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Silicon-Mediated Adjustments in C:N:P Ratios for Improved Beetroot Yield under Ammonium-Induced Stress

Dilier Olivera-Viciedo [1,2,*], Daimy Salas Aguilar [1], Renato de Mello Prado [3], Kolima Peña Calzada [4], Alexander Calero Hurtado [4], Marisa de Cássia Piccolo [5], Mariana Bomfim Soares [3], Rodolfo Lizcano Toledo [6], Guilherme Ribeiro Alves [7], Daniele Ferreira [1], Rosane Rodrigues [1] and Anderson de Moura Zanine [1]

[1] Center of Environment and Agriculture Science, Federal University of Maranhão, Chapadinha 65500-000, Brazil; daimysalas82@gmail.com (D.S.A.); daniele.ferreira@ufma.br (D.F.); rosanerodrig@gmail.com (R.R.); anderson.zanine@ufma.br (A.d.M.Z.)
[2] Institute of Agrifood, Animals and Environmental Sciences, Universidad de O'Higgins, San Fernando 3070000, Chile
[3] Department of Soils and Fertilizers, Faculty of Agricultural and Veterinarian Sciences, São Paulo State University (UNESP), Jaboticabal 14884-900, Brazil; rm.prado@unesp.br (R.d.M.P.); marianabomfims@gmail.com (M.B.S.)
[4] Agronomy Department, University of Sancti Spiritus 'Jose Marti Perez' (UNISS), Sancti Spiritus 60100, Cuba; kolimapena@gmail.com (K.P.C.); alexcalero34@gmail.com (A.C.H.)
[5] Center of Nuclear Energy in Agriculture, University of São Paulo, Piracicaba, SP 13416-970, Brazil; mpiccolo@cena.usp.br
[6] Tolimense Institute of Technical Training Professional, Faculty of Engineering and Agro-Industrial Science, Espinal 733528, Colombia; rodolfolizcano@gmail.com
[7] School of Veterinary Medicine and Animal Science, Federal University of Bahia, Salvador, BA 40170-110, Brazil; alves.gr@hotmail.com
* Correspondence: dilier.olivera@uoh.cl

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Abstract: Nitrogen (N) holds a prominent position in the metabolic system of plants, as it is a main constituent of amino acids, which are the basic building blocks of proteins and enzymes. Plants primarily absorb N in the form of ammonium (NH_4^+) and nitrate (NO_3^-). However, most plants exhibit severe toxicity symptoms when exposed to NH_4^+ as the sole N source. Addressing NH_4^+ stress requires effective strategies, and the use of silicon (Si) has shown promising results. However, there is a lack of underlying studies on the impact of NH_4^+ toxicity on C:N:P stoichiometric balance and the role of Si in these ratios. In this study, we explored the effects of varying NH_4^+ concentrations (1, 7.5, 15, 22.5, and 30 mmol L^{-1}) on the C:N:P stoichiometry and yield of beetroot in hydroponic conditions. Additionally, we investigated whether the application of Si (2 mmol L^{-1}) could mitigate the detrimental effects caused by toxic NH_4^+ levels. The experiment followed a randomized block design based on a 5 × 2 factorial scheme with four replicates. Results revealed that in the presence of Si, both [N] and [P] significantly increased in shoots and roots, peaking at 15 mmol L^{-1} of NH_4^+ in the nutrient solution. While shoot [C] remained stable, root [C] increased with NH_4^+ concentrations of 22.5 and 30 mmol L^{-1}, respectively. Moreover, shoot and root [Si] increased with higher NH_4^+ levels in the nutrient solution. The findings underscored homeostatic instability under the highest NH_4^+ levels, particularly in plants cultivated without Si in the nutritive solution, leading to a reduction in both shoot and root dry matter production.

Keywords: abiotic stress; *Beta vulgaris*; ammonium toxicity; C:N:P stoichiometry; nutrient balance; plant growth; hydroponic conditions; nitrogen assimilation; phosphorus uptake; silicon application

1. Introduction

Nitrogen (N) is an essential macronutrient for plants, obtained from various compounds like nitrate (NO_3^-), urea ($CO(NH_2)_2$), ammonium (NH_4^+), and amino acids. Plants utilize N for multiple metabolic processes, including nucleic acid and protein synthesis,

as well as for signaling and storage functions [1]. According to FAO estimates [2], total global agricultural consumption of elemental N from synthetic fertilizers reached 107.7 Mt in 2018, with China, India, the United States, the EU28, and Brazil accounting for 68% of the total N use. Therefore, N availability is a critical factor determining plant growth across various environments [3,4]. In agriculture, both NH_4^+ and NO_3^- are the primary forms of N absorbed by plants [5]. After absorption, NH_4^+ is assimilated directly into organic compounds without necessitating energy-dependent enzymatic reduction, unlike NO_3^-. Thus, urea, a widely used N fertilizer, is converted into NH_4^+ by the enzyme urease, while NO_3^- is converted into NH_4^+ by nitrate and nitrite reductase enzymes within plants. Additionally, atmospheric nitrogen (N_2) is fixed by nitrogen-fixing bacteria such as *Rhizobium*, Frankia, etc., providing plants with NH_4^+ as well [6]. As a result, the reduced metabolic energy expenditure linked to ammoniacal nutrition can be transformed into increased plant growth, consequently leading to higher production [4,7].

While NH_4^+ is valued as a fertilizer, excessive levels can trigger the generation of reactive oxygen species (ROS), resulting in reductions in cytoplasmic pH, photosynthetic rate, transpiration, and stomatal conductance [4,8]. Exclusive provision of N as NH_4^+ can detrimentally affect numerous plants, leading to low biomass accumulation and ion imbalances [4,7,9]. While NH_4^+ toxicity can affect various plant species, the threshold at which symptoms manifest differs significantly among them. Typically, many cultivated plants such as potato *(Solanum tuberosum* L.), tomato (*Solanum lycopersicum* L.), bean (*Phaseolus vulgaris* L.), pea (*Pisum sativum* L.), strawberry (*Fragaria* × *ananassa*), and mustard (*Brassica juncea* L.) exhibit sensitivity to NH_4^+. In contrast, certain crops like rice (*Oryza sativa* L.), onion (*Allium cepa* L.), cranberry *(Vaccinium macrocarpon*), and blueberry *(Vaccinium corymbosum*) have developed a high tolerance to NH_4^+ [10,11]. Toxic levels of NH_4^+ in plant tissues accumulate when the rate of its conversion to amino acids and amides decreases, relative to its uptake and cellular production through amino acid catabolism, NO_3^- reduction, phenylpropanoid metabolism, and photorespiration [12]. Ammonium toxicity disrupts nutrient balance and metabolic processes, potentially impairing plant growth and productivity [8,13]. The adverse impact of NH_4^+ on nutrient ratios is based on its capacity to decouple mitochondrial electron transport from oxidative phosphorylation, therefore failing to meet the energy demand for nutrient uptake [6,14,15]. One of the detrimental effects of NH_4^+ toxicity is the nutritional imbalances it induces, particularly through its antagonistic effect on calcium, magnesium, and potassium (Ca, Mg, and K) absorption, leading to deficiencies of these nutrients in plants [16]. Additionally, the NH_4^+ toxic effect results in an increase in respiratory intensity, hastening the oxidation of respiratory substrates, without sufficient ATP production [14,17].

A possible alternative to mitigate nutritional disorders caused by high NH_4^+ toxicity in plant tissue is the use of Si [4,7]. Although not considered a plant nutrient, this beneficial element (mostly as monosilicic acid (H_4SiO_4)) is absorbed by plants with concentrations varying between 0.1 and 0.6 mM, which is about two orders of magnitude higher than the concentrations of phosphorus (P) [18]. The beneficial effects of Si have been observed in various plant species, including Si-accumulating and non-accumulating species [19–21]. For example, grasses can even contain higher levels of Si than any of the other inorganic mineral nutrients [19]. Si application has a positive impact on almost all aspects of N nutrition, i.e., absorption, assimilation, and remobilization [3,14,22]. This beneficial effect of Si on overall plant performance has been established under low, optimal, and excessive N supply. In addition to a direct effect on N metabolism, Si supply induces changes in carbon (C) and P stoichiometry in shoots [23,24] and increases nutrient acquisition by roots [21,25], which in turn can contribute to improving N utilization within plant tissues. In rice cultivated under low N supply, the expression levels of N-uptake genes (*OsNTR1.1* and *OsAMT1;1*) remained unaffected or were even down-regulated by Si supplementation, whereas N-assimilation genes (*OsGS2*, *OsFd-GOGAT*, *OsNADH-GOGAT2*, *OsGDH2*, and *OsNR1*) were up-regulated [26]. Furthermore, in non-stressed rice with sufficient N supply, Si nutrition was found to influence the flux from 2-oxoglutarate to amino acid metabolism [27].

Beetroot (*Beta vulgaris* L.) originates from temperate climate regions of Europe and North Africa. According to Sediyama et al. [28], this vegetable is gaining importance in Brazil and is among the ten main vegetables produced in the country. Its cultivation predominantly occurs in the South and Southeast regions, contributing to 77% of the total production, with an average yield ranging between 30 and 40 t ha^{-1} [29]. It has been indicated that N is the most important element applied to beetroot, because it is difficult to find soils containing sufficient amounts of this element in any of its available forms. Insufficient N supply can reduce plant N concentration and photosynthetic rate [4] and simultaneously reduce plant growth and quality of harvestable materials [7]. Optimal N fertilizer application positively impacts yield. However, an oversupply of N does not always lead to increased yield and, in fact, could result in reduced growth and yield, especially for crops where roots and tubers are harvested [4,7,30].

Elemental stoichiometry, which examines the relative proportions of elements such as C, N, and P in organisms and ecosystems, is fundamental in shaping ecosystem dynamics and functioning. The study of C:N:P stoichiometry offers a novel approach to understanding the interactions between plants and soils, as well as the elemental cycling in plant-soil systems, particularly in the context of a changing environment [31–33]. Additionally, the concept of stoichiometric homeostasis highlights the ability of organisms to maintain stable concentrations or ratios of elements within their tissues despite fluctuations in environmental conditions [34]. This understanding is crucial for predicting how nutrient proportions vary among different plant communities in response to various growth conditions or exposure to biotic or abiotic stresses.

Several studies have concluded that C, N, and P stoichiometry in plants tend to decouple under climate change effects [33,35–37], but studies involving NH_4^+ toxicity are lacking. Therefore, stoichiometric homeostasis can be used to predict the strategies used by different plant species under biotic and abiotic stress to cope with limited resources in their environment.

Despite the wealth of research on nutrient stoichiometry, there is still limited understanding of how NH_4^+ toxicity affects the C:N:P ratio, particularly in horticultural crops. Therefore, comprehending the interactions among Si, NH_4^+ toxicity, and nutrient stoichiometry can bolster the advancement of resilient and productive cropping systems in the face of changing environmental conditions.

We hypothesized that plants of beetroot will adjust nutrient conservation strategies to balance the altered elemental stoichiometric homeostasis (C:N:P) and dry matter production according to NH_4^+ concentrations in the presence of Si. Meanwhile, the absence of Si in the nutrient solution could decrease N and P concentrations as well as exacerbate NH_4^+ toxicity due to altered elemental stoichiometric ratios. Therefore, this study aims to evaluate individual and interactive effects of different NH_4^+ concentrations in the presence or absence of Si in the nutrient solution on C:N:P stoichiometry and yield of beetroot grown using hydroponics.

2. Materials and Methods

2.1. Installation and Conduction of the Experiment

The experiment was conducted in a greenhouse located at the Faculty of Agricultural and Veterinary Sciences (FCAV), UNESP Jaboticabal, SP, Brazil (21°15′22″ S and 48°18′58″ W). The aim was to evaluate the influence of Si on the C:N:P stoichiometry and yield parameters of beetroot plants (*Beta vulgaris* L. cv. Early Wonder), under different NH_4^+ concentrations. Plants were cultivated under controlled conditions in a growth chamber, with a light/dark cycle of 13/11 h, temperature regimen ranging from 35 to 25 °C, and relative humidity of approximately 50%. Each experimental unit consisted of a plastic pot with a capacity of 3.8 L, filled with a mixture of coarse vermiculite substrate (90 to 100% particles between 1.19 and 1.50 mm) combined in a 1:1 ratio (*v*/*v*) with superfine particles (90 to 100% particles between 0.21 and 0.33 mm). This substrate mixture ensured adequate porosity and aeration for plant growth.

2.2. Growth Condition

In each pot, six seeds were sown at a depth of 2 cm. Five days after emergence, the seedlings were thinned, leaving only two plants per pot to provide sufficient space for root development. Initially, 100 mL of distilled water per pot was applied for the first 7 days to maintain the required humidity for the seedlings. Distilled water was subsequently substituted with 200 mL of a nutrient solution for each pot [38], with a modification in the source of iron, alternating between Fe-EDTA and Fe-EDDHMA. The pH of the nutrient solution was monitored daily and kept within a range of 5.4 ± 0.3 by adjusting with 0.01 mol L^{-1} sodium hydroxide (NaOH) and/or hydrochloric acid (HCl).

2.3. Experimental Design

The experimental design employed was a completely randomized design, arranged in a factorial scheme of 5 × 2. This corresponded to five concentrations of NH^{4+} (1.0, 7.5, 15, 22.5, and 30 mmol L^{-1}) and the absence and presence of Si (2 mmol L^{-1}), with four replicates. The Si concentration utilized in this study was determined based on the experiments conducted by our research group (GENPLANT) [4,7], and the fact that the solubility of H_4SiO_4 in the nutrient solution is close to this concentration [4,39]. The N source employed was NH_4Cl, with Si provided in the form of H_4SiO_4 (Si = 28.5 g L^{-1}).

2.4. Determination of Dry Matter

The plant material underwent a thorough cleaning process involving rinsing under running water, treatment with a 0.2% detergent solution, followed by a 0.1% hydrochloric acid solution, and a final rinse with deionized water. Afterward, all plant material was placed in paper sacks and dried in a forced air circulation oven (Tecnal TE 394–3—Piracicaba, Brazil) at 65 ± 5 °C until a constant weight was achieved. Subsequent to drying, the total dry mass was measured using a precision digital balance (Sartorius, TS 1352Q37, Goettingen, Germany). The dried material was then pulverized using a Wiley mill equipped with a stainless-steel chamber and blades (IKA-WERKE, GMBH & CO. KG, Staufen im Breisgau, Germany).

2.5. Carbon, Nitrogen, Phosphorus, and Silicon Analysis

For nutrients (N, P, and C), the material collected from each replicate (n = 4) per pot was combined to create a composite sample. We determined the total carbon (C) and nitrogen (N) concentrations in shoots and roots using the dry combustion method (at 1000 °C) in an elemental analyzer (LECO Truspec CHNS) calibrated with the wheat pattern (LECO 502–278) standards for carbon (C = 45.00%) and nitrogen (N = 2.68%). The Si content in shoots and roots was determined following the methodology outlined in reference [40]. Meanwhile, P concentration was determined using a spectrophotometer (model SP-1105) employing the molybdenum antimony colorimetric method. Total N concentration was measured according to the methodology described in [41]. With the C, N, and P concentrations obtained from shoots and roots, we computed the C:P, C:N, and N:P ratios [33].

2.6. Statistical Analysis

The data underwent a two-way analysis of variance (ANOVA) following the verification of variance homogeneity using Levene's F-test. The normality of the data was assessed using the Shapiro–Wilks W test. Mean values were compared using Tukey's test ($p < 0.05$). In this study, we examined the main effects of five ammonium concentrations (NH_4^+) both in the absence and presence of silicon (Si), as well as their interactions (Si × N). All statistical analyses were conducted using the software Agroestat® v. 1.1.0.626 [42].

3. Results

3.1. Nutrient (C, N, P, and Si) Concentrations in Shoots

The ANOVA revealed a significant interaction of N × Si for C concentration [C], N concentration [N], P concentration [P], and Si concentration [Si] in shoots (Figure 1a–d). While [C] remained stable, the interactive effect increased shoot [N] and [P], reaching its highest value at 15 mmol L^{-1} of NH_4^+ in the presence of Si (Figure 1a–c). Thereafter, there was a tendency to decrease [N] and [P] with increasing NH_4^+ levels independently from the use of Si in the nutrient solution. On the other hand, shoot [Si] reached its maximum at the highest NH_4^+ level (30 mmol L^{-1}) in the nutrient solution (Figure 1d).

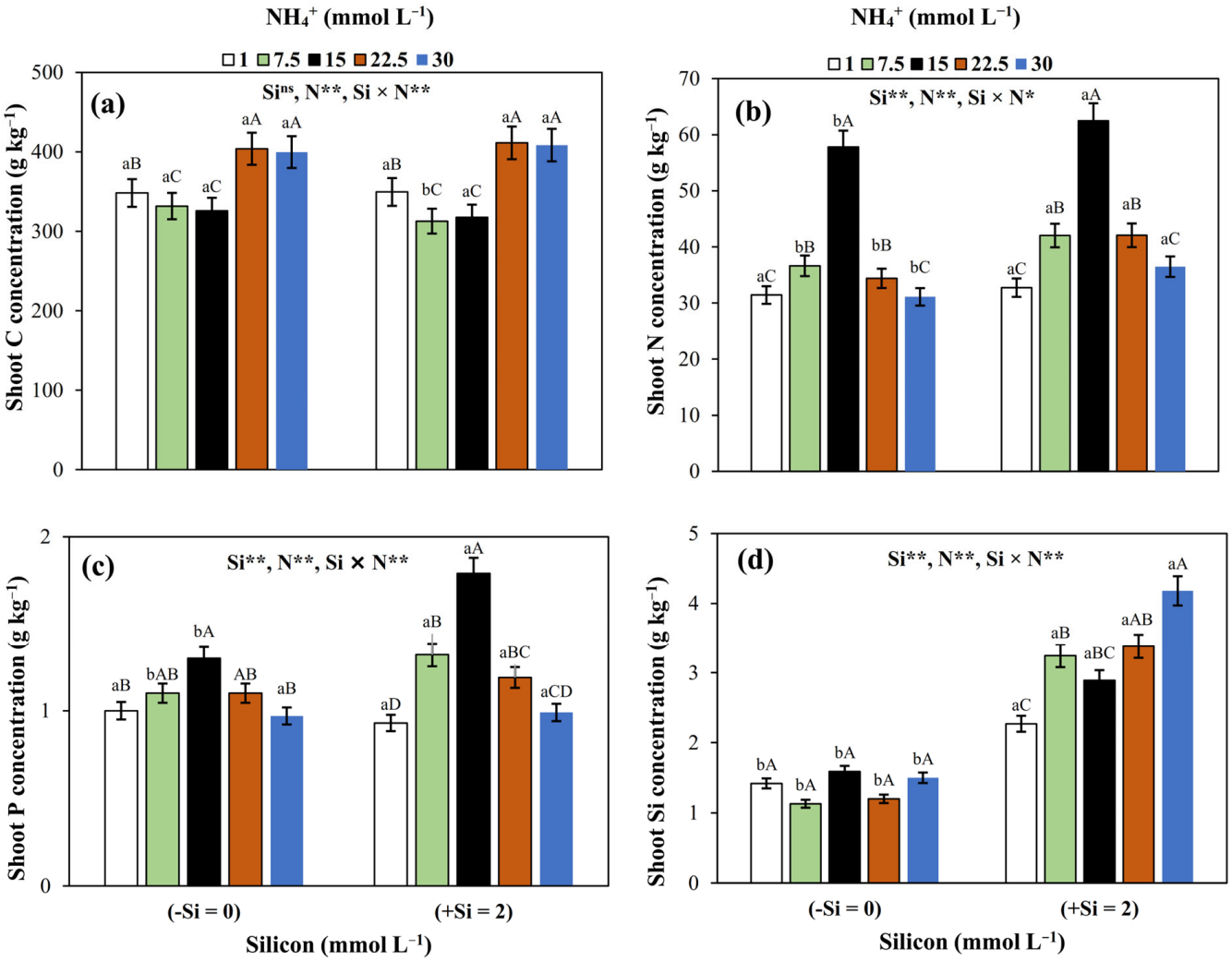

Figure 1. Effects of NH_4^+ concentrations, in the presence (+Si) and absence (−Si) of Si on shoot C concentration (**a**), shoot N concentration (**b**), shoot P concentration (**c**), and shoot Si concentration (**d**) of beetroot plants. Different uppercase letters indicate significant differences between different NH_4^+ concentrations at the same Si concentration, while different lowercase letters indicate significant differences between different Si concentrations within the same NH_4^+ concentration, according to the F test. Error bars show standard errors based on the average values of four replicates (n = 4). * $p \leq 0.05$; ** $p \leq 0.01$; ns, not significant; Si × N, Si–NH_4^+ interaction.

3.2. Nutrient (C, N, P, and Si) Concentrations in Roots

The ANOVA revealed a significant interaction between [Si] and [N] (Si × N) in the roots of beetroot plants depending on the treatment. In the absence of Si, the [C] decreased linearly as NH_4^+ concentration increased up to 30 mmol L^{-1}. In the opposite direction, the presence of Si in the nutrient solution increases the [C] (Figure 2a). On the other hand,

an increase in the concentration of NH_4^+ decreased [N], especially in the plants cultivated without the incorporation of Si in the nutritive solution in the last NH_4^+ concentration (Figure 2b). Both [P] and [Si] in the root increased in the presence of Si in the nutrient solution. Specifically, [P] increased up to 15 mmol L^{-1} of NH_4^+, meanwhile, the addition of Si in the nutrient solution resulted in higher levels of Si in the root of the beetroot, relative to plants without Si supplementation, across all concentrations of NH_4^+ (Figure 2c,d).

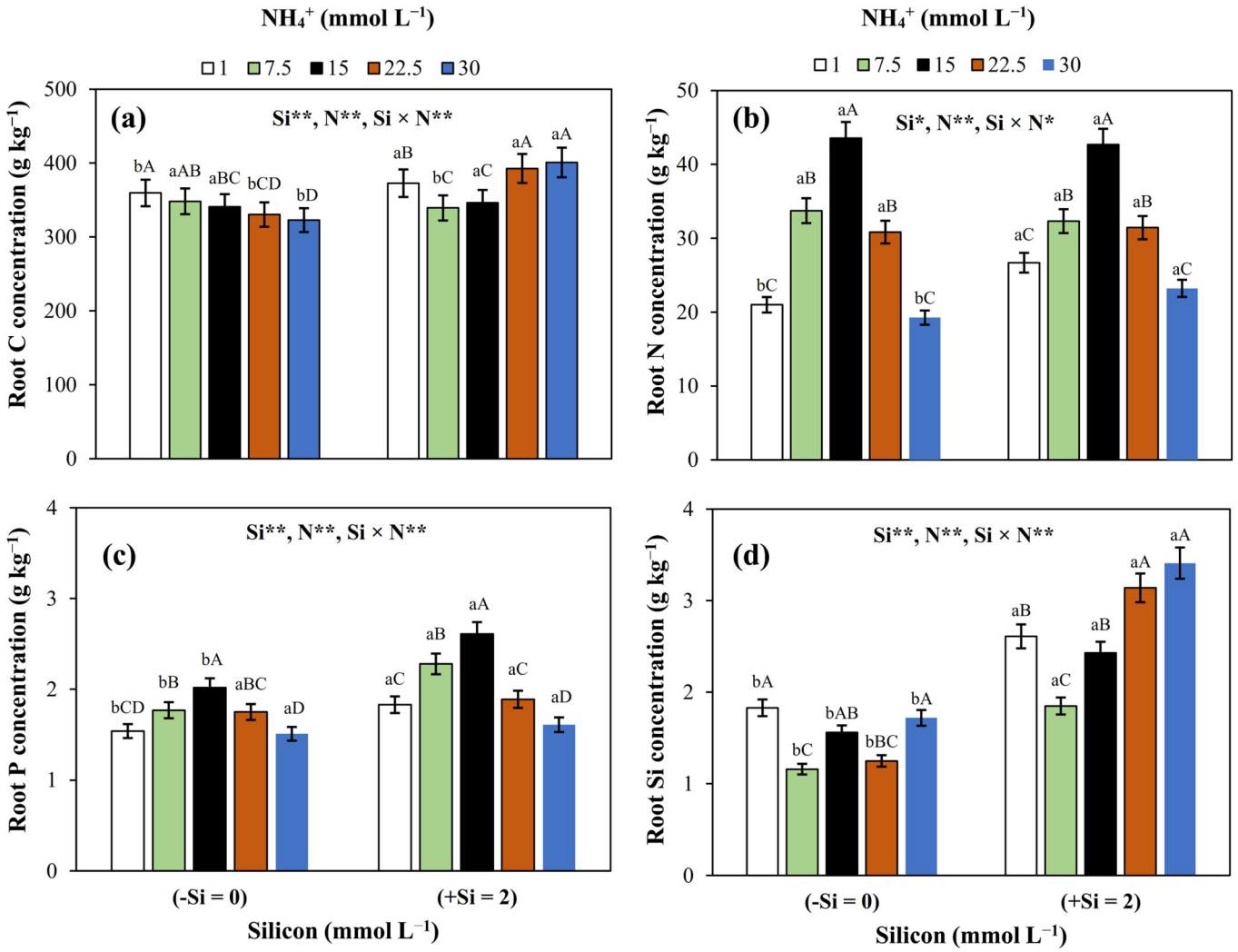

Figure 2. Effects of NH_4^+ concentrations, in the presence (+Si) and absence (−Si) of Si on root C concentration (**a**), root N concentration (**b**), root P concentration (**c**), and root Si concentration (**d**) of beetroot plants. Different uppercase letters indicate significant differences between different NH_4^+ concentrations at the same Si concentration, while different lowercase letters indicate significant differences between different Si concentrations within the same NH_4^+ concentration, according to the F test. Error bars show standard errors based on the average values of four replicates (n = 4). * $p \leq 0.05$; ** $p \leq 0.01$; Si × N, Si–NH_4^+ interaction.

3.3. Dry Matter and C:N, C:P, and N:P Ratios in Shoots

Shoot C:N ratio increased in the absence of Si; however, an interactive effect between Si and N decreased the C:N ratio in the presence of Si for all NH_4^+ concentrations (Figure 3a). Shoot C:P ratio increased under higher NH_4^+ concentration conditions in the nutrient solution, irrespective of the presence or absence of Si, showing an interaction between Si and N (Figure 3b). The highest N:P ratio of the shoot was found in 15 mmol L^{-1} of NH_4^+ concentration in the absence of Si (Figure 3c). Conversely, the N:P ratio increased with the higher NH_4^+ concentration in the presence of Si in the nutrient solution (Figure 3c). We

found a growing increase in the shoots dry matter production up to 15 mmol L^{-1} of NH_4^+ (Figure 3d). From this concentration, the tendency was to gradually decrease, but it was always greater in the presence of Si, when compared to plants without the addition of Si. Shoot dry matter was significantly influenced by the interactive effects between Si and N.

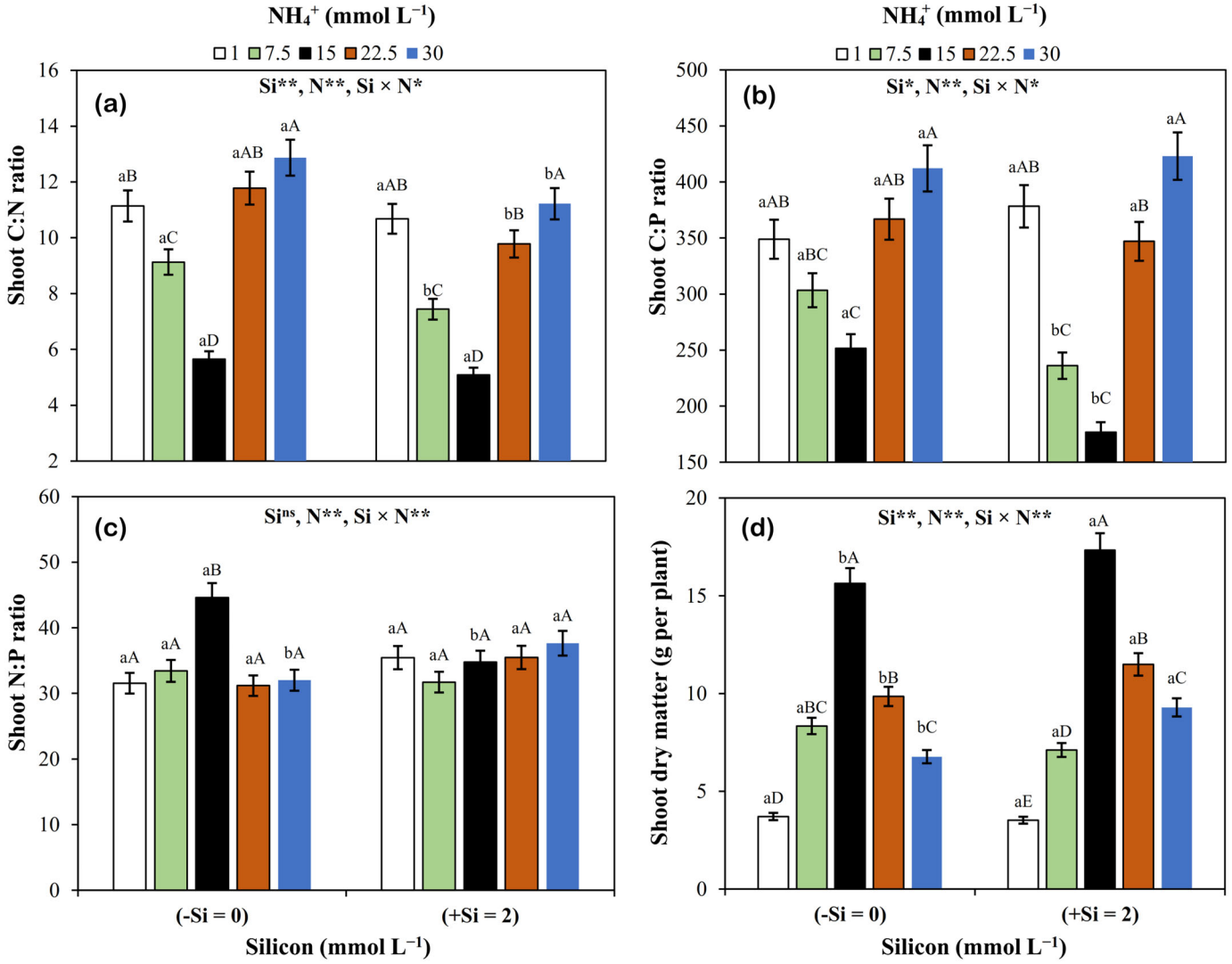

Figure 3. Effects of NH_4^+ concentrations, in the presence (+Si) and absence (−Si) of Si on shoot C:N ratio (**a**), shoot C:P ratio (**b**), shoot N:P ratio (**c**), and shoot dry matter (**d**) of beetroot plants. Different uppercase letters indicate significant differences between different NH_4^+ concentrations at the same Si concentration, while different lowercase letters indicate significant differences between different Si concentrations within the same NH_4^+ concentration, according to the F test. Error bars show standard errors based on the average values of four replicates (n = 4). * $p \leq 0.05$; ** $p \leq 0.01$; ns, not significant; Si × N, Si–NH_4^+ interaction.

3.4. Dry Matter and C:N, C:P, and N:P Ratios in Roots

Root C:N, C:P, and N:P ratios were significantly influenced by the interactive effects of Si × N (Figure 4a–c). In comparison with the plants that grow in the presence of Si, the concentration of 15 mmol of NH_4^+ had a significant positive effect on the C:N ratio of the roots in the absence of Si, while the opposite effect was observed at a higher concentration of 22.5 mmol of NH_4^+ (Figure 4a). C:P ratio decreased in plants supplied with Si under the first three concentrations of NH_4^+ (from 1 mmol L^{-1} to 15 mmol L^{-1}) in the nutrient solution (Figure 4b). However, Si increased the C:P ratio under the last two concentrations of NH_4^+ (from 22.5 mmol L^{-1} to 30 mmol L^{-1}) in the nutrient solution. Except for the first

and last concentrations of NH_4^+ in the nutrient solution, the C:N ratio in the root increased significantly in plants in the absence of Si (Figure 4c). In contrast, root dry matter increased for all treatments in the presence of Si, regardless of the NH_4^+ concentration in the nutrient solution, compared with plants in the absence of Si (Figure 4d).

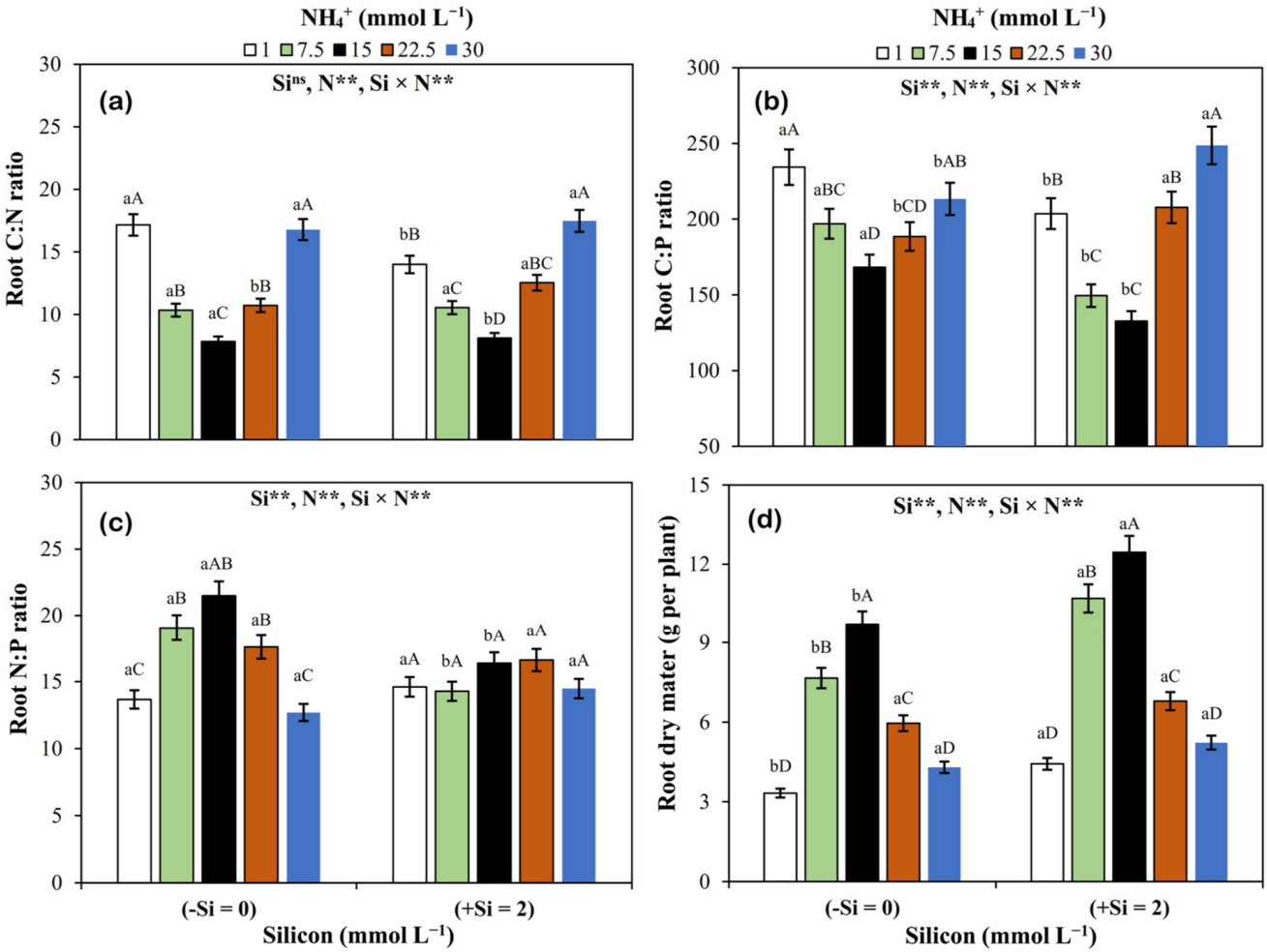

Figure 4. Effects of NH_4^+ concentrations, in the presence (+Si) and absence (−Si) of Si on root C:N ratio (**a**), root C:P ratio (**b**), root N:P ratio (**c**), and root dry matter (**d**) of beetroot plants. Different uppercase letters indicate significant differences between different NH_4^+ concentrations at the same Si concentration, while different lowercase letters indicate significant differences between different Si concentrations within the same NH_4^+ concentration, according to the F test. Error bars show standard errors based on the average values of four replicates (n = 4). ** $p \leq 0.01$; ns, not significant; Si × N, Si–NH_4^+ interaction.

3.5. Visual Evidence of Si-Mediated Suppression of NH_4^+ Toxicity in Beetroot

The benefit of plants treated with Si in the suppression of NH_4^+ toxicity can be seen visually (Figure 5). In the absence of Si, plants had less development, uniform leaf chlorosis, and necrosis at the leaf edge, thus, plants showed lower dry matter accumulation than seedlings grown in the presence of Si in the nutrient solution.

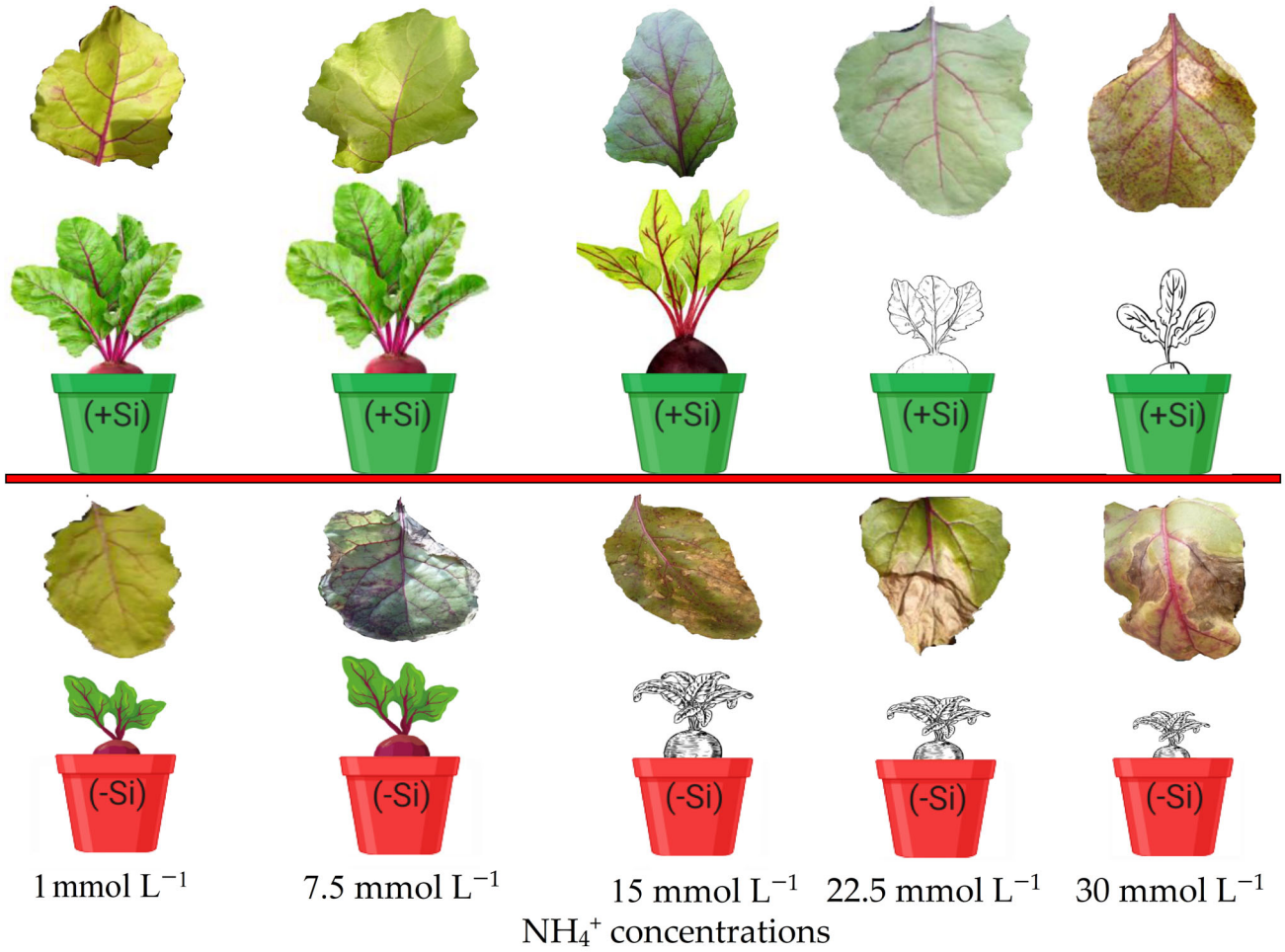

Figure 5. *Beta vulgaris* L. cv. early wonder grown in nutrient solution under different NH_4^+ concentrations in the presence (+Si) and absence (−Si) of Si.

4. Discussion

The use of N supply based on the NH_4^+ form is used in cheap fertilizers such as urea, the use of which can reduce the costs of production and increase farmers' incomes [4]. Unlike NO_3^-, NH_4^+ is directly incorporated into organic compounds without the need for energy-dependent enzymatic reduction [6]. Consequently, the lower metabolic energy expenditure associated with ammoniacal nutrition can be converted into higher plant growth, and thus higher production. However, despite its value as a fertilizer, it is well established that an excess of NH_4^+ can promote the production of reactive oxygen species (ROS), which can cause reductions in cytoplasmic pH, photosynthetic rate, transpiration, and stomatal conductance [4,7,43]. In addition, an excess NH_4^+ can inhibit root growth, and subsequently vegetative shoot growth and yield (Figure 5) [44].

Ammonium toxicity typically occurs in plants when they are exposed to high levels of NH_4^+ in their environment. This can result from various factors such as excessive NH_4^+ accumulation in the soil, imbalances between NH_4^+ and NO_3^- availability, adverse soil conditions like acidic pH and waterlogging, and interference of NH_4^+ with the uptake of other essential nutrients [11].

Several experiments have focused on the relationships between nutrient stoichiometry in plant communities and geographical variations or climatic factors [33,35,45]. However, to the best of our knowledge, few studies have focused on the effects of NH_4^+ toxicity on the C:N:P ratio in horticultural crops.

A strategy that has proven its effectiveness in mitigating the damages caused by excess of NH_4^+ is the use of Si. Although Si is not an essential nutrient, its application

is beneficial. Si application can mitigate the harmful effects of oxidative stress in the photosynthetic apparatus of different crops [4,7] and improve antioxidant responses [21], increasing dry matter by enhancing ionic homeostasis in roots and shoots of different plant species [46]. The addition of Si induces changes in the C:N:P stoichiometry and enhances the stoichiometric homeostasis of sorghum and sunflower plants under salt stress [45]. However, the patterns of plant C:N:P stoichiometry are species-specific and dependent on various factors and ambient conditions [32,33,37].

Plants exposed to high concentrations of NH_4^+ typically show symptoms of NH_4^+ toxicity. At low concentrations (<3 mmol L^{-1}), NH_4^+ is typically the N source preferred by plants, but above a certain threshold, e.g., 15 mmol L^{-1} in beetroot and 30 mmol L^{-1} in radish, NH_4^+ becomes toxic [4,7]. This threshold depends on plant species and on variety or cultivars of the same species [43,47]. Recently, Olivera-Viciedo et al. [4] reported that at the concentration of 30 mmol L^{-1}, NH_4^+ was shown to have negative effects on the total dry biomass, photosynthesis, transpiration, and stomatal conductance of radish seedlings, even in the presence of Si in the nutrient solution, whereas instantaneous water-use efficiency and the green color index increased in the presence of Si.

In this study, we observed that the highest levels of NH_4^+ affected stoichiometric homeostasis and reduced the dry matter by decreasing the shoots and roots [N] and [P], especially in the plants cultivated without Si in the nutritive solution, corroborating our main hypothesis. These findings indicate that the application of Si to the nutrient solution used in hydroponic conditions could provide an effective means of alleviating the unfavorable effects induced by NH_4^+ toxicity in agreement with our previous experiment [4,7]. The beneficial effect of Si is attributed to the stimulation of NH_4^+ ion incorporation through its effect on genes encoding enzymes involved in N metabolism, such as nitrate reductase, glutamine synthetase, and glutamate dehydrogenase [14,16]. As a result, the amount of free NH_4^+ is reduced, thereby having no toxic effect.

While plants can survive with very low Si availability under greenhouse or some controlled laboratory conditions, numerous studies have demonstrated that plants fertilized with Si exhibit increased photosynthesis, water-use efficiency, and consequently, higher biomass production compared to non-Si-fertilized plants [4,7,19,21,48,49]. Higher dry matter of shoots and roots (Figures 3d and 4d) in the presence of Si may be given by a higher [N] and [P] in both plant organs (Figure 1b,c and Figure 2b,c). This positive effect of Si is due to the fact that this element accumulates in the abaxial region of the leaves, leading to more erect plants, with higher light absorption capacity (Figure 5). Consequently, this enhancement can improve photosynthetic efficiency, thereby increasing dry matter production, which would be advantageous to the plant [4,7]. However, it should be noted that there was a more severe effect of NH_4^+ toxicity in the roots than shoots when NH_4^+ concentrations were higher than 15 mmol L^{-1}, probably because roots constitute the first NH_4^+ sensor, and the initial signals of NH_4^+ toxicity appear at the root level with a severe modification of the root architecture that results in a decreases root/shoot ratio, as reported in previous studies [6,50].

5. Conclusions

The addition of Si in the nutrient solution significantly increased both [N] and [P] in shoots and roots. Although shoot [C] remained stable, there was a notable increase in root [C] at NH_4^+ concentrations of 22.5 and 30 mmol L^{-1} in the presence of Si. These results underscore the crucial role of Si in maintaining nutrient balance, particularly evident under high NH_4^+ levels. Plants cultivated without Si in the nutrient solution exhibited diminished shoot and root dry matter production, highlighting the essential function of Si in mitigating the detrimental effects of NH_4^+ toxicity on plant growth and biomass accumulation. Incorporating Si (2 mmol L^{-1}) into the nutrient solution used in hydroponic cultivation could serve as an effective strategy to alleviate the adverse effects induced by NH_4^+ toxicity in beetroot at concentrations up to 15 mmol L^{-1}.

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