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Differential responses produced by silicon (Si) on photosynthetic pigments in two pepper cultivars exposed to water deficiency

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Abstract

This study aims to (i) investigate the silicon action on photosynthetic pigments, as well as (ii) to determine the optimal Si level for each cultivar, and (iii) establish a possible interference on carbon compounds in two *Capsicum annuum* cultivars exposed to water deficiency. For this purpose, a completely randomised factorial design was conducted, composed of four water and Si combinations (water deficit + 0.00 Si, water deficit + 0.25 Si, water deficit + 1.00 Si, and water deficit + 1.75 mM Si) applied on two cultivars (Ikeda and Vermelho Gigante). Some parameters such as relative water content and temperature in leaf, pigments, and carbon compounds were evaluated. The results showed that both cultivars have high water content and temperature in leaf and sucrose content after Si application. The Si application caused reduction in total soluble carbohydrates of two cultivars, with the values of 1.26 and 0.96 mM Si for Ikeda and Vermelho Gigante, respectively. The cultivars presented differential behavior linked to photosynthetic pigments, in which only Vermelho Gigante cultivar showed increase, after 0.99 mM Si treatment.

Keywords: *Capsicum annuum* L., carbohydrates, chlorophylls, drought, silicon.
Abbreviations: ATP_Adenosine triphosphate, cv_cultivar, HCl_hydrochloric acid, $HClO_4$_perchloric acid, LRWC_Leaf relative water content, mM_millimolar, NADPH_nicotinamide adenine dinucleotide phosphate, NaOH_sodium hydroxide, Si_ silicon, $(SiO_2)n.H_2O$_hydrated silica

Introduction

Silicon (Si) is considered a beneficial element to higher plants (Epstein and Bloom, 2004). Its absorption and deposition in cell walls of several organs such as leaf and stem can promote the plant growth and activity (Cunha et al., 2008). It has been frequently linked to physiological, morphological, nutritional, and molecular aspects in plants (Ma, 2004; Epstein and Bloom, 2004; Ma and Yamaji, 2006; Lobato et al., 2009 a).

Pepper (*Capsicum annuum* L.) is a plant used in preparation of foods, condiments, and sauces, being consumed fresh or dehydrated (Sousa et al., 2009). In addition, pepper fruit contain high levels of vitamin A and C (Carvalho et al., 2011). Recent studies reveal that the *Capsicum* genus has medical properties linked to anti-inflammatory characteristics (Barbosa et al., 2002). In relation to productive performance of pepper plants, water deficit is a limiting factor to achieve adequate yield in protected cultivation or under field conditions (Patane and Cosentino, 2010).

The stress is defined as a significant change of optimal conditions, which will induce modifications and consequently responses in plant metabolism (Lobato et al., 2008a). These changes are reversible or irreversible depending on intensity and duration (Larcher, 2006). Additionally, water deficit is a condition of stress to plants (Costa et al., 2011). It represents the main abiotic limitation affecting the production (Chaves and Oliveira, 2004).

The chlorophyll is usually divided to chlorophylls *a* and *b* with greater occurrence in chloroplasts (Candan and Tarhan, 2003). The chlorophyll has large interference with photosynthetic apparatus. They are responsible for the conversion of radiation in energy under form of ATP and NADPH (Lichtenthaler, 2009). For this reason, they are directly related to the photosynthetic efficiency in higher plants. In addition, these structures have instable characteristics, dependence to nutritional supply, sensitive to light, and denaturation under high temperature (Schoefs, 2002).

Positive interference on physiological parameters such as photosynthetic and transpiration rates in plants exposed to water deficit has been attributed to the Si application (Hattori et al., 2005; Gao et al., 2004; Trenholm et al., 2006). The Si application proportioned increases in activities of antioxidant enzymes (Liang et al. 2006) and modifications in chemical proprieties of cell walls (Hossain et al., 2007). On the other hand, the drought produces decrease of photosynthetic pigments (Ahmad and Haddad, 2001). Therefore, these modifications in physiological, biochemical, and structural levels probably will exercise influence on chlorophylls. Nolla et al. (2012) revealed that Si application induces improvement in yield of *Oryza sativa* plants exposed to drought. Ahmed et al. (2011) reported increases in total dry matter of *Sorghum bicolor* subjected to Si and water deprivation. In contrast, several studies reported that water deficit frequently promotes changes in carbon metabolism like as accumulation of sucrose and total soluble in leaf (Lobato et al., 2008b; Oliveira Neto et al., 2009). This retention of carbon compounds in leaf will negatively affect the translocation of organic solutes and consequently the yield.

Results

Modifications induced by the Si on relative water content (RWC) and temperature in leaf

The progressive addition of Si caused significant effect on leaf relative water content (RWC). Here, we report a quadratic equation to explain the Si influence on leaves RWC of both cultivars (Fig 1A). The Si provoked the higher values in Ikeda and Vermelho Gigante cultivars under the concentrations of 1.26 and 1.54 mM Si, respectively. The Si proportioned significant effect in leaf temperature (Fig 1B), and was observed the quadratic equations to relate the Si action in two cultivars exposed to water deficiency. The Si application increased the leaf temperature of both cultivars.

Differential responses produced by Si on photosynthetic pigments

The Si application proportioned significant effect on levels of chlorophyll *a*, in the quadratic equation to relate this effect in both cultivars (Fig 2A). The Si application increased the chlorophyll *a* only in Vermelho Gigante cultivar. The highest value of chlorophyll *a* was observed under concentration of 0.97 mM Si. The Si application also had had significant effect on chlorophyll *b* as well. A quadratic equation was used to describe this interaction (Fig 2B). The positive effect of the Si application on chlorophyll *b* was expressed only in Vermelho Gigante cultivar. A higher value of chlorophyll *b* was observed under concentration of 1.01 mM Si. The application of progressive doses of Si provoked increase in total chlorophyll in Vermelho Gigante cultivar (Fig 2C), under 0.99 mM Si treatment.

Effects of Si application on total soluble carbohydrates (TSC)

The quadratic model could also describe the action of Si treatments on total soluble carbohydrates (TSC) in both cultivars (Fig 3A). The Si application reduced TSC in two cultivars. The lower values achieved in Ikeda and Vermelho Gigante cultivars after 1.26 and 0.96 mM Si application, respectively. The exogenous application of Si significantly provoked the sucrose levels under a quadratic equation linked to this interaction (Fig 3B). The Si induced increase in both cultivars. The starch levels suffered significant effects with Si application in both cultivars, being described through a linear equation (Fig 3C).

Discussion

The Si treatments attenuated the water deficiency effects on leaf relative water content, compared to control treatment. This fact can be linked to absorption, transport, and accumulation of Si in plants (Ma and Yamaji, 2006). Several plants can assimilate Si by passive diffusion. This form of Si

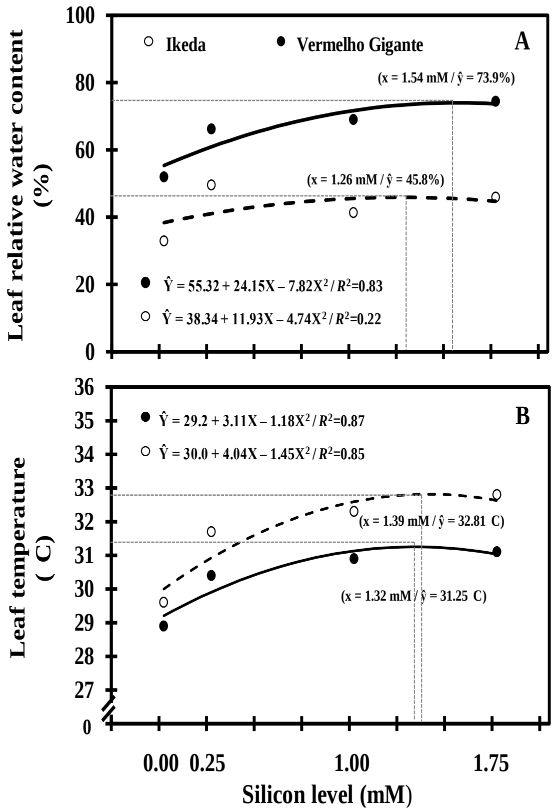

Fig 1. Leaf relative water content (A) and leaf temperature (B) in two *Capsicum annuum* cultivars treated with different silicon levels and exposed to water deficiency.

is transported to xylem with consequent reception in shoot using the transpiratory flux. The Si absorbed by root is transported to shoot and deposited into or out of cell in plant tissues as hydrated silica $(SiO_2)n.H_2O)$. The formation of layer composed of Si has been fundamental in conditions of biotic and abiotic stresses, contributing to reduce the water loss by transpiration and increase of photosynthetic efficiency (Nwugo and Huerta, 2008). The data presented in this investigation suggest beneficial effects proportioned by the addition of Si, corroborating with results on *Lycopersicon esculentum* plants (Romero-Aranda et al., 2006).

The Si application causes increase in leaf temperature. This fact can be explained by the higher amount of this element in leaf tissue combined with lower water absorption during the water restriction. The Si assimilation promotes formation of a double layer of silica and consequently reduction of the transpiration rate. In addition, this element can also be contributing in thermal stability of lipids of the cell membrane during stress. Besides of beneficial effects of Si linked to water retention in plant tissues (Trenholm et al., 2006), this element can contribute indirectly in cell turgescence, attenuating the negative effects of salt stress as reported by Romero-Aranda et al. (2006).

The partial increment that observed in chlorophyll level of Vermelho Gigante after Si application is probably due to a enhancement in maintenance of photosynthetic apparatus, combined with improvement in structural architecture of plant, because the Si deposition keeps the leaf with linear aspect (Fernandes, 2008). This causes a better luminous absorption and increase in photosynthetic capacity (Gong et al., 2005). Streit et al. (2005) reported that plants can adjust the photosynthetic apparatus in agreement with luminous

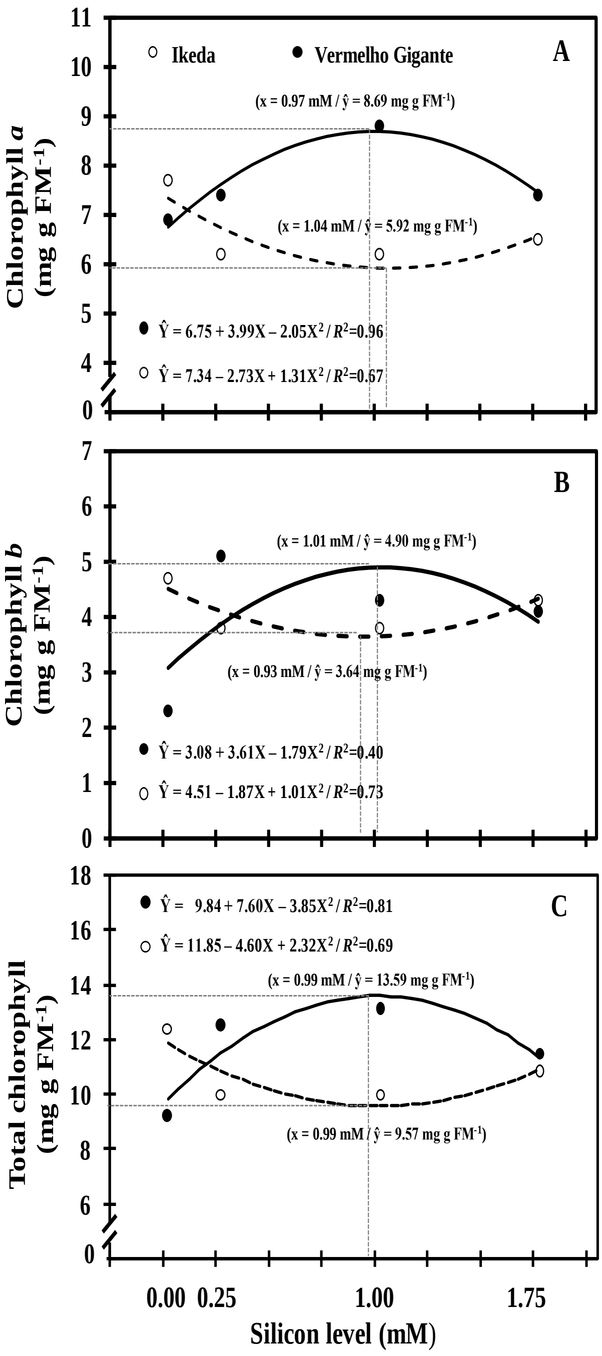

Fig 2. Chlorophyll *a* (A), chlorophyll *b* (B), and chlorophyll total (C) in two *Capsicum annuum* cultivars treated with different silicon levels and exposed to water deficiency.

conditions of environment, which may increase the efficiency of this mechanism. The chlorophyll biosynthesis can be determined mainly by the adequate absorption of nutrients, mainly nitrogen and magnesium and as secondary form by the amount of light absorbed (Blankenship, 2004). However, the light excess will cause oxidative stress in plants decreasing the biosynthesis level or until chlorophyll degradation (Gonçalves, 2009). The results obtained in this study are in agreement with Luz et al. (2009), evaluating chlorophyll levels in *Lycopersicon esculentum* plants under influence of potassium silicate.

The Si action produced increase in level of chlorophyll *b* in Vermelho Gigante cultivar, while Ikeda cultivar presented decrease in this parameter. In agreement with Ahmad and Haddad (2001) this positive response found in Vermelho Gigante is connected to fact that Si utilization reduced the decomposition of photosynthetic pigments during the situation of water stress. This situation is associated also with increase in activity of antioxidant enzymes such as superoxide dismutase and catalase (Gong et al., 2005). Liang et al. (2003) reported that these enzymes have function to avoid the disequilibrium produced during situations of abiotic and biotic stresses. Similar results were found by Lobato et al. (2009a) analyzing Si action in *Capsicum annuum* and Gong et al. (2005) in *Triticum aestivum.*

The levels of total chlorophyll presented contrasting behavior in two cultivars, being found positive results only in Vermelho Gigante cultivar. The water restriction normally promotes reduction in chlorophyll content due to inhibition of biosynthesis and degradation of these pigments. Pilon (2011) reported that the beneficial response of Si application can be linked to better water use efficiency, proportionating higher chlorophyll tenor, and also higher rigidness structural of tissues and by this reason can mitigate the effects produced by water deficit.

The exogenous application of Si reduced the total soluble carbohydrates in leaf of both cultivars. This fact suggests that Si improved the translocation of organic solutes. The results found in this study can explain the increase in yield described by Nolla et al. (2012) on *Oryza sativa* plants exposed to four Si rates. In other words, the Si utilization occasioned fall in levels of total soluble carbohydrates of leaf (sink), and it indicates that these carbon skeletons probably will be transferred to other organs denominated as drains. The increase of this variable in plants under water deficit is associated to process the osmotic adjustment. This increase was revealed in plants exposed to water deficiency as well, compared to control treatment. Similar results were observed by Lobato et al. (2009b), investigating *Capsicum annuum* plants and Mafakheri et al. (2011) on *Cicer arietinum* plants.

The sucrose levels were similarly maximized in both cultivars when treated with Si. The accumulation of sucrose suggests that it is utilized in osmotic adjustment, because plants in normal conditions (irrigated) presented lower values, if compared with deficit + 0 mM Si (data not show). In several higher plants, the sucrose is the main sugar exported form synthesis organs, such as leaf, to drain parts like as stem, root, and flowers, where they will be consumed for growth and/or fruiting (Chaves-Filho and Stacciarini-Seraphin, 2001). The hexoses produced from the sucrose hydrolysis can be used in anabolic or catabolic processes, and also to provide sugar shortage that will contribute in the osmotic adjustment process. The results are similar to those found by Oliveira Neto et al. (2009) measuring chlorophyll levels and carbon compounds in *Sorghum bicolor* subjected to water deficiency.

The Si applications provoked reduction in starch levels in both cultivars. This study revealed that Si can increase the leaf relative water content. Probably, the Si acts as repercussion on supply of this molecule to starch hydrolysis. The water is essential as reagent or substrate in important processes such as starch hydrolysis and consequent formation of other sugars as sucrose, glucose, and fructose (Pimenta, 2004). It can explain the reason that why the starch levels are higher in *Capsicum annuum* plants under water deficiency, compared to treatments exposed to both Si and water deprivation. Therefore, the decrease of starch observed in this study suggests that this carbon suffered hydrolysis and it is probably exported into a direction to sink, in form of other carbons mainly the sucrose, which is the main carbon skeleton transported in plant phloem (Pimentel, 2004).

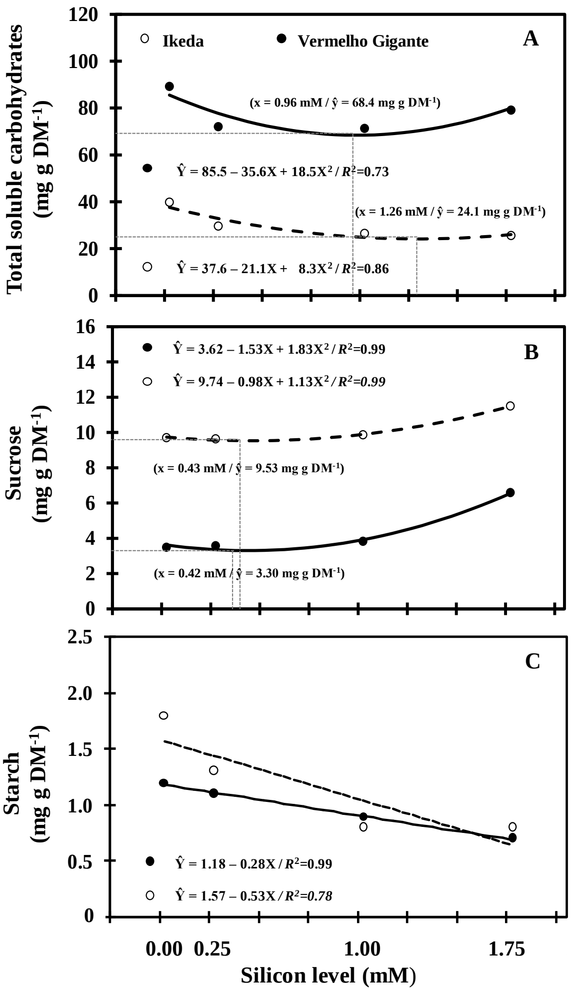

Fig 3. Total soluble carbohydrates (A), sucrose (B), and starch (C) in two *Capsicum annuum* cultivars treated with different silicon levels and exposed to water deficiency.

The behavior linked to reduction of starch can contribute to explain the increase in total dry matter of *Sorghum bicolor* plants exposed to Si application and drought (Ahmed et al., 2011).

Materials and Methods

Location and growth conditions

The study was carried out in the Instituto de Ciencias Agrárias (ICA) of the Universidade Federal Rural da Amazonia (UFRA), Belem city, Para state, Brazil (01°27'S and 48°26'W). Plants remained in the greenhouse without environment control. The minimum, maximum and medium temperatures were 22.1, 35.5, and 28.4°C, respectively. Air relative humidity during experimental period oscillated between 65 and 93%. Photoperiod was 12 h of light/dark.

Plant material, substrate and pot

In this study, seeds of pepper (*Capsicum annuum* L.) cvs. Ikeda and Vermelho Gigante were used. Substrate for plant growth was composed of mixture of sand and silica in proportion of 2:1, respectively. This substrate was autoclaved at 120°C atm^{-1} for 40 min. For semi-hydroponic cultivation, 1.2-L pots (0.15 m in height and 0.10 m in diameter) were equipped with one hole in bottom side and covered with mesh to keep the substrate, and solution absorption by capillarity, being placed into other containers (0.15 m in height and 0.15 m in diameter).

Experimental design and treatments

A completely randomised factorial layout composed of four water and Si combinations (water deficit + 0.00 Si, water deficit + 0.25 Si, water deficit + 1.00 Si, and water deficit + 1.75 mM Si) applied to two cultivars (Ikeda and Vermelho Gigante) experimental design was used with a total of 8 treatments. Experiment was assembled with six replicates and 48 experimental units, as well as one plant in each unit.

Plant culture and Si application

Five seeds were placed in each semi-hydroponic system and thinned to one plant per pot after germination. Control and deficit + 0.00 mM Si treatments received macro and micro nutrients in the form of nutrient solution of Schwarz (1995), without Silicon (Si). Treatments comprised of deficit + 0.25, deficit + 1.00, and deficit + 1.75 mM Si received the same Schwarz nutrient solution, with addition of Si through sodium metasilicate ($Na_2SiO_39H_2O$), in agreement with Liang et al. (2003) and adapted in Laboratorio de Fisiologia Avancada (LFVA).

Water deficit application

The solutions were applied to plants for a period of 45 days, and the nutrient solutions were changed every 5 d at 09:00 h and the pH of the nutrient solution was adjusted to 6.0±0.1 with addition of HCl or NaOH. In 45^{th} day after the experiment implementation, plants of the treatments under deficit + 0.00, deficit + 0.25, deficit + 1.00, and deficit + 1.75 mM Si were subjected to a period of 6 d without nutrient solution (suspension of the water supply), in which the water deficit was simulated from the 65^{th} until 71^{th} day after the experiment started. After this period, physiological parameters were measured in these plants.

Leaf relative water content (RWC)

Leaf relative water content was evaluated with 40 leaf disks with 10 mm diameter being removed from each plant. The calculation was done according to the formula proposed by Slavick (1979): LRWC = [(FM – DM)/(TM – DM)] × 100
Where; FM is fresh matter, TM is turgid matter evaluated after 24 h and saturation in deionised water at 4°C in dark and DM is the dry matter determined after 48 h in oven with forced air circulation at 80°C.

Leaf temperature

The temperature in leaf was evaluated in fully expanded leaves located in the medium third of the branch main under light, using a steady state porometer (LI-COR Biosciences, model 1600) with the gas exchanges evaluated immediately during the period between 10:00 and 12:00 h in all the plants. The irradiance was maintained at 800 μmol m^{-2} s^{-1} during the measurements.

Determination of photosynthetic pigments

The determination of the photosynthetic pigments was carried out with 25 mg of leaf tissue. The samples were homogenized in the dark and in the presence of 2 mL of acetone at 80%

(Nuclear). Subsequently, the homogenate was centrifuged at 5.000 *g* by 10 minutes at 5ºC. The supernatant was removed and the chlorophylls *a*, *b*, and total chlorophylls were quantified using spectrophotometer (Femto, model 700 S), according to the methodology of Lichtenthaler (1987).

Leaf dehydration and sample preparation

Leaves were harvested and placed in an oven with forced air circulation at 70 ± 2ºC for 96 h. After this period, leaf dry matter was triturated and the resulting powder kept in glass containers. These containers were stored in the dark at 15ºC for nutritional and biochemical analysis.

Determination of total soluble carbohydrates and starch

For determination of total soluble carbohydrates, 50 mg of leaf powder was incubated with 5 mL of ultra-pure water at 100ºC for 30 min, centrifuged at 2.000 *g* for 5 min at 20ºC and the supernatant was removed. For determination of starch, 50 mg of powder was incubated with 5 mL of ethanol at 80ºC for 30 min, centrifuged at 2.000 *g* for 10 min at 25ºC, and the supernatant was removed. In addition, a second extraction was carried out with the same powder incubated with 5 mL of 30% $HClO_4$ at 25ºC for 30 min and centrifuged in conditions previously described. The supernatants of the two extractions were mixed. Quantifications of the total soluble carbohydrates and starch were carried out at 490 nm using the method of Dubois et al. (1956), using glucose (Sigma Chemicals) as standard.

Determination of sucrose

The determination of sucrose was carried out with 50 mg of leaf powder incubated with 1.5 mL of solution MCW (methanol, chloroform and water) in the proportion of 12:5:3 (v/v) at 20ºC by 30 min under agitation, centrifuged at 10.000 *g* for 10 min at 20ºC and the supernatant was removed. The sucrose quantification was carried out at 620 nm, in agreement with Van Handel (1968), using sucrose (Sigma Chemicals) as standard.

Data analysis

Data were submitted to variance analysis and when significant differences observed, the Scott-Knott test at 5% level of error probability was applied. Estimators of regression were calculated using the SAS software (1996).

Conclusion

The results that both cultivars presented increase in leaf relative water content, leaf temperature and sucrose content when plants subjected to water restriction and Si application. The cultivars presented different behavior linked to photosynthetic pigments, in which the increase only observed in Vermelho Gigante cultivar, at 0.99 mM Si level. In addition, decreases of total soluble carbohydrates and starch were observed in two cultivars, compared with control plants.

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