Taylor & Francis
Taylor & Francis Group

Journal of Plant Nutrition

ISSN: 0190-4167 (Print) 1532-4087 (Online) Journal homepage: http://www.tandfonline.com/loi/lpla20

Silicon Improves Water Use Efficiency in Maize Plants

Xiaopeng Gao , Chunqin Zou , Lijun Wang & Fusuo Zhang

To cite this article: Xiaopeng Gao , Chunqin Zou , Lijun Wang & Fusuo Zhang (2005) Silicon Improves Water Use Efficiency in Maize Plants, Journal of Plant Nutrition, 27:8, 1457-1470, DOI: 10.1081/PLN-200025865

To link to this article: http://dx.doi.org/10.1081/PLN-200025865

JOURNAL OF PLANT NUTRITION
Vol. 27, No. 8, pp. 1457–1470, 2004

Silicon Improves Water Use Efficiency in Maize Plants

Xiaopeng Gao, Chunqin Zou,* Lijun Wang, and Fusuo Zhang

Key Laboratory of Plant–Soil Interactions, MOE, Key Laboratory of Plant Nutrition, MOA, Department of Plant Nutrition, China Agricultural University, Beijing, P.R. China

ABSTRACT

The influence of silicon (Si) on water use efficiency (WUE) in maize plants (*Zea mays* L. cv. Nongda108) was investigated and the results showed that plants treated with 2 mmol L^{-1} silicic acid (Si) had 20% higher WUE than that of plants without Si application. The WUE was increased up to 35% when the plants were exposed to water stress and this was accounted for by reductions in leaf transpiration and water flow rate in xylem vessels. To examine the effect of silicon on transpiration, changes in stomata opening were compared between Si-treated and nontreated leaves by measuring transpiration rate and leaf resistance. The results showed that the reduction

*Correspondence: Chunqin Zou, Key Laboratory of Plant–Soil Interactions, MOE, Key Laboratory of Plant Nutrition, MOA, Department of Plant Nutrition, China Agricultural University, Beijing 100094, P.R. China; E-mail: zcq0206@hotmail.com.

DOI: 10.1081/PLN-200025865 0190-4167 (Print); 1532-4087 (Online)

in transpiration following the application of silicon was largely due to a reduction in transpiration rate through stomata, indicating that silicon influences stomata movement. In xylem sap of plants treated with 2 mmol L^{-1} silicic acid, the Si concentration was 200-fold higher, while the Ca concentration which is mainly determined by the transpiration rate, was 2.5-fold lower than that of plants grown without Si. Furthermore, the water flow rate in xylem vessels of plants with and without Si was compared. Flow rate in plants with 2 mmol L^{-1} Si was 20% lower than that without Si, which was accounted for by the increased affinity for water in xylem vessels induced by silica deposits. These results demonstrated the role of Si in improving WUE in maize plants.

Key Words: Flow rate; Maize; Silicon; Transpiration; Water use efficiency.

INTRODUCTION

Silicon, the second most abundant element in the earth's crust, interacts with living systems by mechanisms that have remained poorly understood. The correlation between silicon nutrition and water use has been studied in the past, but the results were inconsistent.[1,2] It has been demonstrated that silicon can increase plant defense systems against abiotic and biotic stresses, including water stress.[3–5]

Many studies have clearly shown that transpiration from leaves of some plants is considerably reduced by the application of silicon.[6,7] This was explained by a well-thickened layer of silica gel associated with the cellulose in the epidermal cell walls,[8,9] which may help to reduce water loss, while epidermal cell wall with less silica gel will allow water to escape at an accelerated rate. However, Agarie et al.[6] found that the silicon could influence the stomata light reaction by comparing the leaf conductance under different Si-treatment and different light intensity. Then, how much effect does silicon have on plant water status? Is the leaf transpiration reduction the only way by which Si influences water use of plants? The water transport from root to shoot is mainly through the xylem vessels. In general, radical transport of silicon in roots is forbidden so that almost all of the silicon deposits into the cell walls. Yeo et al.[10] indicated that salt-resistance is attributed to silica nanoparticles deposited in apoplast spaces that contributed to the block of Na^+ into cells and inhibitions of sodium transport in apoplast. Silicon deposited in cell walls interlaces with organic macromolecules (including cellulose, pectin, glycoprotein, and lignin) to form amorphous colloidal complexes with great absorption surfaces. Recent results indicated that 7 nm silica nanoparticles of 1 g possess absorption surfaces with 400 m^2,[11] showing that silica nanoparticles would affect wetting properties of xylem vessels, then affecting transport rate of water or solutes in vessels and changing water use efficiency. Zwieniecki et al.[12] demonstrated that xylem hydraulic resistance can be significantly decreased by increasing the ion concentration in vessels, which is caused by the shrinkage of the pectin matrix in response to the change of ions concentration. The results showed that the xylem was not only a column of dead tissue set inside plant stems passively supplying water to thirsty leaves, but dynamic and live. The objectives of this study were to find the effect of silicon on water use of plants under water stress, which is mainly through water loss from leaves and water transport in xylem.

MATERIALS AND METHODS

Experiment I

Seeds of maize were surface sterilized with H_2O_2 (10%) for 15 min, rinsed thoroughly with distilled water and germinated on moist filter paper for 2 days in an incubator at 25°C. After germination, the seeds were sown in quartz sand in the greenhouse at room temperature. When the second leaf emerged, uniform seedlings were transplanted into 2 L plastic pots containing continuously aerated nutrient solution at the following rate (mmol L^{-1}): K_2SO_4, 0.75; $MgSO_4$, 0.65; KH_2PO_4, 0.25; $Ca(NO_3)_2$; 2.0; Fe-EDTA, 0.1; (μmol L^{-1}) H_3BO_3, 1.0; $MnSO_4$, 1.0; $ZnSO_4$, 1.0; $CuSO_4$, 0.1; $(NH_4)_6Mo_7O_{24}$, 0.005 (modified as Zou et al.[13]). The nutrient solution was prepared using deionized water and renewed every other day. The pH of the nutrient solution was adjusted to 6.0 using 0.01 mol L^{-1} NaOH and/or HCl.

The treatment consisted of 2 levels of Si (0 and 2 mmol L^{-1} silicic acid) and 3 levels of water stress (0, 20, 30% PEG in solution), giving 6 different treatments and each treatment was replicated 3 times. The pots were subjected to a completely randomized design. Two mmol L^{-1} Si concentration used here was based on the experiments carried out by our research group and the fact that the solubility of silicic acid in nutrient solution is close to 2 mmol L^{-1}.[14] Silicon was applied as silicic acid (H_4SiO_4) after the plants being transplanted to the pots. Silicic acid was prepared according to the Okuda and Takahashi.[15] The water stress treatments were applied to plants 30 days after transplanting. The water

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

stress treatments were imposed with polyethylene glycol (PEG6000: final concentration in nutrient solution, 0, 20, 30%) and the plants were further cultured for 3 days. During this period, the transpiration rate and leaf resistance of the middle portions of leaves were measured using *CI—301PS* at 9:00 am of the first and second day after water treatment. *CI—301PS* is a closed-system, portable infrared gas analyzer and a 0.25-L acrylic assimilation chamber configured with a photosynthetically active radiation sensor.[16] For every pot, 2 plants were measured. The water loss was calculated by measuring the water level when the nutrient solution was renewed. The volumes were added to evaluate the total water loss throughout the experiment, which would be necessary when the WUE of plants were calculated. The plants were harvested, and then dry matter was determined. Water use efficiency was expressed in terms of dry matter produced per unit of water consumption.

Experiment II

The germination and growing of plants are the same as described in Experiment I. The treatments consisted of 2 levels of Si (0 and 2 mmol L^{-1} silcic acid) and the pots were arranged in greenhouse as completely randomized design in 4 replicates. After growing for 30 days, they were cut at the base of the shoot. The base was then covered by rubber tube to collect the xylem sap. At 10-min intervals, sap was transferred to a plastic centrifugal tube. The starting and ending time were recorded to evaluate the flow rate. The nutrient concentration in xylem sap was examined using an ICP spectrometer.

All data were analyzed using the statistical software system SAS and significance were assessed with a LSD test at 0.05 probability level.

RESULTS

Effect of Silicon on Growth of Maize Plants and WUE With or Without Water Stress

Effect of added silicon on growth was investigated in maize with or without PEG treatment (Table 1). It can be concluded from data that there was no significant effect of added silicon on fresh or dry weight of maize plants under the condition of this experiment.

Shoot and root dry matter productions were significantly declined with duration of treatment at 0, 20, and 30% PEG addition (Table 1).

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

Table 1. Effect of silicon on the growth of maize. Plants were grown in nutrient solution with or without silicic acid for 30 days and then water treatments as 0, 20, 30% PEG in solution were applied for 3 days before harvest. Mean values of three replicates and analysis of significance are presented.

PEG concentration (%)	Si supply ($mmol\,L^{-1}$)	Fresh weight ($g\,plant^{-1}$)			Dry weight ($g\,plant^{-1}$)		
		Shoots	Roots	Total	Shoots	Roots	Total
0	0	30.4 a	8.0 a	38.4 a	2.68 a	0.55 a	3.23 a
	2	32.0 a	7.8 a	39.8 a	2.73 a	0.55 a	3.28 a
20	0	16.4 b	4.7 bc	21.1 b	1.82 b	0.44 ab	2.26 b
	2	16.7 b	5.0 b	21.6 b	1.84 b	0.49 ab	2.33 b
30	0	11.3 c	3.2 c	14.5 c	1.22 c	0.26 b	1.48 c
	2	11.6 c	3.5 bc	15.1 bc	1.40 bc	0.32 ab	1.72 bc

Table 2. Effect of silicon on water consumption of maize. Plants were grown in nutrient solution with or without silicic acid for 30 days and then water treatments as 0, 20, 30% PEG in solution were applied for 3 days before harvest. Mean values of three replicates and analysis of significance are presented.

PEG concentration (%)	Si supply ($mmol\,L^{-1}$)	Water consumption ($ml\,plant^{-1}$)
0	0	10.1 a
	2	8.5 a
20	0	8.2 a
	2	6.1 b
30	0	6.4 b
	2	5.5 b

This decline was more serious for 30% PEG treatment. Exposed to 30% PEG for 3 days, dry matter weight of plants without Si decreased about 54% and it was about 48% for plants with 2 $mmol\,L^{-1}$ Si application, which indicated Si supply could improve the tolerance of maize to water stress. Results of the present study revealed that water stress had more detrimental effects on shoot and root growth of Si deficient plants than on Si sufficient plants.

The results in Table 2 and Fig. 1 showed that addition of Si could significantly decrease water loss and increase WUE of plants with or without water stress, and this amelioration was more obvious when the plants suffered from water stress.

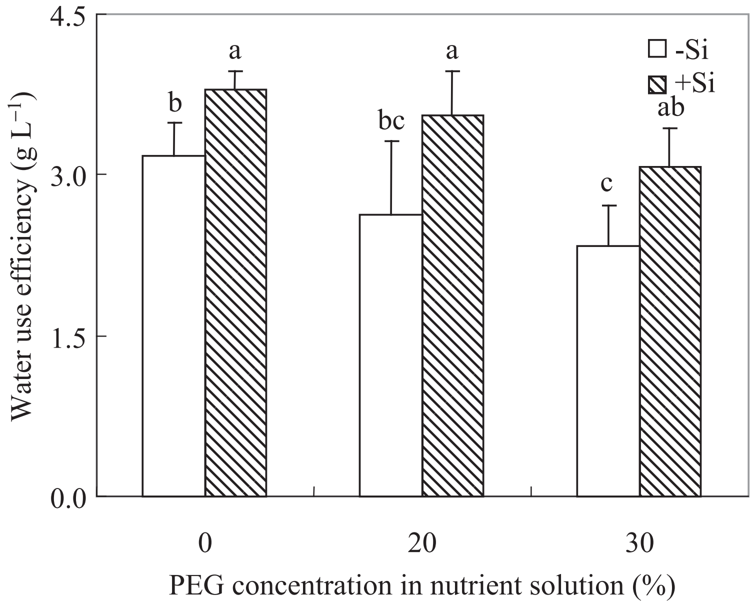

Figure 1. Effect of silicon on water use efficiency of maize plants grown in nutrient solution for 30 d before harvest. Each bar represents a mean of three replicates ± SD.

When the plants suffered from water stress (20 and 30% PEG) for 3 days, the WUE of plants without Si supply was decreased by 17 and 27% respectively. For plants with 2 mmol L^{-1} Si, WUE was only reduced by 5.8 and 19% (Fig. 1). These results showed that plants applied with 2 mmol L^{-1} Si had 20% WUE higher than plants without Si application, and this magnitude was up to 35 and 32% when the plants suffered from 20% PEG and 30% PEG water stress.

Effect of Silicon on Leaf Transpiration Rate and Leaf Resistance With or Without Water Stress

The results presented in Figs. 2 and 3 were based on the fact that the plants suffered from water stress for 24 and 48 h. The leaf transpiration of plants without Si was always higher than plants with Si (Fig. 2), and the leaf resistance was just opposite (Fig. 3). Though water stress decreased transpiration for all plants, the degree of decrease was higher in −Si

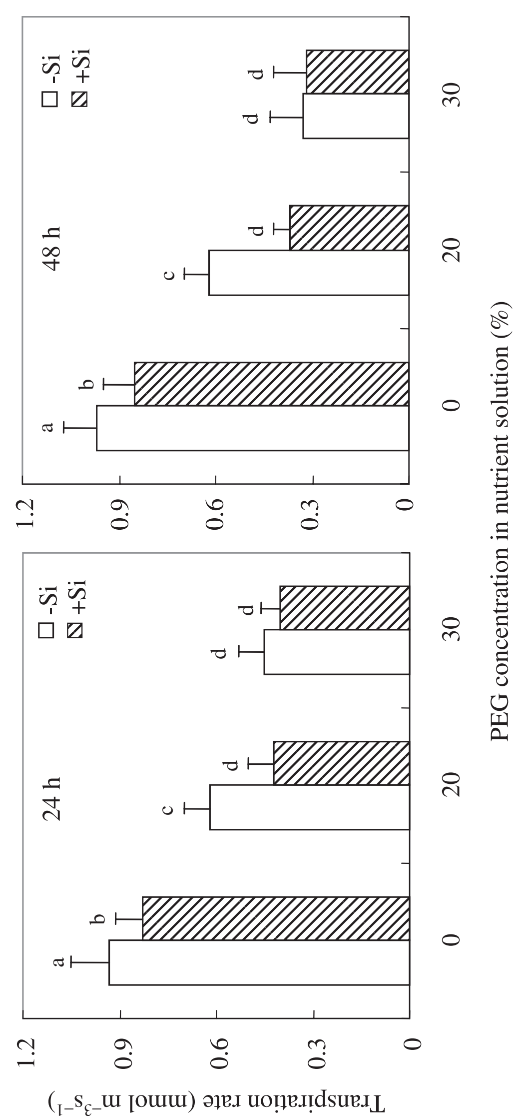

Figure 2. Effect of silicon on leaf transpiration rate of maize plants grown in nutrient solution for 30 d before harvest. Each bar represents a mean of three replicates ± SD. Left: 24 h after water treatment; Right: 48 h after water treatment.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

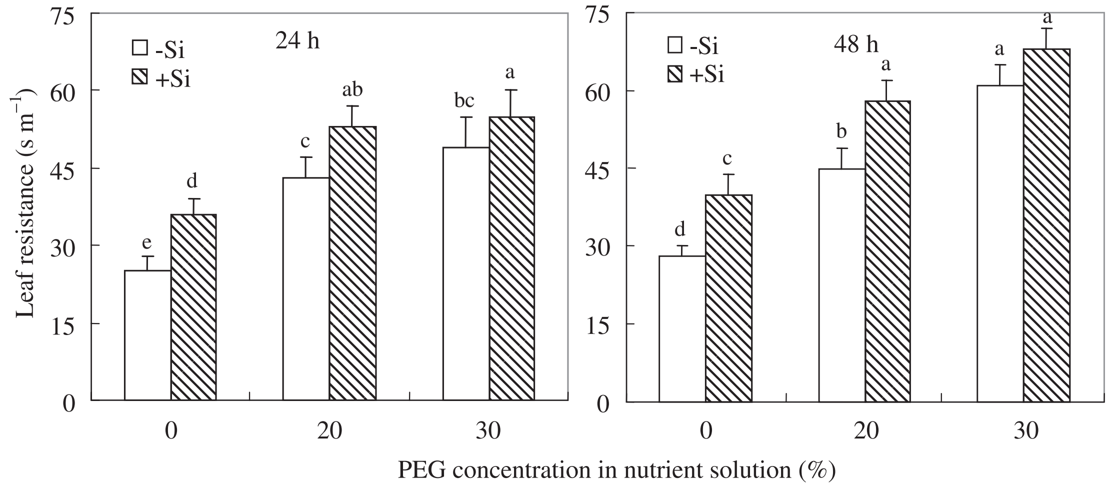

Figure 3. Effect of silicon on leaf resistance of maize plants grown in nutrient solution for 30 d before harvest. Each bar represents a mean of three replicates ± SD. Left: 24 h after water treatment; Right: 48 h after water treatment.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016

treatment than in +Si treatment. For the same water treatment, the transpiration was always higher in −Si-plants than in +Si-plants.

Effect of Silicon on Transport of Xylem Sap and Xylem Sap Nutrient Concentration

The flow velocities of solutes in the plants between different treatments were evaluated by calculating the weight of xylem sap collected per min (Fig. 4). The silicon addition (2 mmol L^{-1} Si) reduced the flow rate about 20%, compared with the treatment without Si application.

Meanwhile, the nutrient concentration in xylem sap of plants with or without Si treatment was investigated (Table 3). The Si concentration in xylem sap of plants with Si treatment was 200-fold higher than in plants without Si treatment. Si concentration in the xylem sap of plants grown in solution without Si was very low, indicating that very low amounts of Si were presented by the contamination from water and the chemicals used to prepare the nutrient solution. Calcium concentration in xylem sap of plants applied with 2 mmol L^{-1} Si was 2.5-fold lower than that in

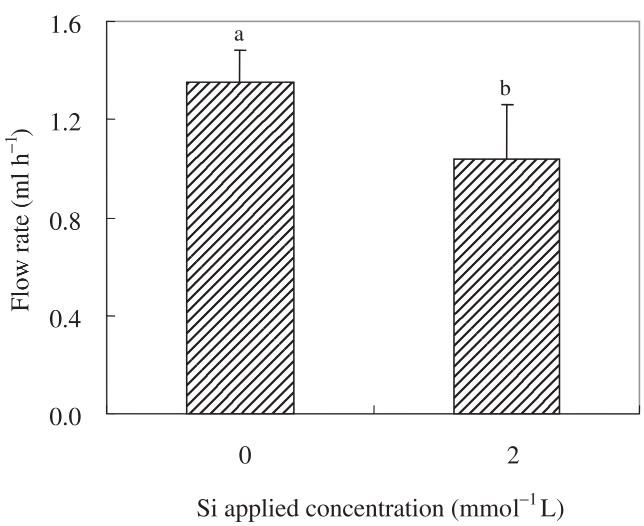

Figure 4. Effect of silicon on flow rate of xylem sap in maize plants grown in nutrient solution for 30 d before harvest. Each bar represents a mean of three replicates ± SD.

Table 3. Effect of silicon on the element concentration of xylem sap. Plants were grown in nutrient solution with or without silicic acid for 30 d before harvest and normal water supply. Mean values of three replicates and analysis of significance are presented.

Si supply ($mmol\,L^{-1}$)	Element concentration ($mg\,L^{-1}$)					
	Si	Ca	Mg	K	Na	P
0	1.6 b	209.8 a	58.4 a	873.9 a	3.1 a	122.5 a
2	191.2 a	83.3 b	34.1 a	912.3 a	4.3 a	85.7 b

xylem sap of plants grown without Si. In this experiment, there were no differences in Mg, K, and Na concentration in xylem sap of maize plants between −Si and +Si treatment. The P concentration in xylem sap of plants fed with Si ($2\,mmol\,L^{-1}$) was significantly lower than that of plants without Si.

DISCUSSION

There was no significant effect of added silicon on plant fresh or dry weight of maize plant under each water treatment in our experiment (Table 1). Match et al.[17] also found that silicon did not significantly improve growth of plant without environment stress, even though the silicon concentration of the shoots was increased 50-fold. If precautions are taken to reduce the silicon contamination in the water and the chemicals used to prepare the culture solution, a positive response of growth to silicon fertilization can be demonstrated.[18] Plant yields significantly declined with the increase of osmotic concentration (Table 1). At a higher osmotic concentration, a positive response of growth to silicon was found. Although the significant effect of Si addition on plant growth was not found under normal water condition (Table 1), it was proved that the WUE of plants with Si treatment was significantly higher than that of plants without Si addition and the magnitude of increase was larger when the plants suffered from water stress (Fig. 1).

It was more important that the water use efficiency (WUE) of +Si-plants was always significantly higher than that of −Si-plants. Compared with treatment without Si, Si addition significantly increased WUE of plants (Fig. 1), and the degree of increase was more significant when the plants suffered from water stress. It could be explained by (1) silicon nutrition of plants may reduce excessive leaf transpiration (Fig. 2). The result was consistent with those reported by other researchers.[1,6,19,20] This observation suggests that Si has a role in improving the water economy of the plants. (2) Silicon can reduce the water loss by decreasing the water flow rate in xylem (Fig. 4). This maybe caused by the increase of appetency to water in xylem vessels because of the deposition of Si on the cell wall.

Silicon always reduced the transpiration of maize plants compared with no Si application (Fig. 2). The leaf resistance showed a highly negative correlation with the transpiration rate (Fig. 3). Many researchers postulated that reduction in transpiration of Si-treated plants might be due to a reduction in transpiration through cuticle thickened by silica deposits.[1,8,20] However, Agarie et al.[6] investigated the effect of silicon on stomata blue-light response and found that Si could influence the stomata opening. So it is hypothesized that the reduction of transpiration is resulted from increased stomata sensitivity and cuticular resistance. Although the difference in transpiration between cuticle and stomata was not distinguished in this experiment, the difference in transpiration between −Si leaves and +Si leaves was always changed with the change of water stress, indicating that the application of silicon may influence the stomata response to water stress. The mechanism on how Si regulates stomata response remains unclear and needs more investigation.

Silica deposits were reported to occur as intracellular inclusions in the secondary wood tissues in the stems of plants.[21] Deposition of silicon in the cell walls had been thought as common phenomena in many plants.[22,23] The xylem vessels under different Si-treatment, composed of dead cells, must have different silica deposits on the walls of vessels. Silicon deposited in cell walls interlaced with organic macromolecules (including cellulose, pectin, glycoprotein, and lignin) to form amorphous colloidal complexes with great absorption surfaces. These nanoparticles would affect wetting properties of xylem vessels, and then affects water or solutes transport rate in vessels and consequently water use efficiency.

In these studies, water flow rate in xylem decreased about 25% as the Si concentration was increased from 0 to 2 $mmol\,L^{-1}$ (Fig. 4). We conformed that this process was induced by the change of hydraulic resistance, which maybe caused by the change of appetency to the water in xylem vessels. This could be confirmed by another fact that +Si-plants had higher WUE.

An increasing rate of transpiration in Si-deficient plants could explain why wilting is easy to occur under water deficiency. In these studies, Ca concentration in the xylem sap of Si-fed maize was decreased (Table 3), but no significant effect of Si on plant growth was found. This fact suggested that Ca concentration decrease was not caused by biomass dilution. Although it is still a controversial question whether Ca uptake by plants is active or passive, most investigators assume Ca uptake to be a passive mass flow-regulated process.[18,24] In this study, Si application significantly decrease the transpiration rate (Fig. 2), which might be a major reason causing Ca uptake decrease. In addition, Si also deposits in the free space of the root,[25] which may also affect Ca uptake through decreasing apoplastic flow by precipitation with Ca. However, the mechanism is not yet clear.

Phosphorus concentration in xylem sap of plants fed with Si was significantly lower than that of plants without Si in our experiment (Table 3). Although Si application can increase the water-soluble phosphorus in soil,[26] Miyake[27] found that application of Si on rice, tomato, cucumber, and bean decreased their capacity for phosphorus uptake under solution-cultured condition. The results of these studies were consistent with theirs, but the mechanism remains unclear.

ACKNOWLEDGMENTS

This study was supported by the National Natural Science Foundation of China (No. 30270788). We gratefully thank Dr. Yuqin at The University of Western Australia for her scientific suggestions and good English correction.

REFERENCES

1. Lewin, J.; Reimann, B.E.F. Silicon and plant growth. Annu. Rev. Plant Physiol. **1969**, *20*, 289–304.
2. Walker, C.D.; Lance, R.C.M. Silicon accumulation and ^{13}C composition as indices of water-use efficiency in barley cultivars. Aust. J. Plant Physiol. **1991**, *18*, 427–434.
3. Epstein, E. The anomaly of silicon in plant biology. Proc. Natl. Acad. Sci. USA **1994**, *91*, 11–17.
4. Blanger, R. Soluble silicon: its role in crop and disease management of greenhouse crops. Plant Dis. **1995**, *79*, 329–336.
5. Zhang, X.; Schmidt, R.E. Antioxidant response to hormone-containing product in Kentucky bluegrass subjected to drought. Crop Sci. **1999**, *39*, 545–551.

6. Agarie, S.; Uchida, H.; Qgata, W.; Kubota, F.; Kaufman, P.B. Effects of silicon on transpiration and leaf conductance in rice plants (*Oryza Sativa* L). Jpn. J. Crop Sci. **1998**, *1* (2), 89–95.
7. Elaward, S.H.; Green, V.E. Silicon on the rice environment: a review of recent research. II Riso. **1979**, *28*, 235–253.
8. Wong, Y.C.; Heits, A.; Ville, J.D. Foliar symptoms of silicon deficiency in the sugarcane plant. 1971 Proc. Cong. Int. Soc. Sugarcane Technol. **1972**, *14*, 766–776.
9. Savant, N.K.; Korndörfer, G.H.; Datnoff, L.E.; Snyder, G.H. Silicon nutrition and sugarcane production: a review. J. of Plant Nutr. **1999**, *22* (12), 1853–1903.
10. Yeo, A.R.; Flowers, S.A.; Rao, G.; Welfare, K. Silicon reduces sodium uptake in rice (*Oryza Sativa* L.) in saline condition and this is accounted for by a reduction in the transpirational bypass flow. Plant Cell Environ. **1999**, *22*, 559–565.
11. Wang, J.; Naser, N. Improved performance of carbon paste ampermeric biosensors through the incorporation of fumed silica. Electroanalysis **1994**, *6*, 571–575.
12. Zwieniecki, M.A.; Melcher, P.J.; Holbrook, N.M. Hydrogel control of xylem hydraulic resistance in plants. Science **2001**, *148*, 107–113.
13. Zou, C.; Shen, J.; Zhang, F.; Guo, S.; Rengel, Z.; Tang, C. Impact of nitrogen form on iron uptake and distribution in maize seedlings in solution culture. Plant Soil **2001**, *235*, 143–149.
14. Raven, J.A. The transport and function of silicon in plants. Biol. Rev. **1983**, *58*, 179–207.
15. Okuda, A.; Takahashi, E. Studies on the physiological role of silicon in crop plants (part 1): discussion on the silicon deficient culture method. J. Sci. Soil. Manure. Jpn. **1961**, *32*, 475–480. In Japanese.
16. Gealy, D.R. Differential response of palmleaf morningglory and pitted morningglory to flooding. Weed Sci. **1998**, *46*, 217–224.
17. Match, T.; Kairusmee, P.; Takahashi, E. Salt-induced damage to rice plants and alleviation effect of silicate. Soil Sci. and Plant Nutr. **1986**, *32*, 295–230.
18. Ma, J.F.; Takahashi, E. Interaction between calcium and silicon in water-cultured rice plants. Plant and Soil **1993**, *148*, 107–113.
19. Yoshida, S.; Ohnishi, Y.; Kitagishi, K. Role of silicon in rice nutrition. Plant Soil **1959**, *5*, 127–133.
20. Yoshida, S.; Kitagishi, K. Histochemistry of silicon in the rice plant. III. The presence of a cuticular-silica double layer in the epidermal tissue. Soil Sci. Plant Nutr. **1962**, *8*, 1–5.
21. Scurfield, G.; Anderson, C.A.; Sefnit, E.R. Silica in woody stems. Aust. J. Bot. **1974**, *22*, 211–229.

22. Jone, L.H.P.; Handreck, K.A. Studies of silica in the oat plant. III. Uptake of silica from soil by plant. Plant and Soil **1965**, *23*, 79–95.
23. Parry, D.W.; Winslow, A. Electron-probe microanalysis of silicon accumulation in the leaves and tendrils of *Pisum sativum* (L.). Ann. Bot. (London) **1977**, *41*, 275–278.
24. Michael, G.; Marschner, H. Influence of varied air humidity and transpiration on mineral uptake and distribution. Z. Pflanzenernaehr Bodenk **1962**, *96*, 200–212.
25. Sangster, A.G. Silicon in the roots of higher plants. Am. J. Bot. **1978**, *65*, 929–935.
26. Mckeague, J.A.; Cline, M.G. Silica in the soil. Adv. Agron. **1963**, *15*, 339–396.
27. Miyake, Y. Silica in soils and plants. Sci. Rep. Fac. Agric. Okayama Univ. Japan **1993**, *81*, 61–79.

Marcel Dekker, Inc.
270 Madison Avenue, New York, New York 10016