

Nutritional and Structural Role of Silicon in Attenuating Aluminum Toxicity in Sugarcane Plants

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Abstract

Purpose: We investigated the interactive role of Si-mediated attenuation to aluminum (Al) toxicity in two sugarcane cultivars ('CTC9002' and 'CTC9003') grown in hydroponic conditions.

Methods: Two pot experiments were distributed in randomized blocks in a factorial design (4×2) with four replications. The treatments consisted of 0, 10, 15, and 20 mg L⁻¹ Al (as aluminum sulfate [Al₂(SO₄)₃·18H₂O]), which were combined with the absence and presence of Si [(2.0 mmol L⁻¹ as potassium silicate (K₂SiO₃)).

Results: Both sugarcane cultivars ('CTC9002' and 'CTC9003') were affected by Al toxicity (above 10 mg L⁻¹), resulting in nutritional disorders and decreasing plant growth, which were drastically reversed by Si addition in the growth medium. Si supplementation decrease Al concentration and translocation to the shoots of both cultivars when Al and Si were simultaneously supplied in the growth medium. We demonstrated that in shoots of both sugarcane seedlings, Si concentration are positively related to the lignin concentrations (ranging from 12.0% to 41% in cv. 'CTC9002' and 12% to 47% in cv. 'CTC9003'). In addition, Si fertilization enhanced mineral nutrition and use efficiency of macros- and micronutrients, irrespective of the cultivar. Therefore, the use of cultivar 'CTC9003' under Si fertilization is more recommended to cope with the adverse effect caused by Al stress.

Conclusions: The findings of this study suggest that Si fertilization in sugarcane seedlings is an economic and viable strategy strongly recommended to cope with the adverse effect caused by Al toxicity at concentrations less than 20 mg L⁻¹, which lead to increase the shoot biomass production.

Introduction

Basic aspects that affect crops productivity, soil is essentially important, which it offers physical support, water, nutrients and others important substance for plant growth [1]. Al are important elements in the soil constitution. In acidic soils, Aluminum ions (Al³⁺) is a phytotoxic form that limit agricultural production [2]. Al³⁺ induce inhibition of root growth, being shorter and thicker, affecting the absorbing nutrients and water. Further, transport molecules more slowly through cells, generating water stress and nutrient deficiencies [3, 4]. In addition, Al³⁺ disturb plant metabolic processes in several crops, including sugarcane plants [1]. Al³⁺ also induce detrimental effects on plant growth and it depends on exposure time and Al concentration [5–7].

The first Al³⁺ impact in plants develop occur in the cell wall, plasma membrane, cytoskeleton, and the cell nucleus, which lead to. Al³⁺ induces nutritional imbalances, favoring nutrient deficiency in plants, such as nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), potassium (K), manganese (Mn), iron (Fe), zinc (Zn), boron (B) and molybdenum (Mo), due to the interference of Al in uptake and utilization processes of these nutrients by plants [5, 8–11]. This effect of Al stress on root growth inhibition (46%) has been previously reported in sugarcane plants [1].

One of the current strategies to mitigate the harmful effects of several abiotic stresses on plants is the Si application, which plays a crucial role in attenuating metal toxicity [12–14], including Al toxicity in rice plants [15, 16], sorghum [17], and corn [18]. The role of Si in increasing Al tolerance in previous studies includes increasing the pH in the growth media and decreasing the uptake and translocation of Al, due to the formation of aluminosilicate complexes (Al-Si) in the external and internal root medium [17, 19–21]. Si can attenuate Al toxicity due to increasing nutrient uptake [16, 22–24], production of antioxidant compounds[25, 26], and increasing nutritional efficiency [27, 28].

Nevertheless, the beneficial effects of Si in stimulating phenolic compound and lignin composition production under various stresses is widely reported in the literature [29–31]. Si incorporation in plant tissue may, to some extent, substitute for the production of C compounds such as cellulose and lignin [32–34]. A recent study showed that the co-deposition of Al and Si in phytoliths is another important mechanism in detoxification of Al [23]. In previous research, it has been suggested that Si attenuates Al toxicity by exudation of phenolic compounds with the Al chelation ability of plant roots [19], and some phenolic compounds can form stable complexes with Al^{3+} , contributing to tissue detoxification [35].

Therefore, in sugarcane plants experiments looking at the amelioration of Al toxicity by Si have not been carried out before. However, it has been demonstrated in previous studies in rice, which are similar gramineous plants [16, 21]. Nevertheless, rice and sugarcane plants are considered typical Si-accumulator species, due to both active and passive mechanisms operating in Si uptake and transport, which increases Si uptake efficiency [36–38].

Sugarcane culture has high Si uptake, and this increases the expectation of using Si to promote the attenuation of Al toxicity. This fact is important because sugarcane is grown in different tropical regions with a predominance of acid soils with higher contents of exchangeable Al [39, 40]. Therefore, our key hypotheses were as follows: (1) Si application could regulate Al-induced damages by decreasing Al concentration in sugarcane seedlings, (2) Si concentration could be positively related with lignin concentration improving sugarcane seedlings response to Al stress, (3) Si fertilization can attenuate the detrimental effects of Al toxicity by enhancing mineral composition and nutrient use efficiency, resulting in a slight high shoot biomass production, and (4) between cultivar, 'CTC9003' showed better performance to Si nutrition as compared to 'CTC9002'. Thus, the objective of this research was to investigate the nutritional and structural role of Si-mediated attenuation of Al toxicity in two sugarcane cultivars ('CTC9002' and 'CTC9003') grown under hydroponic conditions.

Material And Methods

Growth conditions, plant material, and nutrient solution

The experiments were performed under a glass greenhouse at São Paulo State University-UNESP (Jaboticabal, Brazil, with geographic coordinates 21° 15' 22" S and 48° 18' 58" W), between February and September of 2019. The sugarcane seedlings (*Saccharum officinarum* L.) used were Canavieira

Technology Center (CTC), cultivars 'CTC9002' and 'CTC9003'. The main characteristics of CTC cultivars 9002 and 9003 are drought tolerance, good suitability for mechanized planting and have higher sugar levels than other cultivars available on the market [41]. These were grown under natural light conditions, with a 12/12h (light/dark) photoperiod, an average day/night temperature of 26.7/18.2 °C, and relative humidity of $60.0 \pm 15\%$.

Buds of both cultivars were placed in Styrofoam trays (1.7 dm^3) filled with sterilized sand and irrigated with deionized water (without Si). Thirty days after emergence (DAE), sugarcane seedlings were fixed in *Styrofoam* plates for root system immersion in pots (3.8 dm^3) filled with nutrient solution (NS) of Clark [42], pH 4.5 or 5.8, . The NS used for plant growth contained the following composition (in mM): 2.6 Ca, 1.8 K, 0.6 Mg, 6.9 N- NO_3 , 0.9 N- NH_4 , 0.069 P, 0.5 S, 0.5 Cl, 0.038 Fe, 0.007 Mn, 0.019 B, 0.002 Zn, 0,0006Mo, and 0.0005 Cu. Only the Si (2 mmol L^{-1}) and Al ($10, 15$ and 20 mg L^{-1}) varied among the treatments. The NS started with 25% ionic strength and was added over 5 days to acclimate plants. During the next 5 days, the NS concentration was increased to 50%, and the NS was changed to 100% ionic strength when the Al and Si treatments were started until the end of the experiment. The system was kept under constant aeration of the solution by bubbling air supplied by a water pump (ACQ-001, BOYU—China).

Experimental design

During the 35 days of the experimental growth period, two pots experiments were carried out, and distributed in a randomized block design, in a factorial arrangement (4×2). Four replicates/pots for each treatment under each sugarcane cultivar were used. Pots were divided into two plots, cv. 'CTC9002' and cv. 'CTC9003', and 32 pots were allocated for each plot/cultivar. Four treatments, 0, 10, 15, and 20 mg L^{-1} of Al (as $\text{Al}_2(\text{SO}_4)_3 \cdot 18\text{H}_2\text{O}$), were combined with the absence and presence (2.0 mmol L^{-1}) of Si (as K_2SiO_3). The experimental unit consisted of a 3.8-dm^3 polyethylene vessel filled with 2 L of Clark NS with one sugarcane seedling.

Al and Si treatments

After transplant, plants of both sugarcane cultivars following 10 days of acclimatization in Clark NS, containing neutral ($\text{pH} = 5.8$) or acidic NS ($\text{pH} \leq 4.5$). Al treatments (as $\text{Al}_2(\text{SO}_4)_3 \cdot 18\text{H}_2\text{O}$) was initiated and maintained in acidic NS on corresponding pots by adding 0, 10, 15, and 20 mg L^{-1} of Al, during 15 days. After this period, Si addition via NS was started during next 20 days. In treatments that did not received K_2SiO_3 , the K concentrations were balanced using potassium chloride (KCl). Control plants were cultivated in neutral NS. During the growth period (35 days), the pH in neutral or acidic NS was adjusted daily using dilute hydrochloric acid (HCl), and both NS was changed every 5 days.

Experimental methods

Analysis of plant growth

Thirty-five days after stress, sugarcane seedlings were collected and the adhering residues were removed by washing with distilled water, detergent solution (0.2%), hydrochloric acid solution (0.1%), and, finally, twice with deionized water [43]. Subsequently, the plants were separated into roots and shoots, collocated onto paper sacks, and placed in a forced ventilation oven (M214Ai/BEL Analytics Equipment's Ltd.—Brazil) at 60 °C until reach a constant dry mass (DM). After that, root and shoot DMs were immediately measured by a digital scale (Q31711-53/Quimis—Brasil).

Determination of Al, Si, and nutrient concentration and use efficiency

The Al concentration [Al] (g kg^{-1}) in both sugarcane cultivars tissue (shoots and roots) was performed following the methodology of Wang and Wood [44]. Briefly, dried samples were heated at 500 °C for 8 h and treated with 2 M HCl. After filtration of the resulting solution, the total amount of Al was quantified by flame atomic absorption spectrophotometry (Corning 410, Essex, UK) at 324.7 nm.

Si concentration [Si] (g kg^{-1}) in shoots was performed following a two-phase wet-digestion procedure and Molybdenum Blue Colorimetry method as described by Kraska and Breitenbeck [45]. A brief, samples of dried shoots (0.1 g) were placed in 2-mL microtubes and wetted with 10 μL octyl alcohol prior to the addition of 90 μL 30% H_2O_2 . The tubes were tightly capped and placed in a convection oven set at 95°C. After 30 min, 100 μL 50% NaOH was added to the hot tubes, which were vortexed, tightly capped and returned to the oven and incubated at 95°C for a further 4 h. Immediately after digestion, 25 μL of 5 mM NH_4F was added to aid monosilicic acid formation. Si concentrations was determined using ultraviolet spectrophotometer subsystem (SP-1105, Ningbo Hinotec Technology, Shanghai, China) at 410 nm.

Shoot nutrient concentrations of N, P, K, Ca, Mg, S, Cu, Fe, Zn, Mn, and B (macronutrients were expressed in g kg^{-1} , and micronutrients in mg kg^{-1}) were estimated as described previously by Bataglia et al [46]. Shoot material was subjected to either oxidation by sulfuric digestion, to determine the total N concentration or to nitric-perchloric acid digestion, to determine the levels of P, K, Ca, Mg, S, Fe, Mn, Zn, and Cu. P and S were determined by the molybdenum antimony colorimetric method using ultraviolet spectrophotometer subsystem (SP-1105, Ningbo Hinotec Technology, Shanghai, China). The concentrations of K, Ca, Mg, Fe, Mn, Zn, and Cu were estimated in atomic adsorption spectrophotometer (Varian® SpectrAA, 50 B, Varian Medical Systems Australasia, Belrose, NSW,). B was determined colorimetrically by the azomethine-H method at 420 nm using ultraviolet spectrophotometer subsystem (SP-1105, Ningbo Hinotec Technology, Shanghai, China).

Determination of lignin concentration

Shoots samples were subjected to pretreatment to remove proteins and other sensitive substances to the wavelength of 280 nm, according to the method described by Ferrarese et al [47]. Then, dry leaves (300 mg) were homogenized in 50 mM potassium phosphate buffer (7 mL pH, 7.0), and transferred into a centrifuge tube. The pellet was centrifuged ($1,400 \times g$, 4 min) and washed by successive stirring and centrifugation, as follows: twice with phosphate buffer pH 7.0 (7 mL), $\times 3$ with 1% (v/v) Triton X-100 in pH 7.0 buffer (7 mL), 2 with 1 M NaCl in pH 7.0 buffer (7 mL), $\times 2$ with distilled water (7 mL), and $\times 2$ with acetone (5 mL). The pellet was dried in an oven (60 °C for 24 hr) and cooled in a vacuum desiccator. The dry matter obtained was defined as the protein-free cell wall fraction.

The acetyl bromide method of Moreira-Vilar et al [48] was utilized to assess lignin concentration [Lignin] in shoots of both cultivars. Further, 20 mg of the protein-free cell wall sample was mixed with 0.5 mL of acetyl bromide (v / v, in glacial acetic acid) and remained at 70 °C for 30 min until complete digestion. After that, the sample was cooled in ice bath and then 100 µL of hydroxylamine 5 M HCl, 0.9 mL of 2 M NaOH and 6 ml of glacial acetic acid were added. The mixture was centrifuged at $1,400 \times g$ for 5 min, the supernatant collected and taken to a spectrophotometer for reading at 280 nm. The results were expressed in percent (%) of lignin g^{-1} cell wall (CW).

Analysis of data

Dates obtained of variables measured were collected in four replicates, and each replicate/sample was performed in triplicate. The data obtained and presented in this research paper were subjected to multifactorial analysis to test the main effects of the four levels of Al, two levels of Si, and their interactions (Al \times Si). Data were tested for normality by Shapiro and Wilk test and unequal variance by Fisher's exact test at $P < 0.05$. After that, all data were then subjected to a multifactorial analysis of variance (two-way ANOVA) using the R software for statistical computing [49]. Multifactorial-ANOVA was also used to analyse the influence between cultivar. A regression analyses among concentration of lignin and Si included only the Si addition under Al treatments for each cultivar. When F tests were significant at $P < 0.05$, the means were compared using Tukey's multiple range test at $P < 0.05$. All figures were created using GraphPad Prism v8.0 (GraphPad Inc., San Diego, CA, USA).

Results

Influence of Si addition on Al concentration in sugarcane seedlings under Al toxicity

The two-way ANOVA showed the highly significant ($P < 0.0001$) differences between Al and Si, between cultivars and among different Al stress on roots and shoots [Al] (Fig. 1a–d). [Al] in shoots and roots of 'CTC9002' and 'CTC9003' cultivars were markedly increased significantly ($P < 0.0001$) with increasing Al in the growth medium, irrespectively of the presence of Si. However, the highest [Al] was recorded in the cv. 'CTC9002', while the minimum [Al] was recorded in the cv. 'CTC9003' ($P < 0.0001$) (Fig. 1a, b). Si addition

to the growth medium interacted with Al, significantly ($P<0.0001$) decreased shoot [Al] by ~16, 13 and 14% and root [Al] by ~10, ~19 and 22% under 10, 15 and 20 mg L⁻¹ Al respectively in the 'CTC9002' cultivar, whereas in the 'CTC9003' cultivar, the decreases were ~28%, ~35%, and ~30% in shoot Al and ~10%, ~20% to ~27% in root [Al] under 10, 15, and 20 mg L⁻¹ Al, respectively as compared to Al-stressed plants without added Si ($P<0.0001$) (Fig. 1a, b). This supports the idea that Si addition in the growth medium decreased Al uptake and transport to shoots in both sugarcane seedlings.

Influence of Si addition on concentration of Si and lignin in sugarcane seedlings under Al toxicity

The ANOVA revealed a significant interaction ($P<0.0001$) between Al and Si during the last 20 d of the experimental period. Results indicated that the [Si] in shoots of both sugarcane cultivars was significantly ($P<0.0001$) increased with increasing [Al] in the growth medium. Data regarding [Si] in shoots as influenced by Al stress (Fig 2a, b) indicated highly significant difference between cultivars and among Al stress treatments. Cultivar 'CTC9003' had significantly greater [Si] by 11%, 17%, and 13% under 10, 15, and 20 mg L⁻¹ of Al, respectively as compared to cultivar 'CTC9002'.

The results indicated that the [lignin] in shoots of both sugarcane cultivars significant ($P<0.0001$) interaction between Al and Si treatments and between cultivars (Fig. 2c, d). In addition, under Al stress, Si supplementation increased the [lignin] even more compared to the plants without Si ($P<0.0001$) (Fig. 2c, d). Between the cultivars, the highest [lignin] in shoots was obtained in 'CTC9003' as compared to the 'CTC9002' under Si and Al stress treatments ($P<0.0001$) (Fig. 2c, d). The response of different cultivars of sugarcane to different Al stress levels differed significantly ($P<0.0001$). The highest [lignin] in shoots (~14%) was obtained in cultivar 'CTC9003', while the lowest [lignin] was obtained in 'CTC9002', both under Si (2 mmol L⁻¹) and Al (10, 15, and 20 mg L⁻¹) stress treatments as compared to the non-Al-stressed plants and with Si (2 mmol L⁻¹) (Fig. 2c, d).

Using a correlation study involving Si and Al treatments, made it possible to evaluate the strategies of lignin production in shoots of sugarcane seedlings. [Si] in shoots of both sugarcane cultivars, determined for various Al (0, 10, 15, and 20 mg L⁻¹) treatments in the presence of Si (2 mmol L⁻¹) were positively correlated with [lignin] ($r = 0.75$) in 'CTC9002' (Fig. 2e) and in 'CTC9003' ($r = 0.79$) (Fig. 2f).

Influence of Si addition on shoots nutrients concentration of sugarcane seedlings under Al toxicity

Dates pertaining to concentrations of macronutrients and micronutrients showed the highly significant ($P<0.001$) interaction between Si, among different Al stress, and between cultivars (Figs. 3, 4). Applied Al concentrations in the growth medium significantly ($P<0.001$) decreased the concentrations of macronutrients in both sugar cane cultivars (Fig. 3a–l). However, Si addition (2 mmol L⁻¹) under Al stress

increased the concentration of N, P, K, Ca, Mg, and S compared to plants stressed by this metal and without Si (Fig. 3a–l). Furthermore, the helpful effects of added Si were more marked in 'CTC9003' cultivar than cv. 'CTC9002', especially under Al stress (Fig. 3a–l).

Data regarding concentrations of micronutrients were influenced by Al stress (Fig. 4) indicated highly significant ($P<0.001$) difference between Si and cultivars and among Al stress treatments (Fig. 4a–j). However, we observed that under Al stress, the Si addition in the growth medium significantly ($P<0.001$) increased the concentration of Fe, Mn, Zn, Cu, and B compared to plants stressed by Al and without Si (Fig. 4a–j). We found that the cultivar 'CTC9003' had significantly greater concentrations of micronutrients as compared to the cultivar 'CTC9002'. Moreover, the beneficial effects of added Si were more marked in cultivar 'CTC9003' as compared to the cultivar 'CTC9002', particularly in the presence of Al (Fig. 4a–j).

Influence of Si addition on nutrients use efficiency of sugarcane seedlings under Al toxicity

The results indicated a significant ($P<0.0001$) interaction between Si and Al treatments and between cultivars on MaUE (N, P, K, Ca, Mg and S) and MiUE (Fe, Mn, Zn, Cu, and B) in shoots (Figs. 5 and 6). The Al stress significantly ($P<0.0001$) decreased the use efficiency of N, P, K, Ca, Mg, and S in the shoots with an increase in the availability of this metal in the absence of Si (Fig. 5a–l). Nevertheless, under Al stress, the addition of Si significantly ($P<0.001$) increased the shoot MaUEs of both cultivars compared to the non-Al-stressed plants and without Si, except for the Ca-use efficiency (Fig. 5g, h). On the other hand, sugarcane cultivars also differed significantly for this variable. Cultivar 'CTC9003' had significantly greater MaUE and MiUE as compared to the 'CTC9002'. Moreover, cultivar 'CTC9003' were more responsible to Si fertilization for increasing MaUE and MiUE as compared to the cultivar 'CTC9002', particularly in the presence of Al (Fig. 5a–l).

The results related to the use efficiencies of Fe, Mn, Zn, Cu, and B in the shoots of cv. 'CTC9002' and cv. 'CTC9003' of sugarcane plants are shown in Fig. 6 (a, j). The increased Al concentration in the NS significantly ($P<0.0001$) decreased the MiUEs, even when Si was present (Fig. 6a, j). Meanwhile, under Al stress, the addition of Si significantly ($P<0.0001$) increased the use efficiencies of Fe, Mn, Zn, Cu, and B in the shoots of both cultivars (Fig. 6a–j), in particular for boron use efficiency in the higher Al concentration of both sugarcane cultivars (Fig. 6i, j). In addition, between cultivar the beneficial effects of Si addition on increased concentration micronutrient were more prominent in cv. 'CTC9003' than in cv. 'CTC9002', especially in the presence of 15 and 20 mg L⁻¹ of Al.

The results of two-way ANOVA revealed significant ($P<0.0001$) interaction between Si and Al treatments and between cultivar on shoots growth (Fig. 7a, b). Al stress drastically decreased the SDM production of both sugarcane cultivars, but this effect was reversed with the addition of Si in the growth medium (Fig. 7a, b). The addition of Si to the acidic growth medium interacted with Al, improved SDM in both

sugarcane cultivars. Applied Si were effective to mitigate the adverse effects of Al and significantly ($P<0.0001$) mitigated the deleterious effects of Al and improved the SDM by ~10% in 10 mg L⁻¹ Al, ~17% in 15 mg L⁻¹ Al, and ~25% in 20 mg L⁻¹ Al in 'CTC9002' cultivar ($P<0.0001$). However, in the 'CTC9003' cultivar, the increases were ~10%, ~19%, and ~30% in 10, 15, and 20 mg L⁻¹ Al, respectively, compared to the Al-stressed plants and non-Si treated plants ($P<0.0001$) (Fig. 7a, b).

On the other hand, the response of different cultivars of sugarcane to different Al stress and Si treatment differed significantly for this variable. Cultivar 'CTC9003' had higher SDM as compared to the 'CTC9002'. Moreover, the most notable effect of Si on SDM production were in the cultivar 'CTC9003' than 'CTC9002', especially under different Al stress (Fig. 7a, b).

Discussion

From this study, it is obvious that the Si nutrition enhanced the tolerance against Al toxicity in *S. officinarum* plants. We found unraveled how shoot and roots [Al], shoot [Si] and [lignin], shoot mineral composition, shoot NUE, and SDM production of both sugarcane seedlings were modified by Si application under Al toxicity in hydroponic conditions. However, the mechanisms underlying these responses remain poorly understood, especially when it comes to sugarcane crops, classified as higher Si-accumulating plants.

We observed that both sugarcane genotypes behaved differentially to Al depending on their capability to selectively absorb Al. Better performance of cultivar 'CTC9003' was due to its lower [Al] in shoot and roots compared to the 'CTC9002' (Fig. 1a, b). In this sense, Vega et al. [26] also demonstrated differences between barley genotypes regarding Al uptake, and the cultivar with lowest [Al] produced the greatest biomass and vice versa. Similar variations were observed in different plant species and varieties such as barley [31] and sorghum plants [17]. These findings suggest that the Al uptake varied substantially among genotypes and depend on levels of Al and the developmental stages of the studied plants. Thus, it is necessary to develop plants with increased resistance to inhibition of uptake effects of external Al stress.

The ameliorative effect of Si on Al toxicity in both sugarcane seedlings were attributed to a decreased [Al] in roots, which reduced the translocation the phytotoxic Al to the shoots (Fig. 1a, b). This decrease in [Al] is in concordance with our first proposed hypothesis to explain how Si reduced [Al] and this is due to the formation of biologically inactive complexes of hydroxyaluminumsilicates (HAS) inside plant tissues (root epidermal walls) [19]. Another possible mechanism causing Si to decrease the plants to absorb Al³⁺ was earlier reported by Singh et al. [16] in which Si helps the formation unstable silicates with Al in the cytoplasm, inhibiting Al symplastic transport. Another typical response to Al stress described in different papers by Si application resulted from decreasing the phytotoxic Al³⁺ concentration in the external solution by forming Al-Si complexes [20]. Another possible way to relieve or protect plants from Al stress by Si is by Al chelation formation as organic acids in roots and shoots of plants [50]. In addition, Si can negatively regulate the expression of metal transporter genes and thus reduce the metal(lloid)s uptake in

plant cells [4]. Thus, our results suggest that a key mechanism for alleviate Al toxicity in sugarcane seedlings by Si is attributed mostly to the inhibitory effect of phytotoxic Al.

A general increase in shoots [Si] has been observed in both sugarcane cultivars under different Al stress treatments (Fig. 2a, b). Different authors have associated that this genotypic variation in the [Si] in the shoots varied considerably within a species and genotypes due to the different mechanisms of Si uptake (active, passive, and rejective), external concentration applied and developmental stages of the studied plants [38, 51]. However, phytoliths formation, composition, and localization vary among plant species [52, 53]. In general, plants with a high root or shoot Si concentration exhibit enhanced tolerance to abiotic stresses like metal toxicity [54]. According to Ashraf et al [55], these differences in the response of genotypes to Si could be related to the size of bypass flow and/or the properties that affected the polymerization of silicate. Our results are in concordance with the previous findings, in which the higher amount of Si absorb by sugarcane plants occur in a range of pH 3.3 to 7.0 [56]. Similar trends were reported previously in Al-stressed barley plants by Liang et al [57], suggesting that under Al toxicity, increased Si accumulation can be one of the mechanisms by Si induce amelioration to Al stress. Recent studies have shown that plants that accumulate more Si present better responses under stress conditions, in which Si are included in the antioxidative defense system [58]. This experiment findings were to increase Si availability from Si fertilizer application, which need further investigations in field scale. Our results indicate that the amounts of Si accumulated in the sugarcane plants are an important mechanism for Si improving sugarcane tolerance to Al toxicity.

Lignin is one of the most important structural carbon compounds. We found that both sugarcane plants fertilizers with Si showed an increase in [lignin], especially under stress conditions (Fig. 2c, d). These results directly supporting our second hypothesis. They validate that the Si availability are positively related to the [lignin]. Our results may contradict the reports about the relationship between Si and [lignin] under different abiotic stress in different plant species such canola (*Brassica napus* L.) [59], rice (*Oryza sativa* L.) [60], and *Phragmites australis* [61, 62]. They demonstrated that the incorporation of structural Si represents an economic strategy of plants to confront a range of environmental stresses.

However, our study demonstrated that both sugarcane cultivars have significant positive correlations between the concentrations of Si and lignin in shoots, particularly under Al stress conditions. This lignin enrichment under Al stress presumably occurred by different ways. First, the presence of OH groups of phenols are condensed with Si(OH) in biological systems [63]. Second, Si could be associated with lignin-carbohydrate complexes in the wall of epidermal cells [64]. Third, Si helps to increase energy available, leading to plants to synthesize nonstructural organic compounds, like cellulose and lignin [32, 65]. Fourth, Si-induced signal transduction pathways, increasing lignin production [66, 67] and have directly influence the lignin synthesis, mainly by formation of hemicellulose-metal complexes [68]. Other research has suggested that Si enhance [lignin], which increase plant tolerance to Al toxicity in ryegrass [69] and wheat [26, 31], although these processes need to be understood in more depth. Our results suggest that the changes in [lignin] by Si can help us predict how plants will respond to the adverse effects of Al toxicity.

Our study showed that [Al] (above 10 mg L⁻¹ Al) inducing nutritional imbalances of both sugarcane cultivars (Figs. 3 and 4), which resulting ionic and oxidative stress in plants [3, 27]. An interesting result of our study was that Si application increased shoot concentrations of macros- and micronutrients (Figs. 3 and 4). Thus, these results support partially our third hypothesis that the enhancing mineral nutrition by Si under Al toxicity are a common phenomenon under Al stress condition. In concordance with our findings, similar responses of different crop species to Al were earlier reported in barley [26, 31, 57] and sorghum [22]. Besides, Si plays a crucial role in maintaining mineral uptake in acidic conditions by improving metal homeostasis [12, 68, 70]. In addition, Si induces enzyme activation such as H-ATPase that is involved in the nutrient uptake process [3]. Therefore, higher concentrations of macros- and micronutrients was could facilitate several essential processes, like photosynthesis, activation of enzymes, cell division, carbohydrate accumulation, pigments production, synthesis of nucleic acid and proteins, and activate/repress several metabolic processes [3, 68]. Our results suggest that under Al toxicity, Si fertilization play an important role on mineral nutrition to completely understand the resistant mechanisms adopted by species to cope with Al toxicity.

In our results, Si addition improved overall NUE (Figs. 5 and 6), leading to the increased primary productivity of both sugarcane cultivars (Fig. 7). These results support our third hypothesis. In concordance with our findings, recent studies have reported that Si increased total NUE, and these suggest higher biomass accumulation [3, 28]. This study demonstrated that Si application promotes higher SDM of overall nutrients in shoots tissues, likely through enhancing total NUE and thus improving plant biomass. This may be related to the different morphological and physiological functions of these nutrients. Therefore, the beneficial effects of Si on NUE in shoots of both sugarcane cultivars could be directly related to the less [Al] in roots, which reduced its uptake and transport to shoots. These observations suggest that Si fertilization represents an economic strategy of sugarcane seedlings to confront Al stress. These results suggest that the beneficial effects of Si in improving Al tolerance could be attributed to improving overall NUE, favoring shoots biomass production of sugarcane seedlings under Al toxicity conditions.

The SDM yield is the result of complex interactions between different physiological processes. Most of these processes are negatively affected by Al stress. In our experiment, the impair influence of Al toxicity on SDM production was associated with an increasing [Al] in shoots and roots (Fig. 1a-d), a decreasing in the concentrations of macronutrients and micronutrients (Fig. 3 and 4), as well as a diminishing of the overall NUE (Fig. 5 and 6). Similar observation was report in barley plants, in which the growth was harmfully influenced by Al toxicity [26, 31].

As discussed above, the hypothesis assumes that Si application represents an economic and efficient strategy of sugarcane plants to confront Al toxicity. These beneficial effects of Si against Al toxicity are presumably associated with a lower [Al] in shoots and roots (Fig. 1a-d), higher concentrations of macros- and micronutrients (Figs. 3 and 4), and improvement overall NUE (Figs. 5 and 6). In addition, an increase in the [lignin] (Fig. 2c, d) with Si could have induced adaptive response in sugarcane seedlings under Al toxicity, which resulting in higher SDM production (Fig. 7a,b). These beneficial effects of Si improving

plant growth under Al toxicity were previously reported in different species, such as barley [57], rice [15, 16], sorghum [17, 58], corn [18], and wheat [26]. Our main results showed that Si have positive effects on SDM production of both sugarcane seedlings, corroborating our second hypothesis.

Our results also showed that the interaction between Si and Al stress treatment varied between cultivars at the same species. Similar variation were observed in different plant species and varieties such as barley [26, 31] and sorghum [17]. In present study, the ameliorative effects of added Si were more pronounced in cv. 'CTC9003' than cv. 'CTC9002' because present lower [Al], and higher [Si], [lignin], concentration of macros- and micronutrients, NUE of macronutrients and micronutrients, and SDM production. These findings support partially our fourth hypothesis that Si fertilization enhance the response of cultivar 'CTC9003' to adverse effects of Al stress than 'CTC9002'. In concordance with our results, difference response Si application under Al stress between genotypes were observed in experiments with wheat [26, 31], rice [15], and sorghum [17]. Our findings contribute to the current understanding of cultivar 'CTC9003' showed more acclimatization mechanisms to Si fertilization than cultivar 'CTC9002' under Al stress.

Conclusions

We observed that Si addition to growth medium interacted with Al, decreased its uptake and translocation to the shoots of both sugarcane cultivars. In addition, Si concentration had a positive correlated with the lignin concentration, improving the performance of both *S. officinarum* cultivars to cope with Al stress. Furthermore, we showed that the Si fertilization impact in mineral composition and nutrient use efficiency, resulting a slight high shoot biomass production in both cultivars under Al toxicity. Thus, the use of cultivar 'CTC9003' under Si fertilization is more recommended to cope with the adverse effect caused by Al stress. Collectively, our findings suggest that Si fertilization plays an important role in the current understanding of adaptation mechanisms of sugarcane to Al toxicity, leading to improve the plant growth sustainably.

Declarations

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Conflicts of interest/Competing interests. The authors declare that they have no competing interests.

Availability of data and material. 'Not applicable'

Code availability. 'Not applicable'

Consent for publication. This manuscript does not contain any individual person's data. The authors agreed to the publication of the manuscript in this journal.

Authors' contributions: DMMS and GSSJ designed the idea and planned the experiments. GSSJ and JPSJ conducted the experiments. GSSJ, DMMS, JPSJ, and ACH helped conduct parts of the experiments and analyses. DMMS, RMP, and JPSJ contributed reagents/materials/analysis tools. JPSJ assisted with the management and analysis of Si. GSSJ and ACH carried out the statistical analysis. GSSJ, DMMS, RMP, and ACH contributed to data interpretation and validation. GSSJ acquired funding. ACH and GSSJ wrote the first draft of the manuscript, and all authors contributed to the editing of the manuscript. All the authors reviewed and approved the final manuscript.

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Figures

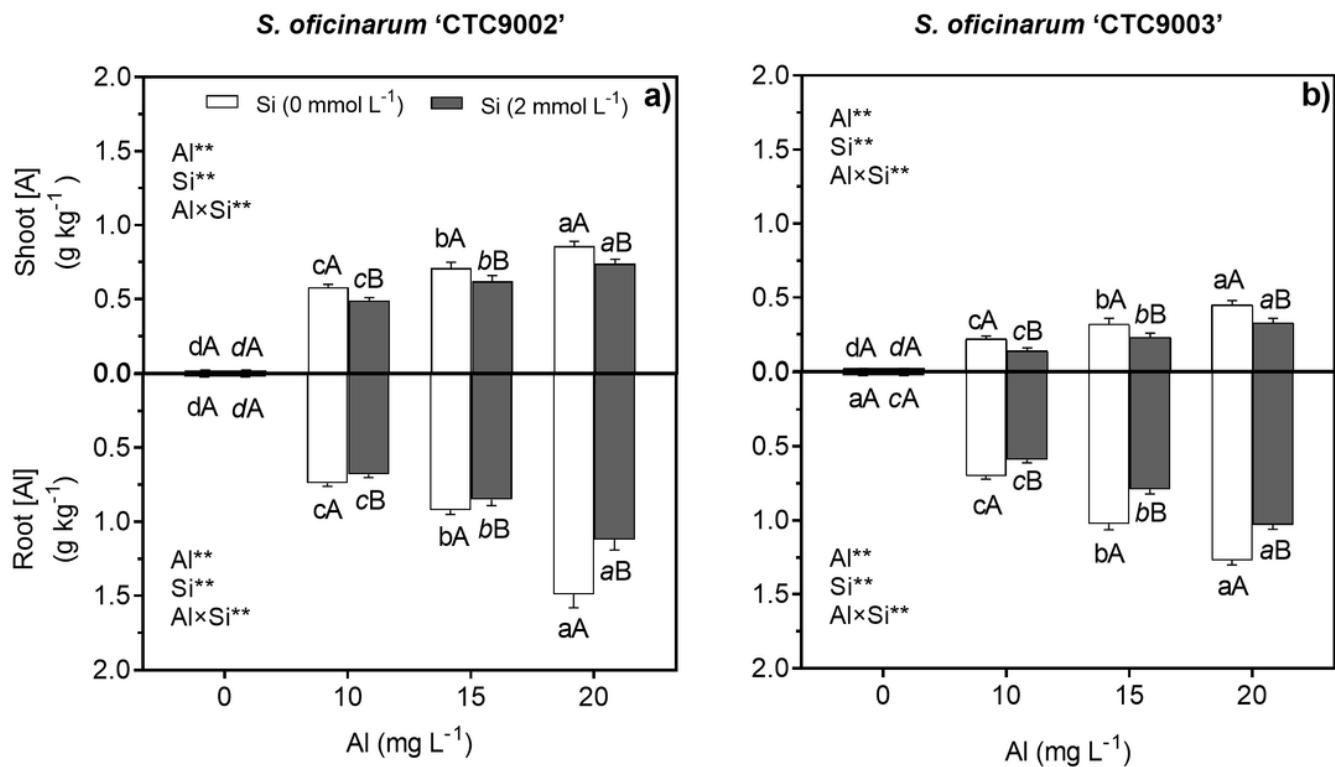


Figure 1

Al concentrations in shoots and roots of cultivar 'CTC9002' (a) and cultivar 'CTC9003' (b) as a function of the Al application (0, 10, 15, and 20 mg L⁻¹) and the absence and presence (2 mmol L⁻¹) of Si. Values are represented by the means of four replications \pm standard deviation (SD). Similar lower case letters (e.g., a, a) do not indicate significant differences among Al concentrations in the absence of Si, similar italicics lower case letters (e.g., a, a) do not indicate significant differences among Al concentrations in the presence of Si, and similar uppercase letters (e.g., A, A) do not indicate significant differences between

the absence and presence of Si treatments at the same Al concentrations, according to the Tukey test ($P<0.05$). ** $P<0.001$, according to the two-way ANOVA. Al × Si, Aluminum–Silicon interaction

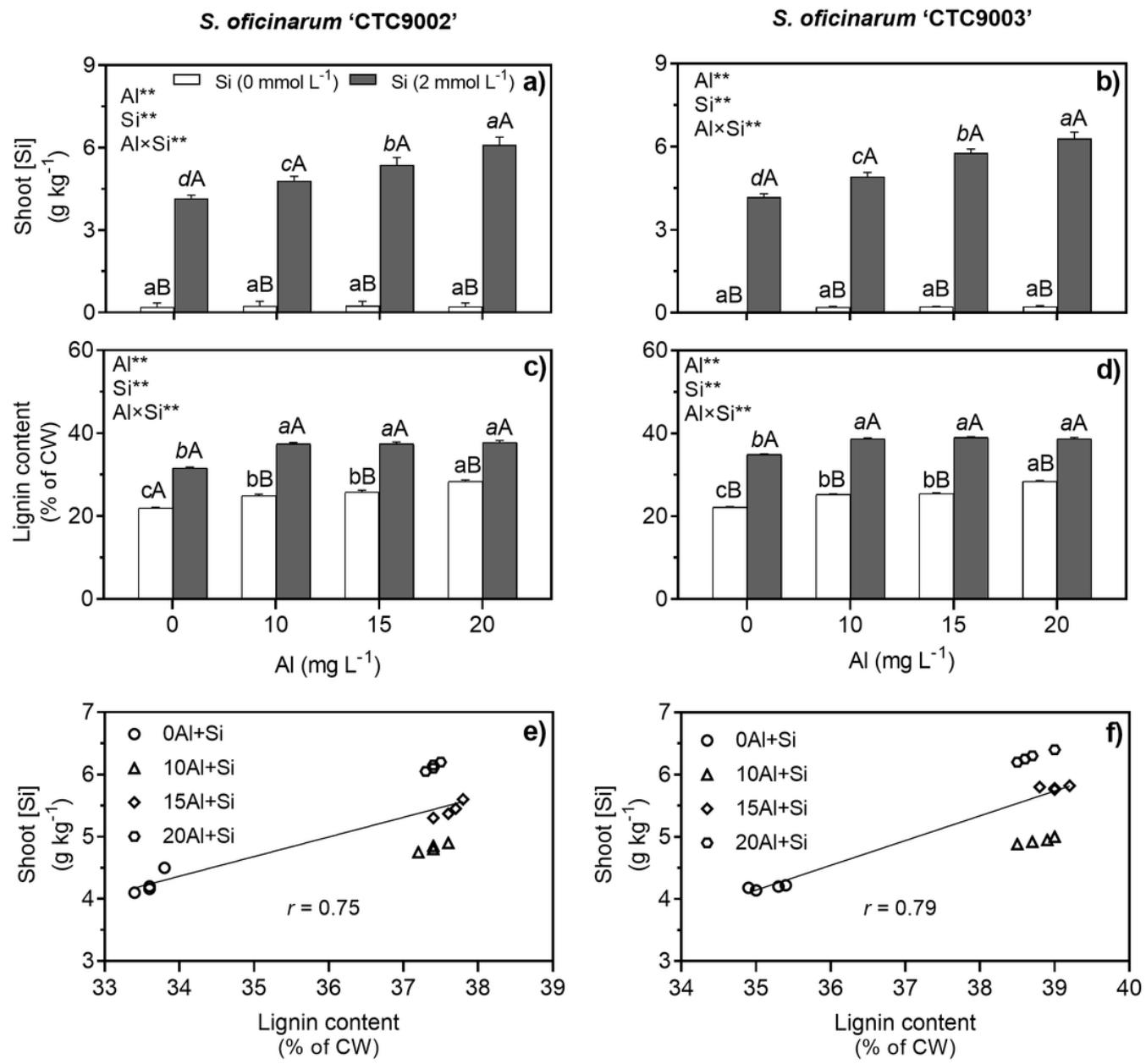


Figure 2

Shoot Si concentration in sugarcane cultivar 'CTC9002' (a) and cultivar 'CTC9003' (b). Shoot lignin concentration in cultivar 'CTC9002' (c) and cultivar 'CTC9003' (d) and correlation analysis between concentration of Si and lignin in 'CTC9002' (e) and 'CTC9003' (f) cultivars. Treatments and statistics as described in Fig. 1

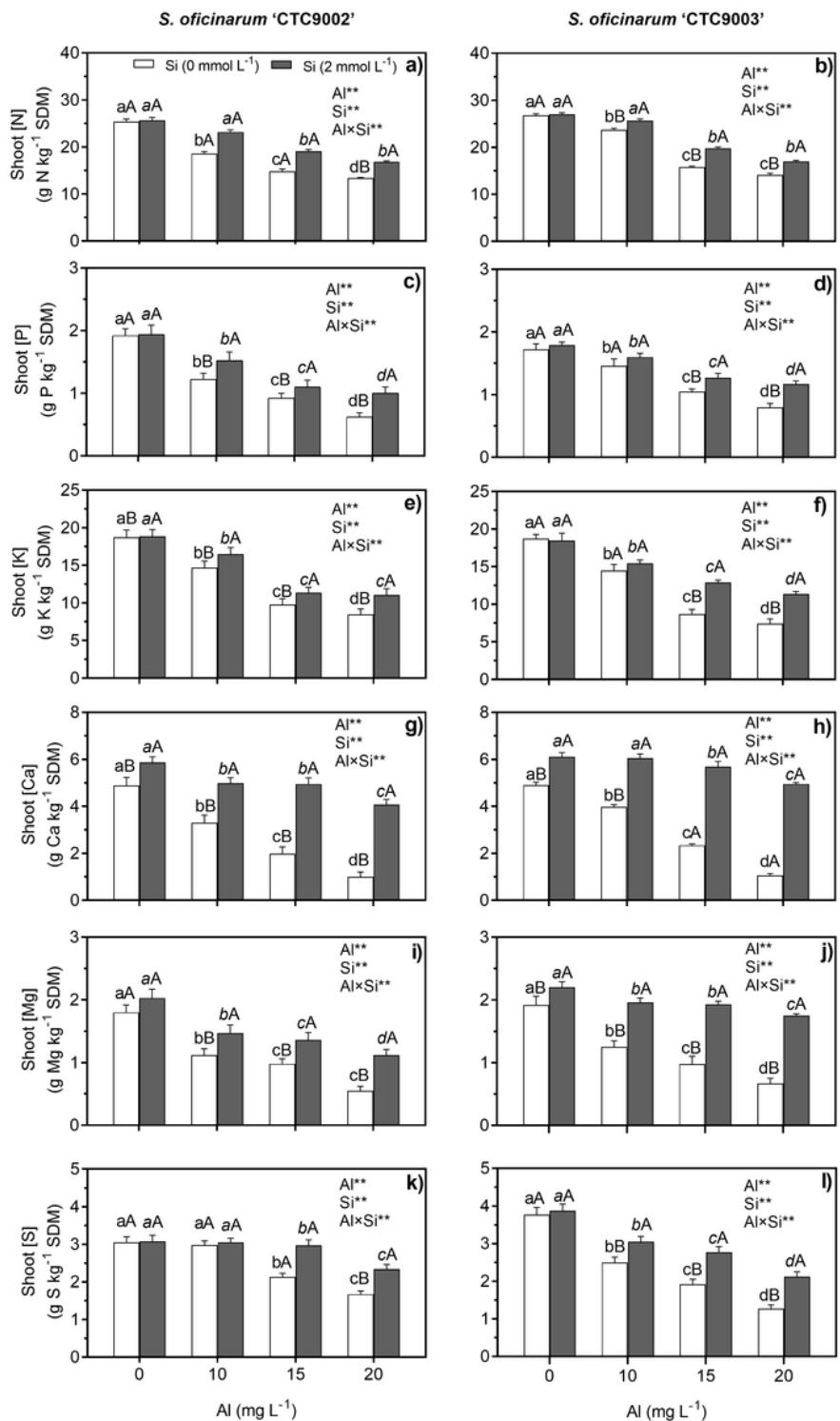


Figure 3

Concentration of macronutrients in the shoots of sugarcane seedlings. Nitrogen concentration in cultivar 'CTC9002' (a) and cultivar 'CTC9003' (b), phosphorus concentration in cultivar 'CTC9002' (c) and cultivar 'CTC9003' (d), potassium concentration in cultivar 'CTC9002' (e) and cultivar 'CTC9003' (f), calcium concentration in cultivar 'CTC9002' (g) and cultivar 'CTC9003' (h), magnesium concentration in cultivar

'CTC9002' (i) and cultivar 'CTC9003' (j), and sulfur concentration in cultivar 'CTC9002' (k) and cultivar 'CTC9003' (l). Treatments and statistics as described in Fig. 1

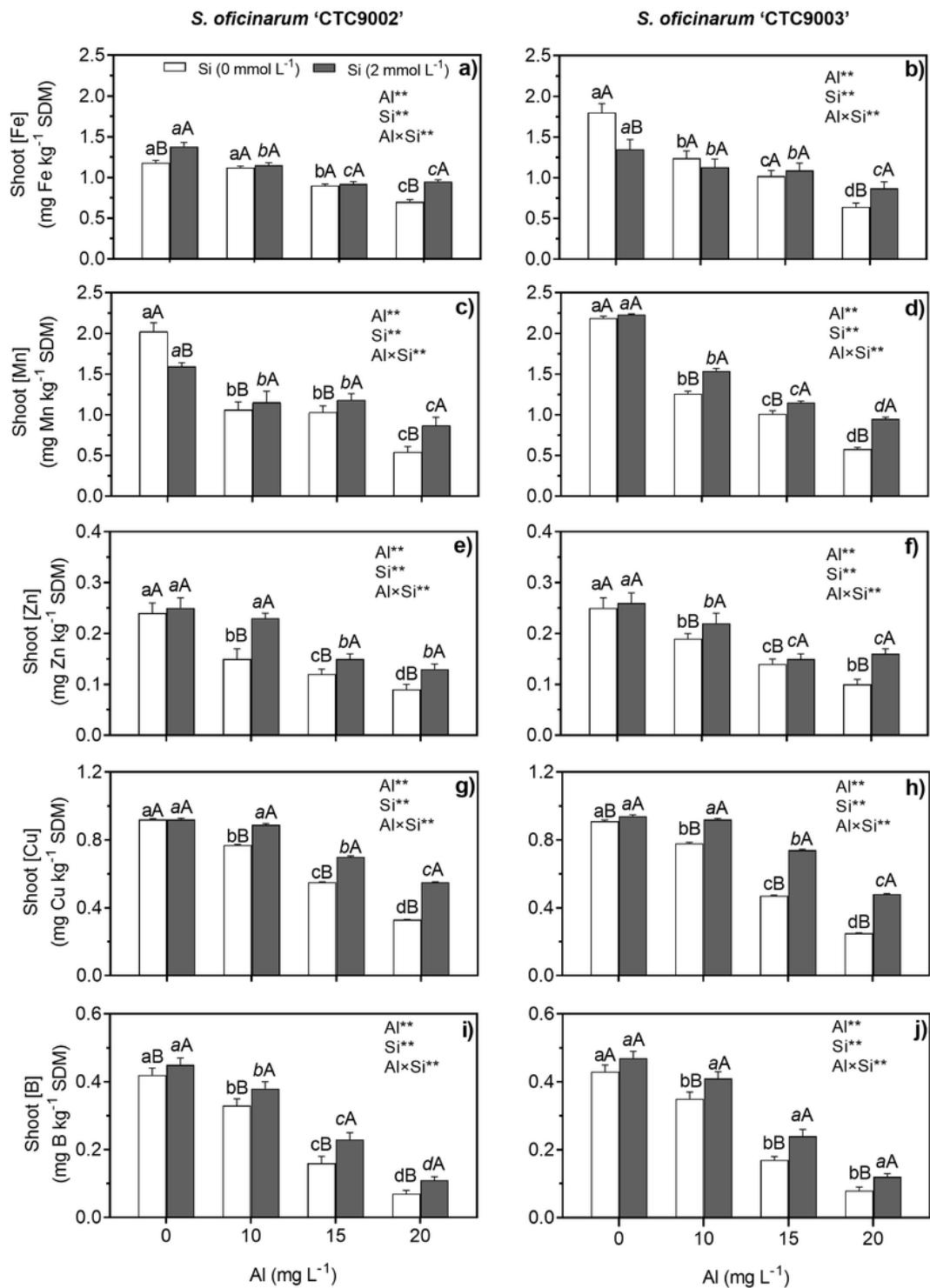


Figure 4

Concentration of micronutrients in the shoots of sugarcane seedlings. Iron concentration in cultivar 'CTC9002' (a) and cultivar 'CTC9003' (b), manganese concentration in cultivar 'CTC9002' (c) and cultivar 'CTC9003' (d), zinc concentration in cultivar 'CTC9002' (e) and cultivar 'CTC9003' (f), copper

concentration on cultivar 'CTC9002' (g) and cultivar 'CTC9003' (h), and boron concentration in cultivar 'CTC9002' (i) and cultivar 'CTC9003' (j). Treatments and statistics as described in Fig. 1

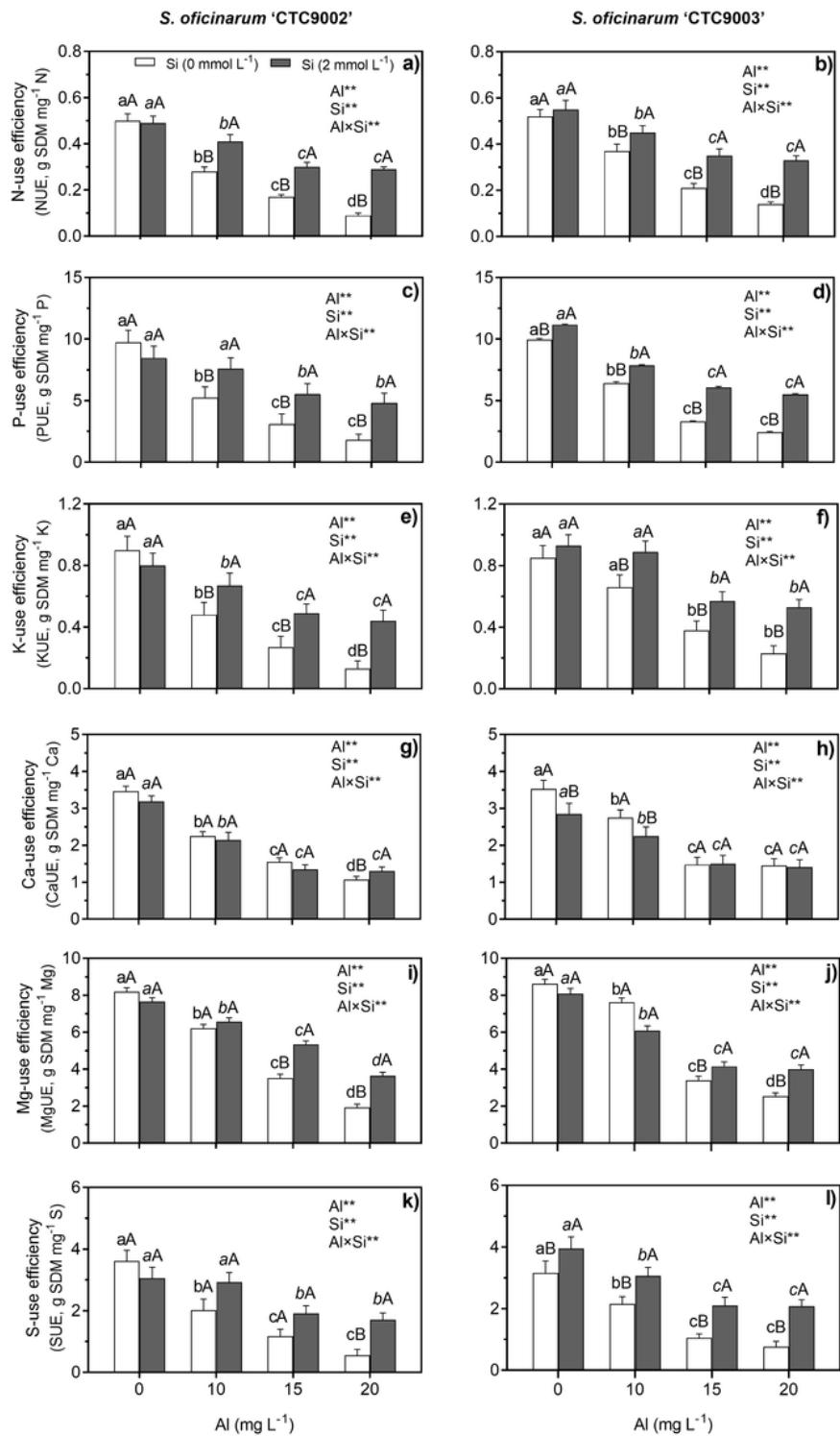


Figure 5

Use efficiency of macronutrients in the shoots of sugarcane seedlings. Nitrogen use efficiency in cultivar 'CTC9002' (a) and cultivar 'CTC9003' (b), phosphorus use efficiency in cultivar 'CTC9002' (c) and cultivar 'CTC9003' (d), potassium use efficiency in cultivar 'CTC9002' (e) and cultivar 'CTC9003' (f), calcium use

efficiency in cultivar 'CTC9002' (g) and cultivar 'CTC9003' (h), magnesium use efficiency in cultivar 'CTC9002' (i) and cultivar 'CTC9003' (j), and sulfur use efficiency in cultivar 'CTC9002' (k) and cultivar 'CTC9003' (l). Treatments and statistics as described in Fig. 1

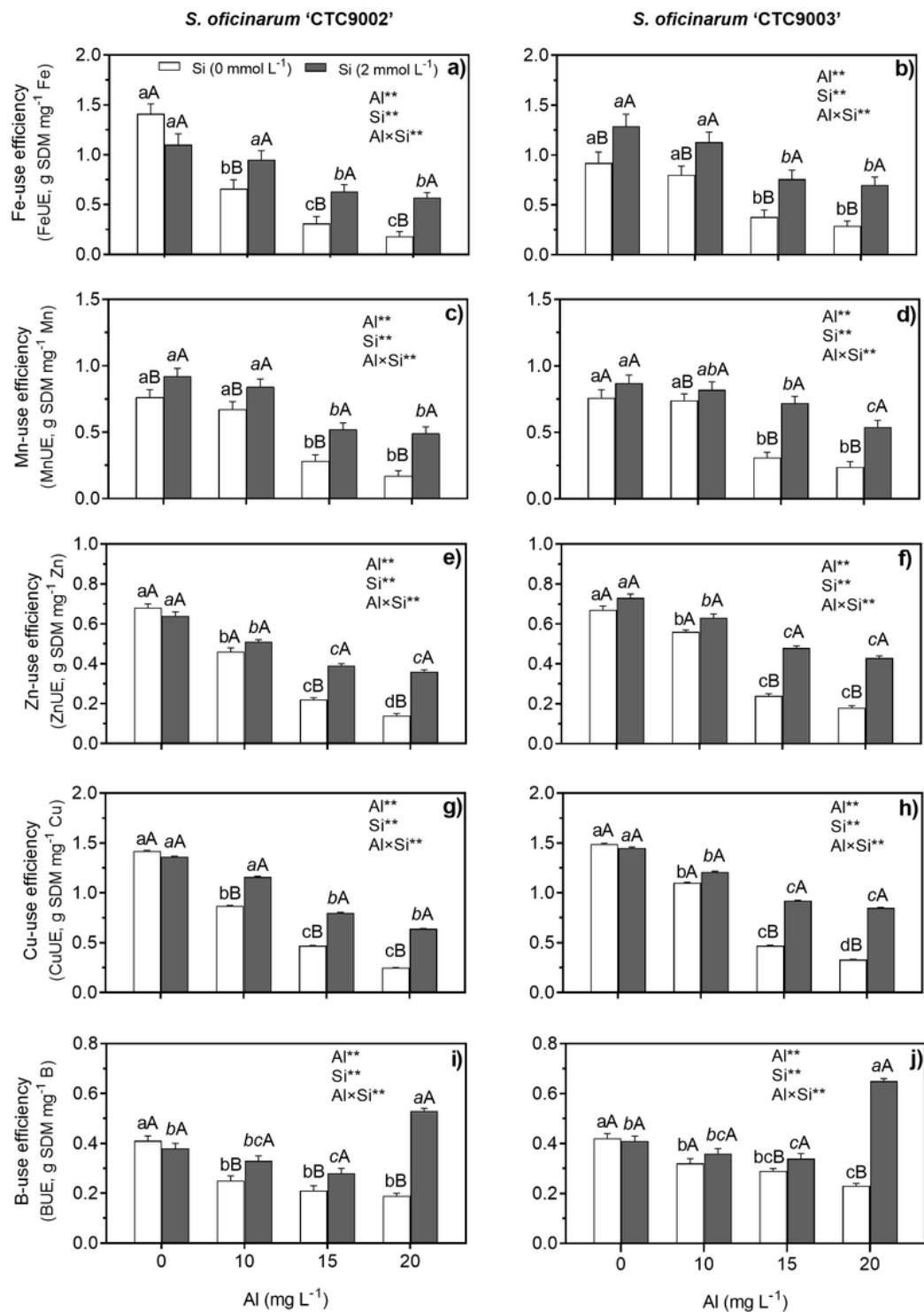


Figure 6

Use efficiency of micronutrients in the shoots of sugarcane seedlings. Iron use efficiency in cultivar 'CTC9002' (a) and cultivar 'CTC9003' (b), manganese use efficiency in cultivar 'CTC9002' (c) and cultivar 'CTC9003' (d), zinc use efficiency in cultivar 'CTC9002' (e) and cultivar 'CTC9003' (f), copper use efficiency in cultivar 'CTC9002' (g) and cultivar 'CTC9003' (h), and boron use efficiency in cultivar 'CTC9002' (i) and cultivar 'CTC9003' (j).

'CTC9003' (d), zinc use efficiency in cultivar 'CTC9002' (e) and cultivar 'CTC9003' (f), copper use efficiency in cv. 'CTC9002' (g) and in cultivar 'CTC9003' (h), and boron use efficiency in cultivar 'CTC9002' (i) and cultivar 'CTC9003' (j). Treatments and statistics as described in Fig. 1

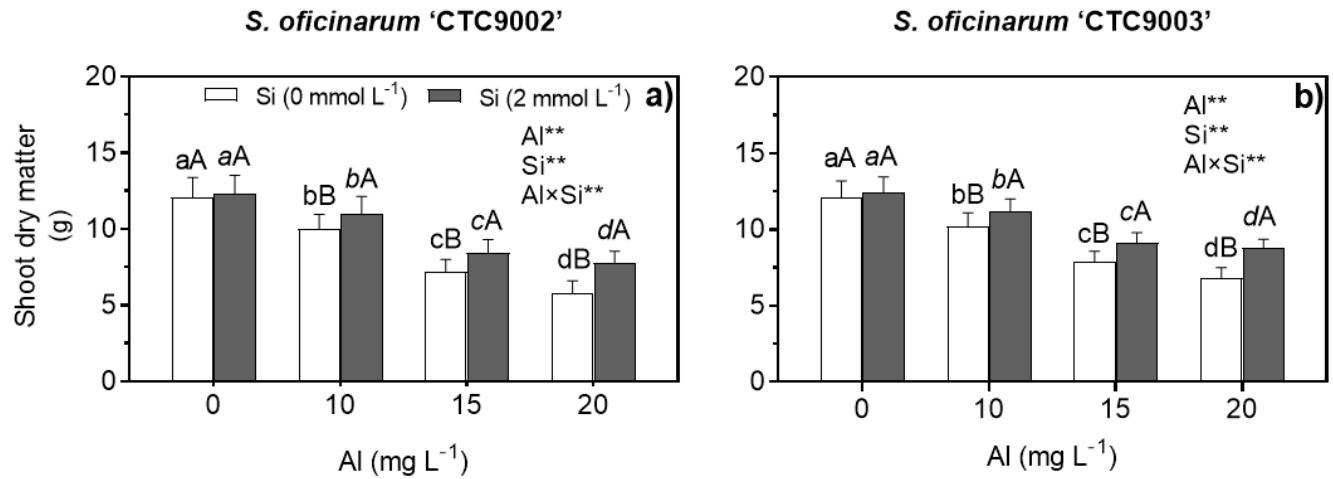


Figure 7

Shoot dry matter production of sugarcane seedlings in cultivar 'CTC9002' (a) and cultivar 'CTC9003' (b). Treatments and statistics as described in Fig. 1