

Si attenuates the transpiration and increases both N assimilation and root development in the tomato under N availabilities

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Abstract

Nitrogen (N) is the most important nutrient in crop productivity and silicon (Si) increases the uptake of nutrients and affect the uptake of N. The objective of this study was to evaluate the effect of Si combined with rates of N on the growth, root development, uptake of N and Si, assimilation of N, and photosynthesis of the tomato plants (*Solanum lycopersicum*). A factorial 3 × 3 was used, with rates of Si 0 (control treatment), 1, and 3 mmol L⁻¹, and rates of N 5 (control treatment), 15, and 25 mmol L⁻¹ in the nutrient solution. The rates of N did not affect the dry mass production and uptake of Si. However, the application of Si improved the plant growth and accumulation of Si and N. Relating to control treatment, the rate of Si 1 mmol L⁻¹ increases the dry mass production and accumulation of Si and N in order of 52, 37, and 54 %, respectively. Although the rate of N did not increase the plant growth, it was verified that the N 15 mmol L⁻¹ improves the concentration and accumulation of N in the shoots, and the relative concentration of chlorophyll with values of 43.5, 67, and 14 %, respectively, compared to the control. The supply of Si under low and high availability of N improved the glutamine synthetase, but at the rate of N 25 mmol L⁻¹, a decrease in the transpiration rate and stomatal conductance was verified. Under the high availability of N, the glutamine synthetase raised 78 % as an effect of Si 3 mmol L⁻¹ compared to control treatment (Si 0 mmol L⁻¹). Nevertheless, the transpiration rate and stomatal conductance decreased 49 and 52 % under that condition. The excess of N 25 mmol L⁻¹ negatively affected the root development, but under that condition, the application of Si increased the root length, root surface, and root hood in order of 70, 40, and 77 % compared to the control treatment. Application of Si is recommended for tomato growth, especially when cultivated with high N availability. The application of silicon enhances the plant growth, root development, nutrient uptake, nitrogen assimilation, and photosynthesis of the tomato plants cultivated under rates of N. We recommend the use of Si 3 mmol L⁻¹ and N 15 mmol L⁻¹ for the tomato plants under the nutrient solution.

Keywords: Nitrogen, Nitrogen assimilation, Photosynthesis, Silicon, *Solanum lycopersicum*, Winrhizo.

Abbreviations: N_Nitrogen; NR_Nitrate reductase; Si_Silicon; SPAD_Indirect chlorophyll determination.

Introduction

The future of food production may be negatively influenced by the global temperature increase, lower availability of drinking water, and soil contamination by toxic elements, causing low productivity and nutritional quality of foods (Adams et al., 2001). Moreover, the world is experiencing the transformation of useful lands into regions with low soil fertility due to the low availability of N (Linguist et al., 2011). Therefore, the high yield of crops requires better management of fertilizers. A possible technique for better management of fertilizers may be the use of beneficial elements such as silicon (Si) associated with nutrients, which increase the nutrient uptake, transpiration, and production of many plant species (Choi et al., 2016; Ma et al., 2004).

Nitrogen (N) is the constituent of all proteins like DNA and plant hormones (Taiz et al., 2017). N has a unique impact on the efficiency of agricultural systems, especially combined with other elements. The production of N fertilizers expends high amounts of energy and is one of the most expensive fertilizers in agriculture. The excessive use of N fertilizers may decrease production and lead to negative

environmental consequences (Xu et al., 2012). Concerning the soluble N fertilizers, the first goal has been to increase the crop yield due to the adjustment of the optimum rate (Firbank, 2005). The non-adjustment of the supply of N, especially at the initial growth, may cause low development and in some cases increase the leaching of N to the environment. Hence, it is necessary to develop technologies that improve the uptake and use of N by the root of the plants in low or high availability conditions. One of the methods of improving uptake and use of N is the combination with other elements, such as silicon (Si). Si fertilizers are widely used to improve the crop yield (Liang et al., 2006). The mechanisms of the uptake of Si and their effects on plant structure and stress alleviation have been well described (Marschner, 2012). Hydroponics studies showed that the presence of Si in the growth medium reduces saline stress, the adverse effects related to the production of plant dry mass, and increases the chlorophyll content in wheat (*Triticum* sp.) (Tuna et al., 2008). That element is also involved in the metabolic and physiological

mechanisms under water stress, which decreases the transpiration rate by the deposition of Si on the leaves as a result of increasing the uptake of Si, preventing excess water loss by transpiration (Gong et al., 2005; Pati et al., 2016). Kamenidou et al. (2009) also reported that a major benefit of the application of Si is the reduction in the rate of transpiration by the accumulation of Si in the leaves.

There is evidence that the interaction N × Si in the plant enhances growth and root development (Lemus et al., 2008; Massey et al., 2007). N is the most demanded nutrient by crops and one of the most limited in agricultural productivity (Nascente et al., 2011). Supply of N in high rates promotes excess increases in the plant height, making it susceptible to tipping as well as the occurrence of pests and diseases (Prabhu et al., 2007), and possible nutrient leaching to the environment. On the other hand, Si is polymerized in the cells of the leaf epidermis, forming a rigid layer (Marschner, 2012) and improving the plant architecture, resulting in high light capture, great photosynthetic activity, less lodging, low risk of disease and pest attack, high capacity of the metabolic system (Gunes et al., 2008), and water-saving (Guerrero et al., 2011). The effect of Si in plants is attributed to the improvements of the plant architecture, leaf transpiration, arrangement, increase in the light uptake, photosynthetic activity (Tamai and Ma, 2008), as well as in the N uptake (Detmann et al., 2012). However, the role of Si in non-grass plants is still poorly studied, especially under rates of N. Thus, the hypothesis is: the supply of Si improves the growth and development of the tomato plants in the conditions of low or high N availability at the initial growth. The objective of this study was to evaluate the effects of Si on the shoots and root development, nutritional attributes, and metabolic and photosynthetic activity of the tomato plants (*Solanum lycopersicum*) under availabilities of N.

Results

Morphological symptoms

Plants were grown under applications of Si at the highest rate of N 25 mmol L⁻¹ showed the greatest root branching, which seemed to give the plants a high specific surface area to uptake water and nutrients. At the highest rate of Si 3 mmol L⁻¹, the plants were upright, with the possibility of greater use of luminosity. The plants grown at low availability of N were chlorotic concerning the plants grown in other availabilities of N.

Dry mass production, minerals in the plant tissue, and SPAD values

Dry mass production of the tomato was affected by the rates of Si (Table 1). The results indicated that the production of shoots was higher on plants that received Si 1 and 3 mmol L⁻¹ compared to those plants that received no Si in the nutrient solution (Table 1). Similar results were observed for the roots dry mass production, which showed higher values with Si 1 mmol L⁻¹ compared to the plants with no Si application in the growth medium (Table 1).

The concentration of total N in the shoots and roots changed as the N rates in the nutrient solution were increased (Table 1). Plants grown with the N rate of 15 and 25 mmol L⁻¹ showed a higher concentration of N in the shoots and roots compared to the plants grown under N 5 mmol L⁻¹ (Table 1). In relation to the concentration of Si in the plant samples,

higher concentrations of Si were found in the roots and shoots supplied with the highest rate of Si (3 mmol L⁻¹) than at Si 1 mmol L⁻¹ or no Si added (Table 1).

The accumulation of total N in the shoots was influenced by the rates of N and Si (Table 1). N rates of 15 and 25 mmol L⁻¹ induced higher accumulation of N in the shoots of the tomato compared to N 5 mmol L⁻¹. The same trend was found in the shoots of plants grown with Si in the nutrient solution, where plants receiving Si 1 and 3 mmol L⁻¹ had higher accumulations of N than plants with no Si supplied (Table 1). In the roots, only the rates of Si changed the accumulation of N (Table 1). Accumulation of Si was significantly higher in the roots of the tomato supplied with Si 3 mmol L⁻¹ compared to no Si supply (Table 1).

The concentration of indirect chlorophyll (SPAD value) was influenced by the rates of N in the nutrient solution. The results showed higher averages in the plants receiving N 15 and 25 mmol L⁻¹ compared to those receiving N 5 mmol L⁻¹ (Table 1).

N-assimilation in the tomato plants

The activity of NR was influenced by the rates of N (Figure 1a). The highest enzyme activity was found in the plants grown at N 15 and 25 mmol L⁻¹ than those at N 5 mmol L⁻¹ (Figure 1a). For the activity of GS, it was found that the interaction N × Si was significant (Figure 1b). For plants grown at N 5 and 25 mmol L⁻¹, the activity of GS was higher under Si 3 mmol L⁻¹ in relation to no Si application. The rates of Si did not change the activity of GS in the plants grown at N 15 mmol L⁻¹. In the nutrient solution with no Si added, it was verified that N 15 mmol L⁻¹ resulted in a higher activity of GS than other rates of N. The plants grown with Si in the nutrient solution, rates of N did not affect the activity of GS.

Photosynthetic activity

The net photosynthesis (Figure 2a), transpiration rate (Figure 2b), and stomatal conductance (Figure 2c) on the tomato leaves showed a significant interaction N × Si (Figure 2). Tomato plants grown at N 15 mmol L⁻¹ and those that received Si 1 mmol L⁻¹ showed lower averages of the transpiration rate and stomatal conductance than those plants that did not receive Si. The results also show that plants grown under N 25 mmol L⁻¹ have higher net photosynthesis, transpiration rate, and stomatal conductance when grown with no Si or with 1 mmol L⁻¹ than plants grown with Si 3 mmol L⁻¹. For the plants that received N 5 mmol L⁻¹, no significance was found among the rates of Si (Figure 2a, 2b, 2c). Plants grown with no Si and with 1 mmol L⁻¹ showed higher values of net photosynthesis, transpiration rate, and stomatal conductance when grown with N 25 mmol L⁻¹ than N 5 mmol L⁻¹ (Figure 2a, 2b, 2c).

The quantum efficiency of photosystem II and the electron transport rate showed a significant interaction N × Si (Figure 2d, 2e). Regarding the plants receiving N 5 and 15 mmol L⁻¹, those with no Si had a higher average than those at Si 1 mmol L⁻¹. However, the plants that received N 25 mmol L⁻¹, the rates of Si did not affect the quantum efficiency of photosystem II and electron transport rates (Figure 2d, 2e). Rates of N were effective only when the plants received Si and the results showed higher efficiency of photosystem II and electron transport rate (Figure 2d, 2e).

Root development

The interaction $N \times Si$ was significant for root length, root surface, root hood unit, and root diameter (Figure 3). For the plants grown with $N\ 25\ \text{mmol L}^{-1}$, the root length was higher at rates of $Si\ 1$ and $3\ \text{mmol L}^{-1}$ than those plants with no Si supplied (Figure 3a). However, at $N\ 15\ \text{mmol L}^{-1}$ and $Si\ 1$ and $3\ \text{mmol L}^{-1}$ the root length was lower than those plants that did not receive Si . For the plants grown under low N availability ($5\ \text{mmol L}^{-1}$), the root length was higher at $Si\ 1\ \text{mmol L}^{-1}$ than those with other rates of Si . For the plants grown with $Si\ 3\ \text{mmol L}^{-1}$, rates of N did not affect the root length. However, under other rates of Si , the supply of N decreased the root length. The root surface (Figure 3b) of plants grown under $N\ 25\ \text{mmol L}^{-1}$ was higher when receiving $1\ \text{mmol L}^{-1}$ relative to those plants that did not receive Si . For the plants grown at $N\ 5\ \text{mmol L}^{-1}$, higher values were found when the plants received $Si\ 1\ \text{mmol L}^{-1}$ than those plants receiving $Si\ 3\ \text{mmol L}^{-1}$. However, under $N\ 15\ \text{mmol L}^{-1}$, the rates of Si did not influence the results. The rates of N had no effect when the plants were grown with $Si\ 3\ \text{mmol L}^{-1}$. Besides, the supply of N decreased the root surface when the plants were cultivated with other rates of Si . The rates of Si changed the amount of the root hood in the plants grown under $N\ 15$ and $25\ \text{mmol L}^{-1}$. However, the Si application did not affect those plants grown with $N\ 5\ \text{mmol L}^{-1}$ (Figure 3c). For the plants grown under $N\ 25\ \text{mmol L}^{-1}$ a higher average was recorded with the application of $Si\ 1\ \text{mmol L}^{-1}$ in relation to other rates of Si . However, under $N\ 15\ \text{mmol L}^{-1}$, the highest averages were found in those receiving no Si and $1\ \text{mmol L}^{-1}$ than $Si\ 3\ \text{mmol L}^{-1}$. Under no Si added, $N\ 15\ \text{mmol L}^{-1}$ provided higher averages of the root hood than other rates of N . At $Si\ 1\ \text{mmol L}^{-1}$, greater amounts of the root hood were observed in those plants that received $N\ 15$ and $25\ \text{mmol L}^{-1}$ than plants receiving $N\ 5\ \text{mmol L}^{-1}$. The plants grown under $Si\ 3\ \text{mmol L}^{-1}$, the higher averages were verified in plants that received $N\ 5$ and $15\ \text{mmol L}^{-1}$ than those grown with $N\ 25\ \text{mmol L}^{-1}$.

The root diameter was affected by the rates of Si only in plants that received $N\ 25\ \text{mmol L}^{-1}$, showing lower values in the plants that received $Si\ 1$ and $3\ \text{mmol L}^{-1}$ than those that with no Si supply (Figure 3d). Plants grown with no Si added and supplied with $N\ 25\ \text{mmol L}^{-1}$ showed higher root diameter than those with $N\ 5$ and $15\ \text{mmol L}^{-1}$. There were no effects of N rates in plants receiving $Si\ 1$ and $3\ \text{mmol L}^{-1}$. The root volume was influenced by the rates of N and Si (Figure 3e, 3f). The results of N showed that the higher averages were observed in the plants grown with $N\ 5$ and $15\ \text{mmol L}^{-1}$ than those cultivated with $N\ 25\ \text{mmol L}^{-1}$ (Figure 3e). Regarding the application of Si , the root volume was higher in the plants exposed to $Si\ 1\ \text{mmol L}^{-1}$ than those exposed to $Si\ 3\ \text{mmol L}^{-1}$ (Figure 3f).

Discussion

The supply of N did not affect dry mass production (Table 1). That result was not expected since the N has large importance in plant growth. A possible explanation could be associated with the amount of N necessary for the initial growth of tomatoes. At the initial growth of tomatoes, the plants require low amounts of N , and its excess causes tipping, self-shading, tissue juiciness, and susceptibility to insects and pathogens (Marschner, 2012). Nevertheless, plants cultivated under a high supply of N led to high chlorophyll concentration (in this study measured by SPAD

values). A high concentration of chlorophyll increases the photosynthetic activity and the synthesis of carbohydrates, which can elevate the free carbohydrate in leaves and hence be attractive for herbivores (Horgan, 2017). Studies have shown that the excessive supply of N affects growth, food consumption, survival, breeding rates, and density of those herbivorous insects (Brodbeck et al., 2001; Khan and Port, 2008; Mattson, 1980; Moon et al., 1995). However, the incidence of pest attack and injuries tends to be reduced using Si in the growth medium (Cai et al., 2009; Datnoff et al., 2001). Si may be concentrated in plant tissue and confers more tissue rigidity, improving the plant architecture and resistance to attack by insects and diseases (Marschner, 2012). In the present study, the positive effects of Si could lead to better tomato plant growth and showed higher dry mass production than those that did not receive Si . These results were also observed by Bastos and Ferreira (2010) in sugarcane. As the rates of Si in the nutrient solution increased, the accumulation of Si increased in the shoots and roots up to $1\ \text{mmol L}^{-1}$ (Table 1). According to Malavolta (2006), the supply of Si provides a better possibility of nutrient uptake and response to N fertilization. The concentration and accumulation of Si were highest only in the shoots and roots of the plants that received $Si\ 3\ \text{mmol L}^{-1}$. Plants that do not receive Si are anatomically fragile and more susceptible to biotic and abiotic stress when compared to those supplied with that element (Mitani and Ma, 2005). The accumulation of Si was higher in the shoots when compared to the roots and that accumulation in the plant tissues lead to an increase in dry mass production (Table 1), as observed by Neu et al. (2017). Previous studies that showed high uptake of Si by roots presented high concentrations in plant tissues and induced specific transporters in xylem associated with transpiration (Neu et al., 2017). In a study with wheat plants, Jarvis (1987) observed that 90 % of the Si uptake was transported from roots to the shoots, as occurred in the present study. Plants cultivated in the soil under normal conditions show concentrations of Si in the plant tissue between 1 and $100\ \text{g kg}^{-1}$ (Elmer and Datnoff, 2014; Epstein, 1999). The low activity of NR was observed in the plants with low availability of N in the nutrient solution ($5\ \text{mmol L}^{-1}$) (Figure 1a). At the low supply of N , low concentration, and accumulation of N were observed in the plant samples, which led to the low activity of NR . Those results indicate that low rates of N decreased the use of energy demanded by NR , however with no effects for dry mass production. It suggests that the initial growth of the tomato requires the low activity of NR sufficient to promote the proper growth of the plants since the early-stage plants require less N (Marschner, 2012). On the other hand, a high supply of N induces high concentration and accumulation of N in the plant tissue and consequently high activity of NR . It indicates that the enzyme NR is responsible for the supply of nitrate since 70 % of N applied in the present study was nitrate. The supply of nitrate increases the activity of NR (Liu et al., 2017). However, even when NR is working in high activity, plants cannot assimilate high amounts of nitrate provided at the initial growth since the plant did not require a high amount of N in that phase. Rates of Si were important for increasing the activity of GS at low ($5\ \text{mmol L}^{-1}$) and high ($25\ \text{mmol L}^{-1}$) supply of N (Figure 1b) that improved the assimilation of ammonium by the tomato plants. Those effects were particularly important in context with low availability of N .

Table 1. Dry mass production, concentration and accumulation of nitrogen and silicon in the shoots and roots, and relative chlorophyll concentration (SPAD) of the tomato plants at the initial growth under rates of nitrogen and silicon in the nutrient solution.

	Dry mass	N		Si		Chlorophyll
	g per plant	g kg ⁻¹		mg per pot		
Shoots						
		Nitrogen rates (mmol L ⁻¹)		Silicon rates (mmol L ⁻¹)		
5	5.60 ^{ns} ± 0.48	17.22 ^b ± 1.10	1.71 ^{ns} ± 0.12	92.42 ^b ± 3.46	9.39 ^{ns} ± 0.88	32.63 ^b ± 0.65
15	6.31 ^{ns} ± 0.51	24.71 ^a ± 1.33	1.79 ^{ns} ± 0.15	154.46 ^a ± 11.99	11.62 ^{ns} ± 1.76	37.17 ^a ± 0.96
25	5.64 ^{ns} ± 0.66	26.94 ^a ± 1.22	2.10 ^{ns} ± 0.12	150.42 ^a ± 17.12	12.08 ^{ns} ± 1.91	37.40 ^a ± 0.93
		Nitrogen rates (mmol L ⁻¹)		Silicon rates (mmol L ⁻¹)		
0	4.36 ^b ± 0.26	25.13 ^{ns} ± 2.01	1.78 ^{ns} ± 0.12	108.62 ^b ± 9.29	7.66 ^b ± 0.59	35.16 ^{ns} ± 1.02
1	6.62 ^a ± 0.36	22.37 ^{ns} ± 1.88	1.76 ^{ns} ± 0.15	148.73 ^a ± 15.97	11.79 ^{ab} ± 1.48	35.92 ^{ns} ± 1.16
3	6.57 ^a ± 0.60	21.36 ^{ns} ± 1.55	2.06 ^{ns} ± 0.13	139.95 ^{ab} ± 17.26	13.63 ^a ± 1.78	36.12 ^{ns} ± 1.24
p value	< 0.01	< 0.01	> 0.05	< 0.01	< 0.01	< 0.01
cv (%)	16.16	13.88	21.23	10.30	14.28	5.49
Roots						
		Nitrogen rates (mmol L ⁻¹)		Silicon rates (mmol L ⁻¹)		
5	0.29 ^{ns} ± 0.07	12.34 ^b ± 0.39	3.24 ^{ns} ± 0.18	3.51 ^{ns} ± 0.84	0.91 ^{ns} ± 0.20	—
15	0.37 ^{ns} ± 0.10	15.57 ^a ± 0.37	3.98 ^{ns} ± 0.33	6.41 ^{ns} ± 1.75	1.54 ^{ns} ± 0.55	—
25	0.31 ^{ns} ± 0.07	17.55 ^a ± 0.28	3.96 ^{ns} ± 0.31	5.60 ^{ns} ± 1.35	1.21 ^{ns} ± 0.28	—
		Nitrogen rates (mmol L ⁻¹)		Silicon rates (mmol L ⁻¹)		
0	0.20 ^b ± 0.06	16.23 ^{ns} ± 0.79	3.57 ^b ± 0.12	3.44 ^b ± 1.04	0.72 ^b ± 0.20	—
1	0.42 ^a ± 0.08	15.54 ^{ns} ± 0.92	3.17 ^b ± 0.21	6.71 ^a ± 1.47	1.33 ^{ab} ± 0.28	—
3	0.34 ^{ab} ± 0.08	15.69 ^{ns} ± 1.06	4.45 ^a ± 0.34	5.37 ^{ab} ± 1.49	1.62 ^a ± 0.52	—
p value	< 0.05	< 0.05	< 0.01	< 0.05	< 0.05	—
cv (%)	26.03	5.96	9.07	26.80	30.99	—

Lowercase letters in each sub column and parameters show a significant difference for the nitrogen or silicon rates. ± standard error; ns not significant; cv coefficient of variation; — not measurable.

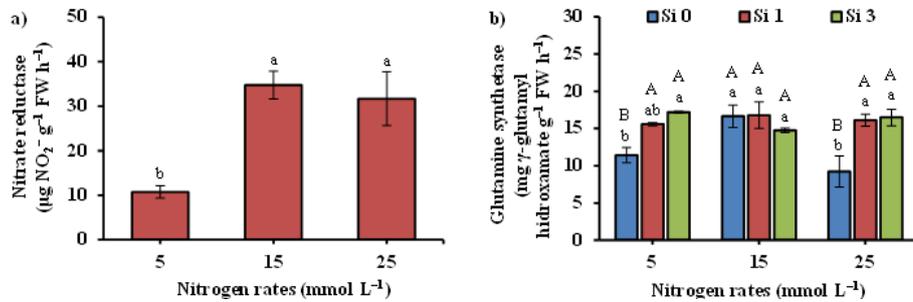


Fig 1. The activity of nitrate reductase and glutamine synthetase in the leaves of the tomato at the initial growth under rates of nitrogen and silicon in the nutrient solution. Coefficient of variation = 22.3 (a) and 14.1 (b) with *p*-value < 0.01. At the figure (a) lowercase letters show a significant difference. In the figure (b), lowercase letters compare rates of silicon within each rate of nitrogen, and capital letters compare rates of nitrogen within each rate of silicon. Error bars indicate standard error.

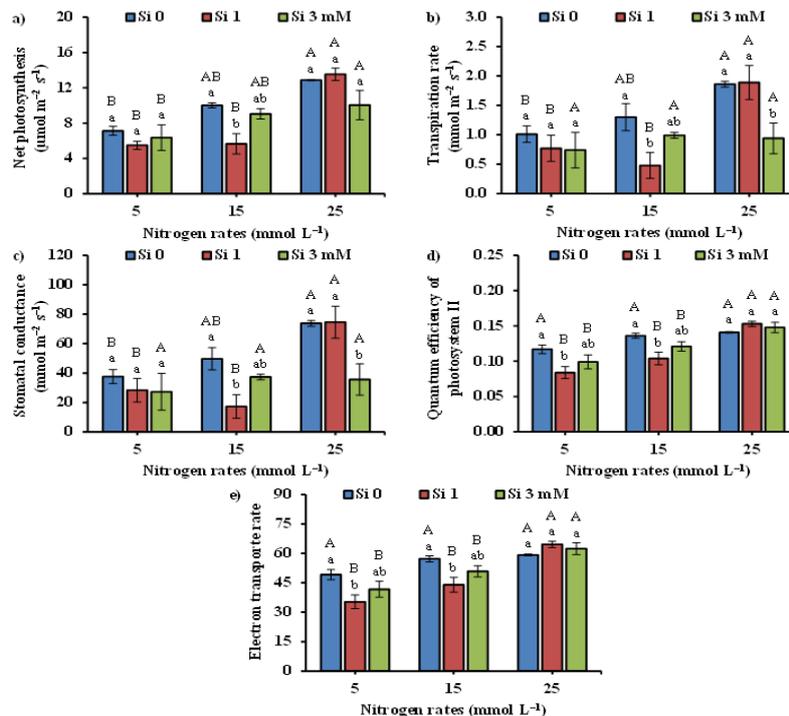


Fig 2. Net photosynthesis, transpiration rate, stomatal conductance, quantum efficiency of photosystem II, and electron transport rate on the leaves of the tomato at the initial growth under rates of nitrogen and silicon in the nutrient solution. Coefficient of variation = 18.6 (a), 33.01 (b), 34.3 (c), 9.74 (d), and 9.73 (e) with *p*-value < 0.05. Lowercase letters compare rates of silicon within each rate of nitrogen, and capital letters compare rates of nitrogen within each rate of silicon. Error bars indicate standard error.

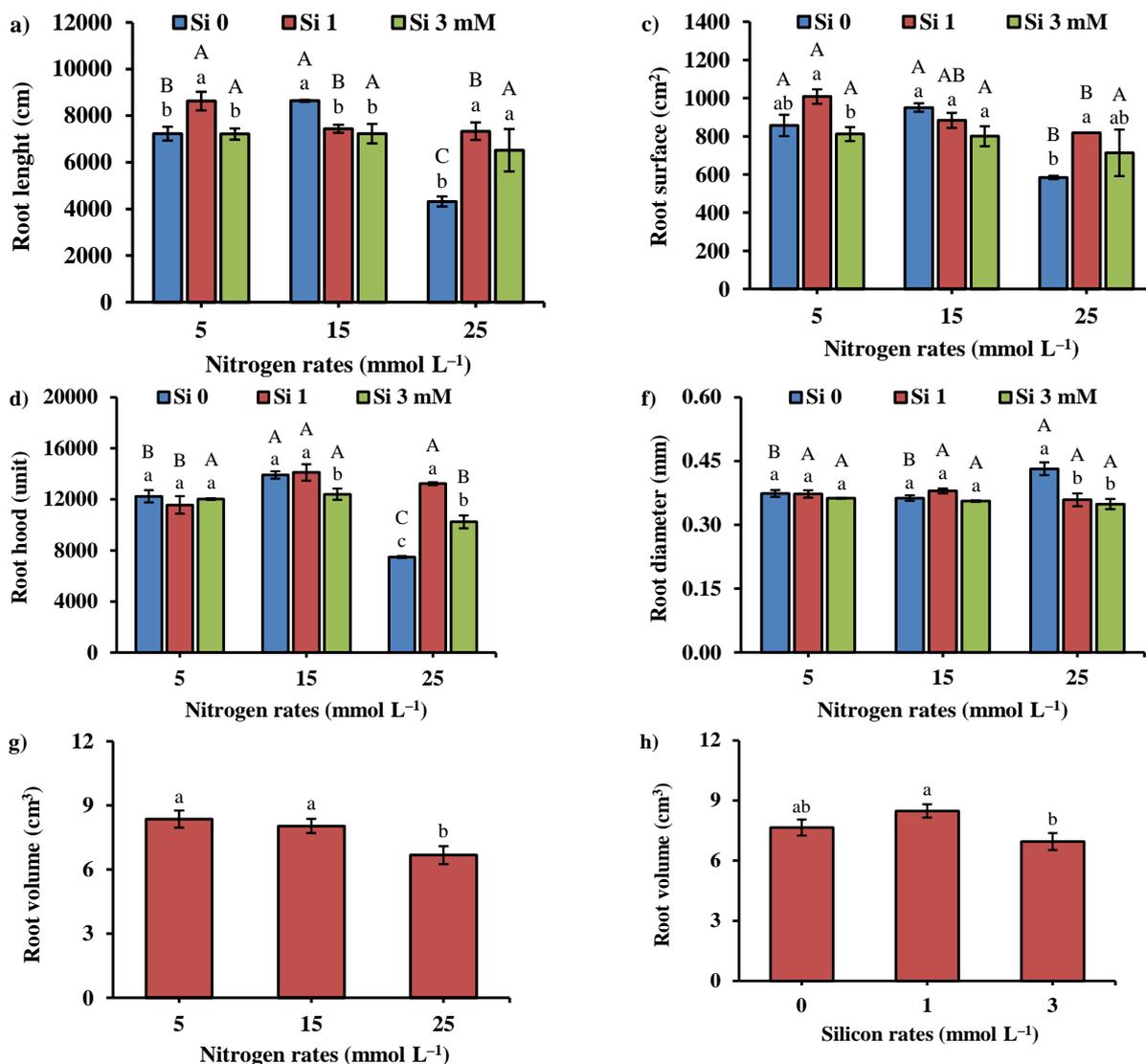


Fig 3. Root length (a), root surface (b), root hood (c), and root diameter (d), and root volume (e, f) of the tomato at the initial growth under rates of nitrogen and silicon in the nutrient solution. Coefficient of variation = 7.73 (a), 9.98 (b), 4.62 (c), 4.60 (d), 5.17 (e), and 13.30 (f) with p -value < 0.01 (a, c, d, e) and < 0.05 (b, f). Lowercase letters compare rates of silicon within each rate of nitrogen, and capital letters compare rates of nitrogen within each rate of silicon. Error bars indicate standard error.

In that context, the application of Si may increase the assimilation of ammonium in the fruit production phase. Possibly, the accumulation of N in the shoot and roots of the tomato increased as a function of Si application and its positive effects in the GS activity. Thus, the increase in the accumulation of N was a result of a higher efficiency of GS promoted by the application of Si. Here, we proposed that the Si could be a catalyzer of GS activity in the tomato plants under low or high availability of N. Kochanová et al. (2014) showed an increase in the activity of GS in the leaves of maize as the supply of Si increases up to 48 h of exposition. However, the authors did not explain the reasons for such an increase. Here, we proposed that the supply of Si increases the expression of the gene coding for GS in low or high availability of N. The photosynthetic rate was highest at the highest rate of N (Figure 2a). High concentrations of N in the shoots at the high rate of N were found, therefore a high SPAD value was observed (Table 1). That situation induces high water consumption to obtain hydrogen and electrons for photosynthesis and hence the stomata become more open (Figure 2a, 2b, 2c). Si 3 mmol L⁻¹ in the nutrient

solution decreased the excessive transpiration (Figure 2b) of the plant and consequently the stomatal conductance (Figure 2c) promoted by the high supply of N (25 mmol L⁻¹). The supply of Si caused an increase in the accumulation of Si in the shoots and roots. That effectively reduced the loss of water by the plant under high nitrogen availability due to the deposition of Si in the cell wall, which reduced the stomatal conductance and transpiration rate. Silicon is polymerized in cells of the leaf epidermis, forming a rigid layer (Marschner, 2012), reducing the loss of excess water, and promoting high photosynthetic activity (Giongo and Bohnen, 2011). Kamenidou et al. (2009) reported decreases in the transpiration rate and increases in the photosynthetic activity in plants grown under Si, as occurred in the current study. These results corroborate other studies involving the supply of Si on crops (Buck et al., 2008; Gholami and Falah, 2013; Osuna et al., 1991; Pati et al., 2016; Prakash et al., 2011). The beneficial effects of Si in the plants may be related to the improvement in root development, water, and nutrient uptake, and upright leaves (Gong et al., 2003; Hattori et al., 2005), providing high water potential of the

leaves, intense green color of the leaves, and great photosynthetic activity.

Application of Si 3 mmol L⁻¹ increases the root length, root surface, and root hood (Figure 3a, b, c), but decreases the root diameter (Figure 3d) at the rate of N 25 mmol L⁻¹. Supplementation of Si in nutrient solution has been reported to improve the morphology and growth of the tomato root system (Lu et al., 2016; Vicedo et al., 2017). However, no studies are showing those effects in a condition of low and high N availability for tomatoes. The present study advances by showing the role of Si in the improvement of root development under high availability of N. Si may increase the uptake of N and improve the metabolism of ammonium by stimulating glutamine synthetase, thus improving root development. Moreover, Si could minimize the excess of transpiration caused by N, possibly improving the efficiency of water uptake and the acquisition of other nutrients like calcium and phosphorus, both are important for root development (Malhotra and Kapoor, 2015).

The structural improvement of the root system by Si could also increase the tolerance of root diseases caused by the genus *Pythium*. The formation of Si polymers inside of the root cells prevents the development of hyphae and stimulate the antioxidant defense system (Fawe et al., 2001). Yi et al. (2018) indicated that Si improved the hydraulic conductance of the root system and reduced oxidative damage in the tomato seedlings. Yi et al. (2018) also showed that under non-stress conditions, Si did not affect the parameters, as observed in our study at N 15 mmol L⁻¹.

Materials and methods

Experimental design and treatments

The experimental design was a complete randomized block with six replications (three for nutrition and production evaluations and three for metabolic determinations) in a 3 × 3 factorial with three rates of Si (0, 1, and 3 mmol L⁻¹) and three rates of N (5, 15, and 25 mmol L⁻¹). Rates of N were based on the following criteria: 15 mmol L⁻¹ is recommended by Hoagland and Arnon (1950); 5 mmol L⁻¹ for low availability (– 10 mmol L⁻¹) acting as a control treatment since N is an essential element, therefore the rate of N 0 mmol L⁻¹ would not allow plant growth; and 25 mmol L⁻¹ for high availability (+ 10 mmol L⁻¹).

Plant materials and environmental conditions

The experiment was conducted with tomato plants (*Solanum lycopersicum*), Serato F1 hybrid in a growth chamber under light conditions of 400 μmol m⁻² s⁻¹, and temperature of 25 °C. The seeds of the tomato were germinated in a plastic tray with sand washed with deionized water. Five days after the plant emerged, the seedlings were irrigated every two days with the nutrient solution of Hoagland and Arnon (1950) with low N availability diluted to 20 % of the ionic strength. When the seedlings reached approximately 5 cm in height, they were transplanted to pots with Hoagland and Arnon (1950) undiluted nutrient solution under N and Si rates. After the transplantation, the experimental units were grown for 47 days. The nutrient solution was renewed every 14 days.

Plant samples and dry mass production

The plant parts were separated into shoots and roots. The plant material related to the metabolic analysis was packed in aluminum bags and immediately frozen in liquid N for storage in the freezer at – 80 °C. The wet samples for the nutritional analysis were collected and dried in an oven at 65 °C with forced air circulation for 72 h. The dry samples (shoots and roots) were weighed and the samples were ground in a Wiley mill for chemical analysis.

Relative concentration of chlorophyll (SPAD values)

SPAD 502 MINOLTA portable equipment was used to quantify the indirect chlorophyll and four readings were taken on the leaves of tomatoes in each experimental pot.

Photosynthetic parameters

The photosynthetic activity was evaluated on the leaves of the tomato using the IRGA WALZ GFS-3000 photosynthesis analyzer, one day before the harvest. Net photosynthesis, transpiration rate, stomatal conductance, quantum efficiency of photosystem II, and electron transport rates were quantified.

Nitrogen and silicon concentrations in the plant samples

In the dried and ground plant samples, sulfuric digestion was performed to assess nitrogen by the Kjeldahl method, according to Malavolta et al. (1997). Silicon was quantified using the method described by Elliott and Snyder (1991), which started with the digestion of ground plant samples using sodium hydroxide and hydrogen peroxide and quantified on a spectrophotometer at 410 nm.

Nitrate reductase (NR, EC 1.7.1.1)

The enzyme activity, according to Mulder et al. (1959), was based on the NO₂⁻ production during the incubation of the leaves *in vitro*, with the addition of a phosphate buffer solution (pH 7) with KNO₃ 0.25 mol L⁻¹ and placing in a water bath at 35 °C for 2 h. The enzymatic reaction was halted using alpha-naphthylamine (NED) and solution of sulfanilamide. The NO₂⁻ produced was quantified on a spectrophotometer at 540 nm. Calculations were based on the curve of standard NO₂⁻.

Glutamine synthetase (GS, EC 6.3.1.2)

The activity was determined by the Elliott (1953) methodology, where portions of leaves were macerated with Tris-HCl solution, and the final extract was centrifuged at 10,000 rpm at 4 °C for 10 min and then subsequently incubated. After incubation, the reaction was stopped with a buffer solution of FeCl₃, TCA, and HCl, and quantified the λ-glutamyl hydroxamate in the final solution on a spectrophotometer at 540 nm.

Roots development

For the morphology analysis of the roots, the system WinRHIZO Pro 2007a coupled to a scanner equipped with an additional light unit was used. Root length, root surface, root hood, root diameter, and root volume were quantified.

The definition of 400 (dpi) was used for measurements of root morphology, as described by Bauhus and Christian (1999).

Statistical analysis

The data of three replications per treatment were submitted for analysis of variance using the Statistical Analysis System (SAS, 2004) and the means were compared by the Tukey test at 5 %. When the interactions of the factors were significant, the means of the first factor were compared within the second factor and vice-versa by the Tukey test at 5 %. When the interaction was not significant, the main effect of each factor was evaluated by comparing averages using the Tukey test at 5 %.

Conclusion

The application of silicon enhances the plant growth, root development, nutrient uptake, nitrogen assimilation, and photosynthesis of the tomato plants cultivated under rates of N. Under low and high availability of N, the high accumulation of Si improves both photosynthesis parameters, associated with transpiration, and activity of glutamine synthetase. We recommend the use of Si 3 mmol L⁻¹ and N 15 mmol L⁻¹ for the tomato plants under the nutrient solution.

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