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Beneficial Role of Silicon on Regulating C, N, and P Stoichiometric Homeostasis and the Growth of Sugarcane Seedlings under Aluminum Toxicity

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Abstract

This study investigates the protective role of silicon (Si) on growth performance, nutrient homeostasis, and C:N:P stoichiometric of sugarcane (*Saccharum* spp.) seedlings under aluminum (Al) stress in hydroponic conditions. Experiments were conducted as a factorial scheme (2×2) in a randomized complete block design (RCBD), with four replications, for each sugarcane cultivar ("CTC9002" and "CTC9003"). They were grown in pots filled with normal Clark nutrient (pH = 5.8 without Al) and acidic Clark nutrient solution (pH = 4.5 with 15 mg L^{-1} of Al, as aluminum sulfate [$Al_2 (SO_4)_3 \cdot 18H_2O$]) in the absence or presence of Si (2 mM, as potassium silicate (K_2SiO_3). Sugarcane seedlings of both cultivars grown under Al stress alone significantly decreased root, culm, and leaf dry biomass, and this adverse effect was reversed by Si supplementation. Added Si also modified nutrient homeostasis of both sugarcane cultivars, and these effects varied depending on plant organs. Si decreased the concentration of C, N, and P and correspondingly increased C:N, C:P, and N:P stoichiometric. In addition, both sugarcane cultivars had a positive response to Si supplementation, but cultivar "CTC9003" is more recommended under added Si to ameliorate the detrimental effects caused by Al toxicity. The findings of this study indicate that Si promoted attenuation of Al-stressed sugarcane seedlings by regulating nutrient and homeostasis stoichiometric, leading to improve dry biomass production.

Keywords Ecological Stoichiometric · Nutrient Homeostasis · *Saccharum officinarum* · Silicon · Plant Organs

1 Introduction

Sugarcane (*Saccharum* spp.) is an important crop in Brazil and worldwide by sugar and ethanol production (Silva et al. 2019). Brazil is a higher sugarcane producer and has extended this crop to numerous areas, which is predominant in acid soils (Sousa Junior et al. 2022). In acid soils, it predominates the phytotoxic Al^{3+} form; thereby, high amounts of Al^{3+} are available to plants, thus affecting several physiological, biochemical, and molecular processes, which decrease plant growth and productivity (Vega et al. 2019). The high presence of Al^{3+} in the soil inhibits root growth, water, and nutrient uptake, which subsequently decreases crop yield (Silva et al. 2019; Singh et al. 2017; Vega et al. 2020). In addition, Al^{3+} induces modifications in the structure and/or functions of cells (Pontigo et al. 2017), plasma membrane (Sade et al. 2016; Singh et al. 2017), nutrient homeostasis (Kostic et al. 2017), and signal transduction pathways (Silva et al. 2019).

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Plants have evolved a diversity of defense mechanisms to cope with different toxic effects caused by Al^{3+}, which are commonly related to Al exclusion and/or internal tolerance mechanisms (Pontigo et al. 2017; Souri et al. 2021). Exclusion mechanisms include the exudation of organic acid anions and/or phenolic compounds by root, which links Al^{3+} and impedes its absorption inside cytosol (Pontigo et al. 2017; Singh et al. 2017). Tolerance mechanisms also include internal detoxification by forming Al complexes with organic constituents in the cytosol, distribution in the vacuole, and improved scavenging of reactive oxygen species (ROS) (Singh et al. 2017; Vaculík et al. 2020).

Si is well known as a non-essential element for plant species, although its presence in the medium growth as a beneficial element helps plants to confront abiotic stress conditions such as drought (Chaiwong and Prom-u-thai 2022; dos Santos et al. 2022; Namjoyan et al. 2021), salinity (Calero Hurtado et al. 2020a; Mahdieh et al. 2015), nutrient toxicity (Olivera et al. 2019; Silva et al. 2020), and nutrient deficiency (Maksimović et al. 2007; Oliveira et al. 2019; Teixeira et al. 2020), including Al stress in different plant species (Pontigo et al. 2015, 2017; Vega et al. 2019, 2020). The mechanisms of Si on the alleviation of Al toxicity are widely studied. Several mechanisms have been recommended to clarify the effects of Si on enhancing plant adaptation under Al stress conditions, such as establishing a mechanical/physical barrier (formed through $Si(OH)_4$ polymerization) for chemical resistance (Kumar et al. 2017) and improving antioxidative defense mechanism (Alzahrani et al. 2018; Calero Hurtado et al. 2020b) and nutrient uptake mechanisms (Calero Hurtado et al. 2019; Kostic et al. 2017). It has been suggested that Si induces a decrease in Al^{3+} uptake, translocation, complexation, and chelation by regulating antioxidant compound biosynthesis and gene expression (Pontigo et al. 2015; Vega et al. 2020; Zhang et al. 2007). Several studies also reported that Si declined the adverse effects of Al stress after the release of root exudates in various plant species (Imtiaz et al. 2016).

An important mechanism of Si in attenuating abiotic stress, including Al toxic, is by regulating nutrient homeostasis (Vaculík et al. 2020). Si can alter macronutrient (e.g., P) availability (Kostic et al. 2017). In addition, Si can also lower the heavy metal toxicity in plants by enhancing the concentration of both macro- as well as micro-nutrients like Ca, Mg, phosphorus (P), K, Zn, iron (Fe), and manganese (Mn) (Etesami and Jeong 2018; Souri et al. 2021) and improving the macro- and micro-nutrients use efficiency (Sousa Junior et al. 2022). Although the beneficial role of Si in the attenuation of Al stress is well established, little is known about its relevance in improving nutrient homeostasis and stoichiometry relationships.

Organic compost formation, including Si, could produce modifications on C, N, and P stoichiometric homeostasis and their ratios, leading to increase plant growth. Consequently, this study aimed to investigate the beneficial role of Si on the distribution and modification of C, N, and P stoichiometric homeostasis and their ratios, as well as dry biomass allocation in sugarcane seedlings under Al toxicity conditions. Therefore, we tested two main hypotheses: (i) Si supplementation may attenuate Al toxicity by improving dry biomass production and promote a higher level of stoichiometric homeostasis; (ii) supplied Si may attenuate Al toxicity by increasing Si concentration and modifying C, N, and P stoichiometric and their distribution in roots, culms, and leaves, favoring dry biomass allocation; and (iii) cultivar "CTC9003" showed better response to Si fertilization than cultivar "CTC9002" under Al stress.

2 Material and Methods

2.1 Plant Material and Growth Conditions

Buds of sugarcane seedlings (*Saccharum officinarum* L.) that used Canavieira Technology Center (CTC) cultivars "CTC9002" and "CTC9003," which were previously identified and characterized as a highly drought resistant genotype (UDOP 2021), were used as the plant material throughout both experiments. Buds grown, seedlings grown, acidic nutrient solution, characteristics of transplanting, acclimation and cultivation of both sugarcane seedlings, data of ionic strength, and constant aeration of the nutrient solution are given by Sousa Junior et al. (2022)

2.2 Experimental Design and Al and Si Treatments

In a study by Souza Junior et al. (2021), fourth levels of 0 mg L^{-1}, 10 mg L^{-1}, 15 mg L^{-1}, and 20 mg L^{-1} of Al (as $Al_2 (SO_4)_3 \cdot 18H_2O$) were used to establish the Al treatments, which were combined with two levels of Si treatments (0 mM and 2 mM). Our research focuses only on two levels of Al treatments, which were started by not adding or adding 15 mg L^{-1} of Al in NS on corresponding pots combined with the absence or presence of Si (2 mM). We thus present in this study the fourth combined treatments: non-Al stress and non-Si addition (-Al-Si), non-Al stress and Si addition (-Al + Si), Al stress and non-Si addition (+ Al-Si), and Al stress and Si addition (+ Al + Si).

2.3 Elemental Analysis

Thirty days after being grown, the sugarcane seedlings were harvested and divided into roots, culms, and leaves. Samples from roots, culms, and leaves were washed with distilled water, detergent solution (0.2%), HCl solution (0.1%), and finally, twice with deionized water (Calero Hurtado et al.

2019). All samples were placed on paper back and dried (60 ℃) using a forced ventilation oven (TE 394–3, Tecnal, Piracicaba, São Paulo, Brazil) to determine total dry biomass (TDB, mg plant^{-1}), root dry biomass (RDB, mg plant^{-1}), culm dry biomass (CDB, mg plant^{-1}), and leaf dry biomass (LDB, mg plant^{-1}). Samples from roots, culms, and leaves were pulverized with a Wiley mill fitted with a stainless-steel chamber and blades (IKA-WERKE, GMBH & CO. KG, Germany). The total concentrations of Si [Si] in roots, culms, and leaves were determined as described by Kraska and Breitenbeck (2010) using a two-phase wet-digestion procedure and the molybdenum blue colorimetry method (details on this methodology are given by Sousa Junior et al. (2022)).

Total concentrations of C [C] and N [N] were determined using a dry combustion (1000 ℃) analyzer (LECO Truspec CHNS) calibrated with the pattern LECO 502–278 of wheat (C = 45.00% and N = 2.68%). Total P concentrations [P] were determined using the molybdenum antimony colorimetric method and an ultraviolet spectrophotometer subsystem (model SP-1105, Ningbo Hinotek Technology, Shanghai, China) (Bataglia et al. 1983). Therefore, the C:N, C:P, and N:P ratios were determined using C, N, and P concentrations.

2.3.1 Statistical Analysis

The data are expressed as the mean of two independent experiments with more standard deviation (SD). Experimental data were analyzed using multifactorial analysis of variance (two-way ANOVA) following normality (Shapiro–Wilk) and homoscedasticity (Bartlett) tests. Differences among means were evaluated by means of the Scott-Knott test. P values ($P < 0.05$) were considered as statistically significant. In addition, the relationship between two response variables was investigated by Pearson correlation. All analyses were performed to test the significance of the observed differences using the R software [(http://www.r-project.org/, (R Core Team 2019)].

3 Results

3.1 Effects of Al and SI treatments on Total Dry Biomass and its Allocation

Total dry biomass (TDB) showed significant interaction among Al and Si treatments between sugarcane cultivars and among plant organs (Fig. 1a, b). Applied Al stress (+ Al-Si) significantly decreased TDB production in roots by 52%, culms by 55%, and leaves by 37% in the cultivar "CTC9002," whereas in "CTC9003," these decrease was by ~ 50% in RDB, 53% in CDB, and 34% in LDB, respectively, as compared to the -Al-Si treatment (Fig. 1a, b). However, the TDB was significantly increased under + Al + Si in RDB by 32%, in CDB by 45%, and in LDB by 16% in the cultivar "CTC9002," whereas in "CTC9003," these increases were 50% in RDB, 49% in CDB, and 19%, respectively, as compared to the -Al-Si treatment (Fig. 1a, b). Moreover, the cultivar "CTC9003" revealed a slight increase in the TDB production under -Al-Si, -Al + Si, and + Al-Si treatments and 8% under + Al + Si and showed a significant difference ($p < 0.0001$) compared to the cultivar "CTC9002" (Fig. 1a, b). Furthermore, in both sugarcane cultivars, higher dry biomass allocation on different plant organs occurred in the following order: leaf > root > culm (with a significant difference, $p < 0.0002$) (Fig. 1a, b).
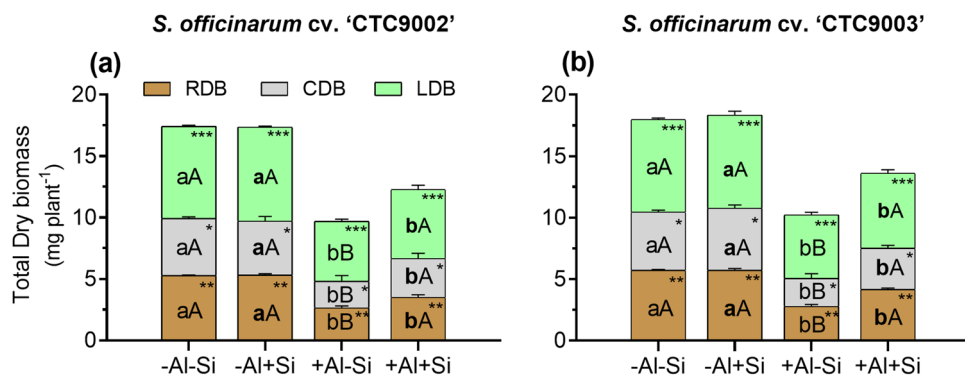

Fig. 1 Dry biomass in roots, culms, and leaves (**a**) in cultivar "CTC9002" and (**b**) in cultivar "CTC9003" in the function of different aluminum (Al) and silicon (Si) availabilities. Treatments: non-Al stress and non-Si addition (-Al-Si), non-Al stress and Si addition (-Al + Si), Al stress and non-Si addition (+ Al-Si), and Al stress and Si addition (+ Al + Si). Normal small letters indicate a significant dif-ference between Al treatments under non-Si addition; bold lowercase letters show a significant difference between aluminum treatments under silicon addition; and capital letters indicate a significant difference between Si treatments under non-Al or Al treatments; *, **, and *** denote a significance among plant organs in the same treatment, according to the Tukey test (ANOVA)

3.2 Effects of Al and Si Treatments on the Concentration of Si, C, N, and P in Different Plant Organs

The two-way ANOVA revealed significant ($p < 0.0001$) interaction between Al and Si treatments between cultivars and among organs on [Si], [C], [N], and [P] (Fig. 2a-h). Si supplementation to the medium growth varied its concentrations between Si and Al treatments between cultivars and among different plant organs. In both sugarcane cultivars, the [Si] was higher (~7%) under +Al+Si compared to -Al+Si (with a significant interaction, $p < 0.0011$)

(Fig. 2a, b). However, the highest [Si] (~8%) was recorded in the cultivar "CTC9003" than in "CTC9002" ($p < 0.0001$) (Fig. 2a, b). Furthermore, the [Si] in both sugarcane cultivars under +Al+Si treatment was similar in the following order: leaf > root > culm, but varied under -Al+Si treatment; in the cultivar "CTC9002," the order of [Si] was culm > leaf > root, while in cultivar "CTC9003" was leaf > culm > root (Fig. 2a, b).

Al stress showed significant variations in the [C] in both sugarcane cultivars promoted by Si supplementation. The cultivar "CTC9003" showed the highest [C] in leaves (10%) and roots (8%) compared to the "CTC9002," whereas this

Fig. 2 Concentration of silicon (Si), carbon, nitrogen, and phosphorous in roots, culms, and leaves of both sugarcane cultivars (**a**) in "CTC9002" and (**b**) in "CTC9003"; carbon concentration in roots, culms, and leaves in cultivar "CTC9002" (**c**) and in cultivar "CTC9003" (**d**); nitrogen concentration in roots, culms, and leaves in cultivar "CTC9002" (**e**) and in cultivar "CTC9003" (**f**); phosphorous concentration in roots, culms, and leaves in cultivar "CTC9002" (**g**) and in cultivar "CTC9003" (**h**) in the function of different aluminum (Al) and Si availabilities. Treatments: non-Al stress and non-Si addition (-Al-Si), non-Al stress and Si addition (-Al+Si), Al stress and non-Si addition (+Al-Si), and Al stress and Si addition (+Al+Si). Normal small letters indicate a significant difference between Al treatments under non-Si addition; bold lowercase letters show a significant difference between Al treatments under Si addition; and capital letters indicate a significant difference between Si treatments under non-Al or Al treatments; *, **, and *** denote significance among plant organs in the same treatment, according to the Tukey test (ANOVA)
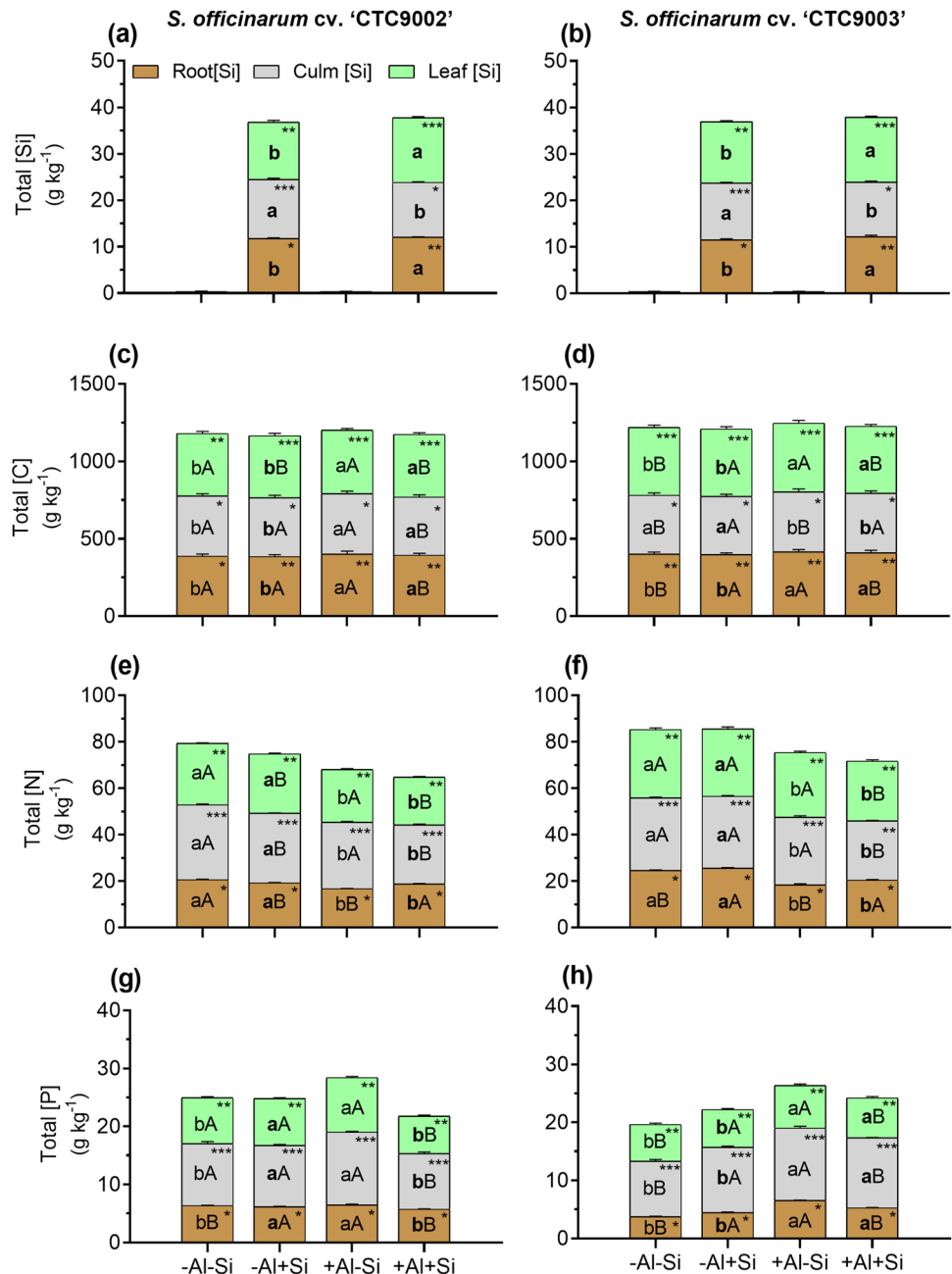
last showed higher (9%) culms [C] in comparison with the cultivar "CTC9003" ($P < 0.0001$) (Fig. 2c, d). However, the [C] increased significantly ($p < 0.0003$) under + Al-Si treatment of both cultivars and in all organs compared to the other treatments, but Si addition (-Al + Si and + Al + Si) decreased the [C] (with a significant difference, $p < 0.001$) compared to the non-Si addition (-Al-Si and + Al-Si). In addition, the order of [C] of each cultivar was leaf > root > culm and among treatments was + Al + Si > + Al-Si > -Al-Si = -Al + Si (Fig. 2c, d).

Similarly, [N] was higher (~ 18%) in leaves and roots in the cultivar "CTC9003" compared to the "CTC9002," but culms [C] showed similar effects in both cultivars ($p < 0.0001$) (Fig. 2e, f). However, under + Al + Si treatments, the [N] decreased significantly ($p < 0.0001$) in comparison to the other treatment (-Al-Si, -Al + Si, + Al-Si) conditions in both. In addition, the order of total [N] was similar for both cultivars culm > leaf > root and among treatments was -Al-Si > -Al + Si > + Al + Si > + Al-Si ($p < 0.0001$) (Fig. 2e, f).

Meanwhile, the total [P] in the culm of the cultivar "CTC9003" was superior by ~ 18% compared to the "CTC9002," whereas total [P] in the cultivar "CTC9002" was higher in roots by 24% and leaves by 18% and showed significant difference ($p < 0.0001$) in comparison with the "CTC9003" (Fig. 2g, h). Moreover, the [P] decreased under + Al + Si treatment in cultivar "CTC9002" compared to the other treatments. Similarly, cv. "CTC9003" decreased total [P] relative to the + Al-Si pots and was higher compared to the -Al-Si and -Al + Si treatments (Fig. 2g, h). In addition, the order of [P] showed similar effects in both cultivars as culm > leaf > root and among treatments was also similar like -Al-Si ≥ -Al + Si > + Al-Si > + Al + Si (Fig. 2g, h).

3.3 Effects of Al and Si Treatments on the Stoichiometric Ratios of C:N, C:P, and N:P and its Allocation in Different Plant Organs.

The ANOVA results exhibited significant ($p < 0.0001$) interaction between Al and Si treatments between cultivars and among plant organs on C:N, C:P, and N:P ratios (Fig. 3a-f). The C:N ratios in the cultivar "CTC9002" during the 35 d of experimental period in the + Al + Si treatment showed similar effects in comparison to the + Al-Si treatment and increased by 14% and ~ 25% compared to the -Al + Si and -Al-Si treatments ($p < 0.0024$), respectively (Fig. 3a). Whereas in the cultivar "CTC9003," the C:N ratio was higher in the + Al + Si treatment, increased by 5%, 19%, and 29% compared to the + Al-Si, -Al + Si, and -Al-Si treatments, respectively, and showed significant difference ($p < 0.0001$) (Fig. 3b).

The C:N ratio distribution in different plant organs showed similar variations (with significant interaction,

$P < 0.0017$) in both sugarcane cultivars, and the order was root > leaf > culm (Fig. 3a, b). Meanwhile, C:N ratio allocation revealed significant ($p < 0.0011$) variations in the cultivar "CTC9002," and the treatment order in roots was + Al-Si > + Al + Si > -Al + Si > -Al-Si, while in culm and leaves, the treatment order was similar as + Al + Si > + Al-Si > -Al + Si > -Al-Si (Fig. 3a), whereas in the cultivar "CTC9003," the C:N ratio allocation showed similar treatment order in root and culm as + Al-Si > + Al + Si > -Al + Si > -Al-Si, while in leaves was + Al + Si > + Al-Si > -Al + Si > -Al-Si ($p < 0.0004$) (Fig. 3b).

Results revealed that C:P ratio in the cultivar "CTC9002" decreased by 10% under + Al-Si treatment and showed a significant difference ($p < 0.001$) compared to the -Al-Si treatment (Fig. 3c). However, Si fertilization under Al stress (+ Al + Si) increased C:P ratio by approximately 28% compared to the + Al-Si treatment, with significant interaction ($p < 0.0001$); however, in the combined -Al + Si and -Al-Si treatments, the C:P ratio showed similar effects, but at the same time, these last treatments increased C:P ratio by 11% in comparison to the combined + Al-Si treatments (Fig. 3c). Likewise, in the sugarcane cultivar "CTC9003," the C:P ratio decreased by approximately 29% in the combined + Al-Si treatment (with a significant difference, $p < 0.0004$) compared to the -Al-Si treatments. However, the C:P ratio increased by ~ 16% in the combined + Al + Si treatment relative to the + Al-Si treatment ($p < 0.0027$) (Fig. 3d).

In order to investigate the effect of the Si treatments on the C:P ratio allocation in different plant organs under Al stress conditions, we found that in both sugar cane cultivars, the C:P ratio allocation was similar and plant organs order was root > leaf > culm ($p < 0.003$) (Fig. 3c, d). However, the C:P ratio showed significant variations between cultivar and among treatments; in the cultivar "CTC9002," the treatment order ($p < 0.001$) in roots and culm were similar like + Al + Si > -Al + Si > -Al-Si > + Al-Si, while in leaves, the order was + Al + Si > -Al-Si > Al + Si > + Al-Si (Fig. 3c). Meanwhile, in the cultivar "CTC9003," the C:P ratio allocation showed similar treatment order in root and culm as + Al + Si > + Al-Si > -Al + Si > -Al-Si, while in leaves, the order was + Al-Si > + Al + Si > -Al + Si > -Al-Si ($p < 0.01$) (Fig. 3b).

Plants treated with combined + Al-Si treatment showed an evident decrease in the N:P ratio by approximately 24% and 43% in cultivars "CTC9002" and "CTC9003," respectively, and showed a significant difference ($p < 0.0001$) compared to the -Al-Si treatments (Fig. 3e, f). Likewise, the N:P ratio in cultivars "CTC9002" and "CTC9003" increased by approximately 16% and 18%, respectively, in the combined + Al + Si treatment (with a significant difference, $p < 0.001$) compared to the + Al-Si treatment (Fig. 3e, f). Consequently, results revealed that the cultivar

Fig. 3 C:N ratios in roots, culms, and leaves in cultivar "CTC9002" (**a**) and in cultivar "CTC9003" (**b**); C:P ratios in roots, culms, and leaves in cultivar "CTC9002" (**c**) and in cultivar "CTC9003") **d**); and N:P ratios in roots, culms, and leaves in cultivar "CTC9002" (**e**) and in cultivar "CTC9003" (**f**) in the function of different aluminum (Al) and silicon (Si) availabilities. Treatments: non-Al stress and non-Si addition (-Al-Si), non-Al stress and Si addition (-Al + Si), Al stress and non-Si addition (+ Al-Si), and Al stress and Si addition (+ Al + Si). Normal small letters indicate a significant difference between Al treatments under non-Si addition; bold lowercase letters show a significant difference between Al treatments under Si addition; and capital letters indicate a significant difference between Si treatments under non-Al or Al treatments; *, **, and *** denote significance among plant organs in the same treatment, according to the Tukey test (ANOVA)
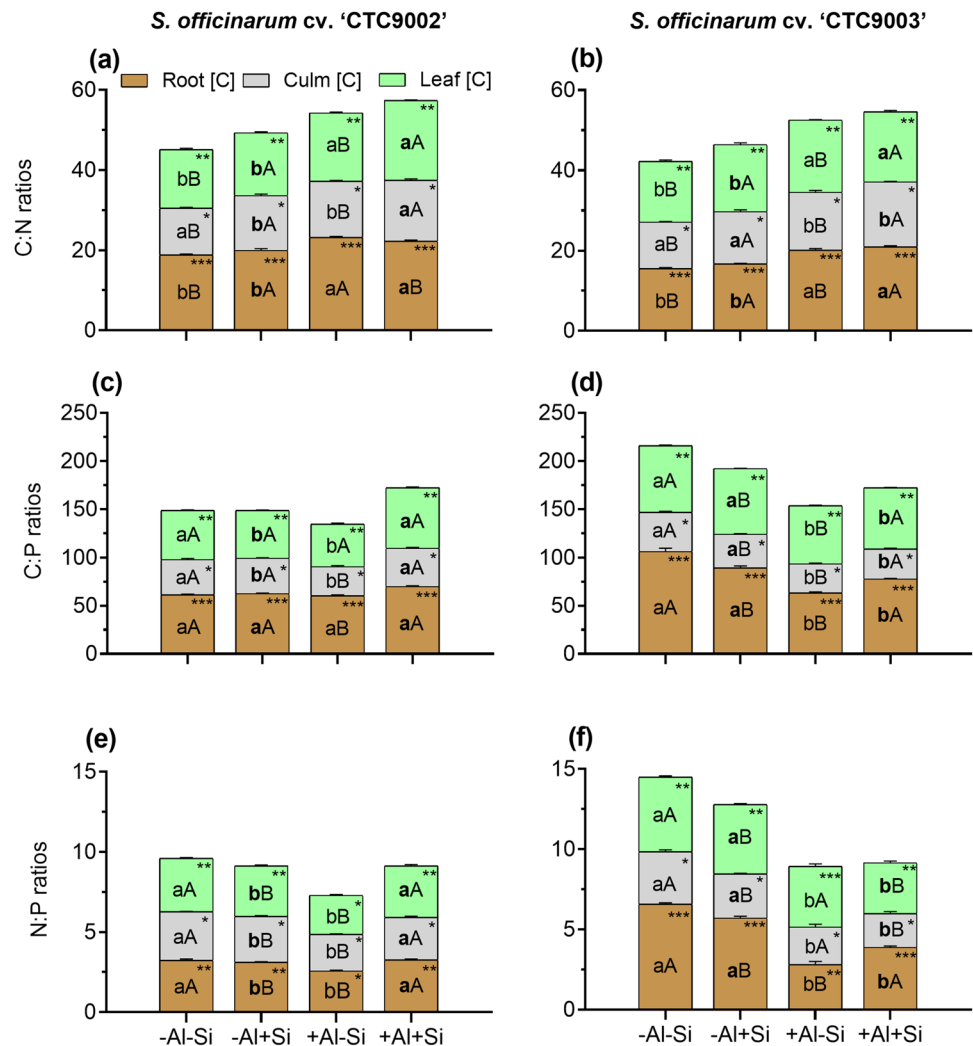
"CTC9003" exhibited a slight increment in the N:P ratio by approximately 51%, 40%, 14%, and 9% in the -Al-Si, -Al + Si, + Al-Si, and + Al + Si treatments, respectively, and showed significant difference ($p < 0.001$) compared to the cultivar "CTC9002" (Fig. 3e, f).

During the 35 d of experimental period, the N:P ratio varied between cultivars and among treatments; in the cultivar "CTC9002," the treatment order was -Al-Si > -Al + Si = + Al + Si > + Al-Si, whereas in the cultivar "CTC9003," the treatment order was -Al-Si > -Al + Si > + Al + Si > + Al-Si ($p < 0.004$) (Fig. 3e, f). Likewise, significant ($p < 0.002$) changes and variations in the allocation of N:P ratio were observed between cultivars, among plant organs and among treatments; for cultivar "CTC9002," the treatment order in roots was + Al + Si > -Al-Si > -Al + Si > + Al-Si, for culm was -Al-Si > -Al + Si > + Al + Si > + Al-Si, and for leaves was -Al-Si > + Al + Si > -Al + Si > + Al-Si (Fig. 3e). Meanwhile, the distribution of N:P ratio in the cultivar "CTC9003," the treatment order was similar in roots and leaves as -Al-Si > -Al + Si > + Al + Si > + Al-Si, while for culm was -Al-Si > -Al + Si > + Al-Si > + Al + Si ($p < 0.001$) (Fig. 3f).

A correlation analysis involving all combined treatments made it possible to evaluate the strategies of C, N, and P allocation to leaves, culms, and leaves of both sugarcane cultivars from the proportion of [C], [N], and [P] in specific plant organs to the total plant [C], [N], and [P] versus dry biomass allocation (dry biomass proportion from the same plant organ divided to the total plant dry biomass) exhibited significant changes and variations between cultivars and among treatments (Figs. 4, 5, and 6).

Results indicating that a negative correlation was observed in the root organ of both sugarcane cultivars "CTC9002" ($r = 0.56$, $p < 0.0196$) and "CTC9003" ($r = 0.51$, $p < 0.0458$) and in leaf organ of cultivar "CTC9003" ($r = 0.56$, $p < 0.0243$), whereas a positive correlation was observed in the culms and leaf organ of both sugarcane cultivars, in culm of cultivar "CTC9002" ($r = 0.34$, $p < 0.0192$) and "CTC9003" ($r = 0.56$, $p < 0.0238$) and in leaves of cultivar "CTC9002" ($r = 0.74$, $p < 0.0003$).

Fig. 4 Correlation analysis between carbon distribution and biomass allocation to roots (top row), culms (middle row), and leaves (bottom row) of both *S. officinarum* cultivars ("CTC9002" and "CTC9003"). Treatments: non-aluminum stress and non-silicon addition (-Al-Si), non-aluminum stress and silicon addition (-Al+Si), aluminum stress and non-silicon addition (+Al-Si), and aluminum stress and silicon addition (+Al+Si). r = correlation coefficient
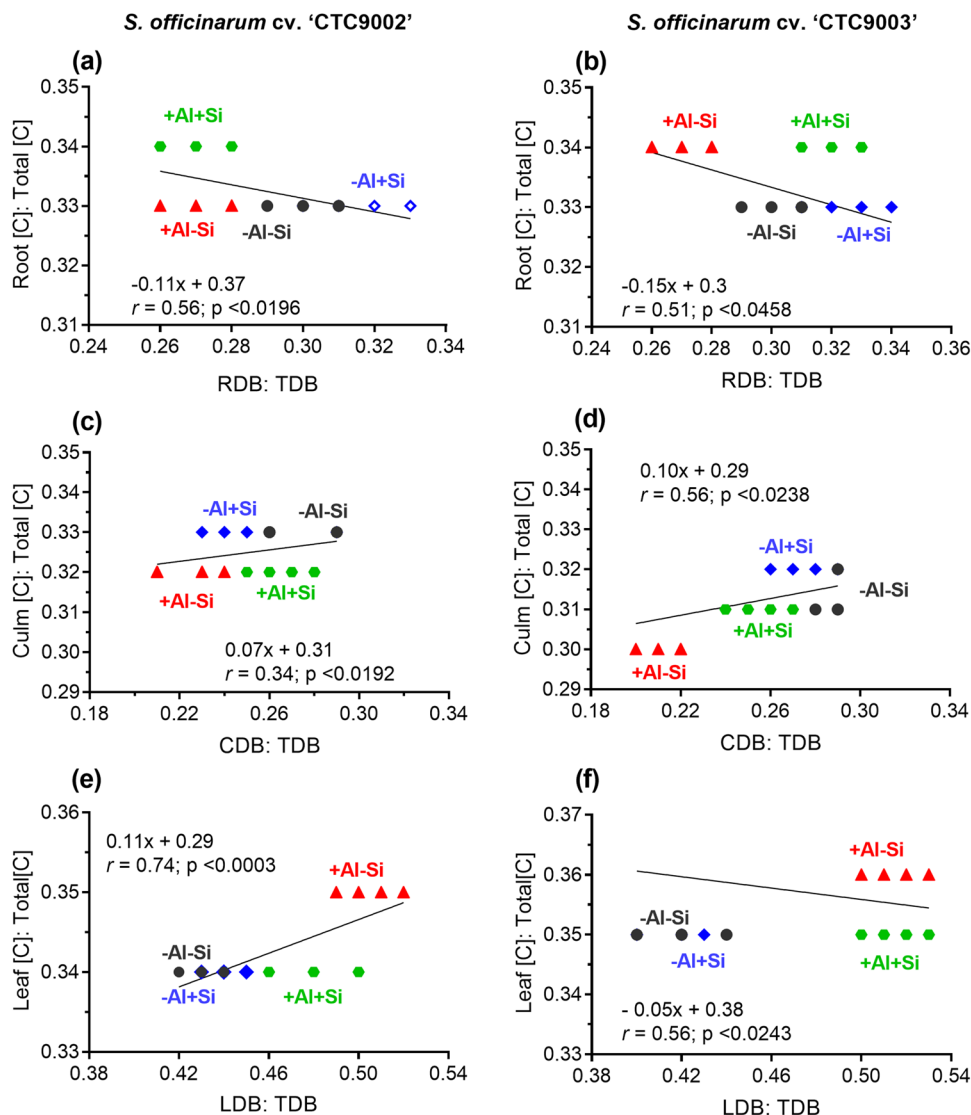

Si nutrition revealed significant variations among plant organs and between sugarcane cultivars. Compared with the +Al-Si treatment, the +Al+Si treatment showed the lowest production of RDB:TDB with higher proportions of root [C]:total [C] ratio in the cultivars "CTC9002," but in the cultivar "CTC9003," it tended to have higher RDB:TDB with the same higher proportions of root [C]:total [C] ratio (Fig. 4a, b). However, in culms of both sugarcane cultivars, the +Al+Si treatment increases linearly the relationship CDM:TDB proportion with a higher culm [C]:total [C] ratio (Fig. 4c-d), but in leaf organs, the response between cultivars was different in the cultivar "CTC9002"; the higher proportions were observed in the +Al-Si treatment compared to the +Al+Si treatment (Fig. 4c), whereas in the cultivar "CTC9003" under +Al+Si treatment, it showed higher LDM:TDB proportion with the lowest leaf [C]:total [C] ratios (Fig. 4d).

Results reveled that proportions root:culm:leaf [N]:total [N] showed negative correlation in cultivar "CTC9002," roots ($r = 0.51$, $p < 0.0424$), culms ($r = 0.57$, $p < 0.0207$), and leaves ($r = 0.50$, $p < 0.0411$) (Fig. 5a, c, e). Similarly, cultivar "CTC9003" showed a negative correlation in culms ($r = 0.61$, $p < 0.0118$) (Fig. 5d); however, a positive correlation in roots ($r = 0.58$, $p < 0.0179$) and leaves ($r = 0.78$, $p < 0.003$) was observed (Fig. 5b, f).

Si supplementation showed significant variations among plant organs and between sugarcane cultivars. Under +Al+Si treatment, the root organ showed the lowest RDB:TDB proportion with higher root [N]:total [N] in cultivar "CTC9002" compared to the -Al+Si treatment (Fig. 5a). However, culm and leaf showed higher RDB:TDB proportion with the lowest root [N]:total [N] compared to the -Al+Si treatment (Fig. 5c, e).

Results indicated that proportions root:culm:leaf [P]:total [P] showed significant variation between cultivars

Fig. 5 Correlation analysis between nitrogen distribution and biomass allocation in roots (top row), culms (middle row), and leaves (bottom row) of both *Saccharum officinarum* cultivars ("CTC9002" and "CTC9003"). Treatments: non-aluminum stress and non-silicon addition (-Al-Si), non-aluminum stress and silicon addition (-Al+Si), aluminum stress and non-silicon addition (+Al-Si), and aluminum stress and silicon addition (+Al+Si). r = correlation coefficient
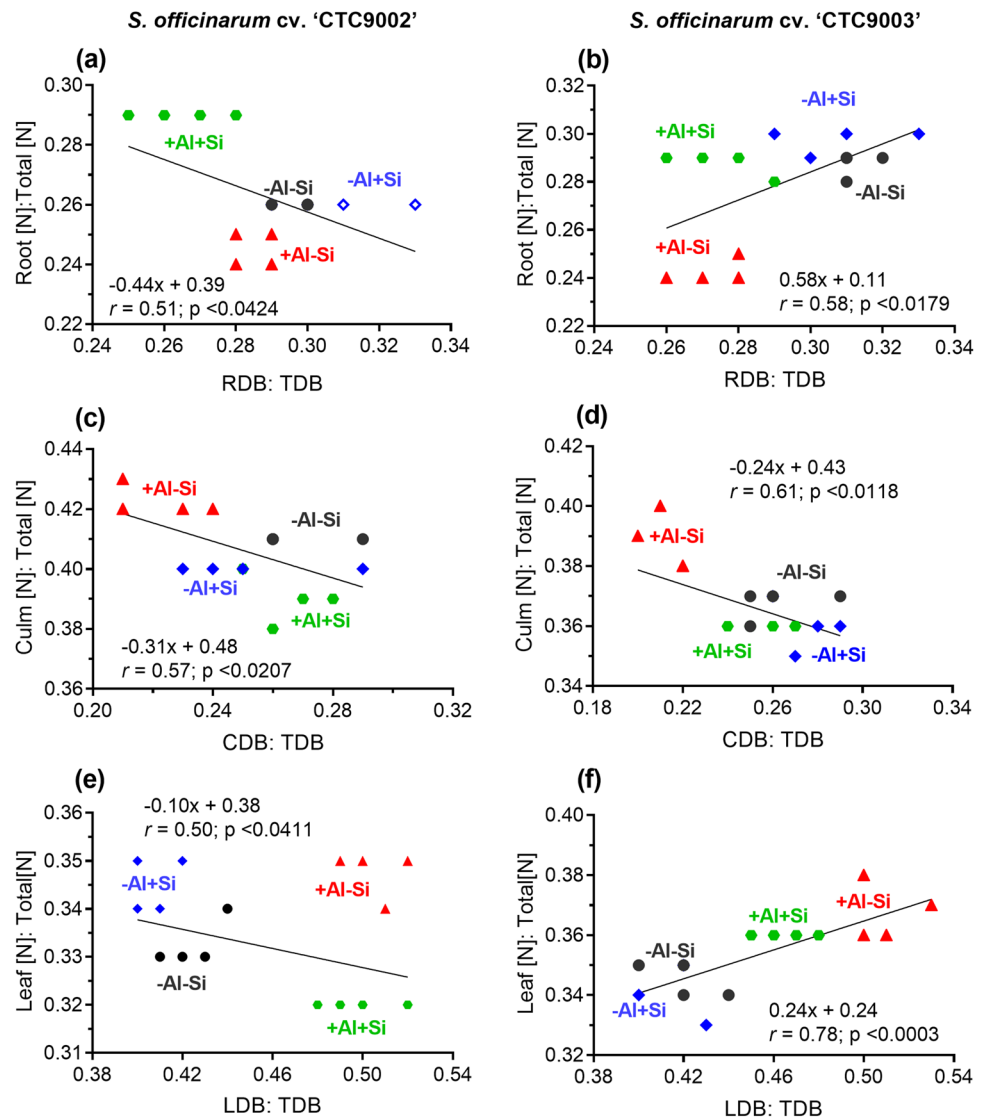
and roots, and leaf [P]:total [P] relationship showed positive correlation in cultivar "CTC9002" (root: $r = 0.51$, $p < 0.0409$; leaf: $r = 0.55$, $p < 0.0290$) (Fig. 6a, c, e) and a negative correlation in cultivar "CTC9003" (root: $r = 0.85$, $p < 0.0001$; leaf: $r = 0.52$, $p < 0.0308$) (Fig. 6b, f). In addition, in culm part, cultivar "CTC9002" revealed a negative correlation ($r = 0.52$, $p < 0.0399$) (Fig. 6c), but culm organ of cultivar "CTC9003" showed a positive correlation ($r = 0.58$, $p < 0.0193$) (Fig. 6d).

Si application exhibited significant variations among plant organs and between cultivars on relationships between RDB:TDB proportion and root [P]:total [P] ratio. Si addition increased RDB:TDB proportion with a higher root [P]:total [P] ratio in cultivar "CTC9002," particularly under + Al + Si treatment as compared to the + Al-Si treatment (Fig. 6a). Conversely, in the cultivar "CTC9003," higher RDB:TDB proportion with the lowest root [P]:total

[P] ratio in all Si treatments was observed, especially in + Al + Si treatment compared to the + Al-Si treatment (Fig. 6b).

In culms of both sugarcane cultivars, Si addition increased CDB:TDB proportion with lowest ulm [P]:total [P] ratio in cultivar "CTC9002" we observed than that in + Al-Si treatment; but, in the cultivar "CTC9003," Si supplementation showed highest CDB:TDB proportion with higher culm [P]:total [P] ratios compared to the + Al-Si treatment (Fig. 6c, d). Conversely, we observe that the higher LDB:TDB proportion was observed under + Al-Si treatment with a higher leaf [P]:total [P] ratio in leaves of the cultivar "CTC9002" compared to the other Si treatments (Fig. 6e). However, the leaves of the cultivar "CTC9003" showed higher LDB:TDB proportion with lower root [P]:total [P] ratio under + Al-Si treatment in comparison with the other Si treatments (Fig. 6f).

Fig. 6 Correlation analysis between a phosphorous distribution and biomass allocation in roots (top row), culms (middle row), and leaves (bottom row) of both *S. officinarum* cultivars ("CTC9002" and "CTC9003"). Treatments: non-aluminum stress and non-silicon addition (-Al-Si), non-aluminum stress and silicon addition (-Al+Si), non-aluminum stress and silicon addition (-Al+Si), and aluminum stress and silicon addition (+Al+Si). *r*=correlation coefficient
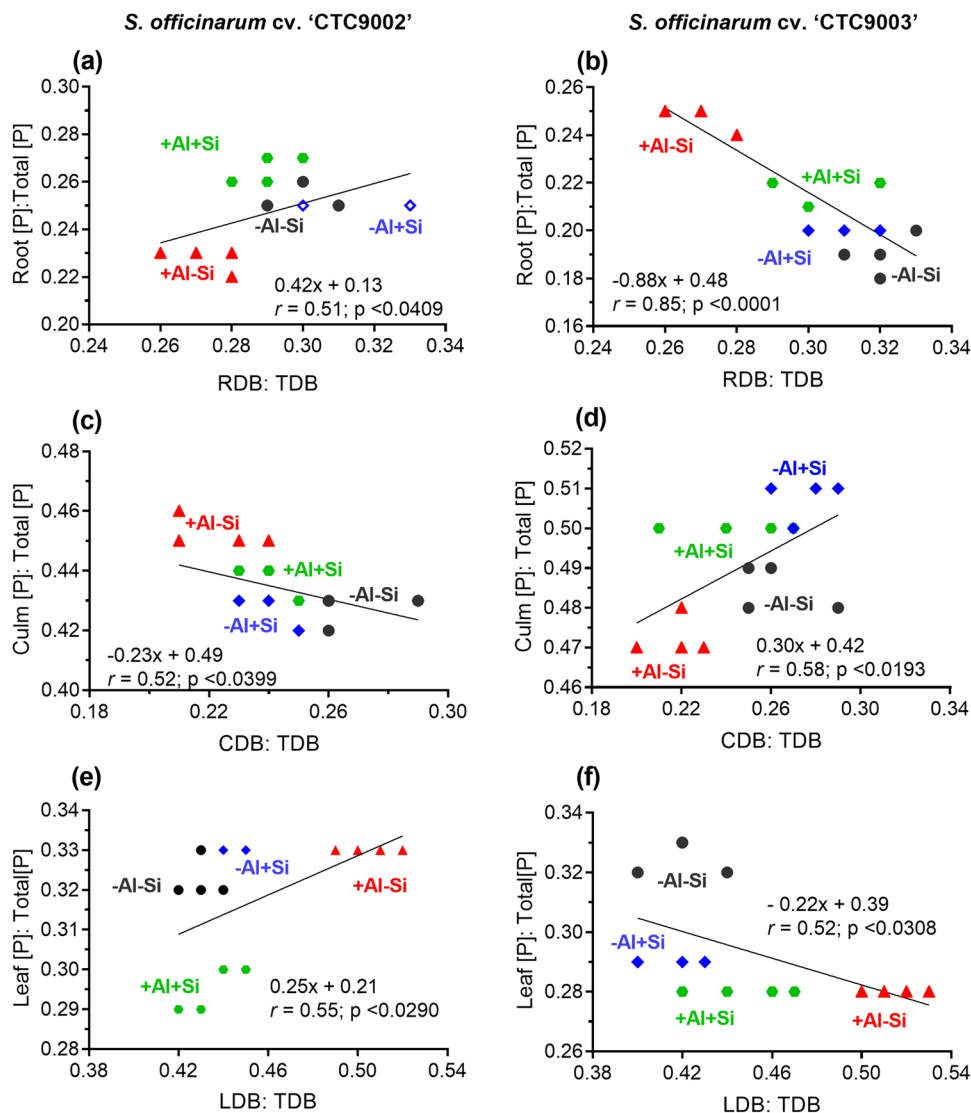
4 Discussion

Plant growth significantly affects by stress conditions. To our knowledge, this is the first describing experimental evidence of dry biomass allocation [Si] and stoichiometric homeostasis distribution in sugarcane (high Si-accumulator) plants under Si and Al stress conditions. Al affected both sugarcane seedling development as RDB, CDB, and LDB, which were severely suppressed, but cultivar "CTC9003" showed lesser effect than the "CTC9002." Root growth inhibition is the first damage of Al toxicity (Pontigo et al. 2017; Silva et al. 2019). Aside from this effect, Al toxicity has been shown that the LDB of both cultivars of *S. officinarum* was usually greater than the RDB and CDB, but RDB was relatively higher than that of CDB. This slight increase of LDB under Al toxicity conditions indicated that the biomass is being allocated in this part, which suggests a lower effect by Al stress as compared to the CDB and RBD, respectively.

Hence, the findings could facilitate a deeper understanding of the potential mechanisms adopted by sugarcane plants under Al stress conditions. Similar observations on Al-induced undesirable effects on plant growth have been made in other plant species under Al toxicity environments, such as grasses (Pontigo et al. 2017), rice (Freitas et al. 2017; Moreno-Alvarado et al. 2017), wheat (Kostic et al. 2017), sugarcane (Silva et al. 2019), and barley (Vega et al. 2019, 2020).

Diverse alternatives to plants confront stress conditions, which is a challenging task for all researchers. Si plays a crucial role in plant growth by its beneficial impacts on water uptake, mineral nutrition, osmolyte accumulation, and antioxidative defense, which increase plant resistance to Al stress (Etesami and Jeong 2018; Vaculík et al. 2020). In the current study, Si attenuated Al stress effects in sugarcane plants by increasing sugarcane growth. Biomass accumulation (RDB, CDB, and LDB) of both Al-stressed sugarcane

cultivars showed a gradually increasing trend under Si addition. Moreover, increased RDB, CDB, and LDB of both *S. officinarum* plants under Al toxicity by Si addition is due to higher levels of stoichiometric homeostasis, corroborating our first hypothesis and suggesting lower effects by Al toxicity.

Although Si addition partially increased RDB in Al-toxic solutions, this improvement in RDB could be related to regulating stoichiometric homeostasis. These findings directly support our starting hypothesis and are in agreement with the increased root development and lateral root formation (Silva et al. 2019). Additionally, Si also helps maintain root growth by decreasing Al uptake (Freitas et al. 2017; Hodson and Evans 2020; Pontigo et al. 2017; Vaculík et al. 2020). The beneficial impacts of Si due to the formation of Al–Si complexes within the root tissues were aluminosilicates or hydroxyaluminosilicates, given their low solubility (Hodson and Evans 2020; Imadi et al. 2016). In addition, LDB and CDB were increased with the Si application of both sugarcane cultivars; we have also observed some level of biomass allocation from leaves to root and culm. The increased LDB by Si supplementation under Al toxicity conditions indicated that a part of the plant's biomass is being allocated to leaves, which suggests a lesser effect of Al stress on LDB than RBD and CDB. Si plays an important role in plant growth due to its beneficial influences on mineral nutrition and enhanced of antioxidative defense mechanism (Pontigo et al. 2017; Souri et al. 2021; Sousa Junior et al. 2022; Vega et al. 2020). We reported the beneficial effects of Si on the growth and Al tolerance of sugarcane cultivars. These improvements in plant growth by Si addition are in agreement with previous observations in wheat (Qian et al. 2016), sorghum (Kopittke et al. 2017), ryegrass (Pontigo et al. 2017), rice (Chaiwong and Prom-u-thai 2022; Moreno-Alvarado et al. 2017), sugarcane (Silva et al. 2019), and barley (Vega et al. 2019, 2020). Therefore, the findings of this study suggest that Si plays an important role in allocating the dry biomass in Al-stressed sugarcane seedlings, which leads to a deeper understanding of the potential mechanisms of Si supplementation in increasing plant tolerance under Al toxicity.

An increase in [Si] in all organs of both sugarcane cultivars was also found when plants were simultaneously supplied with Al and Si. Under non-Al stress conditions, the [Si] in the culm of both sugarcane cultivars were relatively similar and were significantly higher than that in leaves and roots, respectively. One possible explanation for this fact is due to the dilution effect by the lower CDB compared with the RDB and LDB. However, under Al stress conditions, the [Si] in leaves and roots of both sugarcane cultivars was relatively similar and higher than in culm and were significantly higher in the cultivar "CTC9003" than in "CTC9002." As discussed above, the hypothesis assumes that the incorporation of structural Si represents an economic strategy for

plants to confront a range of environmental stresses. These increases in Si uptake might be attributed to the reduction in Al uptake, as reported previously (Sousa Junior et al. 2022), with the subsequent improvement of RDB. Si accumulation in plants greatly varies from plant to plant and in plant tissues because of the architecture of the Si transporter system and prevalent environmental conditions (Ahmad et al. 2019; Calero Hurtado et al. 2020b). However, the formation of Al-Si onto plant tissues could also be involved in the growth-promoting outcome of Si under Al-stressed wheat (Cocker et al. 1998), maize (Wang et al. 2004), and barley (Pontigo et al. 2017). Recent studies have revealed that Si accumulation in plant tissues is controlled by the influx and efflux of Si transporters that could be involved in the differential Si-induced responses to confront with Al stress (Deshmukh et al. 2020; Hodson et al. 2005; Liang et al. 2007; Pontigo et al. 2017). These responses might suggest an increased requirement for [Si] in sugarcane seedlings in order to cope with Al-induced toxicity. Further studies are needed to confirm this assumption.

Plants have evolved a variety of defense mechanisms to survive in metal toxicity environments. Al toxicity showed a significant variation in C, N, and P stoichiometric characteristics. The [C] in leaves and roots of both sugarcane cultivars showed the highest values in the + Al-Si treatment, and the culm [C] then decreased. These results indicated that [C] in leaves and roots were continuously allocated than in culm during the sugarcane growing under Al stress. This effect could be explained by the fact that C provides the structural basis and constitutes 50% of a plant's dry mass (Olivera-Viciedo et al. 2021b). Additionally, [N] and [P] differed remarkably between plant organs, treatments, and cultivars (Fig. 2e–h). The [N] and [P] in culms of both cultivars were slightly higher than in leaves and roots during + Al-Si treatment; thus, [N] was significantly higher in the cultivar "CTC9002" than in "CTC9003"; in contrast, [P] was leaves, culms, and roots that was lower than that of male plants during most months. These results indicate that [N] and [P] decreased under Al stress and decreased the plant growth, which was due to the increasing [Si], which was in agreement with the previous reports of Klotzbücher et al. (2018).

A possible alternative mechanism of Si-mediated Al detoxification in plants enhances the C, N, and P stoichiometric characteristics. At present, there is little information on the effect of Si on the C, N, and P stoichiometric regulations in Al-stressed plants. This study showed significant first-time variations in C, N, and P stoichiometric homeostasis in Al-stressed sugarcane plants. The beneficial role of Si on C, N, and P allocation of Al-stressed sugarcane seedlings was studied. Si tends to decrease [C], [N], and [P] in all plant organs and both sugarcane seedlings under Al toxicity. This suggests that these changes on C, N, and P stoichiometric by Si supplementation are a common phenomenon. These

results partially corroborate our second hypothesis. Therefore, we found slightly higher values of leaves [C] of both sugarcane cultivars under Al toxicity than in [C] in culms and roots, but roots [C] were slightly higher than that in culms, suggesting that C is being allocated to those organs due to the Si application effect as compared with non-Si addition. Fundamentally, this decrease can be explained by Si addition that might cause C to dilute; i.e., when [Si] increases, the concentrations of C and other essentials mineral inevitably decrease. Sugarcane plants incorporate Si as a substitute for organic C, i.e., Si increases C-rich components, such as phenols, lignin, proline, and glycine betaine, and leaves to protect themselves against the adverse effects of Al toxicity (Klotzbücher et al. 2018; Schaller et al. 2012; Sousa Junior et al. 2022; Vega et al. 2019). Another probable explanation for the lower [C] that could be due to Si may decrease transpiration, which leads to the closure of the stomata for long periods of the day, which helps to reduce the rate of assimilation of C and the loss of water, maintaining low C assimilation in low water levels (Khan et al. 2017). Additionally, this marked reduction of [C] by Si is due to the formation of low-energy compounds, such as phytoliths in wall cells (Raven 1983). These results suggest that Si tends to keep a low C stoichiometry in plants grown under Al stress conditions, which leads to important changes in plant responses to Al tolerance.

Al toxicity induces significant changes on [N] in all organs of both sugarcane cultivars. Our results suggested that the growth of sugarcane seedlings under Al toxicity conditions is limited by N. In addition, culm [N] under Si and Al conditions had higher levels than leaves and roots, which suggests that N is being allocated to stems, resulting in a lesser effect of Al on culm [N] as compared to the [N] allocation in leaves and roots. A similar affectation pattern was observed under Al toxicity in barley (Liang et al. 2001) and soybean plants (Balestrasse et al. 2006). One possible explanation for this fact is due to Al toxicity that is closely related to N metabolism, which leads to decreasing the activity of nitrate reductase enzyme (Murad et al. 2020; Sade et al. 2016), glutamine synthetase (GS), as well as glutamate synthase (GOGAT) by Al toxicity (Laîné et al. 2019; Liang et al. 2001). Furthermore, the low [N] may also be associated with C-assimilation capacity (Sardans and Peñuelas 2012) or may be invested in other functions, such as reproduction (Sterner and Elser 2002). In our study, Si application decreased [N] due to the high [Si], which is in agreement with our second hypothesis. This effect is also probably due to the dilutional effect of [N], resulting in higher dry biomass production promoted by Si addition. Additionality, Si plays an important role in N allocation strategies to leaves, culms, and roots to dry biomass accumulation in each organ of both sugarcane cultivars. These results suggest that Si addition can increase the N-use efficiency in Al-stressed

plants, which can maintain higher growth rates at lower [N] (Calero Hurtado et al. 2019; Sousa Junior et al. 2022). These findings indicate that Si induced changes in [N], which may be an important mechanism to predict how plant productivity will respond to Al stress conditions.

Most of the Al-avoidance responses enable plants to adjust to the low availability of resources (water and minerals). P uptake and translocation are complex and vary between species, varieties/cultivars, and organs of the same plant species. Al treatments increased the [P] in roots, culms, and leaves of both sugarcane cultivars. In Al stress plots, the higher [P] is probably due to a dilution effect by lower dry biomass production (RDB, CDB, and LDB) (Olivera-Viciedo et al. 2021a). Our results indicate that the growth of sugarcane plants cultivated under Al stress is limited by P. In addition, we have also observed higher [P] allocation in Al stress condition in both cultivars from culm than in leaves and roots, which leads to a more effective in roots and leaves. These results suggest that higher [P] may have an indirect effect on dry mass production and P uptake under Al toxicity. However, Al-stressed sugarcane seedlings accumulated smaller [P] upon Si application, corroborating our second hypothesis. Si supplementation decreases [P] in the two Al-stressed cultivars in the following order: culm, root, and leaves. A probable explanation for these lower [P] is due to the dilution effect, in which Si promoted an increase the dry biomass production, as was also indicated in a recent study in sorghum (Calero Hurtado et al. 2020a). These results indicate that there is a well-adjusted effect in sugarcane plants under the combination of Al stress and Si application. This effect could also be explicated due to the interference between Si and P in the metabolism of plants (Moreno-Alvarado et al. 2017; Schaller et al. 2012). According to our results, Si addition modifies the P uptake due to the differential use of P by plants (Elser 2006), where P may be more related to plant growth (Sardans and Peñuelas 2012). Another probable role of Si in decreasing [P] under Al toxicity conditions presumably occurs by an increase in the P-use efficiency, converting higher growth rates (Sousa Junior et al. 2022). Additionally, these results suggest that Si addition can keep higher growth rates at lower [P] in Al-stressed sugarcane seedlings, corroborating our second hypothesis. Conversely, other studies also revealed that Si application maintained higher [P] under Al stress conditions, such as barley (Liang et al. 2001; Vega et al. 2019) and wheat plants (Kostic et al. 2017). The findings of this study indicate that the role of Si in the P uptake and translocation in Al-stressed sugarcane plants varies among plant species and varieties/cultivars, which strongly suggests that Si functions in plants Al toxicity conditions are multifaceted and complex.

Changes in C:N, C:P, and C:P ratios can help us predict how plant productivity will respond to future climate

change scenarios. A remarkable variation in stoichiometric relationships of C:N, C:P, and N:P in both sugarcane cultivars under Si and Al stress conditions was documented in this study. This is the first report study on the impact of Al toxicity in the C:N, C:P, and N:P ratios and its allocation to sugarcane plants. Therefore, we also found a lower level of C:N, C:P, and N:P ratios in Al stress plots, which could be associated with decreased dry biomass production. Under Al stress conditions, the C:N ratio was higher with lower growth rates in both sugarcane cultivars, but the C:P and N:P ratios were lesser with lower growth rates. Similarly, root and leaf showed higher C:N ratio compared with the culm and lower C:P and N:P ratios with lower plant growth. To our knowledge, this is the first study describing experimental evidence of the C:N, C:P, and N:P ratios in sugarcane (high Si-accumulator) plants under Al stress conditions. The beneficial role of Si in attenuating the adverse effects of Al toxicity in plant species has been widely accepted (Sousa Junior et al. 2022; Vaculík et al. 2020; Vega et al. 2019, 2020). These findings denote the better sensitivity of both sugarcane cultivars, which is in agreement with previous reports on the differences in Al tolerance (Sousa Junior et al. 2022). Recent studies showed significant variations among genotypes or plant organs at the same plant species under Al stress such as sorghum (Kopittke et al. 2017), grasses (Pontigo et al. 2017), and barley (Vega et al. 2019, 2020). Our study showed for the first time the impacts of Si on C:N, C:P, and N:P ratios and its distribution in both Al-stressed sugarcane cultivars. These beneficial effects of Si also occurred between sugarcane cultivars and in all organs (root, culm, and leaf), corroborating our third hypothesis. These findings provide new evidence that the responses of sugarcane treated with Si under Al stress were remarkably different between plant species. In the current study, Si application increased even the C:N, C:P, and N:P ratios, but also roots and leaves keep higher C:N, C:P, and N:P ratios than that culms in both sugarcane cultivars, which helped to keep higher growth rates of RDB, CDB, LDB, and TDB under Al toxicity conditions. One possible explanation for the higher C:N, C:P, and N:P ratios by Si application were ascribed to decreasing [N] and [P], resulting in higher growth rates. These results indicate that a balancing effect between Al and Si application has occurred in this research. Therefore, Si application under Al stress would have a more obvious effect on N and P uptake than that in C assimilation of sugarcane plants (Si accumulating). One explanation for the increased C:N, C:P, and N:P ratios observed in this studied species may be the availability of Si, as well as the amount absorbed under Al stress conditions (Sousa Junior et al. 2022). This is in agreement with previous studies that have shown a stress mitigation effect from Si due to increasing C:N, C:P, and N:P ratios under toxicity conditions (Calero Hurtado et al. 2020a). These increases produced by Si on C:N, C:P, and N:P ratios

in both cultivars and in their organs may be a crucial mechanism for predicting how plant growth and productivity might respond to Al toxicity. Additionally, this increase in the C:N, C:P, and N:P ratios can prevent decreasing growth caused by Al toxicity and increasing plant development (Haddad et al. 2018; Schaller et al. 2012). These results indicate that Si maintained a balance in Al-stressed sugarcane seedlings, which consequently increased plant growth due to greater use efficiency of N and P (Calero Hurtado et al. 2020a; Sousa Junior et al. 2022). In agreement with our results, the addition of Si in the growth medium has the tendency to increase the C:N, C:P, and N:P ratios as a possible mechanism for Al detoxification in plants.

In previous studies, different responses were observed among plant species, cultivars/varieties/genotypes, and plant organs under Al and Si conditions, such as wheat (Kostic et al. 2017), grasses (Pontigo et al. 2017), barley (Vega et al. 2019, 2020), maize (Sousa et al. 2019), rice (Sousa et al. 2019), and sugarcane (Silva et al. 2019). In the current study, cultivar CTC9003 grown under Al and Si conditions had higher levels of stoichiometric homeostasis and dry biomass production, corroborating our third hypothesis. Contrasting effects between both Al-stressed sugarcane cultivars by Si addition were also observed in the correlation between dry biomass and nutrient ratios. These results suggest that the allocation strategies of C, N, and P to leaves, culms, and roots to dry biomass to each organ of both *S. officinarum* under Si and Al toxicity conditions differ among plant species, varieties/cultivars, and the same plant organ.

Finally, taken together, our findings provide the first stoichiometric homeostasis evidence that Si attenuates the negative effects of Al by increasing Si concentration as well as stoichiometric homeostasis responses in sugarcane plants, which the hypothesis assumes that Si supplementation represents an economic strategy of plants to confront Al toxicity.

5 Conclusions

Our results exhibit that Si supplementation increases the tolerance of sugarcane seedlings grown under aluminum toxicity. Additionally, the beneficial role of Si may be due to the higher levels of stoichiometric homeostasis and dry biomass production of both Al-stressed sugarcane cultivars. Moreover, Si addition impacts stoichiometric changes within sugarcane cultivars because it produces significant changes in C:N, C:P, and N:P ratios, which leads to being an important and crucial mechanism for mitigating the adverse effects caused by aluminum stress. Our findings suggest that the Si addition plays an important role in increasing plant tolerance to Al toxicity, which leads to more sustainable management practices as a key factor for sustainable crop production.

Declarations

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