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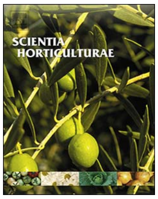

Research Paper

Silicon alleviates ammonium toxicity in cauliflower and in broccoli

Rafael Ferreira Barreto*, Aparecido Alecio Schiavon Júnior, Marcos Aurélio Maggio, Renato de Mello Prado

São Paulo State University (UNESP), School of Agricultural and Veterinarian Sciences, Jaboticabal, Brazil

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ABSTRACT

Plant growth may be higher with a nitrate (NO_3^-) and ammonium (NH_4^+) ratio (N-A ratio), in relation to a particular form of N. However, the NH_4^+ can be toxic. In order to alleviate NH_4^+ toxicity in plants, silicon (Si) can be used. To evaluate the effect of N-A ratios and Si in cauliflower and broccoli, the plants were grown in hydroponic system, using coarse sand substrate. Randomized block design was used, with four replications, in a 3 × 2 factorial scheme, corresponding to total N concentration of 15 mmol L^{-1}, with N-A ratios of 100/0, 50/50 and 0/100, in the absence and presence of Si (2 mmol L^{-1}). The NH_4^+ source was ammonium chloride and as Si source, stabilized sodium and potassium silicate. The results suggest that in cauliflower, the alleviation of NH_4^+ toxicity using Si can be noticed through the increase of the physical integrity of the membranes and in broccoli, the alleviation of NH_4^+ toxicity is associated most with the water use efficiency. Si alleviates NH_4^+ toxicity in cauliflower when the total N concentration is 15 mmol L^{-1} and 50% is supplied in the form of NH_4^+. In broccoli, Si improves the effect of NO_3^- and alleviates NH_4^+ toxicity.

1. Introduction

Ammonium (NH_4^+) is one of the main forms of nitrogen (N) which is responsible for the biosynthesis of amino acids and provides less energetic waste for plants, since it is in a readily assimilable form. However, NH_4^+ accumulation in plant cell leads to oxidative stress, due to the increase in the production of reactive oxygen species, causing toxicity (Bittsánszky et al., 2015). Another consequence of NH_4^+ toxicity is to decrease the accumulation of cations such as potassium (K^+), calcium (Ca^{2+}) and magnesium (Mg^{2+}) (Nasraoui-Hajaji and Gouia, 2014).

Since K^+ and NH_4^+ are very similar in relation to valence and ionic radius, they may not be distinguished by membrane bound-carrier. Thus, at high concentrations of NH_4^+, K^+ uptake decreases (Ten Hoopen et al., 2010). In addition, in NO_3^- fed plants, the external pH usually increases considerably with time, and with NH_4^+ supply, the external pH decreases (Marschner 2012). The consequence of acidification is the lower availability of cations, such as K^+, Ca^{2+} and Mg^{2+} (Ahmad et al., 2006).

In this context, plant growth may be higher with a N-A ratio, in relation to a particular form of N. For example, in broccoli plants fed with low N concentration (3.5 mmol L^{-1}), the highest dry weight was obtained with a N-A ratio of 50/50 (Zaghdoud et al., 2016a). At high N concentration (18 mmol L^{-1}), the highest dry weight of broccoli was obtained in the proportion of 25/75 (Liu and Shelp, 1993). However, in cauliflower plants fed with low N concentration (3.5 mmol L^{-1}), there was no difference in dry weight as a function of the N-A ratios 100/0 and 50/50. In the three studies, symptoms of toxicity in the plants were verified when N was totally supplied in the form of NH_4^+.

In order to alleviate NH_4^+ toxicity in plants, and improves the effect of NO_3^-, Si can be used. For example, in *Brassica napus* fed with 14 mmol L^{-1} of N, Si increased leaf area and fresh weight in N-A ratios ranging from 100/0 to 25/75 (Bybordi 2010).

Despite the importance of brassicas, studies on the role of Si in the mitigation of NH_4^+ toxicity to cauliflower and broccoli are scarce. However, there is a hypothesis that Si can alleviate NH_4^+ toxicity in cauliflower and broccoli crops. Thus, this study aimed to evaluate the effect of Si and N-A ratios on cauliflower and broccoli plants, in hydroponic cultivation.

2. Material and methods

2.1. Plant material and growth conditions

The seeds of cauliflower (*Brassica oleracea* var. Botrytis) cv Barcelona (production cycle = 110 days) and broccoli (*Brassica oleracea* var. Italica) cv BRO 68 (production cycle = 90 days) were sown in polystyrene trays with 128 cells, containing commercial substrate

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* Corresponding author at: Via de Acesso Prof. Paulo Donato Castelane, Vila Industrial, Jaboticabal, São Paulo State, Zip code: 14884-900, Brazil.
E-mail addresses: rafael.fb@outlook.com (R. Ferreira Barreto), alecio.schiavon@syngenta.com (A.A. Schiavon Júnior), marcos.maggio@syngenta.com (M.A. Maggio), rmprado@fcav.unesp.br (R. de Mello Prado).

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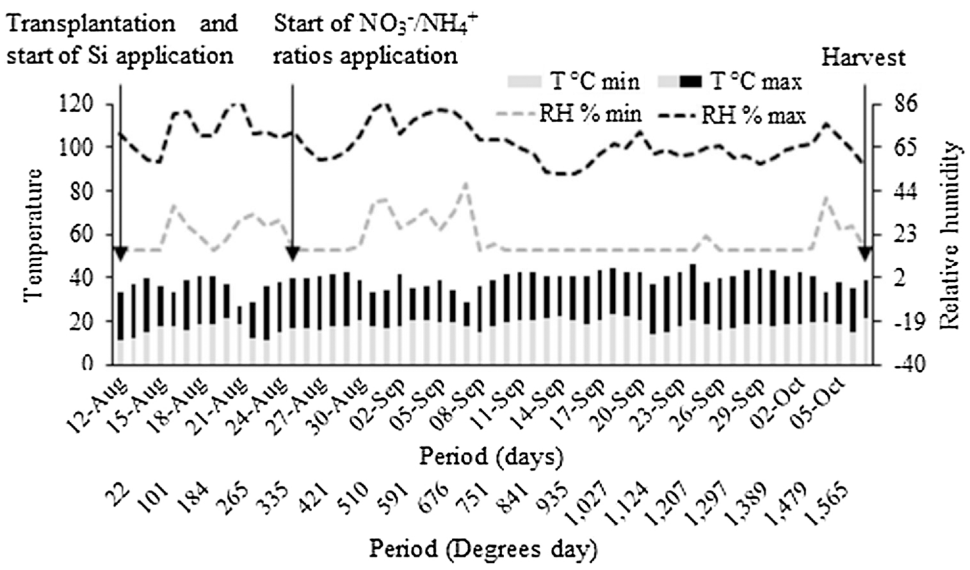

Fig. 1. Temperature and relative humidity at greenhouse during the entire period of experiment.

Table 1
Nutrient solution composition (mmol L^{-1}) at a constant N concentration (15 mmol L^{-1}) and different N-A ratios.

Nutrient source	Nitrate-Ammonium ratios in the nutrient solutions					
	100/0	50/50	0/100	100/0	50/50	0/100
KH_2PO_4	0.50	0.50	0.50	0.50	0.50	0.50
KNO_3	5.00	–	–	5.00	–	–
$Ca(NO_3)_2$	5.00	3.75	–	5.00	3.75	–
$MgSO_4$	1.00	1.00	1.00	1.00	1.00	1.00
KCl	0.19	5.19	5.19	–	5.00	5.00
NH_4Cl	–	7.50	15.00	–	7.50	15.00
$CaCl_2$	–	1.25	5.00	–	1.25	5.00
Stabilized sodium and potassium silicate	–	–	–	2.00	2.00	2.00

Fibramix®, composed of coconut fiber (50%), carbonized rice husk (30%) and ground phenolic foam (20%).

Ten days after sowing (DAS), the cotyledon leaves had fully expanded. When the cauliflower and broccoli showed four and two expanded leaves (24 DAS), respectively, the seedlings were transplanted into 5 L polypropylene pots, filled with coarse sand, which had been previously washed. The plants were watered with 10% of the ionic strength Hoagland nutrient solution (Hoagland and Arnon 1950) until they reach five and three leaves (31 DAS) and with 25% until they reach seven and four leaves (37 DAS), respectively, for cauliflower and broccoli. The greenhouse temperatures and relative humidity were monitored (Fig. 1). Additionally, the period of the experiment was presented in degrees-day. In order to calculate, base temperature of 0 °C was used (Grevsen 1998) and evaluated the daily thermal units accumulated throughout the experiment, according to the equation:

$$DD = (Mt - Bt) + ((MT - Mt)/2); (Bt < Mt)$$

Where:
DD = °-day;
MT = daily maximum temperature;
Mt = daily minimum temperature;
Bt = basal temperature.

2.2. Si and N-A ratios treatments

After the seedling transplanting, Hoagland nutrient solution (Hoagland and Arnon 1950) was applied, to half of cauliflower and broccoli plants, supplemented with 2 mmol L^{-1} silicon, using stabilized sodium and potassium silicate (114.91 g L^{-1} Si and 18.9 g L^{-1} K_2O).

When the cauliflower and broccoli reached seven and four leaves (37 DAS), respectively, Hoagland nutrient solution (Hoagland and Arnon 1950) was modified, in order to supply 15 mmol L^{-1} N in three N-A ratios (100/0, 50/50 and 0/100). The details are shown in Table 1. Final concentration of macronutrients, in mmol L^{-1}, was N 15; P 0.5; K 5.69; Ca 5; Mg 1; S 1. In relation to micronutrients, the only modification recommended by Hoagland and Arnon (1950) was about Fe source, using Fe-EDDHA and twice the recommendation. Modifications with Si and with N-A ratios were balanced varying the concentration of Cl, in order to keep the same concentration of the other nutrients in all treatments. After preparing the solutions, pH was adjusted (5.7 ± 0.2). For cauliflower and broccoli, randomized block design was used, in a 2 × 3 factorial scheme, with four replications.

Until cauliflower and broccoli reached seven and four leaves, respectively, in each pot, 200 mL of nutrient solution had been applied daily. Then, the volume applied was of 300 mL. In the base of the pots, holes and polypropylene plates allowed the nutrient solution retention.

2.3. Total chlorophyll, stomatal conductance, water use efficiency and electrolyte leakage index analysis

Evaluations of chlorophyll, stomatal conductance, water use efficiency and electrolyte leakage index were carried in the fourth and fully expanded leaf of the plants. Total chlorophyll was determined according to the methodology proposed by Lichtenthaler (1987). Stomatal conductance was measured between 8 and 10 am using a portable photosynthesis system, Li-6400 (LI-COR, EUA). Water use efficiency (WUE) was calculated as net photosynthetic rate (*A*) per transpiration rate (*E*):

$$WUE = A/E$$

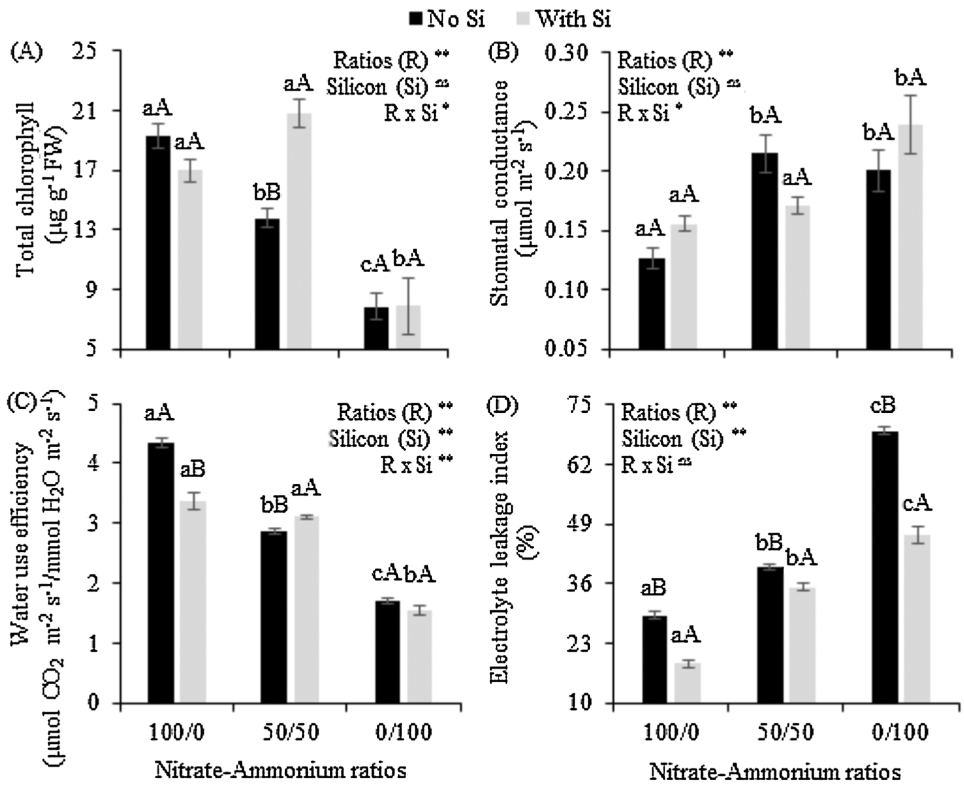

Fig. 2. Effect of Si and N-A ratios on (A) total chlorophyll, (B) stomatal conductance, (C) water use efficiency and (D) electrolyte leakage index of cauliflower shoots. The error bars in the figures represent standard error. Different letters, lowercase between N-A ratios in same Si concentration, and uppercase between Si in same N-A ratio indicate differences ($P < 0.05$, Tukey test) between treatments.

To estimate electrolyte leakage index, the leaves were before rinsed with deionized water. Ten leaf discs (each 6 mm in diameter) were placed in a glass vial. The vials were then filled with 20 mL deionized water maintained at the constant temperature of 25 °C. After 2 h, the initial electrical conductivity (EC1) was measured using an electrical conductivity meter. The samples were autoclaved afterwards at 121 °C for 20 min to completely kill the tissues and release all electrolytes. Samples were then cooled to 25 °C and the final electrical conductivity (EC2) was measured. The electrolyte leakage index (ELI) was expressed following the formula proposed by Dionisio-Sese and Tobita, (1998):

$$ELI = \frac{EC1}{EC2} \times 100$$

2.4. The analysis of N, K, Ca, Mg and Si contents

The analyses of N, K, Ca, Mg and Si contents were carried out in the shoot of the plants, according to the methodology described by Bataglia et al. (1983) and analysis of Si, according to Korndorfer et al. (2004). Based on the contents (C) of nutrients and Si in shoot, and shoot dry weight, the accumulation (A) of these elements was calculated:

$$A = C \times dry\ weight$$

2.5. Plant growth analysis

Leaf area was measured using a leaf-area meter (L-3100, Li-Cor, USA).

The plants were separated into shoot and roots. The roots were washed with running water. The shoot was washed under running water, mild detergent (0.1%), hydrochloric acid solution (0.3%) and deionized water. Plant material was dried out in forced air circulation (65 ± 5 °C), until they reached constant mass. After drying, the dry weight of the shoot and root was obtained.

2.6. Images of roots

The new and thin roots were selected and photographed in the stereomicroscope Leica M205C®.

2.7. Statistic analysis

The data obtained were subjected to analysis of variance, by F test, and then subjected to Tukey test, at 5% probability, in order to compare averages, using the statistical program SISVAR 3.01 (Ferreira, 2011).

3. Results

3.1. Total chlorophyll, stomatal conductance, water use efficiency and electrolyte leakage of cauliflower

In the absence of Si, the authors noticed a decrease of total chlorophyll content with the addition of NH_4^+ to the nutrient solution and in the presence of Si, the total chlorophyll content was higher in N-A ratio of 50/50 (Fig. 2A). In the absence of Si, stomatal conductance increased when NH_4^+ was applied, both in N-A ratios of 50/50 and 0/100. In the presence of Si, the stomatal conductance was higher only in N-A ratio of 0/100 (Fig. 2B). Water use efficiency decreased with the application of NH_4^+, in the absence of Si, and in the presence of Si, there was an increase in water use efficiency in N-A ratio of 50/50 (Fig. 2C). Although the electrolyte leakage index had increased with the application of NH_4^+, the values were lower for plants nourished with Si (Fig. 2D).

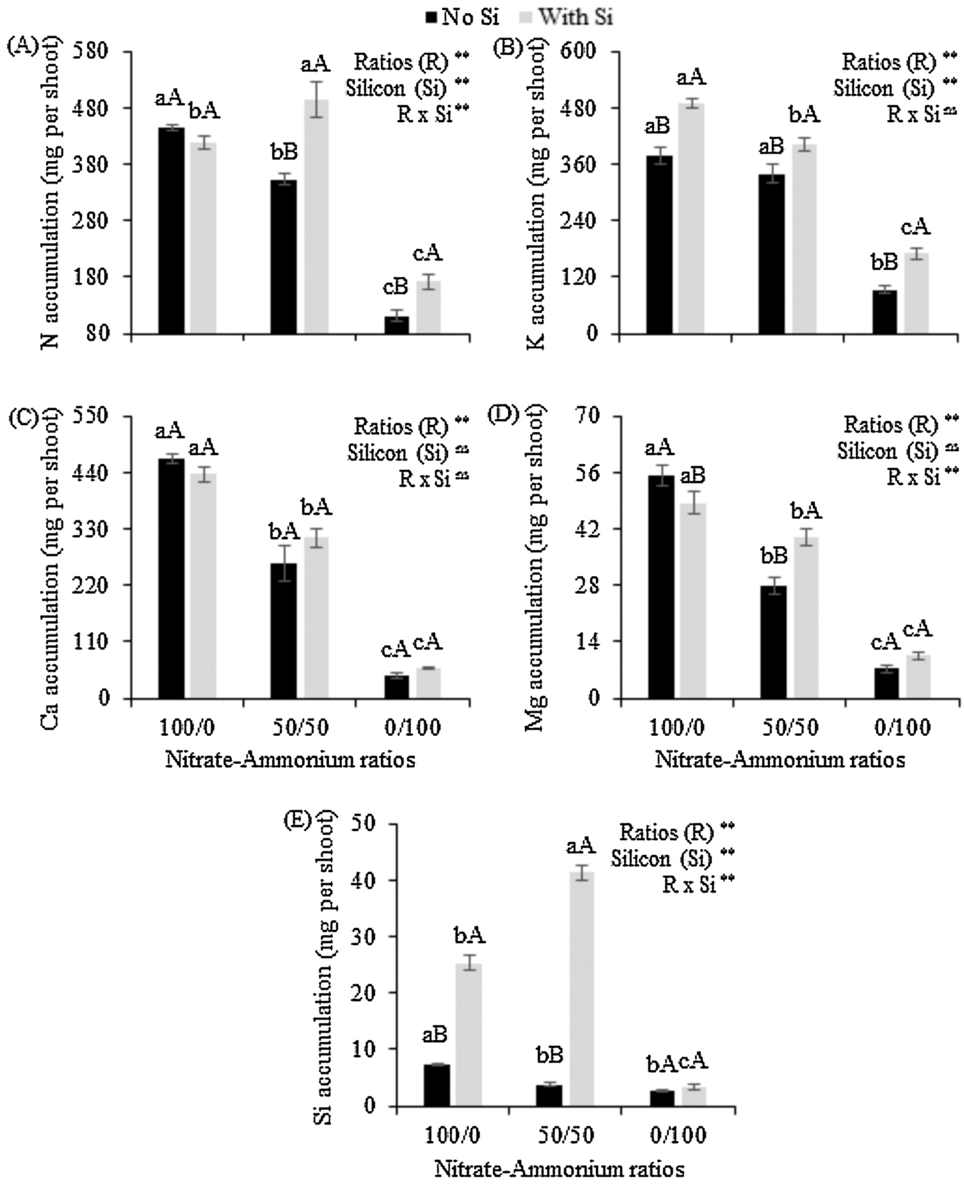

Fig. 3. Effect of Si and N-A ratios on (A) N, (B) K, (C) Ca, (D) Mg and (E) Si accumulation of cauliflower shoot. The error bars in the figures represent standard error. Different letters, lowercase between N-A ratios in same Si concentration, and uppercase between Si in same N-A ratio indicate differences ($P < 0.05$, Tukey test) between treatments.

3.2. The accumulation of N, K, Ca, Mg and Si of cauliflower shoot

In the absence of Si, N accumulation decreased according to the application of NH_4^+. In the presence of Si, N accumulation was higher in N-A ratio of 50/50 (Fig. 3A), with similar effect for Mg accumulation (Fig. 3D). Although K accumulation had decreased with the application of NH_4^+, the accumulation was higher in the presence of Si (Fig. 3B). For Ca accumulation, there was a decrease according to NH_4^+ supply, regardless of Si application (Fig. 3C). In the presence of Si, Si accumulation was higher in N-A ratio of 50/50, and lower in ratio of 0/100. In this same ratio, the authors did not notice any difference for Si accumulation in the absence of the element (Fig. 3E).

3.3. Total chlorophyll, stomatal conductance, water use efficiency and electrolyte leakage of broccoli

Total chlorophyll content was higher in N-A ratios of 100/0 and of 50/50. In ratio of 50/50, in the presence of Si, there was the highest total chlorophyll content (Fig. 4A). Stomatal conductance increased with N supplied in the form of NH_4^+. However, Si decreased the stomatal conductance (Fig. 4B) and increased the water use efficiency in N-A ratios of 100/0 and of 50/50 (Fig. 4C). Electrolyte leakage index increased with NH_4^+ application, both in the absence and presence of Si (Fig. 4D).

3.4. The accumulation of N, K, Ca, Mg and Si of broccoli

Regardless of Si supply, N accumulation in shoot of broccoli decreased when N was totally supplied in the form of ammoniacal (Fig. 5A). Nitrogen supplied in the form of NO_3^- provided higher K accumulation, in the presence of Si, K accumulation was higher in all N-A ratios (Fig. 5B), as well as accumulation of Ca (Fig. 5C) and Mg (Fig. 5D). Si supply provided higher accumulation of this element in N-A ratio of 50/50, and in the absence of Si supply, no difference for

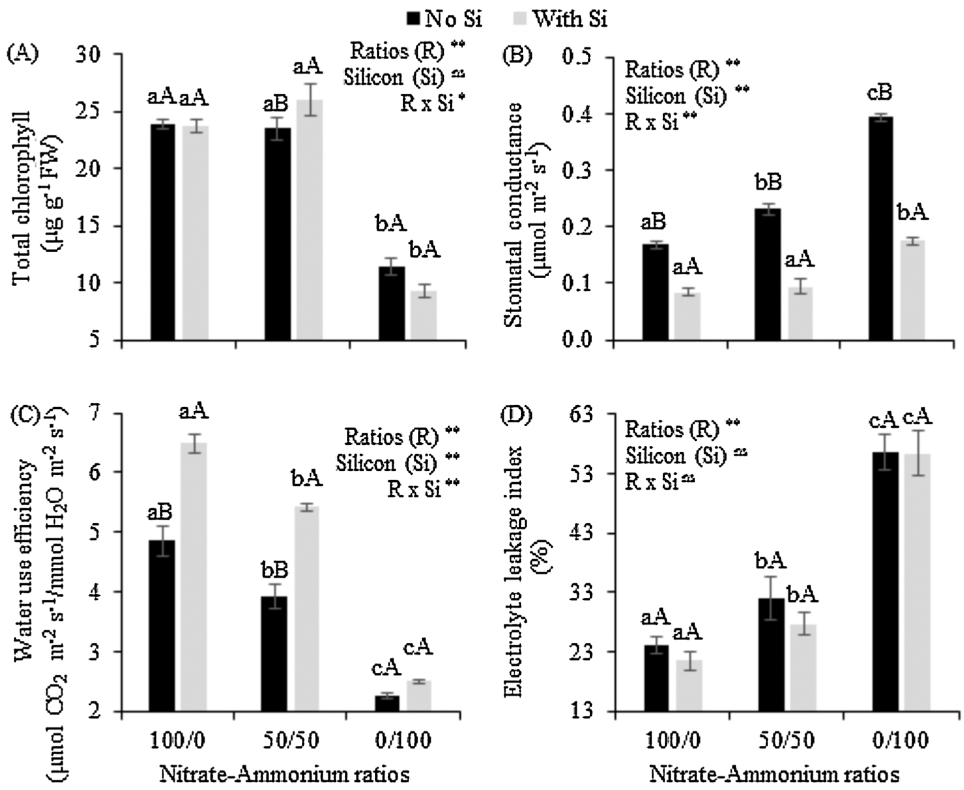

Fig. 4. Effect of Si and N-A ratios on (A) total chlorophyll, (B) stomatal conductance, (C) water use efficiency and (D) electrolyte leakage index of broccoli shoot. The error bars in the figures represent standard error. Different letters, lowercase between N-A ratios in same Si concentration, and uppercase between Si in same N-A ratio indicate differences ($P < 0.05$, Tukey test) between treatments.

accumulation in N-A ratio was noticed (Fig. 5E).

3.5. Plant growth

For cauliflower, the increase of the amount of NH_4^+ in the ratios decreased the leaf area, dry weight of shoots and roots. Nevertheless, Si increased leaf area, regardless of N-A ratio (Fig. 6A). In addition, Si provided an increase in dry weight production of shoots and roots in ratio 50/50 (Fig. 6B and C). For broccoli, in no Si, the increase of the amount of NH_4^+ in the ratios decreased the leaf area. With Si, the leaf area decreased only with 100% NH_4^+ (Fig. 6D). Dry weight of broccoli, both in roots and shoots decreased when N was totally supplied in the form of NH_4^+. However, in the presence of Si, higher production of dry weight of shoots was noticed (Fig. 6E); on the other hand, no effect of the beneficial element for dry weight of roots could be observed (Fig. 6F).

3.6. Images of shoots

After the application of N-A ratios, starting at 37 DAS (25-Aug), the growth of cauliflower fed with 100% NH_4^+ was lower, in relation to the other treatments, until at 59 DAS (17-Sep), cauliflower plants fed 100% NH_4^+ showed severe symptoms of NH_4^+ toxicity, such as necrosis of new leaves and chlorotic dots on old leaves, regardless of the presence or absence of Si. On the same day (17-Sep), broccoli plants fed 100% NH_4^+ were smaller than the other treatments. However, we did not observe the chlorosis or necrosis of the leaves (Fig. 7).

3.7. Images of roots

The roots of cauliflower and broccoli presented a clear coloration with 100% NO_3^-. However, as the amount of NH_4^+ increased, a progressive darkening of the roots of the two crops was noticed, highlighting the NH_4^+ toxicity symptoms, regardless the presence or absence of Si (Fig. 8).

4. Discussion

In cauliflower and in broccoli, the highest total chlorophyll content (Figs. 2 A and 4 A) is related to the highest N accumulation (Figs. 3 A and 5 A) since N is present in the leaf chloroplasts, a constituent of the chlorophyll molecule (Hoertensteiner 2006). These results are due to the presence of Si, in N-A ratio of 50/50, cauliflower and broccoli showed the highest Si accumulation in the shoots (Figs. 3 E and 5 E), indicating that plants have no restriction on the absorption of this beneficial element. Moreover, the most evident role of Si under stress conditions (Epstein 2009) was confirmed in the same ratio, by decreasing the leaf area and shoot dry weight of cauliflower in 6.5% and 23%, respectively (Fig. 6A and B). In broccoli, decreases in leaf area and shoot dry weight was 16.5 and 11%, respectively (Fig. 6D and E) in the absence of Si. In this context, Si increased leaf area and fresh weight of *Brassica napus* with 14 mmol L^{-1} N, in N-A ratios ranging from 100/0 to 25/75 (Bybordi 2010).

Stomatal conductance did not show the same behavior for cauliflower (Fig. 2B) and broccoli (Fig. 4B). Possibly, lower stomatal conductance in plants nourished with Si had increased water use efficiency, being associated to formation of endodermal suberin lamellae (Vatehová et al., 2012). Thus, the highest water use efficiency in broccoli (Fig. 4C) was due to lower transpiration or higher photosynthetic rates when the plants were nourished with Si, and when NH_4^+ was the only N source, Zaghdoud et al. (2016a) also observed lower water use efficiency in broccoli plants fed with 3.5 mmol L^{-1} of N and N-A ratios of 100/0, 50/50 and 0/100.

Under the condition of NH_4^+ excess its conversion rate into amino

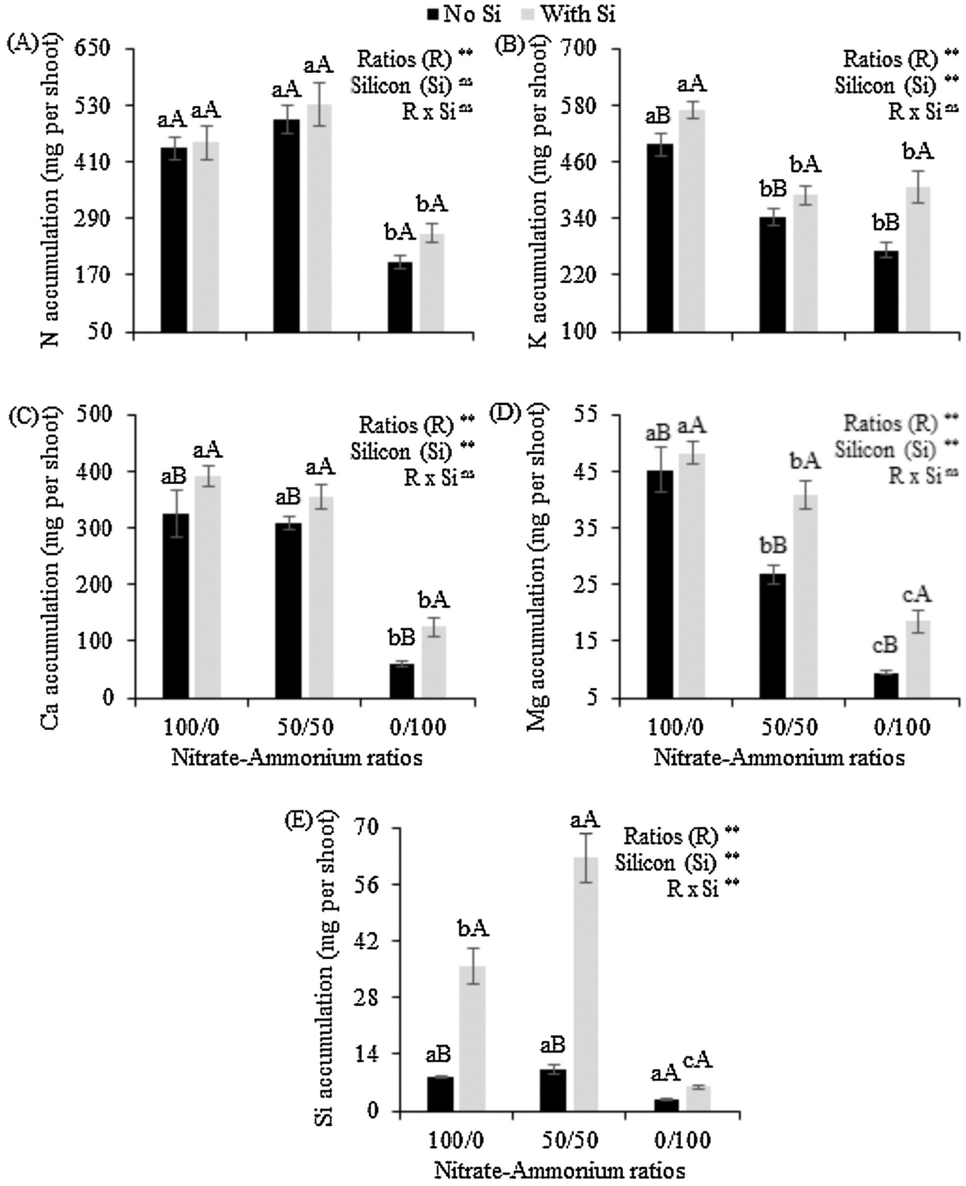

Fig. 5. Effect of Si and N-A ratios on (A) N, (B) K, (C) Ca, (D) Mg and (E) Si accumulation of broccoli shoot. The error bars in the figures represent standard error. Different letters, lowercase between N-A ratios in same Si concentration, and uppercase between Si in same N-A ratio indicate differences ($P < 0.05$, Tukey test) between treatments.

acid is lower than the absorption rate of this nutrient, leading to a NH_4^+ accumulation in plant cell, which results in oxidative stress, due to the increase in the production of reactive oxygen species. Toxicity occurs when this production exceeded the cellular antioxidant capacity (Pandhair and Sekhon 2006), highlighted by the increase of electrolyte leakage index and the increase of NH_4^+ ratio in cauliflower (Fig. 2D) and in broccoli (Fig. 4D). This fact occurs since this index is strongly correlated with the production of hydrogen peroxide, which is a by-product of lipid peroxidation in stressed plants (Liu et al., 2013), inducing the visual symptoms in plants (Fig. 7).

Nevertheless, Si as an effective substance for alleviation of NH_4^+ toxicity is related to the increase of the activity of antioxidant enzymes, which act eliminating reactive oxygen species (Gao et al., 2014). Thus, Si supply was responsible for the lowest electrolyte leakage index in cauliflower plants (Fig. 2D), which was not observed for broccoli plants (Fig. 4D). So, in relation to physiological parameters, the results suggest that the alleviation of NH_4^+ toxicity does not have the same behavior for both crops, since in cauliflower alleviation of NH_4^+ toxicity in ratio of 50/50 (Fig. 6A) is related to the lowest electrolyte leakage index (Fig. 2D) and in broccoli, the alleviation of NH_4^+ toxicity in all ratios, using Si (Fig. 6E) can be related to a higher water use efficiency (Fig. 4C).

In cauliflower and in broccoli, the lowest accumulation of K (Figs. 3 B and 5 B) occurred due to the antagonistic effect of NH_4^+ on this cation, since they are ions which compete for the same absorption sites (Marschner, 2012). In addition, the lowest accumulation of Ca (Figs. 3 C and 5 C) and Mg (Fig. 3D and 5D) was also observed by Ahmad et al. (2006) in cauliflower plants fed with 3.5 mmol L^{-1} of N and N-A ratios of 100/0, 50/50 and 0/100. However, in the presence of Si, both crops show higher accumulation of K, and one possible explanation might be that Si stimulates membrane H^+-ATPase activity, enzyme which is directly related to the K absorption (Liang, 1999). The mechanisms through which Si stimulates the absorption of other cations are still poorly studied. When N was totally supplied in the form of NH_4^+, the damage caused to the root system possibly affected the absorption of nutrients (Li et al., 2014).

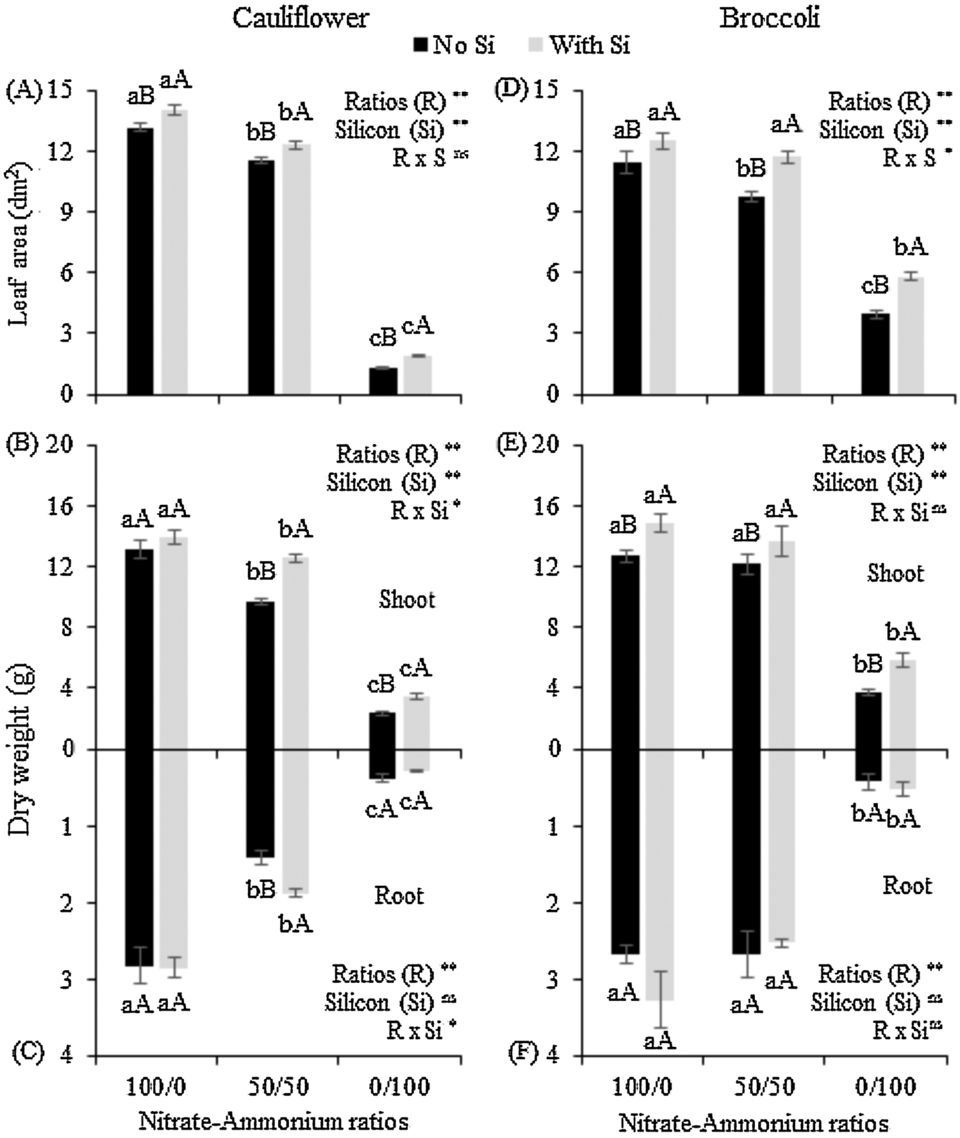

Fig. 6. Effect of Si and N-A ratios on (A) leaf area, (B) shoot dry weight and (C) root dry weight of cauliflower plant; (D) leaf area, (E) shoot dry weight and (F) root dry weight of broccoli plant. The error bars in the figures represent standard error. Different letters, lowercase between N-A ratios in same Si concentration, and uppercase between Si in same N-A ratio indicate differences ($P < 0.05$, Tukey test) between treatments.

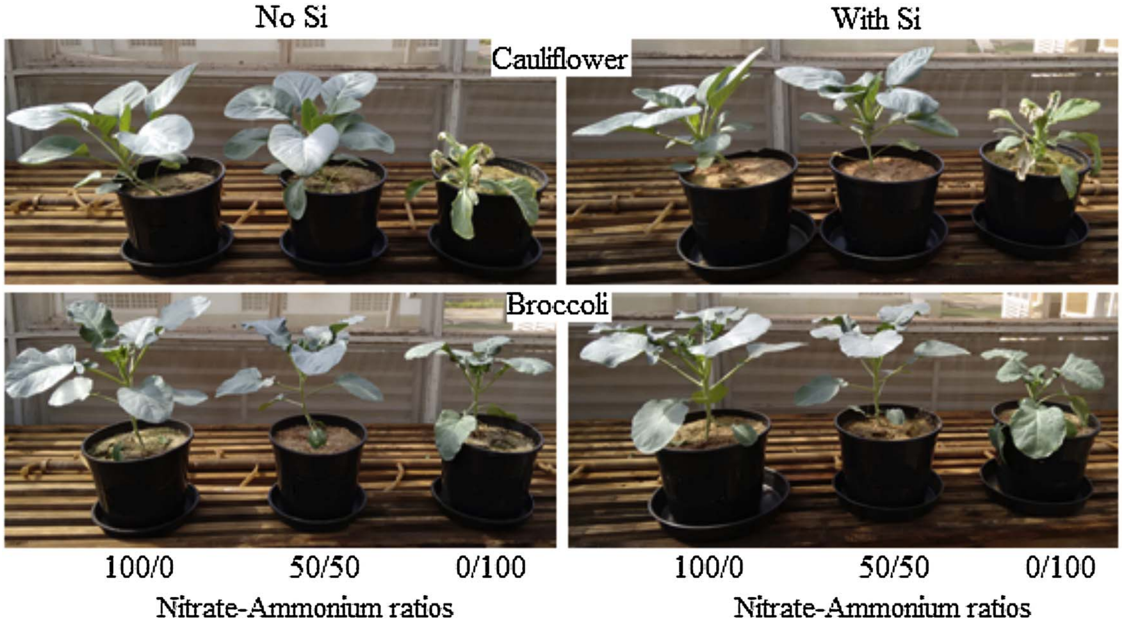

Fig. 7. Effect of Si and N-A ratios on cauliflower and broccoli shoots.

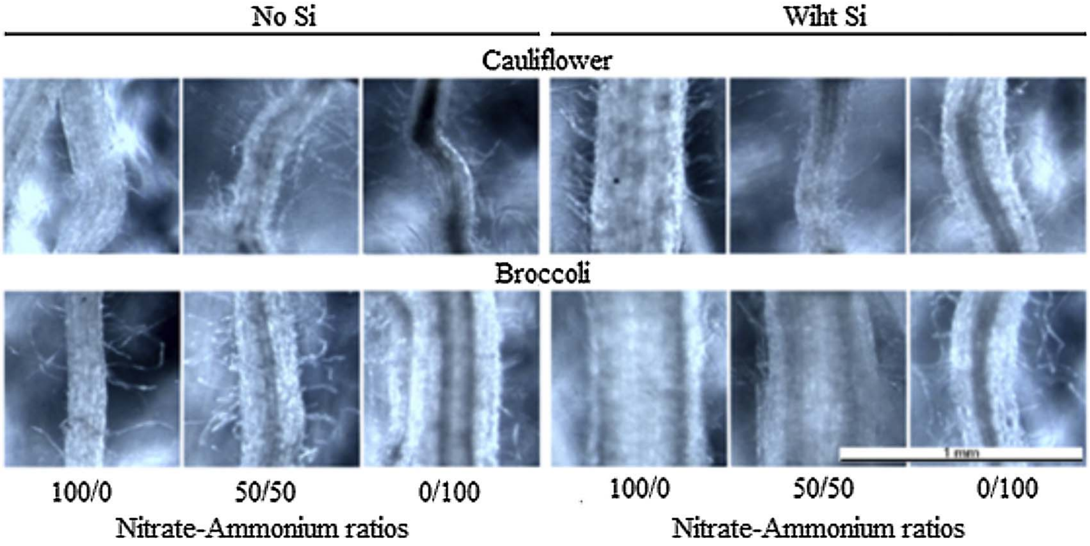

Fig. 8. Effect of Si and N-A ratios on cauliflower and broccoli roots.

In relation to the dry weight production of cauliflower, no other studies were found in literature. Nevertheless, this parameter can be explained by Si benefits, in N-S ratio of 50/50, through the highest water use efficiency (Fig. 2C), the lowest electrolyte leakage index (Fig. 2D) and highest accumulation of N, K, Ca, Mg and Si (Fig. 3), providing alleviation of ammoniacal toxicity (Fig. 6B).

Other studies on broccoli crop indicate that half of total N concentration in the nutrient solution can be in the ammoniacal form, without damaging the dry weight production or the plants (Zaghdoud et al., 2016a; Zaghdoud et al., 2016b), which was confirmed in this study, since the dry weight in N-A ratios of 100/0 and of 50/50 did not show any difference (Fig. 6E). However, Si acting positively in water use efficiency (Fig. 4C), and in accumulation of K (Fig. 5B), Ca (Fig. 5C) and Mg (Fig. 5D) increased the dry weight of the plants.

Thus, the results show that Si alleviates NH_4^+ toxicity in cauliflower when the total N concentration is 15 mmol L^{-1} and 50% is supplied in the form of NH_4^+. In broccoli, Si improves the effect of NO_3^- and alleviates NH_4^+ toxicity.

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