Effects of Silicon and Drought Stress on Tuber Yield and Leaf Biochemical Characteristics in Potato

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ABSTRACT

Silicon has beneficial effects on many crops, mainly under biotic and abiotic stresses. Silicon can affect biochemical, physiological, and photosynthetic processes and, consequently, alleviates drought stress. However, the effects of Si on potato (*Solanum tuberosum* L.) plants under drought stress are still unknown. The objective of this study was to evaluate the effect of Si supply on some biochemical characteristics and yield of potato tubers, either exposed or not exposed to drought stress. The experiment was conducted in pots containing 50 dm³ of a Typic Acrortox soil (33% clay, 4% silt, and 63% sand). The treatments consisted of the absence or presence of Si application (0 and 284.4 mg dm⁻³), through soil amelioration with dolomitic lime and Ca and Mg silicate, and in the absence or presence of water deficit (–0.020 MPa and –0.050 MPa soil water potential, respectively), with eight replications. Silicon application and water deficit resulted in the greatest Si concentration in potato leaves. Proline concentrations increased under lower water availability and higher Si availability in the soil, which indicates that Si may be associated with plant osmotic adjustment. Water deficit and Si application decreased total sugars and soluble proteins concentrations in the leaves. Silicon application reduced stalk lodging and increased mean tuber weight and, consequently, tuber yield, especially in the absence of water stress.

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Abbreviations: DAE, days after emergence; DAP, days after planting; DW, dry weight.

POTATO (*Solanum tuberosum* L.) is quite sensitive to water deficit (Epstein and Grant, 1973; Loon, 1981). This sensitivity can be attributed to its small and shallow root system, which makes the plant ineffective for absorbing water (Gregory and Simmonds, 1992). Short water deficit periods may result in reduced tuber growth, yield, and quality (Costa et al., 1997). Water deficit inhibits photosynthesis as it causes chlorophyll content alterations, harms the photosynthetic apparatus (Costa et al., 1997), and decreases leaf stomatal conductance (Hattori et al., 2005). In addition, it modifies the activity of some enzymes and the accumulation of sugars and proteins in the plant (Nadler and Heuer, 1995; Zhu et al., 2004; Gong et al., 2005), resulting in lower plant growth and yield (Costa et al., 1997).

Plant tolerance to unfavorable conditions, particularly regarding water deficit, has been associated with proline accumulation, which may represent a water loss regulatory mechanism by reducing cell water potential (Fumis and Pedras, 2002) and may also be a biochemical marker of metabolic alterations generated by

different types of stress (Lima et al., 2004). Nadler and Heuer (1995) observed greater accumulation of proline in potato tubers exposed to salinity and water deficit.

Proline is a nonprotein amino acid that is formed in the leaf tissues of plants exposed to water deficit and, together with sugar, is readily metabolized in the leaves after recovery from water stress (Kameli and Losel, 1993). The role of this amino acid is to protect cells from denaturation processes under water and saline stress conditions, due to its high solubility in water (Shevyakova, 1984). Proline is accumulated in the cytoplasm (Leigh et al., 1981) and is found in leaves, stalks, and roots. The accumulation and concentration capacity of this amino acid decreases with leaf age (Sawazaki and Teixeira, 1981). Martinez and Moreno (1992) studied two Peruvian varieties of potato for 10 d under stress and observed that the most–tolerant variety had accumulated more than twice the amount of leaf proline (40 mg g^{-1} dry weight [DW]) than the most–sensitive one (18 mg g^{-1} DW).

Silicon is the second most abundant element in the Earth's crust. Although it is accumulated in large amounts by plants of many families, especially Gramineae and Cyperaceae (Hattori et al., 2005), and even though several studies have demonstrated its beneficial effects in several species (Ma, 2004), Si is still not considered an essential element for plant growth. Its beneficial effects are normally observed under stressing conditions to plants (Ma and Yamaji, 2006), and several studies have demonstrated that Si plays an important role in plant tolerance to environmental stresses (Ma, 2004; Zhu et al., 2004; Gong et al., 2005; Hattori et al., 2005; Gunes et al., 2007a,b, 2008).

Silicon application can decrease the transpiration rate (Agarie et al., 1998b) and electrolyte leakage from leaves (Agarie et al., 1998a), thus preventing the structural and functional deterioration of cell membrane of rice plants (*Oryza sativa* L.) under water deficit conditions. However, Hattori et al. (2005) observed higher transpiration rate, stomatal conductance, and dry matter accumulation under water deficit in sorghum plants [*Sorghum bicolor* (L.) Moench] grown in pots fertilized with Si in relation to plants that did not receive Si. Those authors suggested that the Si effect on greater sorghum tolerance to water deficit resulted from an increased capacity of the plant in absorbing water from the soil.

Gunes et al. (2007a) verified that supplied Si induced higher dry matter yield and proline concentrations in barley plants (*Hordeum vulgare* L.) exposed to excessive sodium and boron in the soil. Zhu et al. (2004) and Gong et al. (2005) observed that cucumber (*Cucumis sativus* L.) and wheat (*Triticum aestivum* L.) plants grown under higher Si availability and exposed to salinity and water deficit, respectively, showed higher protein concentrations in the leaves compared with plants grown without Si. According to those authors, the effect of Si on the greater tolerance of higher plants to drought could be associated with an increase in the action of antioxidant defenses, a reduction in the oxidative damage of functional molecules and membranes, and maintenance of many physiological as well as photosynthetic processes, under water deficit conditions.

Drought stress has been found to increase stomatal resistance, leaf hydrogen peroxide and proline concentrations, and leaf lipid peroxidation in both chickpea (*Cicer arietinum* L.) (Gunes et al., 2007b) and sunflower (*Helianthus annuus* L.) (Gunes et al., 2008). However, Si application decreased their levels and alleviated membrane damage significantly by increasing leaf relative water content.

No information in the literature indicates whether Si applications may have similar beneficial effects on potato under drought stress. The present work aimed to evaluate the effect of Si supply on leaf concentrations of Si, soluble sugars, proteins and proline, and on tuber yield of potato plants grown either with or without exposure to soil water deficits.

MATERIAL AND METHODS

The experiment was performed under greenhouse conditions in Botucatu, São Paulo, Brazil, in 56-L pots, with an effective depth of 30 cm and a hole at the bottom to drain water excess, containing 50 dm^3 of a Typic Acrortox soil (33% clay, 4% silt, and 63% sand). The unamended soil had the following properties: pH (1:2.5 soil/CaCl$_2$ suspension 0.01 mol L^{-1}) 4.0, 22 g dm^{-3} organic matter, 2.1 mg dm^{-3} P, 6.0 mmol$_c$ dm^{-3} Ca, 0.8 mmol$_c$ dm^{-3} Mg, 0.1 mmol$_c$ dm^{-3} K, 78.1 mmol$_c$ dm^{-3} H+Al, and 8.1% base saturation. All the soil chemical attributes were analyzed according to van Raij et al. (2001).

The experiment was arranged in a completely randomized design with a 2 × 2 factorial combination and eight replications. Treatments comprised combinations between the presence or absence of Si supply (284.4 mg dm^{-3} Si), through soil amelioration with dolomitic lime and Ca and Mg silicate, and the presence or absence of water deficit (−0.050 MPa and −0.020 MPa soil water potential values, respectively). Each pot was considered an experimental unit.

To establish the Si treatments, base saturation was increased to 60% (Lorenzi et al., 1997) by applying Ca and Mg silicate to 16 pots, while the other 16 pots received an application of dolomitic lime (Table 1). The finest granulometric portion of the pH–correcting materials, that is, particles smaller than 0.30 mm (50 mesh), was used, to obtain full reaction of the amendments in the soil during the incubation period. Moreover, 150 mg dm^{-3} P (single superphosphate, 18% P$_2$O$_5$), 150 mg dm^{-3} K (potassium chloride, 60% K$_2$O), 5 mg dm^{-3} Zn, and 1 mg dm^{-3} B (fritted trace elements BR12, 9% Zn and 1.8% B) were added. The soil was then wetted to field capacity, covered with polyethylene film, and incubated for 30 d to 25°C.

After the incubation period, soil samples from the pots were air-dried and analyzed for pH in CaCl$_2$, P, H+Al, K, Ca, and Mg. Base saturation was calculated (van Raij et al., 2001), and the soluble Si concentration was determined using a 0.01 mol L^{-1} CaCl$_2$ solution (Korndörfer et al., 2004). Silicon determination was performed by beta-molybdosilicic complex formation

(Kilmer, 1965), using a spectrophotometer at 660 nm. Results are shown in Table 2.

The potato cultivar Bintje was planted on 15 Sept. 2005, at a 15 cm depth, using one seed tuber per pot with diameter size between 30 and 50 mm, containing vigorous shoots. Emergence occurred 9 d after planting (DAP).

Nitrogen was supplied in three split applications at 4, 14, and 25 d after emergence (DAE), using 44, 17.6, and 14 mg dm^{-3} N, respectively, as urea. Boron was sprayed to leaves (0.5% boric acid solution) at 45 DAE. For leaf spraying, an amount equivalent to 200 L of solution ha^{-1} was applied, using a backpack sprayer with constant pressure.

Soil water potential was monitored with conventional mercury tensiometers (13-mm diameter, with a ceramic porous cup connected with tubing to a mercury manometer), which we constructed according Richards (1941), and installed on the planting date at a 15 cm depth, in four replications each treatment (16 pots). After plant emergence and before the water deficit treatments were established, water additions were performed when the mean water potential in the soil reached −0.020 MPa. The treatments with soil water potentials of −0.020 and −0.050 MPa were established at 10 DAE and maintained until 60 DAE. Required water additions were performed according to recommendations by Oliveira and Valadão (1997) and by the soil water retention capacity curve. The soil water retention capacity curve was determined in the laboratory, according to the pressure plate methodology recommended by Richards (1949) and Topp et al. (1993). Water additions were performed manually and calculated so as to increase tension values until the field capacity for all treatments whenever the established tensions were reached. Total water applied was 323 and 392 mm, respectively, in the treatments with or without water deficit.

When plants were at 40 DAE, four leaves per pot (third expanded leaves counting from the plant apex) were collected for Si and biochemical determinations. Two leaves of each pot were dried in a forced-air oven at 65°C for 72 h, ground to pass a 40-mesh stainless steel screen and subjected to Si concentration determinations. The other two collected leaves were wrapped in baking paper, immersed in liquid nitrogen, and then stored in a freezer (−20°C) for later biochemical analyses.

Silicon concentration in the leaves was assayed according to Elliott and Snyder (1991) procedure, adapted by Korndörfer et al. (2004). Samples of plant tissue weighing 0.1 g were wetted with 2 mL of 50% H$_2$O$_2$ in polyethylene tubes. Three mL of 50% NaOH at room temperature was added to each tube. Tubes were placed in a double boiler for 1 h and then in an autoclave at 138 kPa for 1 h. After atmospheric pressure was reached, tubes were removed and 45 mL of water was added. The tubes rested for 12 h. After, one 1-mL aliquot of the super-natant was set aside and 15 mL of water, 1 mL of HCl (500 g L^{-1}), and 2 mL of ammonium molybdate were added. After 5 to 10 min, 2 mL of oxalic acid (500 g L^{-1}) were added. Silicon was determined with a spectrophotometer at a wavelength of 410 nm.

To determine total soluble sugars and total soluble proteins concentrations, 0.5-g aliquots of fresh (frozen) leaves were ground in a porcelain mortar and pestle containing 5 mL of a buffer phosphate solution pH 6.7 0.2 mol L^{-1}, centrifuged at 5000 rpm for 10 min and the supernatant (extract) was collected and frozen (−20°C) for later determinations (Lima et al., 1999). The method described by Dubois et al. (1956), modified by Lima et al. (1998), was used to determine total soluble sugars. Total soluble proteins concentration determination was accomplished using the method described by Bradford (1976). Proline concentrations were determined using the method described by Bates et al. (1973) and Torello and Rice (1986).

Stalk lodging was determined at 60 DAE. Lodging was evaluated via the relation between the number of lodged stalks (stalks touching the ground) and the total number of stalks, with the result expressed as percentage.

The crop cycle lasted 87 d. It was considered finished when 80% of the plants showed stalk yellowing. The number of tubers per plant, mean tuber weight, and tuber yield (g plant^{-1}) were evaluated 10 d after the stalks were completely dry. The tubers were separated from the soil, brushed, and then counted and weighed. After, tubers were sliced, dried in a forced-air oven at 65°C for 72 h, and weighed to determine tubers dry weight (g plant^{-1}).

Data were subjected to analysis of variance, and means were separated using Fisher's protected LSD test at the 0.05 probability level.

RESULTS AND DISCUSSION

Silicon concentrations in the leaves were affected by drought, Si, and the interaction of drought × Si (Table 3). Under water stress, the application of Si resulted in higher concentration of this element in the leaves of potato plants and, when Si was applied, water deficit resulted in greater Si accumulation in the leaves (Table 4).

Potato is considered a non–Si–accumulating plant (Marschner, 1995). According to Mitani and Ma (2005), non-accumulating plants such as tomato (*Lycopersicon esculentum* Mill.) have lower densities of Si transporters from the apoplast

Table 1. Chemical characteristics and rates of materials used in the experiment.

Products	SiO$_2$	CaO	MgO	ECCE[†]	Rate
	———— g kg^{-1} ————			%	g dm^{-3}
Dolomitic limestone	–	390	130	90	2.68
Ca and Mg silicate	227	420	120	82	2.94

[†]Effective calcium carbonate equivalence.

Table 2. Soil chemical characteristics after period of wet incubation. Mean of 16 replicates.

Silicon application	pH (CaCl$_2$)	P	H+Al	K	Ca	Mg	Base saturation	Soluble Si
		mg dm^{-3}	———— mmol$_c$ dm^{-3} ————				%	mg dm^{-3}
No Si (limestone)	4.6a[†]	57.9a	50.4a	2.7a	35.7a	8.7a	52a	2.4b
With Si (silicate)	4.6a	57.7a	48.6a	3.0a	41.4a	9.3a	56a	3.8a
ANOVA	NS[‡]	NS	NS	NS	NS	NS	NS	***
CV (%)	3.7	17.3	13.6	17.3	22.2	19.5	15.0	14.3

***Significant at the 0.001 probability level.

[†]Values in column followed by the same letter are not significantly different at P ≤ 0.05 according to LSD test.

[‡]NS, not significant at the 0.05 probability level.

Table 3. Silicon, proline, total soluble sugar, and total soluble protein concentration in leaves, stems lodging, tuber number per plant, tuber mean weight, tuber yield, and tuber dry weight of potato crop affected by drought stress and Si application, and ANOVA significance.

Treatments	Si in leaves	Proline	Total soluble sugars	Total soluble proteins	Stems lodging	Tuber no.	Tuber mean wt.	Tuber yield	Tuber dry wt.
	% of DW[†]	µmol g^{-1} of FW[†]	mg g^{-1} of FW	% of FW	%	no. plant^{-1}	g	——— g plant^{-1} ———	
Drought stress									
No stress	0.39b[‡]	1.1b	2.7a	3.0a	50.1a	32.3a	31.2a	941.4a	243.8a
With stress	0.43a	1.9a	2.4b	2.8a	49.6a	30.6a	32.3a	833.4b	225.6a
Silicon application									
No Si	0.39b	1.4b	2.8a	3.0a	61.1a	31.0a	30.1a	828.4b	223.6b
With Si	0.44a	1.7a	2.3b	2.8b	38.6b	31.8a	33.4a	946.4a	245.8a
				ANOVA					
Drought stress (D)	*	**	*	NS[§]	NS	NS	NS	**	NS
Silicon application (S)	*	*	*	*	**	NS	NS	**	*
D × S	*	NS	*	*	*	NS	*	*	NS
CV (%)	12.0	8.4	7.1	11.2	8.9	22.3	14.6	9.5	14.2

*Significant at the 0.05 probability level.

**Significant at the 0.01 probability level.

[†]DW, dry weight; FW, fresh weight.

[‡]Values in column, within each factor (drought stress and Si application), followed by the same letter are not significantly different at P ≤ 0.05 according to LSD test.

[§]NS, not significant at the 0.05 probability level.

into the symplast and have a defect in the Si transporters from cortex cells into the xylem. The data obtained in the present paper may indicate that, under water deficit conditions, this Si absorption mechanism is changed. Silicon is an element

Table 4. Effect of drought stress and Si application on the Si, total soluble sugar, and total soluble protein concentration in leaves, stems lodging, tuber mean weight, and tuber yield of potato plants.

Drought stress	Silicon application	
	No Si	With Si
	Si in leaves, % of DW[†]	
No stress	0.37aA[‡]	0.42bA
With stress	0.41aB	0.47aA
	Total soluble sugars, mg g^{-1} of FW[†]	
No stress	2.8aA	2.5aB
With stress	2.7aA	2.1bB
	Total soluble proteins, % of FW	
No stress	3.0aA	2.9aA
With stress	3.0aA	2.6aB
	Stems lodging, %	
No stress	63.4aA	36.8aB
With stress	58.8bA	40.5aB
	Tuber mean weight, g	
No stress	28.6aB	36.0aA
With stress	31.6aA	30.1bA
	Tuber yield, g plant^{-1}	
No stress	868.3aB	1014.6aA
With stress	788.5aB	878.3bA

[†]DW, dry weight; FW, fresh weight.

[‡]Values followed by same lowercase letter in the columns and uppercase letter in the rows are not significantly different at P ≤ 0.05 according to LSD test.

found abundantly in the soil; however, the Si concentration available to plants in the soil solution is normally low (Hattori et al., 2005). Lower water availability probably resulted in higher Si concentration in soil solution or promoted leaf DW reduction, resulting in greater Si concentration in plants with water stress. Mitani and Ma (2005) also observed an increase in Si absorption by tomato plants subjected to higher concentrations of the element in the nutrient solution.

As to proline concentrations, it can be seen that water deficit resulted in higher values, regardless of Si application (Table 3). Water deficit increased proline concentrations in bean (*Phaseolus vulgaris* L.) (Sawazaki and Teixeira, 1981), barley (Gunes et al., 2007a), chickpea (Gunes et al., 2007b), sunflower (Gunes et al., 2008), and potato plants (Sasilaka and Prasad, 1994; Nadler and Heuer, 1995). The capacity to accumulate proline observed during the water stress period has been associated with plant tolerance to this unfavorable condition (Sawazaki and Teixeira, 1981). Martinez and Moreno (1992) observed higher proline accumulation in a potato cultivar tolerant to water stress, in relation to a susceptible cultivar.

Potato plants that received Si applications showed higher proline concentrations in the leaves, regardless of the soil water condition (Table 3). This could be related to a more efficient osmotic adjustment. Gunes et al. (2007b, 2008) observed that Si applications provided higher Si and proline concentrations in chickpea and sunflower plants exposed to drought stress. Probably a more efficient osmotic adjustment as a function of higher proline concentrations is part of the tolerance mechanism to water deficit; Si seems to encourage this mechanism in potato plants.

Total soluble sugar concentrations in the leaves were affected by drought, Si, and the interaction of drought × Si (Table 3). There was a reduction in total soluble sugar concentrations in the treatment that received Si (Table 4). This decrease was more marked in the presence of water deficit, precisely the opposite of what was observed for proline concentrations (Table 4). According to Aziz et al. (1997), hexoses and sucrose constitute part of the solutes accumulated in the cytoplasm of plant cells under water deficit conditions, which could be related to osmotic adjustment. However, sugar and soluble protein concentrations in potato plants exposed to water or saline stress may vary from cultivar to cultivar, regardless of proline accumulation (Sasilaka and Prasad, 1994). It is therefore possible that the results obtained here concerning total soluble sugars and proline concentrations are related to characteristics of the cultivar used.

Zhu et al. (2004) and Gong et al. (2005) observed higher protein concentrations in cucumber and wheat plants that received Si than in plants that did not receive Si when exposed to saline and water stress, respectively. However, we observed that total soluble protein concentrations were smaller in the treatment involving Si, especially under a water deficit condition, precisely the opposite of what was observed for proline concentration (Table 3 and 4). The reason for this reduction may be the breakdown of proteins to supply a carbon skeleton for proline synthesis (Stewart, 1981).

Stalk lodging was affected by the Si application and the interaction of drought × Si (Table 3). The application of Si produced a decrease of this variable under both soil water conditions (Table 4). In the treatment without Si application, greater water availability provided greater lodging in relation to the treatment under water deficit. Gong et al. (2005) observed that the application of Si maintained higher water potential and content in wheat plants exposed to drought compared with plants that did not receive Si. Silicon accumulation in the leaves, and its association with the cuticle, as well as its polymerization in plant tissues may also have contributed to decrease the stalk lodging percentage observed in the present work, since it confers greater mechanical resistance to tissues (Ma, 2004).

The number of tubers per plant was not influenced by the factors studied (Table 3). Tuber mean weight was affected by the interaction of drought × Si (Table 3). This variable was significantly increased with the application of Si only in the absence of water deficit, while higher soil water availability resulted higher tuber weight only when Si was applied (Table 4).

Tuber yield (g plant⁻¹) was influenced by all factors (Table 3). The evaluation of the interaction shows that Si application increased this variable under both water conditions, but with stronger effects under higher water availability (Table 4). These results demonstrate that higher Si availability in the soil is beneficial to potato crops, also increasing tuber dry weight, regardless of water conditions (Table 3). The yield benefit obtained resulted from enhanced tuber filling, probably as a consequence of greater production of photoassimilates, or due to changes in photoassimilates partitioning. Gong et al. (2005) and Hattori et al. (2005) verified that supplied Si provides higher photosynthesis and shoot dry matter in wheat and sorghum plants, respectively.

CONCLUSIONS

Higher Si availability in the soil and water deficit resulted in higher Si accumulation in potato plant leaves. Water deficit and Si applications caused proline concentrations to increase, whereas total sugars and soluble proteins in the leaves were reduced. Silicon supply reduced stalk lodging, increasing mean tuber weight, tuber dry weight, and tuber yield, especially in the absence of water deficit.

References

Agarie, S., N. Hanaoka, O. Ueno, A. Miyazaki, F. Kubota, W. Agata, and P.B. Kaufman. 1998a. Effects of silicon on tolerance to water deficit and heat stress in rice plants (*Oryza sativa* L.), monitored by electrolyte leakage. Plant Prod. Sci. 1:96–103.

Agarie, S., H. Uchida, W. Agata, F. Kubota, and P.B. Kaufman. 1998b. Effects of silicon on transpiration and leaf conductance in rice plants (*Oryza sativa* L.). Plant Prod. Sci. 1:89–95.

Aziz, A., J. Martin-Tanguy, and F. Larher. 1997. Plasticity of polyamine metabolism associated with high osmotic stress in rape leaf disc and with ethylene treatment. Plant Growth Regul. 21:153–163.

Bates, L.S., R.P. Waldren, and I.D. Teare. 1973. Rapid determination of free proline for water-stress studies. Plant Soil 39:205–207.

Bradford, M.M. 1976. A rapid and sensitive method for the qualification of microgram quantities of protein utilizing the principle of protein dye binding. Anal. Biochem. 7:248–254.

Costa, L.D., G.D. Vedove, G. Gianquintoi, R. Giovanardi, and A. Peressotti. 1997. Yield, water use efficiency, and nitrogen uptake in potato: Influence of drought stress. Potato Res. 40:19–34.

Dubois, M., K.A. Gilles, J.K. Hamilton, P.A. Rebers, and F. Smith. 1956. Colorimetric method for determination of sugars and related substances. Anal. Chem. 28:350–356.

Elliott, C.L., and G.H. Snyder. 1991. Autoclave-induced digestion for the colorimetric determination of silicon in rice straw. J. Agric. Food Chem. 39:1118–1119.

Epstein, E., and W.J. Grant. 1973. Water stress relation of the potato plant under field conditions. Agron. J. 65:400–404.

Fumis, T.F., and J.F. Pedras. 2002. Variação nos níveis de prolina, diamina e poliaminas em cultivares de trigo submetidas a déficits hídricos. Pesqui. Agropecu. Bras. 37:449–459.

Gong, H., X. Zhu, K. Chen, S. Wang, and C. Zhang. 2005. Silicon alleviates oxidative damage of wheat plants in pots under drought. Plant Sci. 169:313–321.

Gregory, P.J., and L.P. Simmonds. 1992. Water relations and growth of potatoes. p. 214–246. *In* P.M. Harris (ed.) The potato crop: The scientific basis for improvement. 2nd ed. Chapman and Hall, London.

Gunes, A., A. Inal, E.G. Bagci, and S. Coban. 2007a. Silicon-mediated changes on some physiological and enzymatic

parameters symptomatic of oxidative stress in barley grown in sodic–B toxic soil. J. Plant Physiol. 164:807–811.

Gunes, A., D.J. Pilbeam, A. Inal, E.G. Bagci, and S. Coban. 2007b. Influence of silicon on antioxidant mechanisms and lipid peroxidation in chickpea (*Cicer arietinum* L.) cultivars under drought stress. J. Plant Interact. 2:105–113.

Gunes, A., D.J. Pilbeam, A. Inal, and S. Coban. 2008. Influence of silicon on sunflower cultivars under drought stress, I: Growth, antioxidant mechanisms, and lipid peroxidation. Commun. Soil Sci. Plant Anal. 39:1885–1903.

Hattori, T., S. Inanaga, H. Araki, P. An, S. Morita, M. Luxová, and A. Lux. 2005. Application of silicon enhanced drought tolerance in *Sorghum bicolor*. Physiol. Plant. 123:459–466.

Kameli, A., and D.M. Losel. 1993. Carbohydrates and water status in wheat plants under water stress. New Phytol. 125:609–614.

Kilmer, V.J. 1965. Silicon. p. 959–962. *In* C.A. Black (ed.) Methods of soil analysis: Chemical and microbiological properties. Vol. 2. Agron. Monogr. 9. ASA, Madison, WI.

Korndörfer, G.H., A. Nolla, and L.A. Oliveira. 2004. Análise de silício: Solo, planta e fertilizante. Tech. Bull. 02. Universidade Federal de Uberlândia, Uberlândia, MG, Brazil.

Leigh, R.A., N. Ahmad, and R.G.W. Jones. 1981. Assessment of glicine betaine and proline compartmentation, by analysis of isolated beet vacuoles. Physiol. Plant. 153:34–41.

Lima, G.P.P., O.G. Brasil, and A.M. Oliveira. 1999. Poliaminas e atividade da peroxidase em feijão (*Phaseolus vulgaris* L.) cultivado sob estresse salino. Sci. Agric. 56:21–25.

Lima, G.P.P., A.A.H. Fernandes, A.C. Cataneo, M.P. Cereda, and O.G. Brasil. 1998. Alterações na atividade da peroxidase e no conteúdo de carboidratos em mandioca cultivada *in vitro* sob estresse salino. Sci. Agric. 55:413–417.

Lima, M.D.S., N.F. Lopes, M.A. Bacarin, and C.R. Mendes. 2004. Efeito do estresse salino sobre a concentração de pigmentos e prolina em folhas de arroz. Bragantia 63:335–340.

Loon, C.D. 1981. The effect of water stress on potato growth, development, and yield. Am. Potato J. 58:51–69.

Lorenzi, J.O., H.S. Miranda Filho, and B. van Raij. 1997. Raízes e tubérculos. p. 221–229. *In* B. van Raij et al. (ed.) Recomendações de adubação e calagem para o Estado de São Paulo. 2nd ed. Tech. Bull. 100. Inst. Agronômico Campinas, SP, Brazil.

Ma, J.F. 2004. Role of silicon in enhancing the resistance of plants to biotic and abiotic stresses. Soil Sci. Plant Nutr. 50:11–18.

Ma, J.F., and N. Yamaji. 2006. Silicon uptake and accumulation in higher plants. Trends Plant Sci. 11:392–397.

Marschner, H. 1995. Mineral nutrition of higher plants. 2nd ed. Academic Press, London.

Martinez, C.A., and U. Moreno. 1992. Expresiones fisiologicas de resistencia a la sequia en dos variedades de papa sometidas a estres hidrico. Rev. Bras. Fisiol. Veget. 4:33–38.

Mitani, N., and J.F. Ma. 2005. Uptake system of silicon in different plant species. J. Exp. Bot. 56:1255–1261.

Nadler, A., and B. Heuer. 1995. Effect of saline irrigation and water deficit on tuber quality. Potato Res. 38:119–123.

Oliveira, C.A.S., and L.T. Valadão. 1997. Manejo da água do solo no cultivo da batata. Tech. Commun. 3. Embrapa Hortaliças, Brasília, DF, Brazil.

Richards, L.A. 1941. Soil moisture tensiometer materials and construction. Available at http://www.ars.usda.gov/SP2User-Files/Place/53102000/pdf_pubs/P0015.pdf (verified 5 Mar. 2009). USDA–ARS, Washington, DC.

Richards, L.A. 1949. Methods of measuring moisture tension. Soil Sci. 68:95–112.

Sasilaka, D.P.P., and P.V.D. Prasad. 1994. Salinity effects on *in vitro* performance of some cultivars of potato. Rev. Bras. Fisiol. Veget. 1:1–6.

Sawazaki, H.E., and J.P.F. Teixeira. 1981. Variação do teor de prolina em folhas de feijão em função da disponibilidade de água no solo. Bragantia 40:47–56.

Shevyakova, N.I. 1984. Metabolism and the physiological role of proline in plants under conditions of water and salt stress. Sov. Plant Physiol. 30:597–608.

Stewart, C.R. 1981. Proline accumulation: Biochemical aspects. p. 243–259. *In* L.G. Paleg and D. Aspinall (ed.) The physiology and biochemistry of drought resistance in plants. Academic Press, New York.

Topp, G.C., Y.T. Galganov, B.C. Ball, and M.R. Carter. 1993. Soil water desorption curves. p. 569–579. *In* M.R. Carter (ed.) Soil sampling and methods of analysis. Lewis, Boca Raton, FL.

Torello, W.A., and L.A. Rice. 1986. Effect of NaCl stress and proline and cation accumulation in salt sensitive and tolerant turfgrasses. Plant Soil 93:227–241.

van Raij, B., J.C. Andrade, H. Cantarella, and J.A. Quaggio. 2001. Análise química para avaliação da fertilidade de solos tropicais. Instituto Agronômico, Campinas, SP, Brazil.

Zhu, Z., G. Wei, J. Li, Q. Qian, and J. Yuet. 2004. Silicon alleviates salt stress and increases antioxidant enzymes activity in leaves of salt-stressed cucumber (*Cucumis sativus* L.). Plant Sci. 167:527–533.