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Silicon: A Benefic Element to Improve Tolerance in Plants Exposed to Water Deficiency

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Additional information is available at the end of the chapter

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1. Introduction

The silicon (Si) is an abundant element in terrestrial superficie [1], however its availability to plants is normally low [2]. According to Matichenkov & Calvert [3], the chemically active Si forms in soil are represented by soluble monosilicic acid ($\text{Si}(\text{OH})_4$) that is soluble and weakly adsorbed, as well as acid polisilicic, which are compound organosilicates.

Si is considered an benefic element to higher plants [4], being that the absorption process must be active or passive [5], and deposition in cell walls of several organs such as leaf and stem can promote beneficial effects [6], and for this reason has been frequently linked to physiological, morphological, nutritional, and molecular aspects in plants [7-10].

In plants this nutrient is assimilated mainly by roots, and capacity to accumulate in tissues is variable [11], being several monocots such as *Oryza sativa* and *Triticum aestivum* considered silicon accumulator, with absorption active by root system, and it present leaf levels normally higher than 10.0 g kg^{-1} of Si [12]. In other hand, many dicots like as *Phaseolus vulgaris* and *Glycine max* are characterized as not accumulator of silicon, and its presents passive absorption, with leaf tenors minors than 5.0 g kg^{-1} of Si [13].

In tissues, about of 99% of silicon is found in silic form and less than 1% is colloidal or ionic form, which is the soluble form [14]. Therefore, the storage sites of silicon in plants normally are responsible to improve leaf and plant architectures and also others metabolic processes like as gas exchanges [15], photosynthetic pigments [16], and antioxidant system [17], in

which it results in better performance linked to growth, development, and yield parameters [18] (Figure 1).

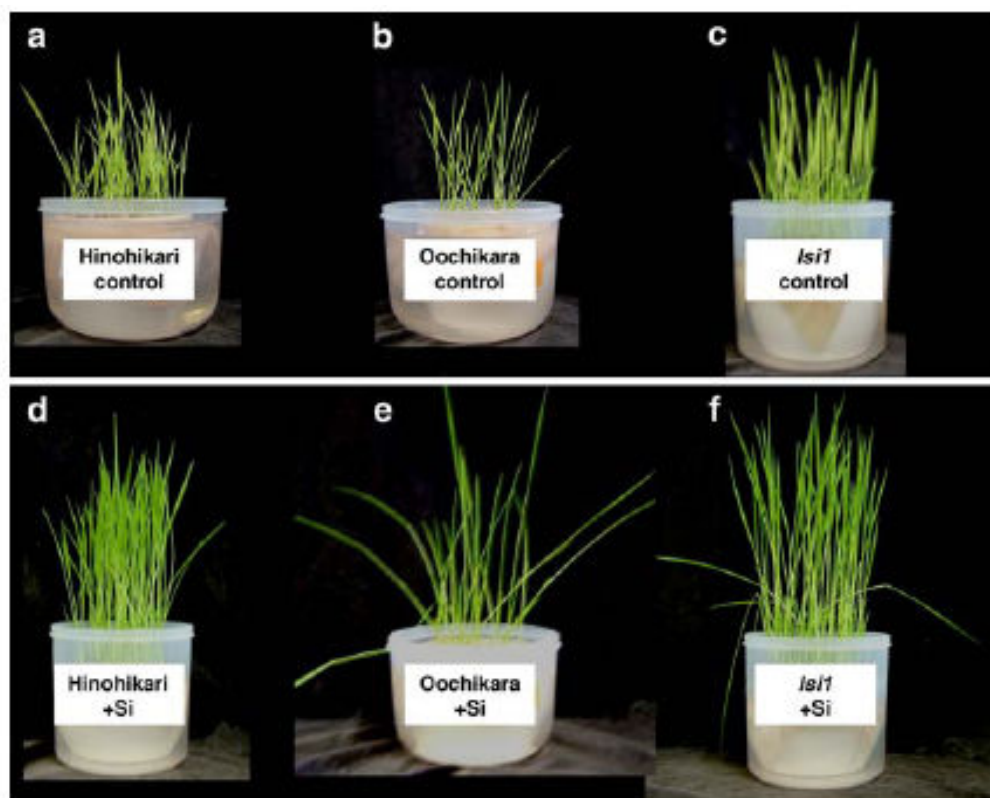


Figure 1. Effects of Si-treatment on growth of cvs. Hinohikari, Oochikara and *lsi1* mutant. Aspects of wild type rice cvs. Hinohikari (a, d), Oochikara (b, e) and *lsi1* mutant (c, f) were observed after control nutrient treatment of rice seedlings (a, b, c) and 14-day silicic acid treatment of rice seedlings (d, e, f) [7].

Drought is one of the key sources of abiotic stress, since it induces smaller growth and development rates, flower aborting, and decreases crop yields during the vegetative, reproductive, and maturation stages [19]. Usually, drought consequences on plants are studied in controlled/artificial conditions through water restriction.

Vascular plants present several strategies to minimize the negative effects induced by water deficiency, being morphological modifications like increase in root size [20] and reduction in leaf area [21]. Other responses are frequently reported, such as reductions in CO_2 assimilation by leaf through stomatal closing, membrane damage and disturbed activity of various enzymes, especially those of CO_2 fixation and adenosine triphosphate (ATP) synthesis. Enhanced metabolite flux through the photorespiratory pathway increases the oxidative load on the tissues as both processes generate reactive oxygen species. Injury caused by reactive oxygen species to biological macromolecules under drought stress is among the major determinants to growth.

The stress occasioned by lower water supply to plant is defined as water deficit, being responsible to active responses in plant such as over-expression of genes linked to osmotic ad-

justment [22], modifications in physiological parameters as water potential, stomatal closing [23], and decrease in photosynthesis rate [24], besides reduction in cell metabolism with negative consequences on growth and production.

Gas exchanges like as leaf water potential, stomatal conductance, and transpiration rate has been used mainly to explain mechanisms affected during drought [25]. When the water availability in soil decrease, normally the water potentials of soil and leaf also are reduced, and it will provoke as consequence turgescence loss in plant cells, mainly in leaf, causing stomatal closing and limiting the gas exchanges [26].

The water potential describes the water amount, in which the water is moved in direction to potentials more negatives, and it differences of potential reveal water flux in soil-plant-atmosphere system [27]. In general, the leaf water potential is depending to soil water potential, water flux in system, and transpiration rate [28].

Attenuation of negative effects induced by the silicon application has been frequently described in plants exposed to water deficiency, such as Hattori et al. [2] investigating *Sorghum bicolor* plants related interference on gas exchanges. Results obtained by Ahmad & Haddad [29] working *Triticum aestivum* plants revealed influence positive on antioxidant enzyme activities. In addition, Lobato et al. [30] studying *Capsicum annuum* plants reported maximization in proline synthesis.

2. Objective

Aims of this chapter is to define (i) silicon and water deficit, to explain (ii) on silicon sources, uptake system and transporters into plant, and detection form in tissue, and to present (iii) the silicon action on gas exchanges and photosynthetic pigments in plants exposed to water restriction.

3. Silicon sources

The silicon uptake using metal salts of silicic acid normally requires their hydrolysis prior to their uptake. In either case they would affect the ionic balance of the system. The proposed mechanism for the solubilization of silica by PNO or MNO is novel and probably involves polarization of surface silica layer through interaction with the oxygen of the pyridine N-oxides. In the solubilization, PNO and MNO are regenerated, as evidenced by the fact that clear water containing freshly prepared PNO/MNO-silica complexes slowly deposits granular silica [31-32].

Based in overview related, a research was conducted by Ranganathan et al. [33] with *Oryza sativa* plants exposed to pyridine N-oxide (PNO), 4-morpholino pyridine N-oxide (MNO), and sodium metasilicate (SMS) aiming to test silicon sources on their ability to enhance the plant silicon content.

The suggestion that enhanced silica deposition is linked to the ability of the rice plant to combat abiotic and biotic stresses is further supported by SEM and EDX analysis of silicon distribution in the rice leaves. In the absence of added silicon, the leaves exhibited a scattered profile of silicon distribution (Figure 2). The leaves treated with MNO, PNO or SMS showed enhanced silicon content and localization of silicon bodies in leaf bundle sheath cells, particularly in the primary and secondary cell wall.

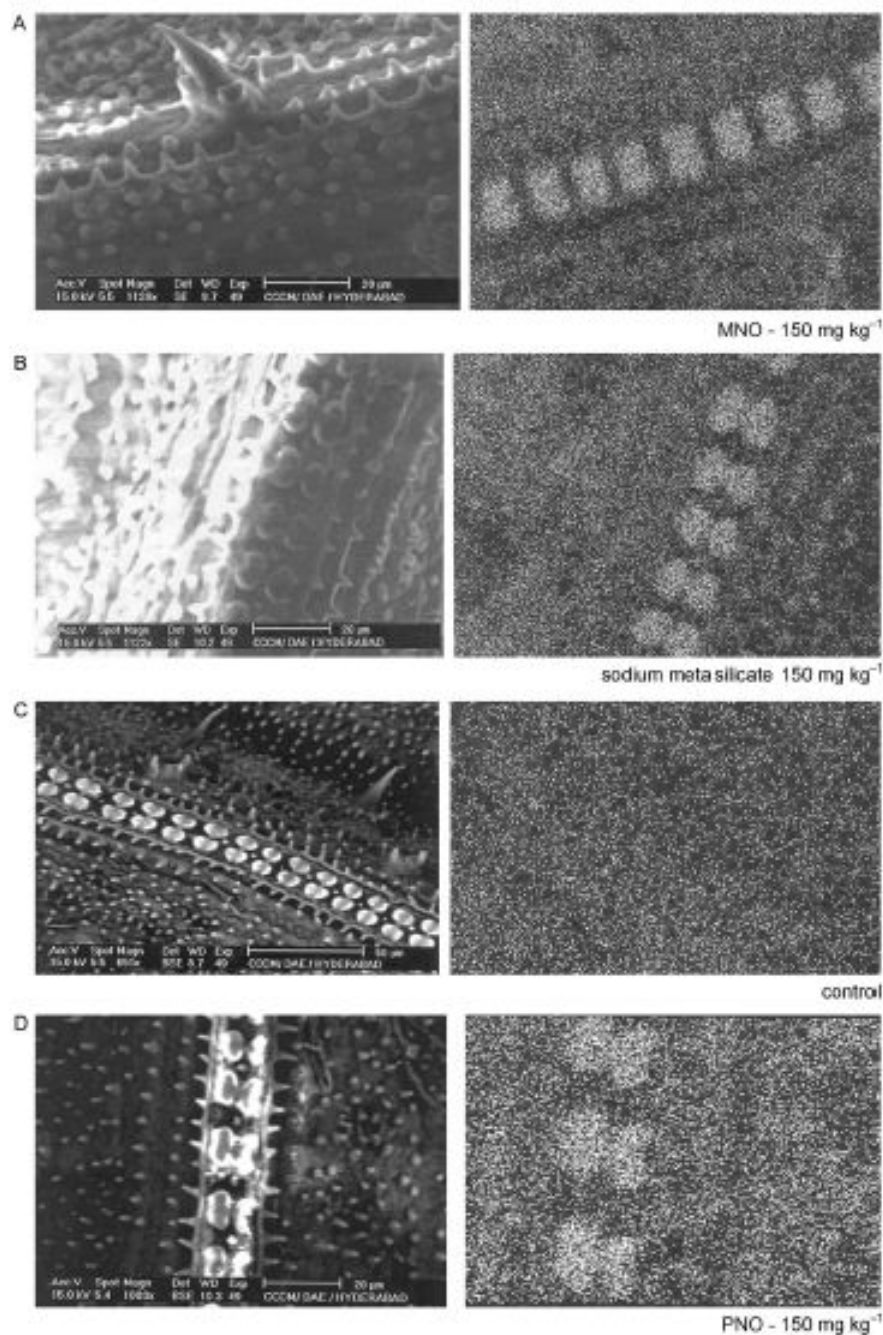


Figure 2. Scanning electron micrograph of silicon mapping (right) and its corresponding bundle sheath cells (left). Application of A - 150 mg kg⁻¹ MNO, B - 150 mg kg⁻¹ sodium silicate, C - control, and D - 150 mg kg⁻¹ PNO [33].

Electron microscopy and in situ X-ray analysis of rice leaves reflect the differences in silicon distribution and cell wall structure between silicon treated and untreated plants [34-36]. The SEM pictures show that PNO and MNO enhanced the silica deposition on the leaves of rice plants concomitant with the localization of silicon bodies in leaf bundle sheath cells and in the primary and secondary cell walls [33].

4. Uptake system and transporters linked to silicon

For decades, rice has been known as the most effective silicon-accumulating species, although the mechanisms involved in high silicon uptake are poorly understood. One of the reasons is, unlike other minerals, the genotypic difference in silicon concentration of rice is too small to be utilized for comparative study on silicon uptake by rice roots [8]. With finality to resolve this problem, a research conducted by Ma et al. [8] working low-silicon mutant (*lsi1*) and wild-type of *Oryza sativa* plants revealed that there are least two transporters involved in silicon transport from nutritive solution to the xylem (Figure 3 and 4).

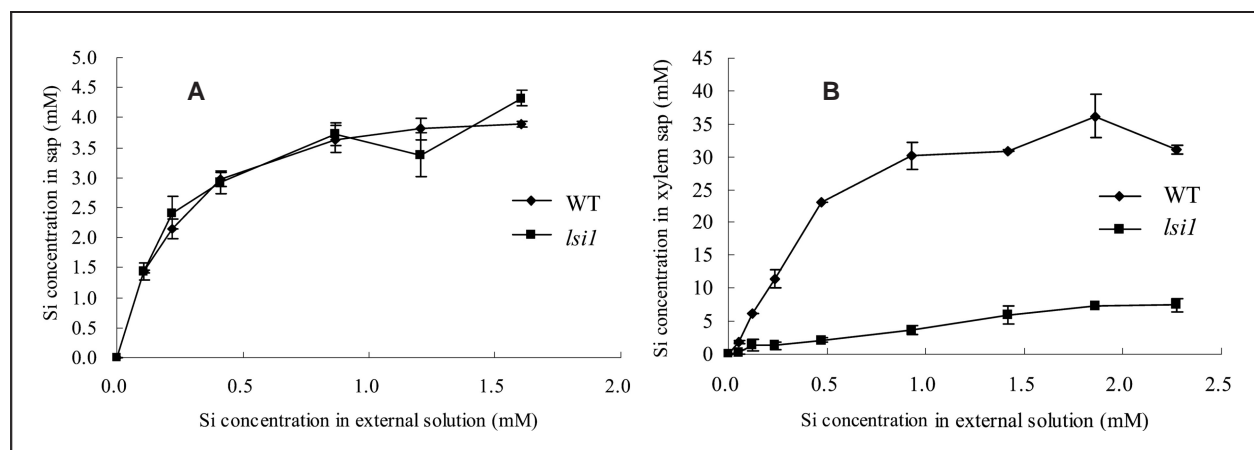


Figure 3. Concentration of silicon in the symplastic solution of *Oryza sativa* root tips (A), and concentration of silicon in the xylem sap (B) of rice cultured in silicon solution at various concentrations. Seedlings (26 d old) of wildtype (WT) and mutant (*lsi1*) rice were cultured in half-strength Kimura nutrient solution containing various concentrations of silicon. The stem was severed after 8 h, and the xylem sap was collected for 30 min. Values are means \pm SD of three replicates [8].

A kinetic study showed that the silicon concentration in the root-cell symplast increased with increasing silicon concentration in external solution but saturated at a higher silicon concentration in both lines (Figure 3 A). Again, there was no significant difference in the silicon concentration of symplastic solution between the wild type and the mutant. These results suggest that silicon transport from the external solution to the root cortical cells is mediated by a type of transporter and that the transporter of the mutant is identical to that of the wild type [8].

Other kinetic study on xylem loading of silicon was then conducted in the wild-type and mutant rice. In contrast to the silicon concentration in the root cortical cell symplast, the sili-

concentration in the xylem sap was much higher in the wild type than in the mutant (Figure 3 B). In the mutant, the silicon concentration in sap increased gradually with increasing silicon concentration in the external solution without saturation. In the wild-type rice, the silicon concentration in the xylem sap also increased with increasing silicon concentration in the external solution (Figure 3 A), but it was saturated at a higher concentration [8].

The silicon concentration in the xylem sap of the wild type was higher than 30 mM at 0.9 mM silicon supply (Figure 3 B). This concentration was much higher than that in root-cell symplast (Figure 3 A), suggesting that silicon is transported from the root cells to the xylem also against a concentration gradient. The curve of Figure 2 B also suggests that the release of silicon into the xylem is mediated by a type of transporter in the wild type [8].

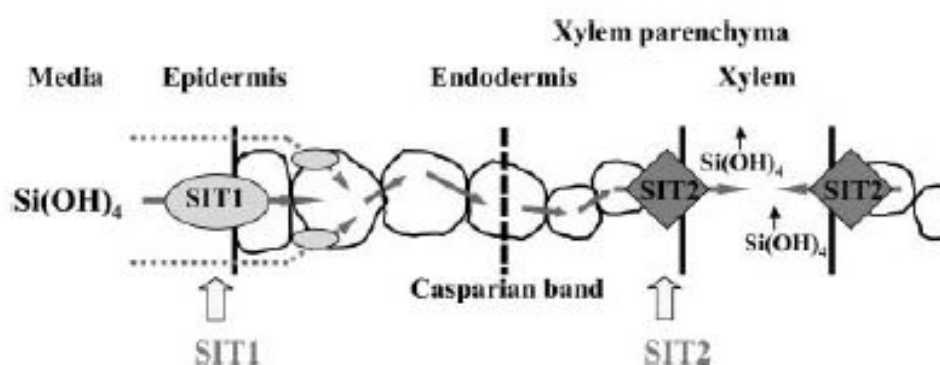


Figure 4. Schematic representation of the silicon uptake system in rice roots. SIT1, Silicon transporter from external solution to cortical cells. SIT2, Silicon transporter for xylem loading [8].

Above results suggest that at least two transporters are involved in the silicon uptake by rice roots (Figure 4). One is located on the plasma membrane of root cortical cells (SIT1, silicon transporter 1), which transport silicon from external solution to the root cortical cells. The other is located on the plasma membrane of xylem parenchyma cells (SIT2, silicon transporter 2), which is responsible for releasing silicon into the xylem. These transporters may have different affinities for silicic acid (Figure 3). Our results also clearly showed that the mutant is defective in xylem loading of silicon rather than transport of silicon from the external solution to the root cell [8].

5. Detection technique

Despite the abundance of studies of the effects of Si fertilizers and electron-microscopic observations of silica depositions within plants[13, 37-39], few of the morphological analysis of silica deposition in rice tissues have used histochemical staining and conventional microscopic techniques available to field researchers.

Although there are a few reports using X-ray scanning analytical microscopy, which described silica deposition detected in a dicot plant such as *Arabidopsis halleri* [40-41], X-ray scan-

ning microscopy have been broadly applied for analysis of silica bodies and other elements in rice tissues [42-45].

Therefore, study carried out by Isa et al. [7] optimized a technique for silica body specific staining to visualize silica deposits in rice tissue by bright field microscopy and a technique for determining the in situ content of elements, including silica, by X-ray scanning microscopy.

The samples were fixed in FAA solution, and fixed samples were transferred and incubated in accordance with the methods of Kaufman et al. [46] and Morikawa & Saigusa [47], with minor modifications. Benzene-equilibrated samples were stained in 0.1% crystal violet lactone solution (in benzene) to visualize the silica bodies.

Silica bodies were observed in the motor cells of the leaf blades of cv. Hinohikari at the maximum tillering stage (Figure 5 A), and silica opal was also observed in the blades (Figure 5 B). In enlarged images of silica cells located along the vascular bundles of cv. Hinohikari treated with silicic acid for 14 days, accumulation of silica was observed as clear X shapes (Figure 5 C) [7].

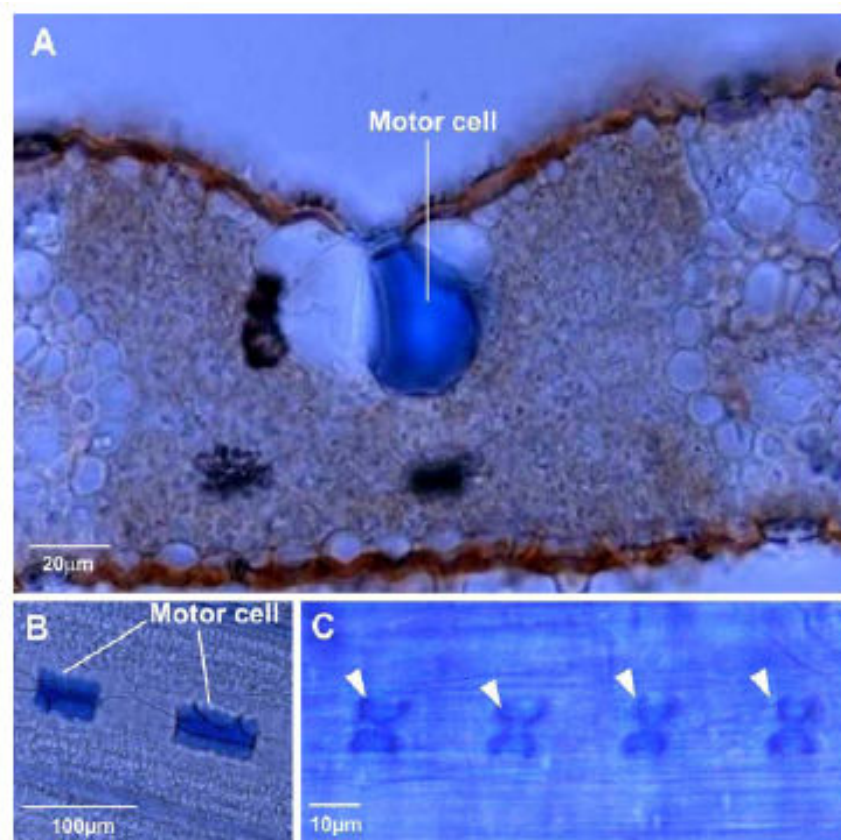


Figure 5. Crystal violet lactone staining of motor cell and silica body in leaf blade of cv. Hinohikari. A, motor cell and silica bodies in cross-section of leaf blade; B, rice opals in motor cells of leaf blade; C, a line of X-shaped silica bodies in leaf sheath. Rice opals in motor cells and silica bodies in epidermis cells were stained with crystal violet actone using leaf blade of cv. Hinohikari in paddy field at the maximum tillering stage. Motor cells and X-shaped silica bodies are indicated by lines and arrow heads, respectively [7].

Crystal violet lactone staining was an effective method of visualizing various shapes of silica opals and silica bodies deposited on the walls of the epidermal cells of leaf blades and stems, forming X-shaped silica cuticles along the vascular bundles (Figure 5 C) [7].

Successful staining reactions for observing silica bodies in plant tissues have been developed; they involve the use of methyl red, silver amine chromate, and crystal violet lactone [46, 48]. In accordance with the reactivity of the silanol groups on the surfaces of the silica bodies, the crystal violet lactone dye stains the silica bodies exclusively, clearly allowing their shapes to be observed [7].

6. Attenuation of negative effects produced by silicon in physiological parameters of plants exposed to water limitation

Benefits of silicon actuation recently reported on physiological parameters such as transpiration [10], stomatal conductance [49], and photosynthesis [50] were reported in several species. In addition, pepper crops, more specifically *Capsicum annuum* exercises strong influence on Brazilian market, and there is necessity to investigate silicon action on this crop. A study aiming to respond these questions was organized with five water and silicon combinations (control, deficit + 0.00, deficit + 0.25 deficit + 1.00, and deficit + 1.75 μM Si) applied to two cultivars (Ikeda and Vermelho Gigante) with a total of 10 treatments.

The water deficit promoted a decrease in leaf relative water content in two cultivars, and 0.25, 1.00, and 1.75 μM Si did not consistently increase this variable for Ikeda, although it was maintained at levels closer to the deficit. Leaf relative water content in Vermelho Gigante for all Si concentrations was slightly higher than the deficit + 0 μM Si (Figure 6 A).

Stomatal conductance was significantly reduced due to water deficit in both cultivars, compared with the control. Ikeda applied with 1.00 and 1.75 μM Si had higher stomatal conductance compared with deficit + 0 μM Si, while Vermelho Gigante had higher values at 0.25 and 1.75 μM Si (Figure 6 B).

The water deficit caused significant reduction in transpiration in Ikeda and Vermelho Gigante cultivars (Figure 6 C). Exogenous application of 0.25, 1.00, and 1.75 μM Si promoted attenuation of symptoms induced by water deficit. The treatments with added silicon were not statistically different.

The leaf relative water content of treatments under silicon application was maintained at levels closer to the control treatment, and this is linked to silicon action that was probably absorbed by plant, and deposited mainly in epidermal cell wall [51]. Additionally, the Si can contribute to higher resistance of xylem vessels [8], which are structures responsible by water transport into plant [52]. Therefore, plants with firmer xylem vessel walls can potentially avoid problems in these structures during drought or extreme heat, besides increasing water volume assimilated by plants [53]. Romero-Aranda et al. [54] investigating silicon effects on *Lycopersicon esculentum* plants under salt stress corroborate the data in this investigation.

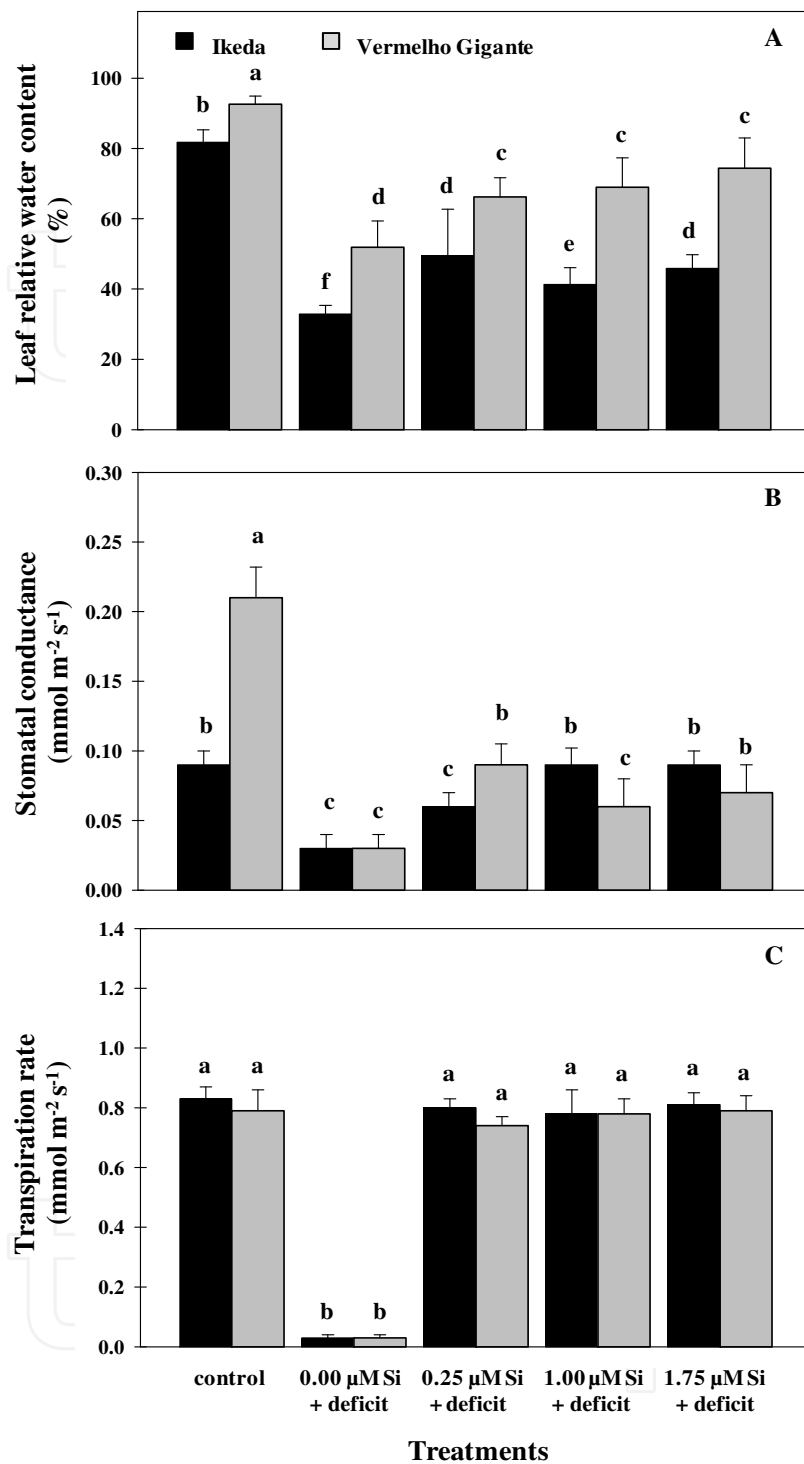


Figure 6. Leaf relative water content (A), stomatal conductance (B), and transpiration rate (C) in two pepper cultivars treated with silicon and exposed to water deficiency. Means followed by the same letter are not significantly different by the Scott-Knott test at 5% of probability. The bars represent the mean standard error [15].

The Si application attenuated the effects of water deficit, indicating intermediary levels in relation to stomatal conductance, and consequently, possible maintenance in gas exchange. A fall in this parameter will affect directly water relations, limiting the assimilation of car-

bon dioxide (CO_2) and water flux (H_2O) through stomata [55]. The stomatal mechanism will reduce the CO_2 assimilation, causing a reduction in photo-assimilate production and losses in yield [56]. Similar results were observed by Gong et al. [57] evaluating the silicon effects on *Triticum aestivum* plants under water deficit, with stomatal conductance being kept at intermediary levels in relation to control plants.

Silicon promoted attenuation in symptoms linked to water deficiency in transpiration rate, because during plant absorption in form of monosilicic acid (H_4SiO_4) [58], silicon accumulates in the leaf, forming a layer double of silicon. This accumulation promotes a reduction in transpiration and decrease water loss by the plant [59-60], but still contributing to maintenance of adequate transpiration rate. In addition, the transpiration process in plants is carried out by the stomatal present in leaf and cuticle normally in stem [61]. Agarie et al. [62] found improvement linked to transpiration rates in *Oryza sativa* plants cultivated with Si. Similar results on maintenance of transpiration were reported previously by Lobato et al. (2009a) studying the protective action of silicon in *Capsicum annuum* under water deficit.

7. Silicon promotes increase in chlorophylls of plants exposed to water deficit

Study conducted by Locarno et al. [63] described increase in level of chlorophyll a, and consequent repercussion on amount of chlorophyll total. Ávila et al. [64] investigating interaction between silicon and nitrogen reported also increase in level of chlorophyll a in *Oryza sativa* plants. In other hand, the drought normally promotes significant decrease in photo-synthetic pigments [65-66].

Therefore, there is limited information linked to silicon action on chlorophyll levels in plants submitted to water deficit. Based in previous results described, Silva et al. [16] carried out an experiment with *Lycopersicon esculentum* plants submitted to water deficiency and silicon, being five water and silicon combinations (control, deficit + 0.00, deficit + 0.25, deficit + 1.00, and deficit + 1.75 μM Si) applied to two cultivars (Super Marmande and Santa Cruz) totalizing 10 treatments. This study had aim of explain silicon action on chlorophylls.

Water deficit promoted reduction not significant in relation to level of chlorophyll a in control treatment for Super Marmande, while Santa Cruz presented significant reduction (Figure 7 A). Applications of silicon in treatments deficit + 0.25, deficit + 1.00, and deficit + 1.75 μM Si promoted an increase in levels of chlorophyll a to both cultivars.

Cultivars evaluated under water deficit presented a reduction in chlorophyll b (Figure 7 B), when compared to control plants. Silicon applications in concentrations of 0.25, 1.00, and 1.75 μM Si provoked oscillations in this parameter. In treatments exposed to silicon, the levels of chlorophyll b presented better performances in concentrations of 1.00 and 1.75 μM Si for Super Marmande and Santa Cruz cultivars, respectively, being these treatments statistically equals to control to both cultivars.

Water deficiency occasioned significant decrease in total chlorophyll evaluated in both cultivars (Figure 7 C). Silicon in concentrations of 0.25, 1.00, and 1.75 μM Si induced a progressive increase in total chlorophyll. The better result was obtained in treatment exposed to concentration of 1.75 μM Si, and this treatment is statistically equal to control.

The reduction in chlorophyll a for both cultivars is a consequence of water restriction, in which will induce probably the production of peroxidative enzymes, and these enzymes are associated to degradation of chlorophyll a in thylakoid membrane [67]. In cultivars exposed to water deficit, silicon application proportioned increase in levels of chlorophyll a, indicating synthesis of new pigments, and maintenance of chlorophyll a previously existing. Donega [68] also affirmed that silicon uses promotes improvement in plant architecture and increase in photosynthesis. In other hand, the deposition of silicon in cell wall increased your tissue resistance, and it will keep plants with better performance linked to leaf position and interception of light [69-70]. Results of this research are similar and corroborate study carried out by Lobato et al. (2009a) investigating *Capsicum annuum* plants under water deficit, as well as Ahmad & Haddad [29] working with *Triticum aestivum* plants under water deficiency and silicon utilization reported similar results.

Water deficiency occasioned decrease chlorophyll b due to water restriction in substrate. Chlorophyll b was positively affected by silicon application, and this fact is associated to Si accumulation in epidermal cells localized in shoot, in which it will promote indirect protector effect on photosynthetic apparatus, and consequently decrease in damages provoked by water restriction in this parameter. The reduction in chlorophyll b in plants under water deficiency probably is resulting of disorders in chloroplast and modifications in relation proteins/lipids responsible by formation of pigment-protein complex [71-72]. Similar results on increase in chlorophyll b were observed by Locarno et al. [63] studying *Rosa* spp. plants under silicon application.

Results obtained in total chlorophyll indicate that plants under water deficit and treated with silicon presented increase in this parameter, and a relationship observed (data not shows) between leaf water potential and total chlorophyll can explain this fact, because adequate water amount in leaf tissue works probably maintaining stability of chloroplasts and consequently the functions carried out by the chlorophylls like as absorption and transport of energy.

In other hand, plants exposed to water deficit presented decrease, being probably linked to decrease in nitrogen absorption, in which is an essential element in formation of chlorophyll molecules. Plants under nitrogen application presented increase in chlorophyll amounts [64], as well as silicon promotes modifications on nitrogen metabolism [73]. Water works as vehicle responsible by nitrogen conduction and other nutrients during absorption through root system [74]. In other hands, during situations of water deficiency can there lower water assimilation, producing a negative interference linked to nitrogen assimilation. Therefore, this fact will generate minor amount of δ -aminolevulinate, which is chlorophyll precursor [75]. Tranaviciene et al. [76] investigating *Triticum aestivum* plants under different nitrogen levels observed that level of chlorophyll increased in consequence of increase in amount of nitrogen applied.

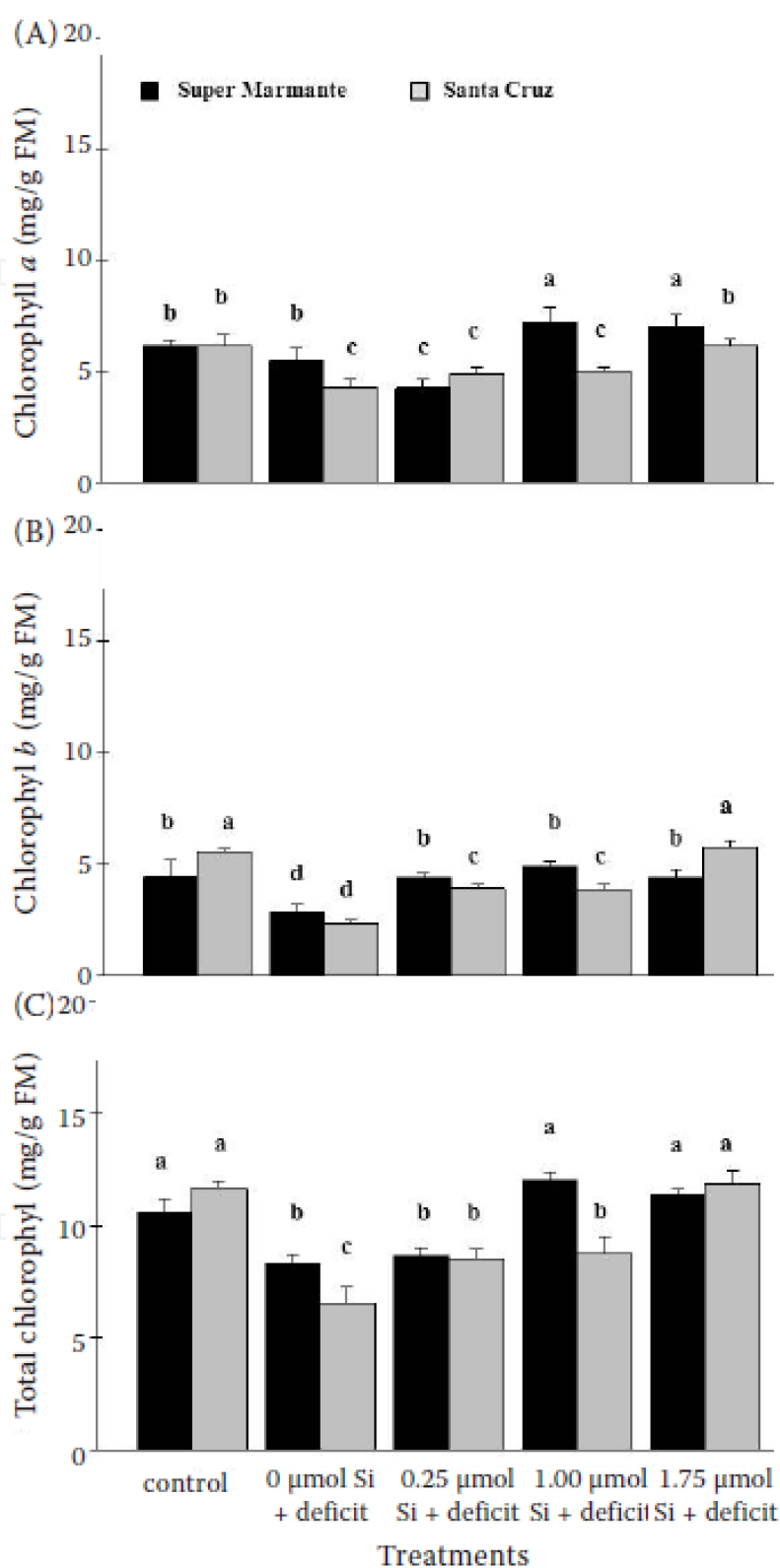


Figure 7. Chlorophyll a (A), chlorophyll b (B), and total chlorophyll (C) in two tomato cultivars treated with silicon and exposed to water deficiency. Means followed by the same letter are not significantly different by the Scott-Knott test at 5% of probability. The bars represent the mean standard error [16].

8. Final considerations

This chapter was structured with novel informations that can represent an important source to students, teachers, researchers, scientists and farmers on silicon action linked to attenuation of water deficit in higher plants. It revealed results and concepts on water deficiency and your consequences on plants, as well as silicon utilization with finality to improve tolerance during inadequate water supply. In addition, it presented a simple and efficient technique to carry detection of element beneficial in tissue. Based in recent results, was also demonstrated as silicon is assimilated, transported, and accumulated in several plant organs. Besides to prove positive interference on gas exchanges and photosynthetic pigments in plants exposed to water restriction.

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