accumulation (B and D) of macronutrients (Ca and Mg) respectively, in sugarcane seedlings submitted to eight Al concentrations.

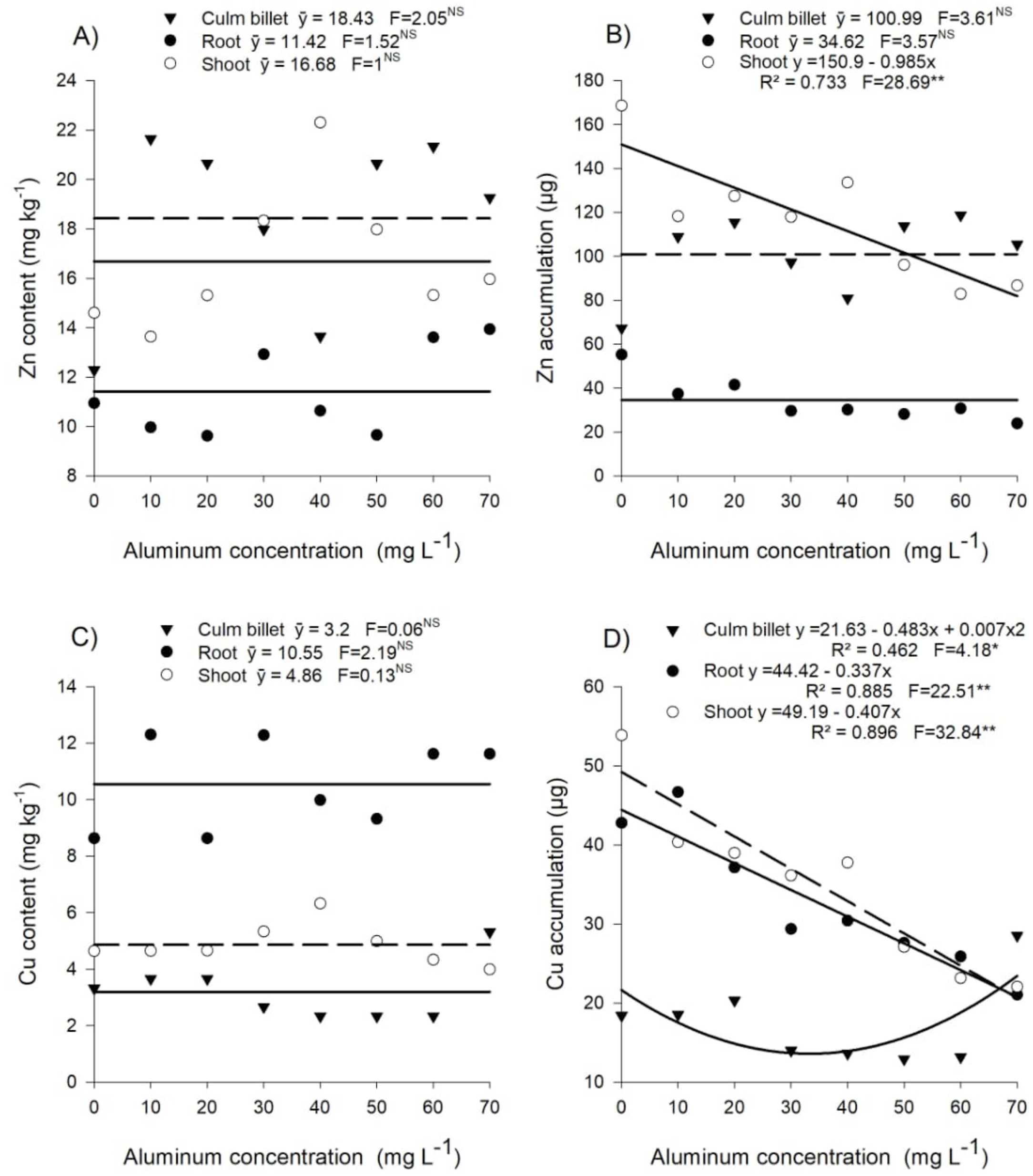

Figure 4: Content (A and C) and accumulation (B and D) of micronutrients (Zn and Cu) respectively, in sugarcane seedlings submitted to eight Al concentrations.

It probably explains why N content increased in the root and decreased in the shoot. In addition, it may also be related to the high nitrogen uptake efficiency, possibly because in a more acid pH, as observed in this study, N in the anion form (NO_3^-) was favored over N as ammonia because the nitrate form has an optimum pH below 6 for absorption due to the co-transport of H^+ (Ullrich, 1987). Also, Al limits the absorption of other cations, including NH_4^+, as observed by Nichol et al. (1993), who indicated that Al treatment suppressed the movement of cations such as NH_4^+ through the plasma membrane, but facilitated the movement of anions (NO_3^-).

However, nitrogen use efficiency decreased with increasing Al concentrations, i.e., the amount of dry matter produced per unit of N absorbed decreased as Al toxicity increased. It can be explained by the interference of Al in the metabolism of N, such as in the translocation and reduction of nitrate in the roots (Gomes et al., 1985) to decrease N in the shoot and hence limit dry matter production by plants. Another fact related to the low N use efficiency is related to changes in the root growth because Al inhibits it (Zhao; Shen 2018).

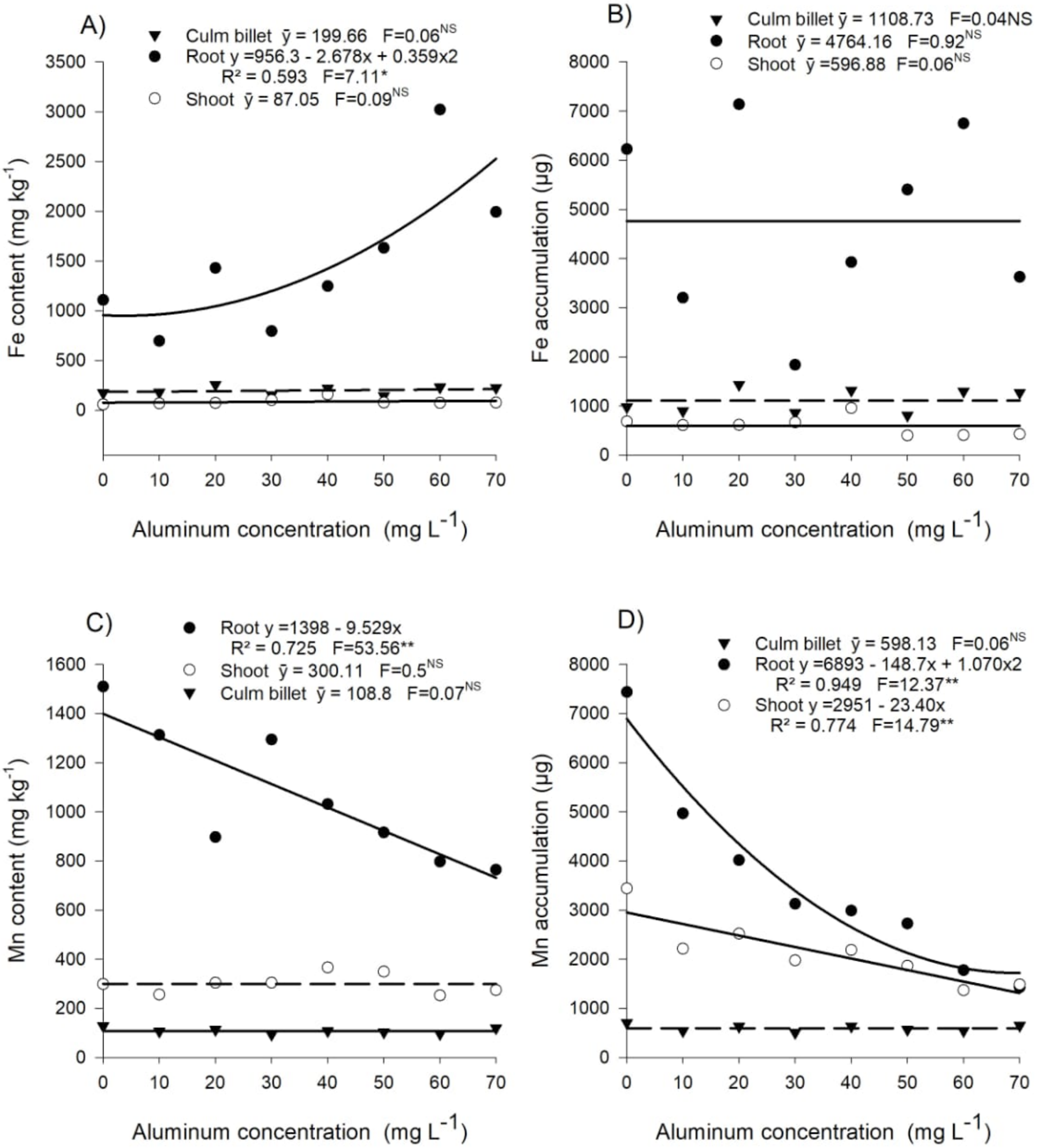

Figure 5: Content (A and C) and accumulation (B and D) of micronutrients (Fe and Mn) respectively, in sugarcane seedlings submitted to eight Al concentrations.

Calcium uptake and translocation efficiencies (Figure 6D and E) increased linearly as Al concentrations increased in the nutrient solution. However, use efficiency decreased linearly as Al increased in the solution, which represented 68% in the concentration of 70 mg L^{-1} compared to plants without the presence of Al (Figure 6F). The nutrients Ca showed an increase in uptake efficiency, even with an increase in Al concentrations. However, it diverges from the literature because, in general, aluminum toxicity in plants has been associated with reduced uptake and translocation of calcium (Foy; Fleming; Armiger, 1969) and cations. The efficiency of calcium translocation explains the increase in calcium in the shoot of plants with increasing concentrations of Al, as seen in Figure 3A. Conversely, in study of Edward and Horton (1977) pointed out that aluminum toxicity in peach was not related to inhibition in translocation of Ca. The increase in Al concentrations increased the Ca translocation efficiency of the plants, which increased the content and accumulation in the shoot.

Phosphorus uptake and translocation efficiencies were not significantly affected by the concentrations of Al in the nutrient solution, but the efficiency of use decreased due to the increase in Al concentrations, with a 40% reduction in the concentration of 70 mg L^{-1} Al compared to the control (Figure 7A, B and C). Potassium showed no adjustment for uptake and translocation efficiencies, with no significant effect of Al concentrations (Figure 7D and E). However, use efficiency was negatively and linearly affected by the increased Al concentrations, with a 59% decrease in concentration of 70 mg L^{-1} Al compared to the control treatment (Figure 7F).

Studies show that P and K absorption may be little affected by Al toxicity (Mariano; Keltjens, 2007). In addition, the ability to maintain the absorption and translocation of P is a plant tolerance mechanism for Al (Cambraia et al., 1991), so that the presence of aluminum does not interfere with the phosphorus absorption and translocation efficiency in plants. Therefore, for this sugarcane genotype, Al does not influence the absorption efficiency of K and P, as a result of less drastic reductions in plant accumulation.

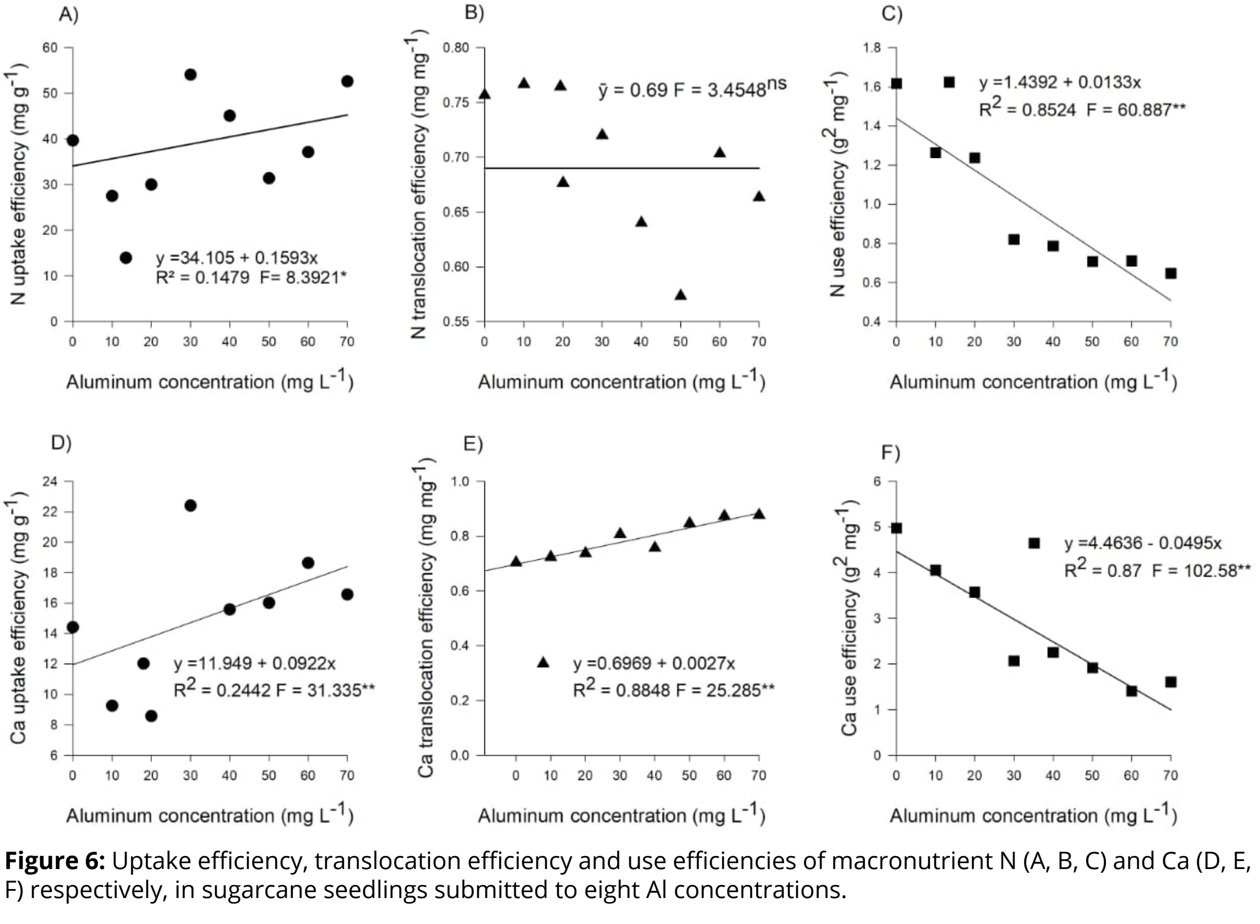

Figure 6: Uptake efficiency, translocation efficiency and use efficiencies of macronutrient N (A, B, C) and Ca (D, E, F) respectively, in sugarcane seedlings submitted to eight Al concentrations.

Magnesium uptake efficiency behaved quadratically to increased Al concentrations (Figure 8A). Translocation efficiency showed a linear increase with increasing Al concentrations in the solution (Figure 8B). However, use efficiency presented a contrary behavior, decreasing linearly with Al concentrations, with a 50% reduction in the concentration of 70 mg L^{-1} Al relative to plants that received no Al in the nutrient solution (Figure 8C). Sulfur uptake and translocation efficiencies showed no significant adjustment for Al concentrations (Figure 8D and E). However, use efficiency showed a linear decrease as Al concentrations increased, with plants submitted to higher concentrations of Al, showing a 49% reduction in the concentration of 70 mg L^{-1} Al compared to control plants (Figure 8F).

Regarding micronutrients, uptake efficiency showed a linear positive behavior for Fe as Al concentrations increased (Figure 9A). However, for Mn showed no significant effect (Figure 9D). Translocation efficiency showed presented a positive linear growth for Mn with increasing Al concentrations (Figure 9E), and for Fe, no significant adjustment was observed (Figure 9B), as well as for Zn (Figure 10B) and Cu (Figure 10E). The use efficiency for Fe and Mn showed a linear decrease with increasing Al concentrations, reaching 73% and 25%, respectively, in the concentration of 70 mg L^{-1} Al in relation to the control (Figure 9C and F).

For Fe and Mn, the effect of Al toxicity was reversed. For Fe, as already demonstrated by Salvador et al (2000) in guava, which worked under concentrations of Al, the toxicity of Al limits the translocation of Fe to the aerial part of plants, a fact verified in this work, because, although the plants absorb Fe in the presence of Al, the nutrient was not transported efficiently, consequently, there was less participation in the metabolism and reduced efficiency of use in the conversion of dry mass. However, for Mn, Al increased the translocation efficiency of Mn.

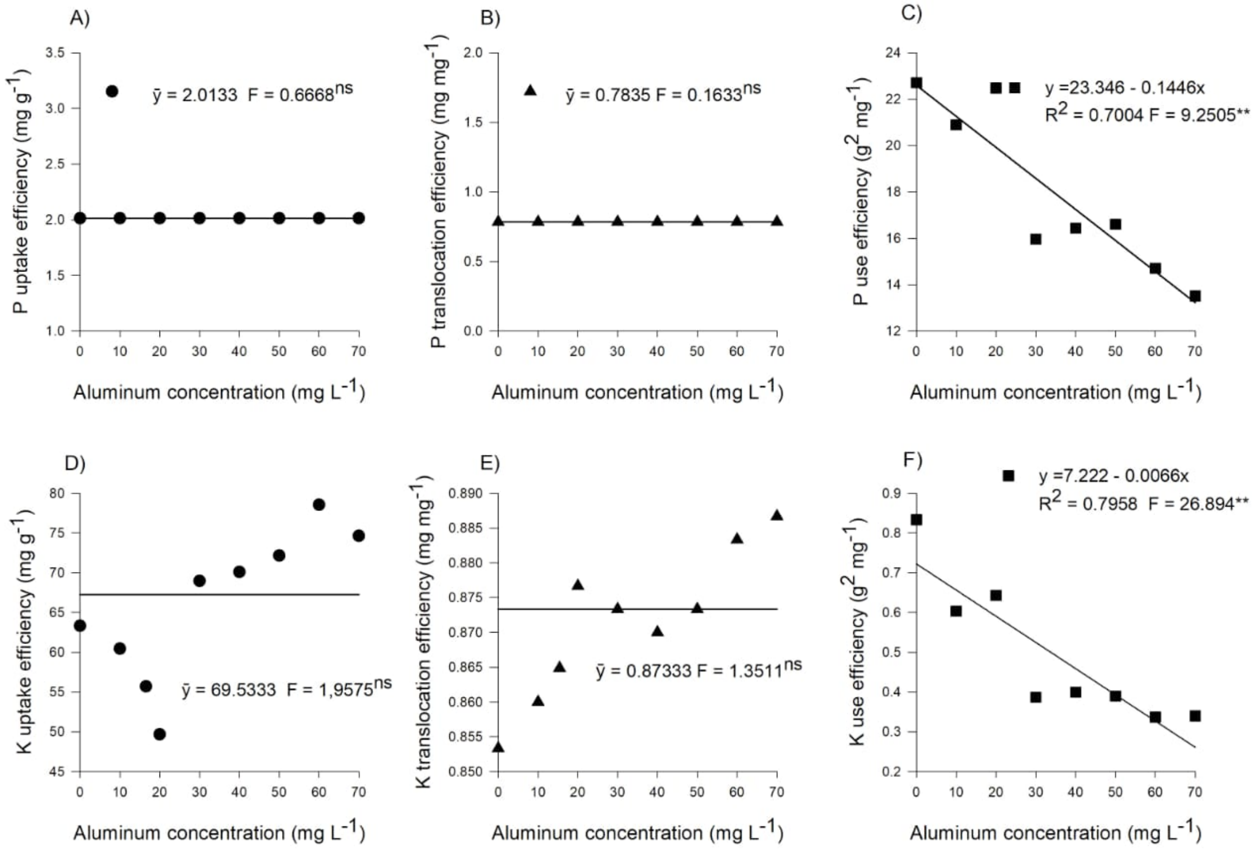

Figure 7: Uptake, translocation, and use efficiencies of micronutrients P (A, B, C) and K (D, E, F) respectively, in sugarcane seedlings submitted to eight Al concentrations.

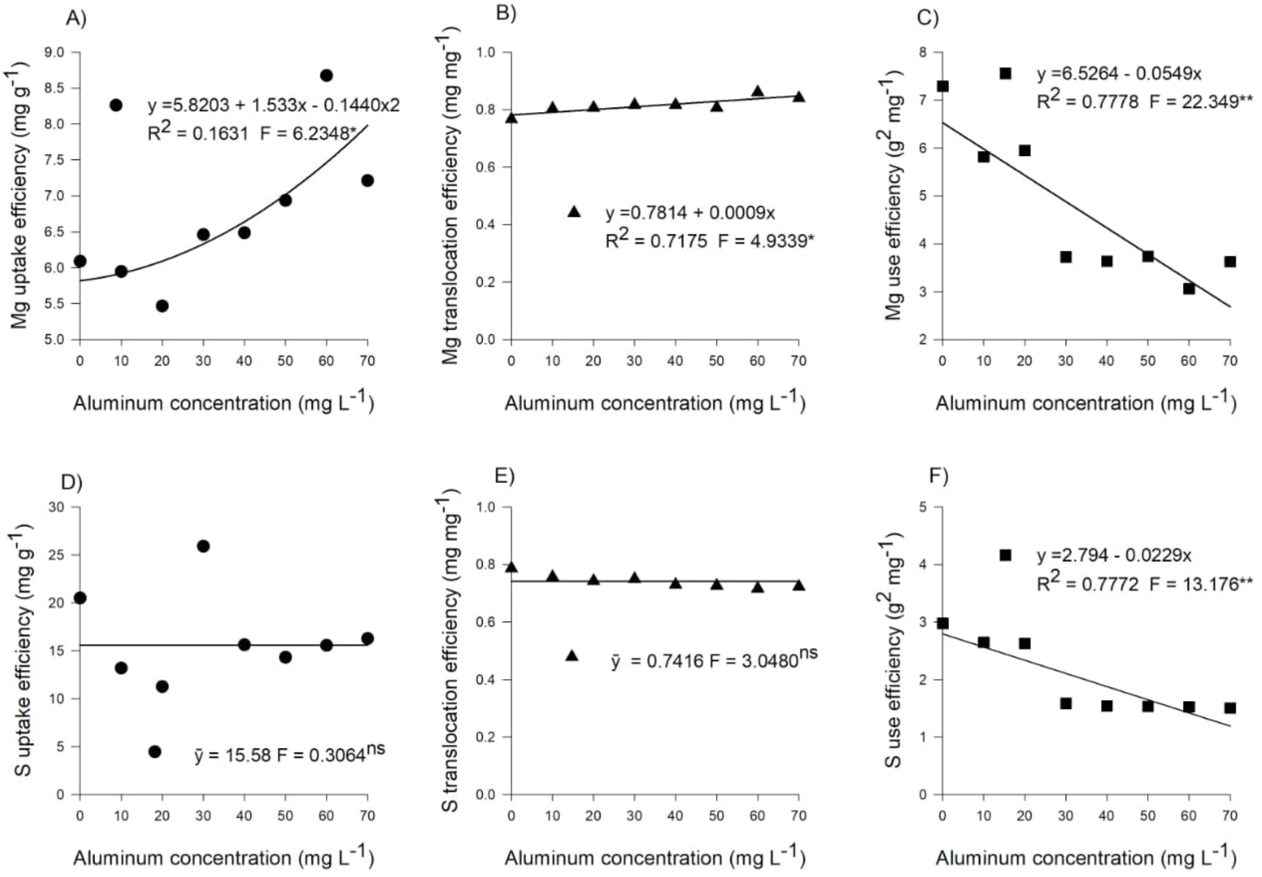

Figure 8: Uptake, translocation, and use efficiencies of micronutrients Mg (A, B, C) and S (D, E, F) respectively, in sugarcane seedlings submitted to eight Al concentrations.

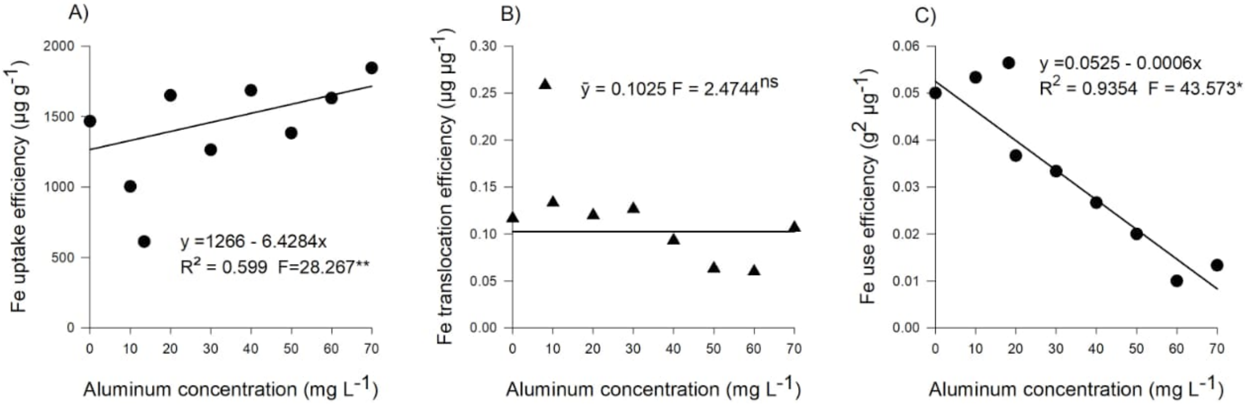

Figure 9: Uptake, translocation, and use efficiencies of micronutrients Fe (A, B, C) and Mn (D, E, F) respectively, in sugarcane seedlings submitted to eight Al concentrations.

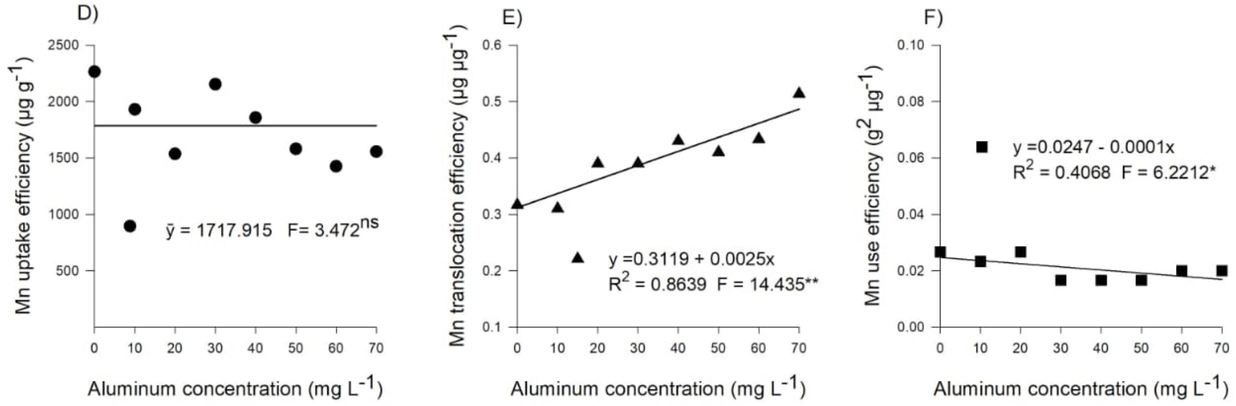

Figure 9: Continuation.

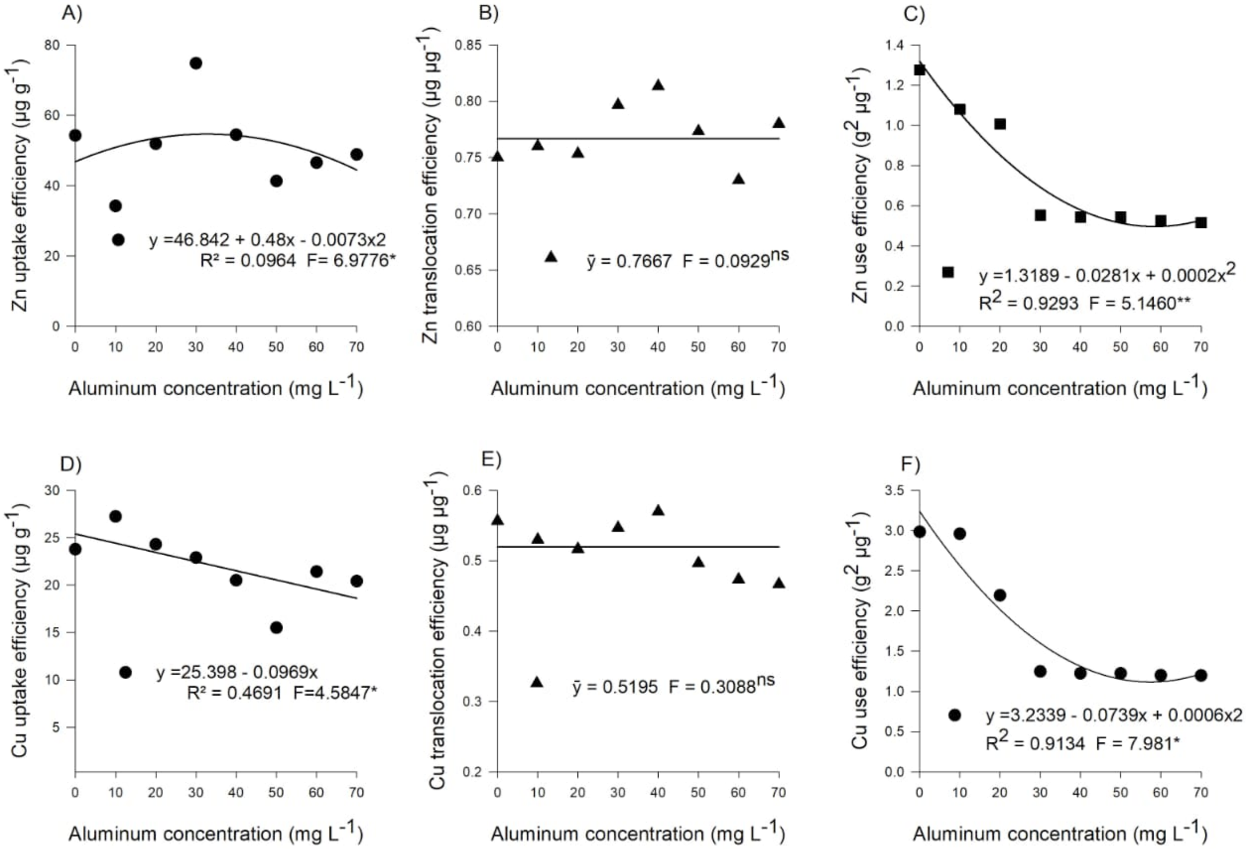

Figure 10: Uptake, translocation, and use efficiencies of micronutrients Zn (A, B, C) and Cu (D, E, F), and Al (G, H, I) respectively, in sugarcane seedlings submitted to eight Al concentrations.

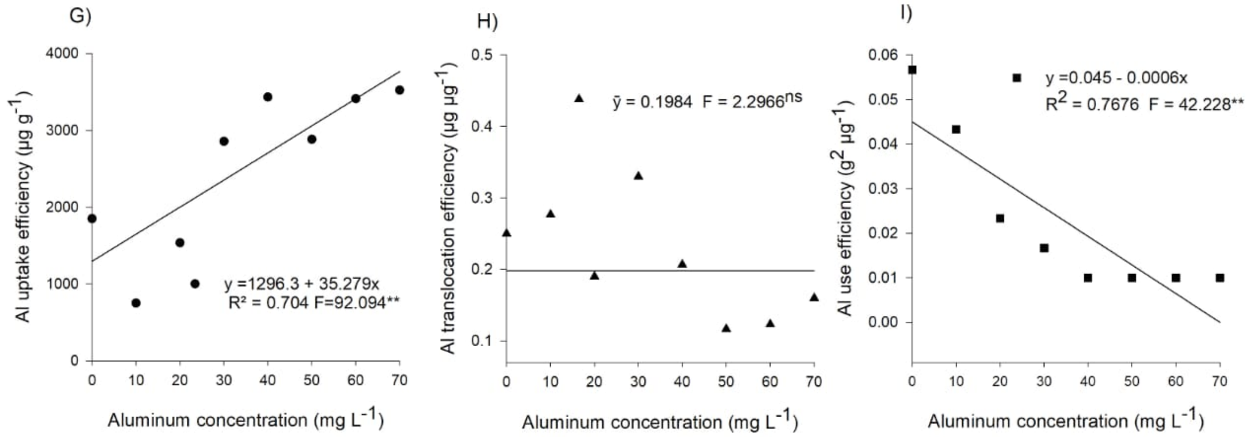

Figure 10: Continuation.

The uptake efficiency showed a quadratic behavior for Zn (Figure 10A), negative linear behavior for Cu (Figure 10D), and positive linear for Al (Figure 10G) as Al concentrations increased. Use efficiency showed a significant effect for all micronutrients, decreasing as Al concentrations increased. However, micronutrients Zn and Cu showed a negative quadratic behavior, with a 59% reduction at the highest concentration of Al (70 mg L^{-1}) for both micronutrients compared to the control (Figure 10C and F). The translocation efficiency of Al showed no significant adjustment, and use efficiency was reduced linearly (Figure 10H and I).

In general, for the micronutrient Zn and Cu, the absorption efficiency was reduced by the lower accumulation of these nutrients in the presence of Al. It is known that the greatest effects caused by the toxicity of Al is the reduction in the absorption of nutrients, mainly cations divalent, in this case, aluminum ions can bind to the cell surface and form a positively charged region, thereby inhibiting the adsorption of positively charged cations on the cell surface (Zhao; Shen, 2018), however for this cane genotype, this was not clear for the other divalent cations (Ca, Mg, Fe and Mn).

In general, the presence of aluminum at increasing concentrations reduced macronutrient use efficiency in a decreasing order: Ca (69%) > N (60%) > K (59%) > Mg (50%) > S (49%) > P (40%). Micronutrients presented the following decreasing order: Fe (73%) > Zn (59%) = Cu (59%) > Mn (25%).

Nutrient use efficiency has been drastically reduced in the presence of Al, mainly for macronutrients, since these variables are directly related to the genetic characteristics of each crop and/or cultivar (Baligar; Fageria; He, 2001) and the environmental interference provided by the presence of Al, interfering with nutrient accumulation. According to these authors, one of the factors that change use efficiency under stress conditions is a reduction in nutrient accumulation in order to reduce plant metabolism. It was verified in this study, which presented high reductions in nutrient accumulation in the shoot. Therefore, the presence of Al reduced use efficiency of all the analyzed nutrients in the sugarcane crop.

This cultivar is susceptible to Al toxicity because it has low nutrient use efficiency when subjected to high concentrations of this toxic element, leading to a reduction in dry matter (Fageria; Baligar; Li, 2008). Moreover, uptake efficiency increased for some nutrients, while transport efficiency, in general, was not affected by the presence of Al.

The macronutrients Ca, N, and K had the lowest use efficiency under aluminum toxicity. These nutrients are essential for crop development, standing out in the extraction and export by sugarcane, being the three most required macronutrients for this crop (Orlando Filho, 1993). Likewise, the highest reductions in use efficiency were verified for the most required micronutrients by sugarcane (Orlando Filho, 1993). Thus, high reductions in dry matter and plant height led to losses in efficiency, mainly in the use of the most demanded nutrients during the plant cycle.

Therefore, the presence of toxic Al concentrations mainly affects nutrient use efficiency in sugarcane seedlings. Although there is an increase in uptake efficiency, transport efficiency, in general, is limited, reducing the participation of nutrients in plant metabolism and conversion to biomass (Giannakoula et al., 2008), possibly due to the action of Al in the enzymatic reactions related to the movement and use of nutrients (Bojórquez-Quintal et al., 2017; Zhao; Shen, 2018).

Root volume showed a linear reduction as Al concentration increased, with a 56% decrease at the minimum concentration (0 mg L^{-1}) relative to the maximum concentration (70 mg L^{-1}) (Figure 11A). Shoot dry matter presented a quadratic reduction with the increased Al concentrations, with a trend to remain constant from 40 mg L^{-1} of Al. The same effect was also found for root dry matter, with a reduction of over 60% at the concentration of 70 mg L^{-1} of Al compared to the control. Cutting dry matter had no significant effect ($P>0.05$), with an average weight of 5.6 g at the maximum Al concentration (Figure 11B).

The reduction in the root and shoot dry matter found in this study was also observed by Sousa, Cazetta and Nascimento, (2018) in 24 sugarcane genotypes, Barbosa et al. (2017) with wheat and Riaz et al. (2018) with trifoliate orange. Therefore, the increased aluminum contents lead to a decrease in root and shoot dry matter production (Wang et al., 2016; Sousa; Cazetta; Nascimento, 2018). Root ends are the most affected, and their response to Al occurs very quickly, which indicates that at first, Al inhibits root cell expansion and elongation, and then cell division is inhibited (Ecco; Santiago; Lima, 2014).

Plant height presented a negative quadratic effect as Al concentrations increased, being more affected up to the dose of 59 mg L^{-1}, with a height of approximately 25.7 cm, but softening from it (Figure 11C). This same result was also found by Sousa, Cazetta and Nascimento, (2018) in different sugarcane genotypes. Riaz et al. (2018) and Wang et al. (2016) worked with trifoliate orange and alfalfa, respectively, and also observed a decrease in plant height. It means that regardless of the crop, high aluminum contents in the medium affect plant growth.

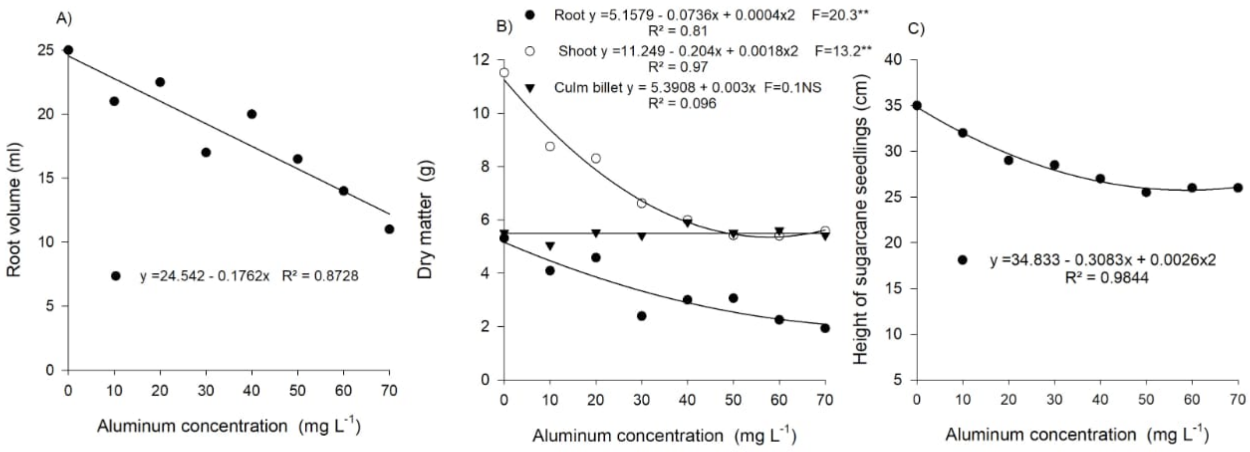

Figure 11: Root volume (A), Root, culm billet, and shoot dry matter (B) and height of sugarcane seedlings (C) submitted to different Al concentrations.

CONCLUSIONS

The increased aluminum concentrations decreased nutrient use efficiency, explaining the high reduction in plant dry matter. Also, it did not affect transport efficiency but increased the uptake efficiency of some nutrients. The presence of aluminum in increasing concentrations reduced use efficiency in the following decreasing order: calcium (69%) > nitrogen (60%) > potassium (59%) > magnesium (50%) > sulfur (49%) > phosphor (40%). For micronutrients, the following decreasing order was observed: iron (73%) > zinc (59%) = copper (59%) > manganese (25%). The very sensitive shoot reduction up to 40 mg L^{-1} due to aluminum toxicity was related to a reduction in nitrogen, phosphor, potassium, sulfur, calcium, and magnesium accumulation and phosphor content, which followed the same reduction pattern of the shoot growth.

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