



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

Gilmar da Silveira Sousa Junior¹ · Alexander Calero Hurtado² · Jonas Pereira de Souza Junior² · Renato de Mello Prado² · Durvalina Maria Mathias dos Santos¹

Received: 16 June 2021 / Accepted: 21 July 2021 / Published online: 4 August 2021
© Springer Nature B.V. 2021

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.

Keywords Abiotic stress · Macronutrients · Micronutrients · *Saccharum officinarum* · Silicon

1 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

[56]. Al are important elements in the soil constitution. In acidic soils, Aluminum ions (Al³⁺) is a phytotoxic form that limit agricultural production [69]. 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 [17, 58]. In addition, Al³⁺ disturb plant metabolic processes in several crops, including sugarcane plants [56]. Al³⁺ also induce detrimental effects on plant growth and it depends on exposure time and Al concentration [2, 16, 55].

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

✉ Gilmar da Silveira Sousa Junior
gilmar.ssjr@hotmail.com

¹ Department of Biology Applied to Agriculture, School of Agricultural and Veterinarian Sciences, São Paulo State University (UNESP), Via de acesso Prof. Paulo Donato Castellane s/n, P. C. 14884-900, Jaboticabal, São Paulo, Brazil

² Department of Agricultural Sciences – Soil and Fertilizer Sector. School of Agricultural and Veterinarian Sciences, São Paulo State University (UNESP), Via de acesso Prof. Paulo Donato Castellane s/n, P. C. 14884-900, Jaboticabal, São Paulo, Brazil

(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 [4, 24, 43, 49, 55]. This effect of Al stress on root growth inhibition (46%) has been previously reported in sugarcane plants [56].

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 [1, 42, 54], including Al toxicity in rice plants [21, 57], sorghum [31], and corn [59]. 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 [12, 31, 47, 65]. Si can attenuate Al toxicity due to increasing nutrient uptake [25, 26, 32, 57], production of antioxidant compounds [46, 63], and increasing nutritional efficiency [8, 30].

Nevertheless, the beneficial effects of Si in stimulating phenolic compound and lignin composition production under various stresses is widely reported in the literature [53, 62, 66]. Si incorporation in plant tissue may, to some extent, substitute for the production of C compounds such as cellulose and lignin [7, 15, 52]. A recent study showed that the co-deposition of Al and Si in phytoliths is another important mechanism in detoxification of Al [26]. 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 [12]; and some phenolic compounds can form stable complexes with Al^{3+} , contributing to tissue detoxification [51].

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 [47, 57]. 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 [14, 36, 38].

Sugarcane culture has high Si uptake, and this increases could be 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 [10, 22]. Therefore, we hypothesized that supplied Si may attenuate Al toxicity in sugarcane seedlings by decreasing Al concentration, increasing Si concentration and enhancing lignin concentration, mineral composition and nutrient use efficiency, favoring shoot dry biomass production. Furthermore, we also hypothesized that both sugarcane cultivars show significant variations in response to the Al and Si application, thereby cultivar ‘CTC9003’ exhibit better performance to Si application under Al stress

than the cultivar ‘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.

2 Material and Methods

2.1 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 Canaveira 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 [60]. These were grown under natural light conditions, with a 12/12 h (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 [11], 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).

2.2 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 $Al_2(SO_4)_3 \cdot 18H_2O$), were combined with

the absence and presence (2.0 mmol L^{-1}) of Si (as K_2SiO_3), obtaining the following combination treatments: 0Al-Si: non-Al stress and non-Si addition; 0Al+Si: non-Al stress and 2 mmol L^{-1} of Si; 10Al-Si: addition of 10 mg L^{-1} of Al and non-Si addition; 10Al+Si: addition of 10 mg L^{-1} of Al and 2 mmol L^{-1} of Si; 15Al-Si: addition of 15 mg L^{-1} of Al and non-Si addition; 15Al+Si: addition of 15 mg L^{-1} of Al and 2 mmol L^{-1} of Si; 20Al-Si: addition of 20 mg L^{-1} of Al and non-Si treatment; and 20Al+Si: addition of 20 mg L^{-1} of Al and 2 mmol L^{-1} of Si. The experimental unit consisted of a 3.8-dm^3 polyethylene vessel filled with 2 L of Clark NS with one sugarcane seedling.

2.3 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.

2.4 Experimental Methods

2.4.1 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 [27]. 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 $60 \text{ }^\circ\text{C}$ until reach a constant dry mass (DM). After that, root and shoot DMs were immediately measured by a digital scale (Q31711–53/Quimis—Brasil).

2.4.2 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 [64]. Briefly, dried samples were heated at $500 \text{ }^\circ\text{C}$ 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 [33]. A brief, samples of dried shoots (0.1 g) were placed in 2-mL microtubes and wetted with $10 \text{ } \mu\text{L}$ octyl alcohol prior to the addition of $90 \text{ } \mu\text{L}$ 30% H_2O_2 . The tubes were tightly capped and placed in a convection oven set at $95 \text{ }^\circ\text{C}$. After 30 min, $100 \text{ } \mu\text{L}$ 50%NaOH was added to the hot tubes, which were vortexed, tightly capped and returned to the oven and incubated at $95 \text{ }^\circ\text{C}$ for a further 4 h. Immediately after digestion, $25 \text{ } \mu\text{L}$ of 5 mM NH_4F was added to aid monosilicic acid formation. Si concentrations was determined using ultraviolet spectrophotometer subsystem (SP-1105; Ningbo Hinotek 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. [6]. 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 Hinotek 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 Hinotek Technology, Shanghai, China).

2.4.3 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. [18]. 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 ($1400 \times g$, 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 ($60 \text{ }^\circ\text{C}$ for 24 h) 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. [41] 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 $1400\times g$ 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).

2.5 Analysis of Data

Data 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 [48]. Multifactorial-ANOVA was also used to analyze the influence between cultivars. 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).

3 Results

3.1 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). We found that 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). [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. Shoot and root [Al] decreased significantly ($P < 0.0001$) under 10Al + Si, 15Al + Si, and 20Al + Si treatments in cultivar 'CTC9002' by ~16, 13 and 14% and by ~10, ~19 and 22%, respectively; whereas in the 'CTC9003' cultivar, the decreases were ~28%, ~35%, and ~30% in shoot [Al] and ~10%, ~20% to ~27% in root [Al], respectively as compared to the 10Al-Si, 15Al-Si, and 20Al-Si treatments ($P < 0.0001$) (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.

3.2 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 35 d of experimental period.

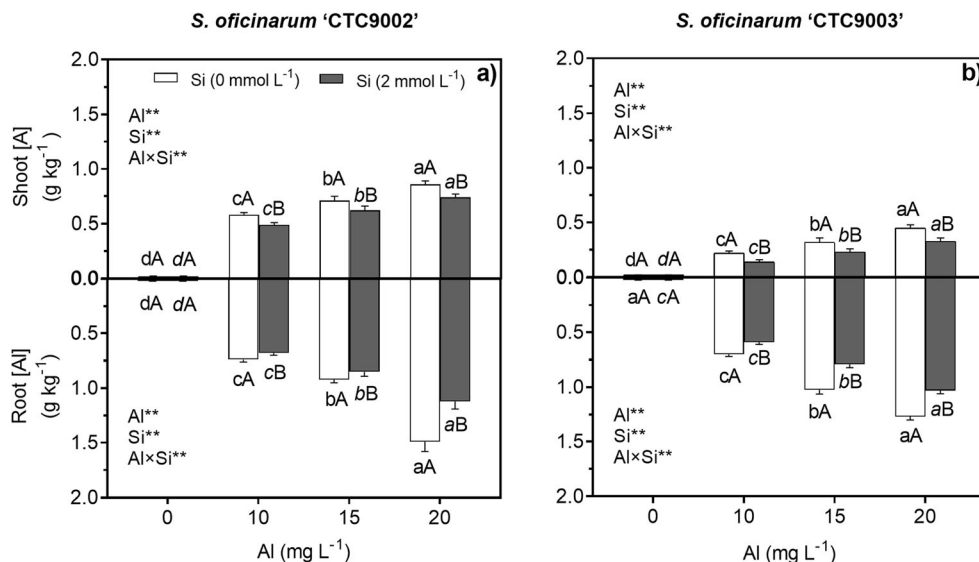


Fig. 1 Al concentrations in shoots and roots of cultivar 'CTC9002' (a) and cultivar 'CTC9003' (b) as a function of the Al application (0, 10, 15, and 20 mg L^{-1}) and the absence and presence (2 mmol L^{-1}) of Si. Values are represented by the means of four replications \pm standard deviation (SD).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

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 \times Si, Aluminum–Silicon interaction

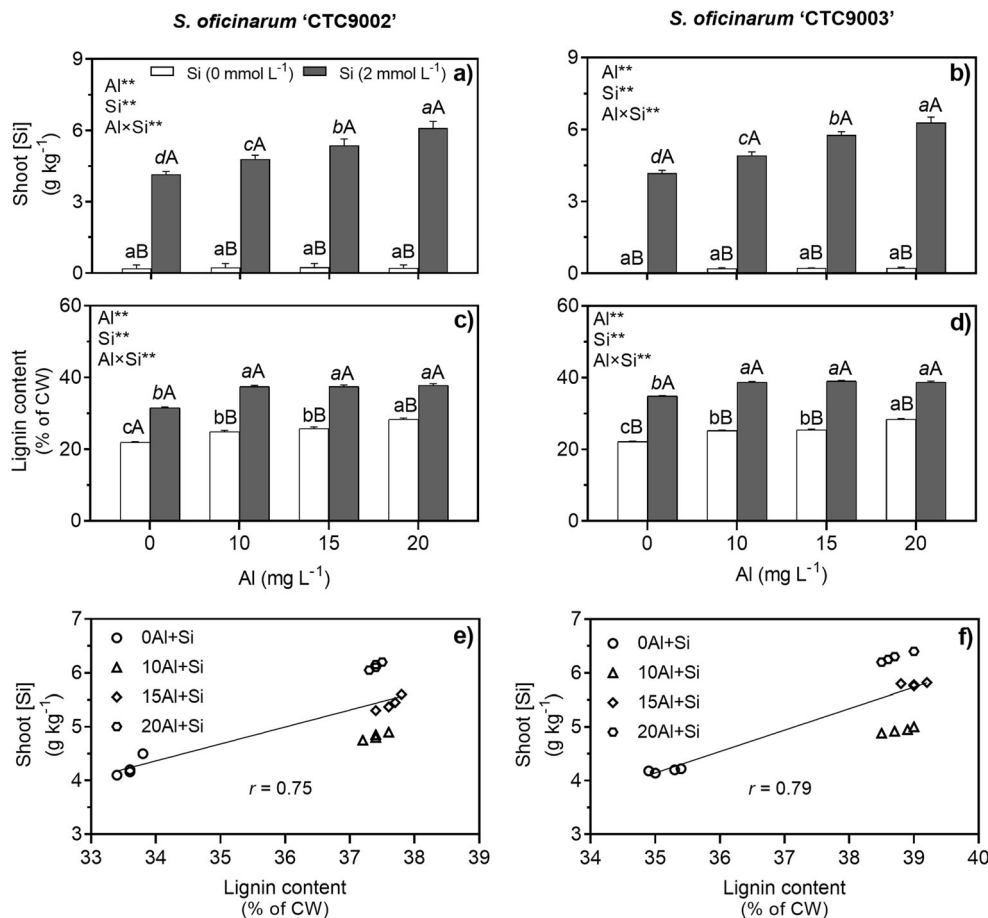
Results indicated that the [Si] in shoots of both sugarcane cultivars was significantly ($P < 0.0001$) increased with increasing Al treatments in the growth medium. Data regarding [Si] in shoots are influenced by increasing Al stress (Fig. 2a, b) indicated highly significant difference between cultivars 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 the cultivar ‘CTC9002’. In both Al stressed sugarcane cultivars all combined treatments (10Al + Si, 15Al + Si, and 20Al + Si) increased shoot [Si], and showed significance difference ($P < 0.0004$) compared to the 0Al + Si treatment, but the highest increases 47% and 51% in the cultivars ‘CTC9002’ and ‘CTC9003’, respectively, were obtained with the application of the 20Al + Si treatments in comparison to the 0Al + Si treatment. Similarly, the 10Al + Si and 15Al + Si treatments increased shoot [Si] by 13 and 29% in the cultivar ‘CTC9002’ and ~18 and 38% in the cultivar ‘CTC9003’ relative to the 0Al + Si treatment Fig. 2a, b).

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 ($P < 0.0001$). [lignin] in shoots increased under 10Al + Si, 15Al + Si, and 20Al + Si treatments as average by ~14% and ~19% in the cultivars ‘CTC9002’ and ‘CTC9003’, respectively, and showed significant difference ($P < 0.0003$) compared to the 0Al + Si treatment (Fig. 2c, d). However, shoots [lignin] under non-Si addition conditions, increased in all 10Al-Si, 15Al-Si, and 20Al-Si treatments in both sugarcane cultivar as compared to the 0Al-Si treatment, especially in the 20Al-Si treatment (26% increase in the cultivar ‘CTC9002’ and 29% in the cultivar ‘CTC9003’), whereas the 10Al-Si and 15Al-Si treatments showed similar effect on increasing [lignin] shoots and these increased were of 14 and 16% in the cultivar ‘CTC9002’ and ‘CTC9003’, respectively compared to the 0Al-Si treatment (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

Fig. 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



positively correlated with [lignin] ($r = 0.75$) in ‘CTC9002’ (Fig. 2e) and in ‘CTC9003’ ($r = 0.79$) (Fig. 2f).

3.3 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 and 4). Applied Al concentrations in the growth medium significantly ($P < 0.001$) decreased the concentrations of macronutrients in both sugar cane cultivars, irrespectively of the addition of Si (Fig. 3a–l). However, the concentration of N, P, K, Mg, and S under 0Al + Si treatment not showed significant difference ($P = 0.2153$), except for Ca concentration ($P < 0.0001$) for both cultivars compared to the 0Al-Si treatment. In addition, the concentration of all macronutrients increased in 10Al + Si, 15Al + Si, and 20Al + Si treatments and showed significant ($P < 0.0011$) difference in comparison with the 10Al-Si, 15Al-Si, and 20Al-Si treatments (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 the concentration of Zn and Cu in the cultivar ‘CTC9002’ not showed significant ($P = 0.5177$) difference between 0Al-Si and 0Al + Si treatments (Fig. 4e, g), but Mn concentration increased under the effects of 0Al-Si treatment relative to the 0Al + Si treatment ($P < 0.0001$) (Fig. 4c). Whereas the concentration of Fe and B increased in 0Al + Si treatment and showed significant ($P < 0.0034$) difference than that observed in response to the 0Al-Si treatment (Fig. 4a, i). However, in the cultivar ‘CTC9003’ the concentration of Mn, Zn and B not exhibited significant ($P = 0.5177$) difference between 0Al-Si and 0Al + Si treatments (Fig. 4d–j), but Fe concentration was higher in 0Al-Si treatment than that in 0Al + Si treatment (Fig. 4b) ($P < 0.0031$), while Cu concentration increased in 0Al + Si treatment than that under 0Al-Si treatment ($P < 0.0022$) (Fig. 4h). Nevertheless, the concentration of Fe, Mn, Zn, Cu, and B increased in 10Al + Si, 15Al + Si, and 20Al + Si treatments and showed significant ($P < 0.001$) difference compared to that in 10Al-Si, 15Al-Si, and 20Al-Si treatments (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).

3.4 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). Applied Al stress showed an exacerbate decreasing in MaUE use efficiency in the shoots of both sugarcane cultivars, inclusive with the presence of Si in the growth medium (Fig. 5a–l). The MaUE use efficiency in the shoots of the ‘CTC9002’ not showed significant ($P < 0.0001$) effects between 0Al-Si and 0Al + Si treatments (Fig. 5a–k). However, cultivar ‘CTC9003’, showed significant responses in MaUE use efficiency in the shoots, N, K and Mg use efficiency not exhibited significant ($P = 0.6028$) difference between 0Al-Si and 0Al + Si treatments (Fig. 5b–j). However, the use efficiency of P and S increased in 0Al + Si treatment than that observed under 0Al-Si treatment ($P < 0.001$) (Fig. 5d, l). While Ca use efficiency increased in 0Al-Si treatment compared to the 0Al + Si treatment ($P < 0.0031$) (Fig. 5h). Nevertheless, shoot MaUEs of both cultivars were higher under 10Al + Si, 15Al + Si, and 20Al + Si treatments and showed significant ($P < 0.001$) difference compared to that in 10Al-Si, 15Al-Si, and 20Al-Si treatments (Fig. 5a–l). Cultivar ‘CTC9003’ had significantly greater MaUE as compared to the ‘CTC9002’. Moreover, cultivar ‘CTC9003’ were more responsible to Si fertilization for increasing MaUE 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. 6 a–j). Meanwhile, the use efficiencies of Fe, Zn, Cu, and B in shoots of the cultivar ‘CTC9002’ not revealed significant ($P = 0.7305$) difference between 0Al-Si and 0Al + Si treatments (Fig. 6a–i). While, Mn-use efficiency was higher in 0Al + Si treatment than that observed in response to the 0Al-Si treatment ($P < 0.0021$) (Fig. 6c). However, in the ‘CTC9003’ the use efficiency of Mn, Zn, Cu, and B not showed significant ($P = 0.5518$) difference between 0Al-Si and 0Al + Si treatments (Fig. 6d–j). Whereas the Fe-use efficiency increased under 0Al + Si treatment

Fig. 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

relative to the 0Al-Si treatment ($P < 0.0011$) (Fig. 6b). In addition, between cultivar the beneficial effects of Si

addition on increased concentration micronutrient were more prominent in cultivar ‘CTC9003’ than that

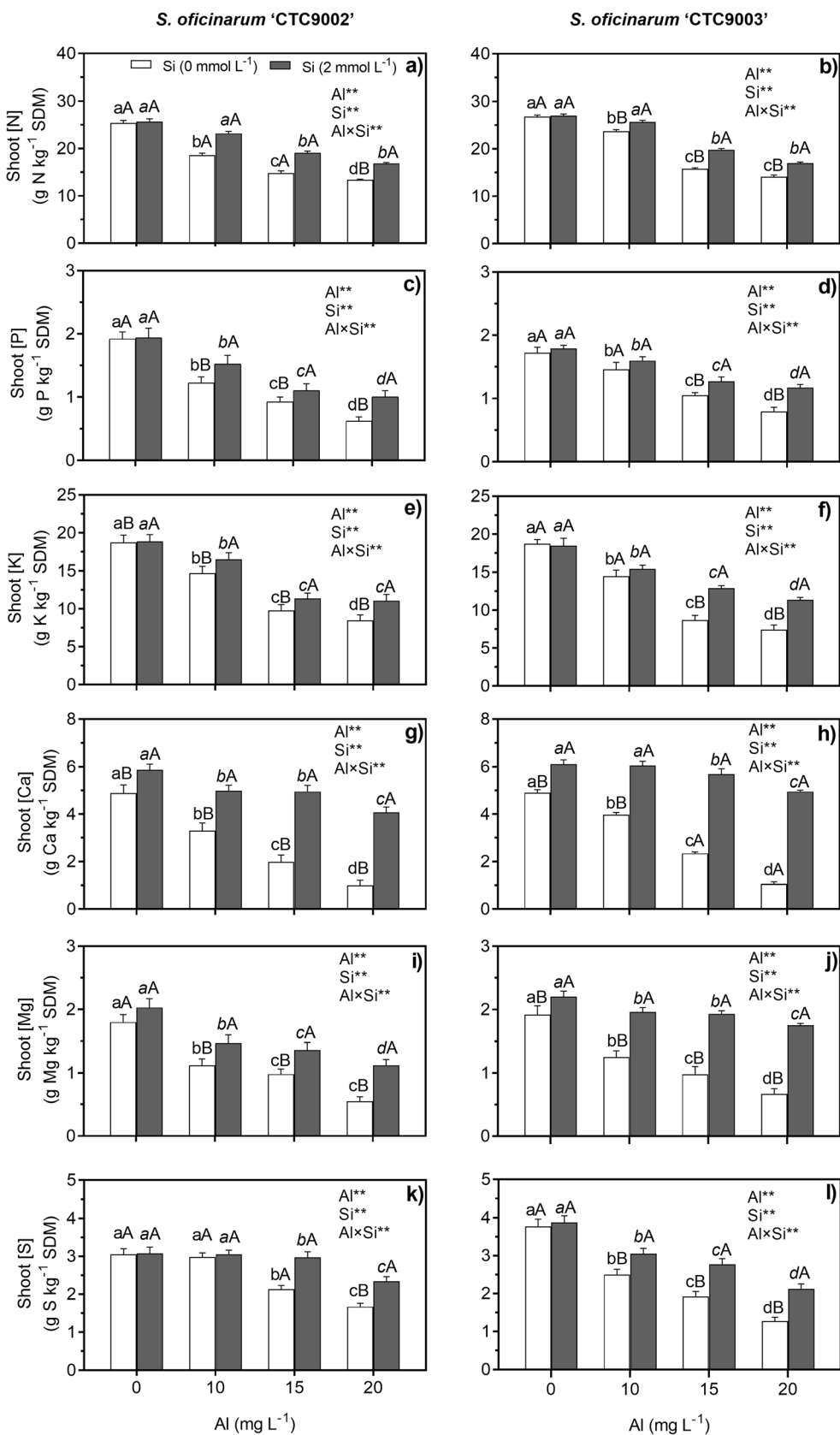
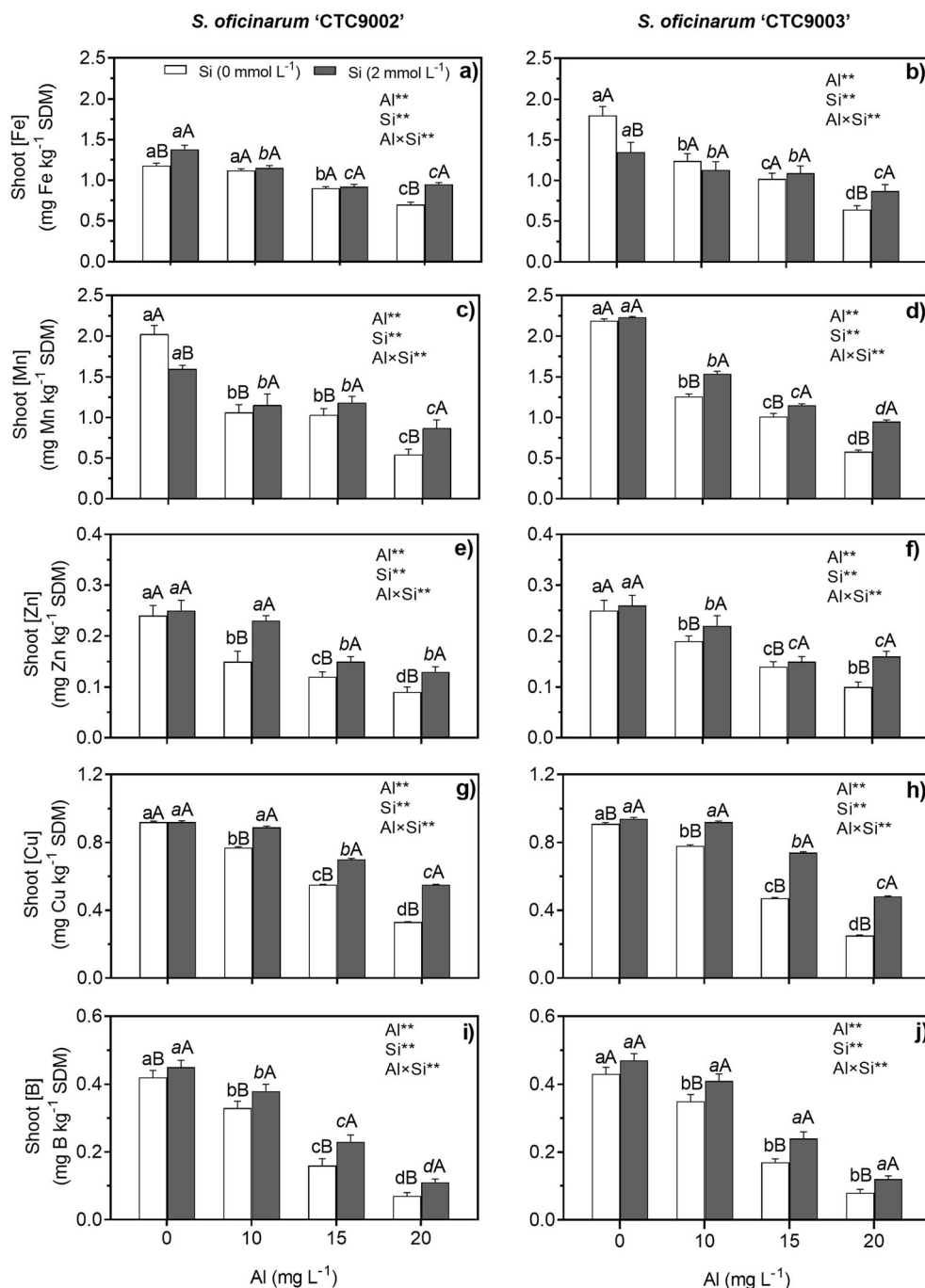


Fig. 4 Concentration of micronutrients in the shoots of sugarcane seedlings. Iron concentration in cultivar ‘CTC9002’ (a) and cultivar ‘CTC9003’ (b), manganese concentration in cultivar ‘CTC9002’ (c) and cultivar ‘CTC9003’ (d), zinc concentration in cultivar ‘CTC9002’ (e) and cultivar ‘CTC9003’ (f), copper concentration in 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



‘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 showed an exacerbate decreasing 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 SDM in both sugarcane cultivars not exhibited significant difference ($P = 0.8439$) difference between 0Al-Si and 0Al + Si treatments. However, the SDM was increased in cultivar ‘CTC9002’ by

~10, ~17 and ~25% and in ‘CTC9003’ by ~10%, ~19%, and ~30% cultivars, under the effects of 10Al + Si, 15Al + Si, and 20Al + Si treatments and significantly ($P < 0.0001$) mitigated the deleterious effects of Al toxicity compared to the 10Al-Si, 15Al-Si, and 20Al-Si treatments (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).

4 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. [63] 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 [62] and sorghum plants [31]. 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) [12]. Another possible mechanism causing Si to decrease the plants to absorb Al^{3+} was earlier reported by Singh et al. [57] 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 Al^{3+} concentration in the external solution by forming Al-Si complexes [65]. 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 [5]. In addition, Si can negatively regulate the expression of metal transporter genes and thus reduce the metal(loid)s uptake in plant cells [17]. 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 [14, 37]. However, phytoliths formation, composition, and localization vary among plant species [34, 39]. In general, plants with a high root or shoot Si concentration exhibit enhanced tolerance to abiotic stresses like metal toxicity [13]. According to Ashraf et al. [3], 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 3.3–7.0 [40]. Similar trends were reported previously in Al-stressed barley plants by Liang et al. [35], 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 [9]. These 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.) [23], rice (*Oryza sativa* L.) [29], and *Phragmites australis* [52, 68]. 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 [67]. Second, Si could be associated with lignin-carbohydrate complexes in the wall of epidermal cells [28]. Third, Si helps to increase energy available, leading to plants to synthesize nonstructural organic compounds, like

cellulose and lignin [44, 52]. Fourth, Si-induced signal transduction pathways, increasing lignin production [19, 20] and have directly influence the lignin synthesis, mainly by formation of hemicellulose-metal complexes [61]. Other research has suggested that Si enhance [lignin], which increase plant tolerance to Al toxicity in ryegrass [50] and wheat [62, 63], 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 [30, 58]. An interesting result of our study was that Si application increased shoot concentrations of macro- 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 [35, 62, 63] and sorghum [32]. Besides, Si plays a crucial role in maintaining mineral uptake in acidic conditions by improving metal homeostasis [1, 45, 61]. In addition, Si induces enzyme activation such as H-ATPase that is involved in the nutrient uptake process [58]. Therefore, higher concentrations of macro- 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 [58, 61]. 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 [8, 58]. 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 (Figs. 3 and 4), as well as a diminishing of the overall NUE (Figs. 5 and 6). Similar observation was report in barley plants, in which the growth was harmfully influenced by Al toxicity [62, 63].

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 macro- 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 previous reported in different species, such as barley [35], rice [21, 57], sorghum [9, 31], corn [59], and wheat [63]. 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 [62, 63] and sorghum [31]. 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 macro-

Fig. 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

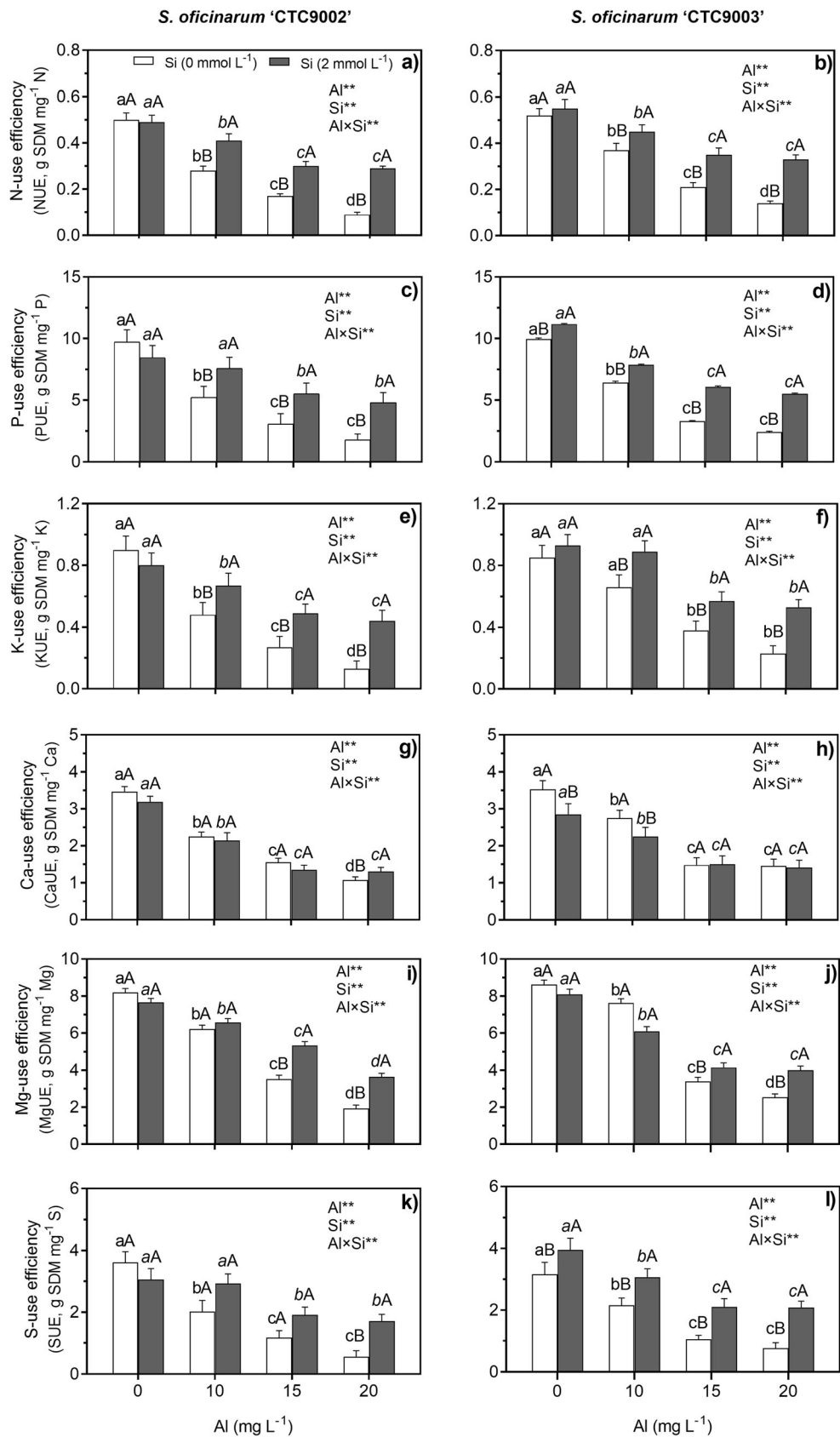
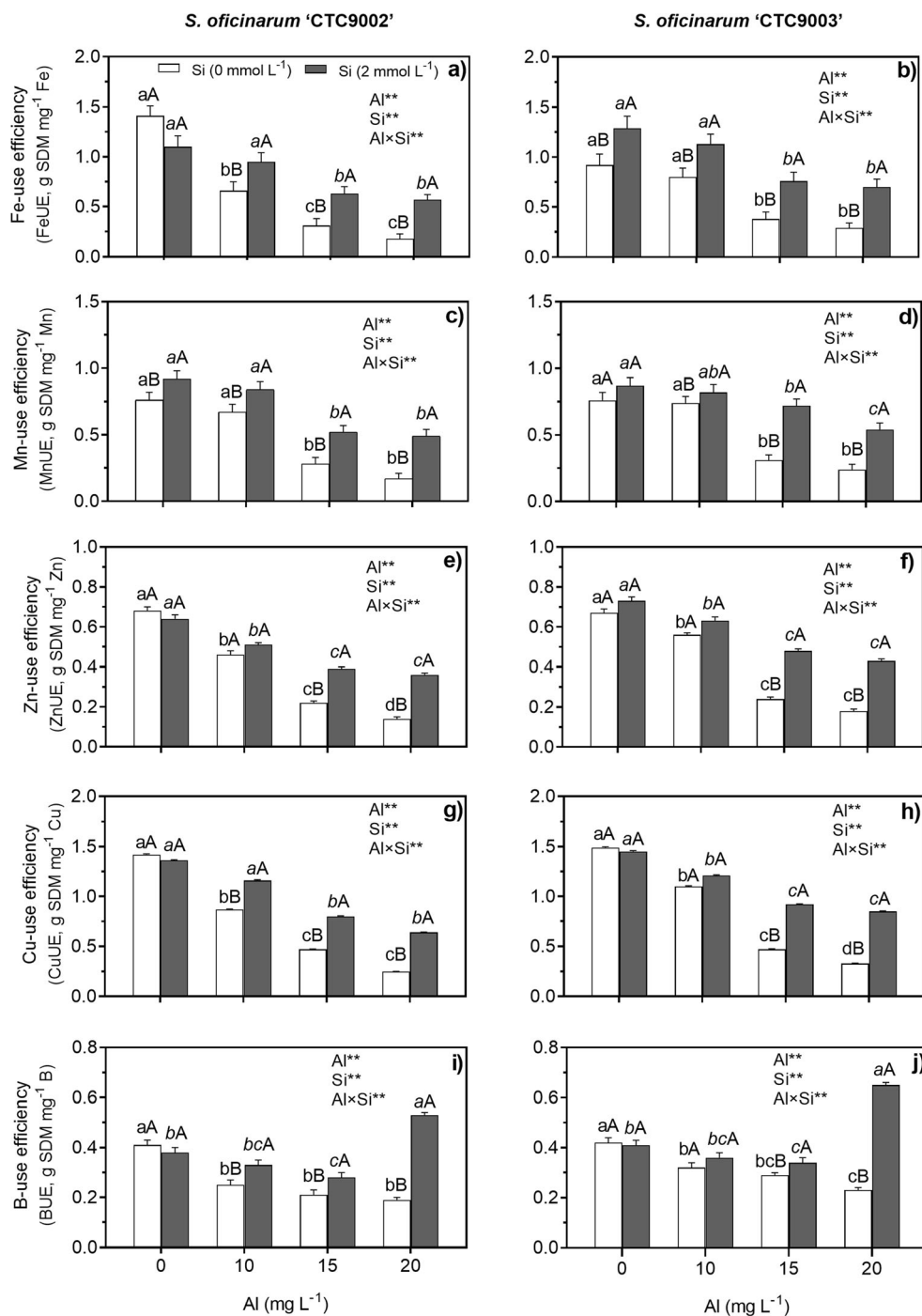


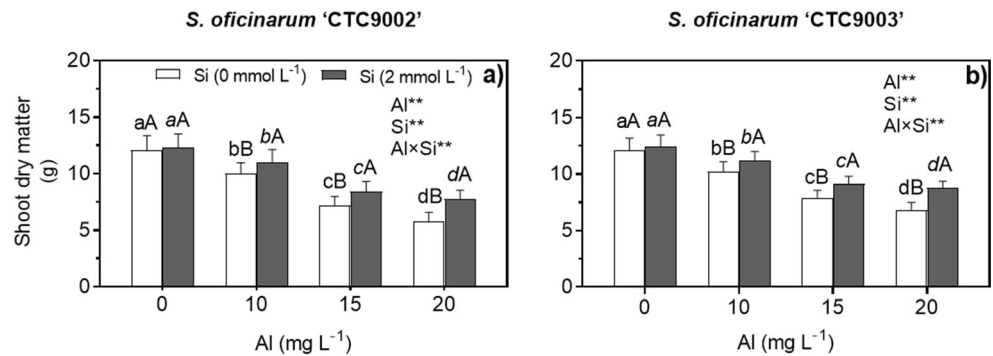
Fig. 6 Use efficiency of micronutrients in the shoots of sugarcane seedlings. Iron use efficiency in cultivar ‘CTC9002’ (a) and cultivar ‘CTC9003’ (b), manganese use efficiency in cultivar ‘CTC9002’ (c) and cultivar ‘CTC9003’ (d), zinc use efficiency in cultivar ‘CTC9002’ (e) and cultivar ‘CTC9003’ (f), copper use efficiency in 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



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 that ‘CTC9002’. In concordance with our results, difference response Si

application under Al stress between genotypes were observed in experiments with wheat [62, 63], rice [21], and sorghum [31]. Our findings contribute to the current understanding of cultivar ‘CTC9003’ showed more acclimatization mechanisms to Si fertilization than cultivar ‘CTC9002’ under Al stress.

Fig. 7 Shoot dry matter production of sugarcane seedlings in cultivar ‘CTC9002’ (a) and cultivar ‘CTC9003’ (b). Treatments and statistics as described in Fig. 1



5 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.

Acknowledgments This work was partially supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES) (Finance Code 001). We would also like to thank São Paulo State University—UNESP, School of Agricultural and Veterinarian Sciences—FCAV, for providing the facilities necessary for this research.

Code Availability Not applicable.

Author Contribution 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.

Funding The project was financially supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brazil (CAPES) – Brazil [Finance Code 001].

Data Availability Not applicable.

Declarations

Ethics Approval and Consent to Participate No animal or human subjects were used in this work. This manuscript is an original paper and has not been published in other journals. The authors agreed to keep the copyright rule.

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.

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

References

- Adrees M, Ali S, Rizwan M, Zia-ur-Rehman M, Ibrahim M, Abbas F, Farid M, Qayyum MF, Irshad MK (2015) Mechanisms of silicon-mediated alleviation of heavy metal toxicity in plants: a review. *Ecotoxicol Environ Saf* 119:186–197. <https://doi.org/10.1016/J.ECOENV.2015.05.011>
- Arunakumara KKIU, Walpola BC, Yoon MH (2013) Aluminum toxicity and tolerance mechanism in cereals and legumes – a review. *J Korean Soc Appl Biol Chem* 56:1–9. <https://doi.org/10.1007/s13765-012-2314-z>
- Ashraf M, Afzal M, Ahmed R et al (2010) Alleviation of detrimental effects of NaCl by silicon nutrition in salt-sensitive and salt-tolerant genotypes of sugarcane (*Saccharum officinarum* L.). *Plant Soil* 326:381–391. <https://doi.org/10.1007/s11104-009-0019-9>
- Balestrasse KB, Gallego SM, Tomaro ML (2006) Aluminium stress affects nitrogen fixation and assimilation in soybean (*Glycine max* L.). *Plant Growth Regul* 48:271–281. <https://doi.org/10.1007/s10725-006-0010-x>
- Barceló J, Poschenrieder C (2002) Fast root growth responses, root exudates, and internal detoxification as clues to the mechanisms of aluminium toxicity and resistance: a review. *Environ Exp Bot* 48: 75–92. [https://doi.org/10.1016/S0098-8472\(02\)00013-8](https://doi.org/10.1016/S0098-8472(02)00013-8)
- Bataglia OC, Teixeira JPF, Furlani PR et al (1983) Métodos de análise química de plantas. 1st edn. Instituto Agronômico de Campinas, Campinas
- Brackhage C, Schaller J, Bäucker E, Dudel EG (2013) Silicon availability affects the stoichiometry and content of calcium and micro nutrients in the leaves of common reed. *Silicon* 5:199–204. <https://doi.org/10.1007/s12633-013-9145-3>

8. Calero Hurtado A, Chiconato DA, de Prado RM et al (2019) Silicon attenuates sodium toxicity by improving nutritional efficiency in sorghum and sunflower plants. *Plant Physiol Biochem* 142:224–233. <https://doi.org/10.1016/j.plaphy.2019.07.010>
9. Calero Hurtado A, Chiconato DA, de Prado RM et al (2020) Different methods of silicon application attenuate salt stress in sorghum and sunflower by modifying the antioxidative defense mechanism. *Ecotoxicol Environ Saf* 203:110964. <https://doi.org/10.1016/j.ecoenv.2020.110964>
10. Castanho RB, Souto TS (2013) A importância da orizicultura na constituição do espaço geográfico: evolução e dinâmica da produção de arroz no período de 1930 a 2010 em Ituiutaba (Minas Gerais – MG, Brasil) e a inserção de novas culturas. *Cuad Geogr Rev Colomb Geogr* 23:93–107. <https://doi.org/10.15446/rcdg.v23n1.32465>
11. Clark RB (1975) Characterization of phosphatase of intact maize roots. *J Agric Food Chem* 23:458–460. <https://doi.org/10.1021/jf60199a002>
12. Cocker KM, Evans DE, Hodson MJ (1998) The amelioration of aluminium toxicity by silicon in higher plants: solution chemistry or an in planta mechanism? *Physiol Plant* 104:608–614. <https://doi.org/10.1034/j.1399-3054.1998.1040413.x>
13. Debona D, Rodrigues FA, Datnoff LE (2017) Silicon's role in abiotic and biotic plant stresses. *Annu Rev Phytopathol* 55:85–107. <https://doi.org/10.1146/annurev-phyto-080516-035312>
14. Deshmukh R, Sonah H, Belanger R (2020) New evidence defining the evolutionary path of aquaporins regulating silicon uptake in land plants. *J Exp Bot* 71:eraa342. <https://doi.org/10.1093/jxb/eraa342>
15. Deus ACF, de Mello PR, de Cássia Félix Alvarez R et al (2020) Role of silicon and salicylic acid in the mitigation of nitrogen deficiency stress in rice plants. *Silicon* 12:997–1005. <https://doi.org/10.1007/s12633-019-00195-5>
16. Emamverdian A, Ding Y, Mokherdoran F, Xie Y (2015) Heavy metal stress and some mechanisms of plant defense response. *Sci World J* 2015:1–18. <https://doi.org/10.1155/2015/756120>
17. Emamverdian A, Ding Y, Xie Y, Sangari S (2018) Silicon mechanisms to ameliorate heavy metal stress in plants. *Biomed Res Int* 2018:1–10. <https://doi.org/10.1155/2018/8492898>
18. Ferrarese MLL, Zottis A, Ferrarese-Filho O (2002) Protein-free quantification in soybean (*Glycine max*) roots. *Biologia (Bratisl)* 57:541–543
19. Fleck AT, Nye T, Repenning C et al (2010) Silicon enhances suberization and lignification in roots of rice (*Oryza sativa*). *J Exp Bot* 62:2001–2011
20. Fleck AT, Schulze S, Hinrichs M, Specht A, Waßmann F, Schreiber L, Schenk MK (2015) Silicon promotes exodermal casparian band formation in Si-accumulating and Si-excluding species by forming phenol complexes. *PLoS One* 10:e0138555. <https://doi.org/10.1371/journal.pone.0138555>
21. Freitas LB, Fernandes DM, Maia SCM, Fernandes AM (2017) Effects of silicon on aluminum toxicity in upland rice plants. *Plant Soil* 420:263–275. <https://doi.org/10.1007/s11104-017-3397-4>
22. Geraldo Oliveira E, Miziara F, Ferreira ME (2014) Fatores determinantes e cenários futuros sobre a expansão da cana-de-açúcar na região de Cerrado no Centro-Oeste mineiro. *Ateliê Geográfico* 9:79–103. <https://doi.org/10.5216/ag.v9i1.29101>
23. Hashemi A, Abdolzadeh A, Sadeghipour HR (2010) Beneficial effects of silicon nutrition in alleviating salinity stress in hydroponically grown canola, *Brassica napus* L., plants. *Soil Sci Plant Nutr* 56:244–253. <https://doi.org/10.1111/j.1747-0765.2009.00443.x>
24. Haynes RJ (2014) A contemporary overview of silicon availability in agricultural soils. *J Plant Nutr Soil Sci* 177:831–844. <https://doi.org/10.1002/jpln.201400202>
25. Hernandez-Apaolaza L (2014) Can silicon partially alleviate micronutrient deficiency in plants? A review. *Planta* 240:447–458. <https://doi.org/10.1007/s00425-014-2119-x>
26. Hodson MJ, Evans DE (2020) Aluminium/silicon interactions in higher plants- an update. *J Exp bot* eraa024. 71:6719–6729. <https://doi.org/10.1093/jxb/eraa024>
27. Hurtado AC, Chiconato DA, de Mello PR et al (2021) Silicon alleviates sodium toxicity in sorghum and sunflower plants by enhancing ionic homeostasis in roots and shoots and increasing dry matter accumulation. *Silicon* 13:475–486. <https://doi.org/10.1007/s12633-020-00449-7>
28. Inanaga S, Okasaka A, Tanaka S (1995) Does silicon exist in association with organic compounds in rice plant? *Soil Sci Plant Nutr* 41:111–117. <https://doi.org/10.1080/00380768.1995.10419564>
29. Klotzbücher T, Klotzbücher A, Kaiser K, Vetterlein D, Jahn R, Mikutta R (2018) Variable silicon accumulation in plants affects terrestrial carbon cycling by controlling lignin synthesis. *Glob Chang Biol* 24:e183–e189. <https://doi.org/10.1111/gcb.13845>
30. Kochian LV, Hoekenga OA, Piñeros MA (2004) How do crop plants tolerate acid soils? Mechanisms of aluminum tolerance and phosphorous efficiency. *Annu Rev Plant Biol* 55:459–493. <https://doi.org/10.1146/annurev.arplant.55.031903.141655>
31. Kopittke PM, Gianoncelli A, Kourousias G, Green K, McKenna BA (2017) Alleviation of Al toxicity by Si is associated with the formation of Al–Si complexes in root tissues of Sorghum. *Front Plant Sci* 8:2189. <https://doi.org/10.3389/fpls.2017.02189>
32. Kostic L, Nikolic N, Bosnic D, Samardzic J, Nikolic M (2017) Silicon increases phosphorus (P) uptake by wheat under low P acid soil conditions. *Plant Soil* 419:447–455. <https://doi.org/10.1007/s11104-017-3364-0>
33. Kraska JE, Breitenbeck GA (2010) Simple, robust method for quantifying silicon in plant tissue. *Commun Soil Sci Plant Anal* 41:2075–2085. <https://doi.org/10.1080/00103624.2010.498537>
34. Li H, Zhu Y, Hu Y, Han W, Gong H (2015) Beneficial effects of silicon in alleviating salinity stress of tomato seedlings grown under sand culture. *Acta Physiol Plant* 37:1–9. <https://doi.org/10.1007/s11738-015-1818-7>
35. Liang Y, Yang C, Shi H (2001) Effects of silicon on growth and mineral composition of barley grown under toxic levels of aluminum. *J Plant Nutr* 24:229–243. <https://doi.org/10.1081/PLN-100001384>
36. Liang Y, Sun W, Zhu YG, Christie P (2007) Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: a review. *Environ Pollut* 147:422–428. <https://doi.org/10.1016/j.envpol.2006.06.008>
37. Ma JF (2004) Characterization of the system and molecular mapping of the silicon transporter gene in rice. *Plant Physiol* 136:3284–3289. <https://doi.org/10.1104/pp.104.047365>
38. Ma JF, Yamaji N (2006) Silicon uptake and accumulation in higher plants. *Trends Plant Sci* 11:392–397. <https://doi.org/10.1016/j.tplants.2006.06.007>
39. Ma JF, Yamaji N (2008) Functions and transport of silicon in plants. *Cell Mol Life Sci* 65:3049–3057
40. Miles N, Manson AD, Rhodes R, van Antwerpen R, Weigel A (2014) Extractable silicon in soils of the south African sugar industry and relationships with crop uptake. *Commun Soil Sci Plant Anal* 45:2949–2958. <https://doi.org/10.1080/00103624.2014.956881>
41. Moreira-Vilar FC, de Siqueira-Soares RC, Finger-Teixeira A et al (2014) The acetyl bromide method is faster, simpler and presents best recovery of lignin in different herbaceous tissues than Klason and Thioglycolic acid methods. *PLoS One* 9:e110000. <https://doi.org/10.1371/journal.pone.0110000>
42. Olivera D, Prado R, Lizcano R et al (2019) Silicon supplementation alleviates ammonium toxicity in sugar beet (*Beta vulgaris* L.). *J Soil Sci Plant Nutr* 19:413–419. <https://doi.org/10.1007/s42729-019-00043-w>

43. Panda Anjib K, Baluška F (2015) Aluminum stress adaptation in plants. 1st edn. Springer, Cham, Switzerland
44. Penning de Vries FWT, Brunsting AHM, Van Laar HH (1994) Products, requirements and efficiency of biosynthesis a quantitative approach. *J Theor Biol* 45:339–377. [https://doi.org/10.1016/0022-5193\(74\)90119-2](https://doi.org/10.1016/0022-5193(74)90119-2)
45. Pontigo S, Ribera A, Gianfreda L, de la Luz Mora M, Nikolic M, Cartes P (2015) Silicon in vascular plants: uptake, transport and its influence on mineral stress under acidic conditions. *Planta* 242:23–37. <https://doi.org/10.1007/s00425-015-2333-1>
46. Pontigo S, Godoy K, Jiménez H, Gutiérrez-Moraga A, Mora ML, Cartes P (2017) Silicon-mediated alleviation of aluminum toxicity by modulation of al/si uptake and antioxidant performance in ryegrass plants. *Front Plant Sci* 8:642. <https://doi.org/10.3389/fpls.2017.00642>
47. Qian L, Chen B, Chen M (2016) Novel alleviation mechanisms of aluminum phytotoxicity via released Biosilicon from Rice straw-derived biochars. *Sci Rep* 6:1–11. <https://doi.org/10.1038/srep29346>
48. R Core Team (2019) R: a language and environment for statistical computing. 2015. 4
49. Rahman M, Lee S-H, Ji H, Kabir A, Jones C, Lee KW (2018) Importance of mineral nutrition for mitigating aluminum toxicity in plants on acidic soils: current status and opportunities. *Int J Mol Sci* 19:3073. <https://doi.org/10.3390/ijms19103073>
50. Ribera-Fonseca A, Rumpel C, de la Mora ML et al (2018) Sodium silicate and calcium silicate differentially affect silicon and aluminum uptake, antioxidant performance and phenolics metabolism of ryegrass in an acid Andisol. *Crop Pasture Sci* 69:205. <https://doi.org/10.1071/CP17202>
51. Sasaki M, Yamamoto Y, Matsumoto H (1996) Lignin deposition induced by aluminum in wheat (*Triticum aestivum*) roots. *Physiol Plant* 96:193–198. <https://doi.org/10.1111/j.1399-3054.1996.tb00201.x>
52. Schaller J, Brackhage C, Dudel EG (2012) Silicon availability changes structural carbon ratio and phenol content of grasses. *Environ Exp Bot* 77:283–287. <https://doi.org/10.1016/j.envexpbot.2011.12.009>
53. Sheng H, Chen S (2020) Plant silicon-cell wall complexes: identification, model of covalent bond formation and biofunction. *Plant Physiol Biochem* 155:13–19. <https://doi.org/10.1016/j.plaphy.2020.07.020>
54. Shi G, Cai Q, Liu C, Wu L (2010) Silicon alleviates cadmium toxicity in peanut plants in relation to cadmium distribution and stimulation of antioxidative enzymes. *Plant Growth Regul* 61:45–52. <https://doi.org/10.1007/s10725-010-9447-z>
55. Silva S (2012) Aluminium toxicity targets in plants. *J Bot* 2012:1–8. <https://doi.org/10.1155/2012/219462>
56. da Silva RG, Rosa-Santos TM, de Castro França S et al (2019) Microtranscriptome analysis of sugarcane cultivars in response to aluminum stress. *PLoS One* 14:e0217806. <https://doi.org/10.1371/journal.pone.0217806>
57. Singh VP, Tripathi DK, Kumar D, Chauhan DK (2011) Influence of exogenous silicon addition on aluminium tolerance in rice seedlings. *Biol Trace Elem Res* 144:1260–1274. <https://doi.org/10.1007/s12011-011-9118-6>
58. Singh S, Tripathi DK, Singh S, Sharma S, Dubey NK, Chauhan DK, Vaculik M (2017) Toxicity of aluminium on various levels of plant cells and organism: a review. *Environ Exp Bot* 137:177–193. <https://doi.org/10.1016/j.envexpbot.2017.01.005>
59. de Sousa A, Saleh AM, Habeeb TH, Hassan YM, Zrieq R, Wadaan MAM, Hozzein WN, Selim S, Matos M, Abdelgawad H (2019) Silicon dioxide nanoparticles ameliorate the phytotoxic hazards of aluminum in maize grown on acidic soil. *Sci Total Environ* 693:133636. <https://doi.org/10.1016/j.scitotenv.2019.133636>
60. UDOP (2021) CTC launches variety of sugarcane that produce more adaptable to the Brazilian cerrado
61. Vaculik M, Lukačová Z, Bokor B, Martinka M, Tripathi DK, Lux A (2020) Alleviation mechanisms of metal(loid) stress in plants by silicon: a review. *J Exp Bot* 71:6744–6757. <https://doi.org/10.1093/jxb/eraa288>
62. Vega I, Nikolic M, Pontigo S, Godoy K, Mora MLL, Cartes P (2019) Silicon improves the production of high antioxidant or structural phenolic compounds in barley cultivars under aluminum stress. *Agronomy* 9:388. <https://doi.org/10.3390/agronomy9070388>
63. Vega I, Rumpel C, Ruíz A, Mora ML, Calderini DF, Cartes P (2020) Silicon modulates the production and composition of phenols in barley under aluminum stress. *Agronomy* 10:1138. <https://doi.org/10.3390/agronomy10081138>
64. Wang C, Wood FA (1973) A modified aluminum reagent for the determination of aluminum after HNO₃-H₂SO₄ digestion. *Can J Soil Sci* 53:237–239. <https://doi.org/10.4141/cjss73-035>
65. Wang Y, Stass A, Horst WJ (2004) Apoplastic binding of aluminum is involved in silicon-induced amelioration of aluminum toxicity in maize. *Plant Physiol* 136:3762–3770. <https://doi.org/10.1104/pp.104.045005>
66. Weber F, Liao W, Barrantes A et al (2019) Silicate-phenolic networks: coordination-mediated deposition of bioinspired tannic acid coatings. *Chem Eur J* 25:9870–9874. <https://doi.org/10.1002/chem.201902358>
67. Williams RJP (1986) Introduction to silicon chemistry and biochemistry. In: *Silicon biochemistry*, 1st ed. Wiley., Hoboken, NJ, USA, pp. 24–29
68. Xia S, Song Z, Van Zwieten L et al (2020) Silicon accumulation controls carbon cycle in wetlands through modifying nutrients stoichiometry and lignin synthesis of *Phragmites australis*. *Environ Exp Bot* 175:104058. <https://doi.org/10.1016/j.envexpbot.2020.104058>
69. Zhang J, He Z, Tian H, Zhu G, Peng X (2007) Identification of aluminium-responsive genes in rice cultivars with different aluminium sensitivities. *J Exp Bot* 58:2269–2278. <https://doi.org/10.1093/jxb/erm110>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.