Journal of Plant Nutrition

Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713597277

EFFECT OF SILICON APPLICATION ON SORGHUM ROOT RESPONSES TO WATER STRESS

Kaori Sonobe[a]; Taiichiro Hattori[b]; Ping An[a]; Wataru Tsuji[a]; Anthony Egrinya Eneji[c]; Sohei Kobayashi[d]; Yukio Kawamura[e]; Kiyoshi Tanaka[f]; Shinobu Inanaga[g]

[a] Arid Land Research Center, Tottori University, Tottori, Japan [b] Field Production Science Center, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan [c] College of Agronomy and Biotechnology, China Agricultural University, Beijing, China [d] Rhizosphere Environment Research Team, National Agriculture Research Center for Hokkaido Region, Hokkaido, Japan [e] Department of Applied Biological Chemistry, Kinki University, Oosaka, Japan [f] Faculty of Agriculture, Tottori University, Tottori, Japan [g] Tottori Institute of Industrial Technology, Tottori, Japan

Online publication date: 01 December 2010

To cite this Article Sonobe, Kaori , Hattori, Taiichiro , An, Ping , Tsuji, Wataru , Eneji, Anthony Egrinya , Kobayashi, Sohei , Kawamura, Yukio , Tanaka, Kiyoshi and Inanaga, Shinobu(2011) 'EFFECT OF SILICON APPLICATION ON SORGHUM ROOT RESPONSES TO WATER STRESS', Journal of Plant Nutrition, 34: 1, 71 — 82

To link to this Article: DOI: 10.1080/01904167.2011.531360

URL: http://dx.doi.org/10.1080/01904167.2011.531360

Journal of Plant Nutrition, 34:71–82, 2011

ISSN: 0190-4167 print / 1532-4087 online
DOI: 10.1080/01904167.2011.531360

EFFECT OF SILICON APPLICATION ON SORGHUM ROOT RESPONSES TO WATER STRESS

Kaori Sonobe,[1] Taiichiro Hattori,[2] Ping An,[1] Wataru Tsuji,[1] Anthony Egrinya Eneji,[3] Sohei Kobayashi,[4] Yukio Kawamura,[5] Kiyoshi Tanaka,[6] and Shinobu Inanaga[7]
[1]*Arid Land Research Center, Tottori University, Tottori, Japan*
[2]*Field Production Science Center, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan*
[3]*College of Agronomy and Biotechnology, China Agricultural University, Beijing, China*
[4]*Rhizosphere Environment Research Team, National Agriculture Research Center for Hokkaido Region, Hokkaido, Japan*
[5]*Department of Applied Biological Chemistry, Kinki University, Oosaka, Japan*
[6]*Faculty of Agriculture, Tottori University, Tottori, Japan*
[7]*Tottori Institute of Industrial Technology, Tottori, Japan*

□ *To analyze how silicon (Si) fertilizer improves plant growth under water stress, we investigated the growth and root responses of sorghum seedlings to Si application. Seedlings were grown hydroponically at two Si levels (0 and 1.78 mM) and under two water stress conditions simulated with polyethylene glycol. The reduction in dry weight due to stress was alleviated by Si application, accompanied by an increase in root water uptake. Silicon application decreased the osmotic potential of the roots without affecting their water content, showing that osmotic adjustment occurred to increase water uptake. An assessment of root solutes suggested that soluble sugar and amino acids (alanine and glutamic acid) were osmolytes responsible for this adjustment. Root anatomical traits related to water transport were not affected by the Si application. These results improved our understanding of the physiological mechanisms that underlie the Si-induced increases in sorghum growth and water uptake under water stress.*

Keywords: root, silicon, sorghum, water uptake, water stress

INTRODUCTION

Soil water deficits sufficiently severe to reduce crop yield are a common problem in the world's arid and semi-arid regions. Grain sorghum

Received 23 January 2009; accepted 29 March 2009.
Address correspondence to Kaori Sonobe, Arid Land Research Center, Tottori University, 1390 Hamasaka, Tottori, Tottori 680-0001, Japan. E-mail: beno_alfa@hotmail.com

[*Sorghum bicolor* (L.) Moench] serves as a staple food in these regions, since this crop species is more tolerant to water deficit than other species, such as maize (Farré and Faci, 2006). The growth of sorghum plants, however, is suppressed greatly by a temporal, severe water deficit in the seedling stage (Mastrorilli et al., 1999). Alleviating this growth suppression requires a further improvement of the sorghum's water stress tolerance, especially during the initial growth stages.

Silicon (Si) is an agronomically important fertilizer element that enhances plant tolerance to abiotic stresses (Hodson and Evans, 1995; Epstein, 1999; Ma, 2004; Liang et al., 2003, 2005). Past studies of Si application to maize plants have revealed that the application decreased leaf transpiration rates under water stress and thereby improved the plant's water status (Gao et al., 2004, 2006). On the other hand, Si application to sorghum plants increased leaf transpiration rates (stomatal conductance) and consequently alleviated the reduction of photosynthetic rates by water stress (Hattori et al., 2005). In recent studies, antioxidant processes were activated by Si under water stress in maize (Kaya et al., 2006) and wheat (Gong et al., 2005, 2008). Thus, Si application affects some physiological traits to enhance plant tolerance to water stress, although the physiological mechanisms responsible for these effects are not fully understood in the context of using Si fertilizer in the arid and semi-arid cropping systems.

In our previous experiment, Si application to sorghum seedlings resulted in maintaining a high photosynthetic rate, high stomatal conductance, and high leaf transpiration rates under water stress (Hattori et al., 2005). Recently, we found that these effects were accompanied by increased plant water uptake (Hattori et al., 2008; Sonobe et al., 2009). In general, plant water uptake is mainly regulated by the root system, as reviewed by Kramer and Boyer (1995). Our previous results therefore indicate that Si application improved water uptake in sorghum roots and consequently enhanced the plant tolerance to water stress. Further analyses that focus on sorghum roots and water uptake are required to better understand physiological mechanisms responsible for the Si-enhanced plant tolerance to water stress.

Root water uptake is regulated by several anatomical and physiological traits, such as the diameter and number of the xylem vessels, and by the solute content associated with osmotic adjustment (Kramer and Boyer, 1995; Cruz et al., 1992). These traits play important roles in root water uptake under water stress (Salih et al., 1999; Cruz et al., 1992; Ogawa and Yamauchi, 2006; Sharp et al., 1990). However, few studies have investigated whether Si application affects root characteristics under water stress. This study therefore aimed to assess the effects of Si application on root anatomical and physiological traits in sorghum seedlings in water stress conditions.

MATERIALS AND METHODS

Plant Materials and Growth Conditions

Seeds of sorghum (cv. 'Gadambalia') were surface-sterilized with 5% (w/v) Benlate (Hokko Chemical Industry Co., Tokyo, Japan) solution for 10 min, and were held for 20 h at 28°C in the dark to promote germination. Germinated seeds were rolled in wetted filter paper and kept for two days at 28°C under the same conditions. Three days after sowing (DAS), the seedlings were transplanted into 20- or 8-L plastic hydroponic containers filled with the Hoagland and Arnon culture solution (Hoagland and Arnon, 1938). The transplanted seedlings were grown under a 16/8-h (day/night) cycle at 28/23°C, with 30%/40% relative humidity and 450 μmol m^{-2} s^{-1} photosynthetically active radiation, in a controlled-environment chamber (GC-A, Fuji Electric Co. Ltd., Tokyo, Japan). The concentration of the culture solution was increased from 1/4 strength to 1/2 and full strength at 3, 7, and 18 DAS, respectively, in response to changes in seedling size. The culture solution was continuously aerated and was renewed every three days. The solution pH was adjusted daily to 6.5 using 0.1 M hydrochloric acid (HCl) or 1 M potassium hydroxide (KOH). Deionized water was used to prevent contamination of the culture solution by Si. This experimental procedure had been used in our previous study (Sonobe et al., 2009).

Silicon and Water Stress Treatments

Sorghum seedlings were grown at two Si concentrations (0 and 1.78 mM; −Si and +Si) and two levels of water stress (with and without polyethylene glycol 6000; −PEG and +PEG). Thus, we used four growth treatments: −Si−PEG, +Si−PEG, −Si+PEG, and +Si+PEG.

Silicon application in the +Si−PEG and +Si+PEG treatments started at three DAS by following the procedure in Okuda and Takahashi (1961). At 10 DAS, PEG was added to the culture solution of the +PEG treatments to produce an osmotic potential of −0.2 MPa (10% PEG in the solution), leading to the development of mild water stress. The osmotic potential was decreased to −0.4 MPa at 13 DAS and to −0.6 MPa at 16 DAS (13 and 15% PEG in the solution). The treatment procedure was the same as the one used in our previous study (Sonobe et al., 2009).

Plant Sampling and Dry Weight Determination

For each treatment, five seedlings were sampled at 12, 15, and 23 DAS for the determination of plant dry weight and mineral content. The seedlings were separated into shoots and roots, dried at 80°C for 72 h, and weighed. On the same sampling dates, the segments of roots from 0 to 10 cm from the root tip were excised for measurement of their water content, osmotic potential, amino acids content, and sugar content. The excised root segments were sealed in plastic tubes and frozen in liquid N_2 for storage at −80°C until the analyses. Furthermore, roots were harvested at 23 DAS and fixed in methanol for anatomical assessment.

Measurement of Plant Water Relations

Plant water uptake was measured at 12, 15, and 23 DAS by the gravimetric method. In each treatment, five seedlings were transferred into 500-mL polyethylene bottles (one seedling per bottle) two days before the measurement and were grown under the same treatment conditions. Each seedling was weighed every two hours during the light period (16 h). The seedlings were harvested to determine root dry weight and to calculate water uptake rate per unit root dry weight. The water uptake rates between 6 and 10 h after the beginning of the light period were used, since the rates were stable during this period.

For the measurement of root osmotic potential, the frozen root segments were thawed for 30 min at room temperature, and were then homogenized with a glass rod. The cell sap was extracted by centrifugation for 20 min at 11 000*g*. The osmotic potential of the cell sap was measured with a freezing-point-depression osmometer (OM801, Vogel, Giessen, Germany). The root segments were also dried at 80°C for 72 h to calculate their water content.

Measurement of Root Solute Contents

The frozen root segments were homogenized in liquid N_2 before extraction of the solutes in 85% ethanol. The total sugar and total amino acid contents in the ethanol extracts were determined by the anthrone and ninhydrin method, respectively (Yemm and Willis, 1954; Moore and Stein, 1954). The total amino acid content was expressed as mg asparagine equivalent per gram fresh weight. Furthermore, the content of each amino acid was analyzed for the root samples at 23 DAS by using an automatic amino acid analyzer (Hitachi L 8500, Hitachi, Tokyo, Japan). Only major amino acids ($>10^{-1}$ μmol g^{-1} root fresh weight) are presented in Table 1. Contents of potassium (K), calcium (Ca), and magnesium (Mg) in the roots were measured with an atomic absorption spectrophotometer (AA-6700, Shimadzu, Kyoto, Japan).

Root Anatomical Characteristics

Manual sections of the basal part of nodal roots were prepared and were stained with 2% fluoroglucinol dissolved in 80% ethanol (w/v). A light microscope with a digital camera was used to capture images of each section. The digital images were used to measure the diameter of the roots and their

TABLE 1 Content of each amino acid in sorghum plants grown at two silicon concentrations (0 and 1.78 mM, −Si and +Si) and under two levels of water stress (−PEG and +PEG) for 23 DAS

		Contents of each amino acid (μmol gFW^{-1})											
PEG treatment	Si treatment	Asp	Glu	Thr	Asn	Gln	Ala	Ser	P-Ser	Pro	Gly	Val	Total
−PEG	−Si	0.47^{a}	0.89^{b}	0.14^{a}	1.15^{a}	0.96^{a}	0.35^{bc}	0.39^{a}	0.22^{a}	0.00^{c}	0.09^{b}	0.23^{a}	6.14^{b}
	+Si	0.37^{a}	0.74^{b}	0.11^{a}	0.77^{a}	0.61^{ab}	0.30^{c}	0.30^{a}	0.17^{a}	0.07^{bc}	0.06^{b}	0.18^{a}	4.99^{b}
+PEG	−Si	0.16^{b}	0.50^{b}	0.08^{a}	0.46^{a}	0.42^{ab}	0.66^{b}	0.25^{a}	0.14^{b}	0.29^{ab}	0.22^{ab}	0.12^{a}	5.10^{b}
	+Si	0.12^{b}	1.44^{a}	0.11^{a}	0.45^{a}	0.31^{b}	3.15^{a}	0.46^{a}	0.18^{a}	0.35^{a}	0.34^{a}	0.21^{a}	10.54^{a}
Source of variation													
	PEG	**	NS	NS	*	**	**	NS	*	**	**	NS	*
	Si	NS	**	NS	NS	NS	**	NS	NS	NS	NS	NS	*
	PEG × Si	NS	**	NS	NS	NS	**	*	*	NS	NS	NS	*

Parameter values within a column followed by different letters differ significantly ($P < 0.05$, Scheffé's test). NS, *, and ** represent non-significance and significance at $P < 0.05$ and <0.01, respectively (two-way ANOVA). Only the contents of major amino acids ($>10^{-1}$ μmol g^{-1} root fresh weight) were showed. The amino acids are: Asp-Aspartic acid, Glu-Glutamic acid, Thr-Threonine, Asn-Asparagine, Gln-Glutamine, Ala-Alanine, Ser-Serine, P-Ser-phospho Serine, Pro-Proline, Gly-Glycine, Val-Valine.

xylem vessels, and the number of xylem vessels in the Adobe Photoshop software (version 7.0, Adobe Systems Inc., San Jose, CA, USA).

Statistical Analysis

Our previous studies showed that the effect of Si on sorghum growth was expressed only under water stress (Hattori et al., 2005, 2008; Sonobe et al., 2009) We therefore analyzed the data separately for unstressed and stressed treatments to focus on the effect of Si application under water stress. Two-way analysis of variance was performed on the data of both shoot and root dry weights, and shoot to root ratio. Means were compared by the Scheffe's test at the 5% level of probability. On the data of root anatomical traits, *t*-test was performed for the comparison with significance at $P < 0.05$.

RESULTS

Shoot and Root Dry Weights

Addition of PEG to the culture solution (i.e., exposure to water stress) decreased sorghum shoot dry weights at 15 and 23 DAS (Table 2). The extent of the decrease was greater at 23 DAS than at 15 DAS. Elevating the Si concentration by 1.78 mM significantly increased shoot dry weight only at 23 DAS in the +PEG condition, (Table 2): thus, the Si-induced increase in shoot dry weight depended on both the water stress and the duration of the stress. ANOVA showed that the effects of Si and the Si × DAS interaction were statistically significant only for the +PEG treatment. Similar results were

TABLE 2 Shoot and root dry weights and the shoot-to-root ratios of sorghum plants grown at two silicon concentrations (0 and 1.78 mM, −Si and +Si) and under two levels of water stress (−PEG and +PEG) at 12, 15, and 23 days after sowing (DAS). Data are the means of five plants

DAS	Si treatment	Shoot dry weight (g)		Root dry weight (g)		Shoot/Root ratio	
		−PEG	+PEG	−PEG	+PEG	−PEG	+PEG
12	−Si	0.09[b]	0.09[c]	0.05[b]	0.04[c]	1.94[a]	1.99[a]
	+Si	0.09[b]	0.09[c]	0.04[b]	0.04[c]	2.03[a]	2.30[a]
15	−Si	0.15[b]	0.13[c]	0.08[b]	0.07[bc]	1.86[a]	1.92[a]
	+Si	0.15[b]	0.13[c]	0.08[b]	0.06[bc]	1.73[a]	2.09[a]
23	−Si	0.80[a]	0.23[b]	0.49[a]	0.10[b]	1.77[a]	2.54[a]
	+Si	0.83[a]	0.41[a]	0.53[a]	0.21[a]	1.52[a]	2.01[a]
Source of variation							
	DAS	**	**	**	**	NS	NS
	Si	NS	**	NS	**	NS	NS
	DAS × Si	NS	**	NS	**	NS	NS

Parameter values within a column followed by different letters differ significantly ($P < 0.05$, Scheffé's test). NS, *, and ** represent non-significance and significance at $P < 0.05$ and <0.01, respectively (two-way ANOVA).

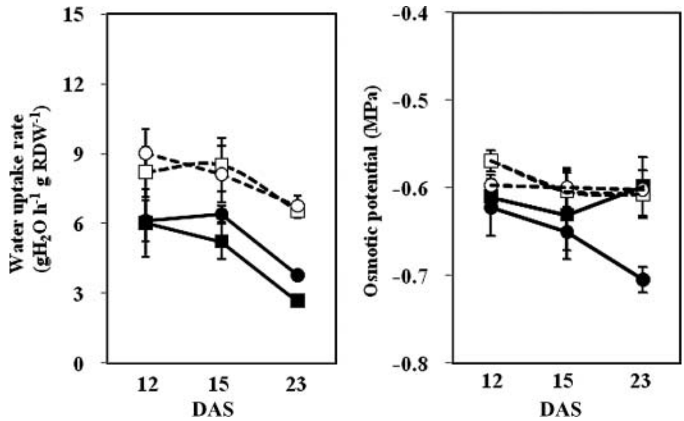

FIGURE 1 Water uptake rate (left) and root osmotic potential (right) of sorghum plants grown at following conditions for 12, 15, and 23 days after sowing (DAS): −Si−PEG (open square), −Si+PEG (closed square), +Si−PEG (open circle), and +Si+PEG (closed circle). Data are the means of five replications; range bars are standard errors; RDW, root dry weight.

also observed for root dry weight. The shoot to root ratio was not affected significantly by Si, PEG, and their interaction (Table 2).

Root Water Relations

The rate of root water uptake decreased significantly with the +PEG treatment throughout the experimental period (Figure 1). Under the +PEG condition, +Si seedlings showed a higher rate of root water uptake, especially at 23 DAS, than the −Si seedlings (3.77 vs. 2.65 gH_2O $gRDW^{-1}$, $P = 0.023$). At 23 DAS, +Si seedlings in the +PEG treatment also showed a significantly negative root osmotic potential (i.e., a high potential to maintain water uptake), compared to the −Si seedlings (−0.71 vs. −0.62 MPa, $P = 0.024$, Figure 1). The water content of the roots was slightly affected by the Si and PEG treatments (data not shown).

Root Solute Content

For the +Si+PEG condition, root amino acid content increased from 12 DAS to 23 DAS, whereas, for the other conditions, the content remained stable throughout the experimental period (Figure 2). Si application significantly increased the root amino acid content in the +PEG treatment at 23 DAS (0.61 vs. 0.41 g gFW^{-1}, $P = 0.015$). A Si-induced increase was likewise observed for root sugar content in the +PEG treatment at 23 DAS, although this increase was not statistically significant (Figure 2). Analyzing each amino acid furthermore showed that Si application increased alanine and glutamic acid under +PEG condition. Such an increase was not detected for root Ca, K, and Mg contents throughout the experiment period (Figure 3).

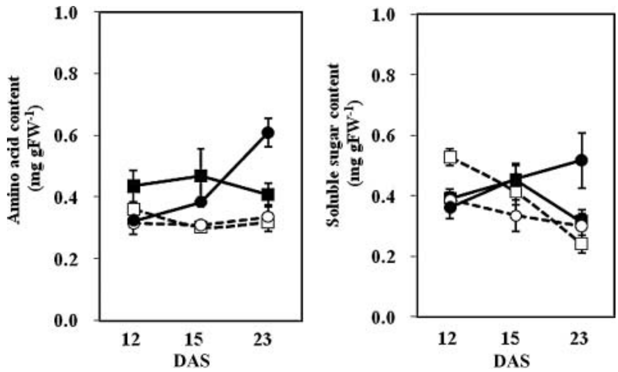

FIGURE 2 Root amino acid content (left, asparagine equivalent) and sugar content (right) of sorghum plants grown at following conditions for 12, 15, and 23 days after sowing (DAS); −Si−PEG (open square), −Si+PEG (closed square), +Si−PEG (open circle), and +Si+PEG (closed circle). Data are the means of five plants; range bars are standard errors.

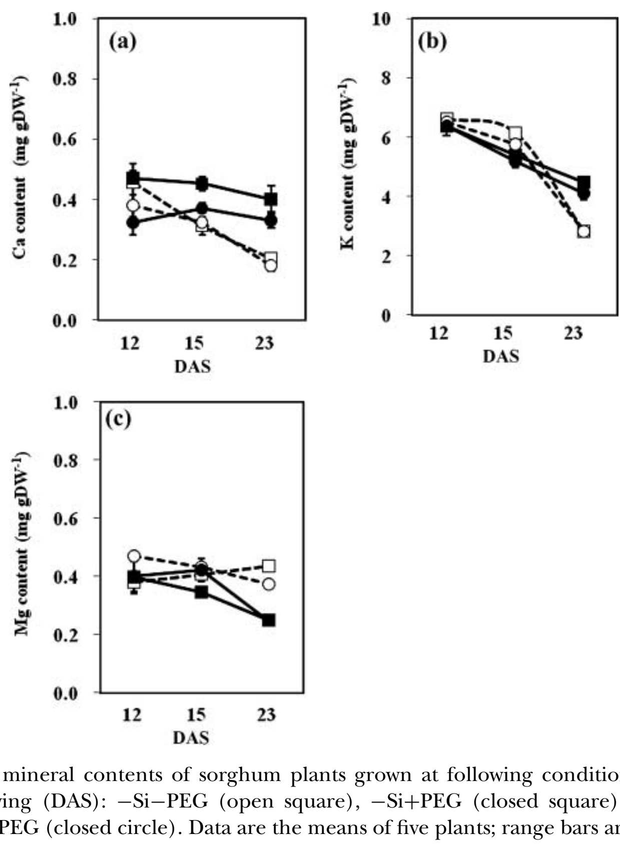

FIGURE 3 Root mineral contents of sorghum plants grown at following conditions for 12, 15, and 23 days after sowing (DAS): −Si−PEG (open square), −Si+PEG (closed square), +Si−PEG (open circle), and +Si+PEG (closed circle). Data are the means of five plants; range bars are standard errors.

TABLE 3 Diameters of roots and xylem vessels and number of xylem vessels in sorghum seedlings grown at two silicon concentrations (0 and 1.78 mM, −Si and +Si) and under two levels of water stress (−PEG and +PEG). Data are the means of three plants

		Root diameter (mm)			Vessel diameter (mm)			Number of vessels		
		Internode								
PEG treatment	Si treatment	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd
−PEG	−Si	0.71	1.11	1.48	0.11	0.15	0.19	6.80	9.40	11.90
	+Si	0.72	1.12	1.55	0.10	0.16	0.20	7.00	9.80	12.90
		NS	NS	NS	NS	NS	NS	NS	NS	NS
+ PEG	−Si	0.83	1.04		0.12	0.14		8.40	10.80	
	+Si	0.83	1.21		0.12	0.16		8.20	10.30	
		NS	*		NS	NS		NS	NS	

NS and * represent non-significance and significance at $P < 0.05$, respectively (*t*-test).

Root Anatomical Characteristics

The root anatomical traits that we evaluated did not change in response to Si addition in either PEG treatment, with the exception of the second-nodal-root diameter that increased significantly in the +Si+PEG treatment (Table 3). The emergence of the second nodal root coincided with the beginning of the +PEG treatment at 10 DAS.

DISCUSSION

In the past pot experiment, Si application to sorghum seedlings resulted in an increased plant water uptake with a decreased shoot to root (S/R) ratio (i.e., increased root surface area) (Hattori et al., 2005). However, the effect of Si on S/R ratio was not observed for sorghum seedlings grown in hydroponic conditions in the study of Hattori et al. (2008). Due to these contrasting results, the mechanisms of the Si-increased plant water uptake remain unclear. The current study showed a result similar to that of the latter study (Table 2), thus demonstrating that, under at least hydroponic conditions, Si application increases water uptake of sorghum plants without affecting the S/R ratio. The increase in water uptake might be achieved by affecting hydraulic conductance (Hattori et al., 2008). Therefore several anatomical and physiological traits involved with hydraulic resistance were investigated in current study.

In our previous study, sorghum shoot dry weight increased in response to Si application under water stress for only 23 DAS (Sonobe et al., 2009). However, statistical tests for the interaction effect between Si and sampling date had not been conducted. The current analyses showed that the effect of the Si × DAS interaction was statistically significant for both shoot and root dry weights under water stress. This result demonstrated that the effect of Si application depends on the duration of water stress. This effect may appear only between 15 and 23 DAS. Such an effect was also observed for the rate of root water uptake. These results indicate that the Si-induced increase in dry weights was attributable to the enhancement of water uptake by Si.

This enhancement, observed for 23 DAS, coincided with the development of a significantly more negative root osmotic potential. The water content of the roots at 23 DAS was only slightly affected by Si application. Thus, the more negative root osmotic potential showed that an active adjustment of root osmotic potential occurred in response to Si application. This active osmotic adjustment is one of the physiological mechanisms responsible for plant adaptation to water stress (Sharp et al., 1990). As a result, this adjustment might lead to the development of a large water potential gradient between the culture solution and the roots that would serve as a driving force for plant water uptake (Hsiao and Xu, 2000). The diameter and number of the xylem vessels, associated with hydraulic conductance in roots (Cruz et al., 1992), did not change as a result of Si application (Table 3). These results support our contention that the application triggered an active osmotic adjustment in sorghum roots to consequently enhance the plant's tolerance of water stress.

Osmotic adjustment often occurs as a result of the accumulation of osmolytes such as amino acids, soluble sugars, and minerals (Morgan, 1984; Premachandra et al., 1992; Hare and Cress, 1997). Kaya et al. (2006) reported that, in maize, the content of proline, a key osmolyte, decreased in response to Si treatment. So far, few data are available to conclude whether Si application affects root osmolyte content under water stress, and what osmolyte contributes to the osmotic adjustment by Si. Our results show that the amino acid contents were significantly increased by Si application for 23 DAS under water stress (Figure 2), and that this increase was accompanied by an increased root water uptake (Figure 3). Furthermore, the amino acids increased by Si application were identified as alanine and glutamic acid (Table 1). Thus, these amino acids were considered as the osmolytes responsible for active osmotic adjustment in sorghum roots in response to Si application.

Our results also showed that the active osmotic adjustment induced in sorghum roots by Si application led to the development of a great water potential gradient that promoted water uptake under water stress. This osmotic adjustment would be one of the physiological mechanisms capable of improving sorghum's tolerance of water stress. Other physiological mechanisms, such as expression of water-channel proteins, may be involved in root water uptake (Maurel et al., 1993; Steudle and Peterson, 1998; Katsuhara et al., 2003). In our preliminary analysis, the content of a class of water channel proteins (aquaporins) in sorghum roots was not affected by Si application. Further studies to analyze root water uptake and the associated physiological characteristics would be needed if we are to thoroughly understand the mechanisms underlying the Si-promoted plant growth and water uptake for improving sorghum water stress tolerance in the arid and semi-arid cropping systems.

ACKNOWLEDGMENT

This study was supported by a grant from the 21st Century Center of Excellence (COE) program of the Japan Society for the Promotion of Science.

REFERENCES

Cruz, R. T., W. R. Jordan, and M. C. Drew. 1992. Structural changes and associated reduction of hydraulic conductance in roots of *Sorghum bicolor* L. following exposure to water deficit. *Plant Physiology* 99: 203–212.

Epstein, E. 1999. Silicon. *Annual Review of Plant Physiology and Molecular Biology* 50: 641–664.

Farré, I., and J. M. Faci. 2006. Comparative response of maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* L. Moench) to deficit irrigation in a Mediterranean environment. *Agricultural Water Management* 83: 135–143.

Gao, X., C. Zou, L. Wang, and F. Zhang. 2004. Silicon improves water use efficiency in maize plants. *Journal of Plant Nutrition* 27: 1457–1470.

Gao, X., C. Zou, L. Wang, and F. Zhang. 2006. Silicon decreases transpiration rate and conductance from stomata of maize plants. *Journal of Plant Nutrition* 29: 1637–1647.

Gong, H. J., K. M. Chen, Z. G. Zhao, G. C. Chen, and W. J. Zhou. 2008. Effects of silicon on defense of wheat against oxidative stress under drought at different developmental stages. *Biologia Plantarum* 52: 592–596.

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

Hare, P. D., and W. A. Cress. 1997. Metabolic implications of stress induced proline accumulation in plants. *Plant Growth Regulation* 21: 79–102.

Hattori, T., S. Inanaga, H. Araki, S. Morita, M. Luxova, and A. Lux. 2005. Application of silicon enhanced drought tolerance in *Sorghum bicolor*. *Physiologia Plantarum* 123: 459–466.

Hattori, T., K. Sonobe, H. Araki, S. Inanaga, P. An, and S. Morita. 2008. Silicon application improves water uptake by sorghum through the alleviation of stress-induced increase in hydraulic resistance. *Journal of Plant Nutrition* 31: 1482–1495.

Hoagland, D. R., and D. I. Arnon. 1938. The water-culture method for growing plants without soil. In: *University of California College Agricultural Experiment Station Circular*. Berkeley, CA: University of California.

Hodson, M. J., and D. E. Evans. 1995. Aluminum-silicon interactions in higher plants. *Journal of Experimental Botany* 46: 161–171.

Hsiao, T. C., and L. K. Xu. 2000. Sensitivity of growth of roots versus leaves to water stress: Biophysical analysis and relation to water transport. *Journal of Experimental Botany* 51: 1595–1616.

Katsuhara, M., K. Koshio, M. Shibasaka, and K. Kasamo. 2003. Expression of an aquaporin at night in relation to the growth and root water permeability in barley seedlings. *Soil Science and Plant Nutrition* 49: 883–888.

Kaya, C., L. Tuna, and D. Higgs. 2006. Effects of silicon on plant growth and mineral nutrition of maize grown under water stress conditions. *Journal of Plant Nutrition* 29: 1469–1480.

Kramer, P. J. and J. S. Boyer. 1995. *Water Relations of Plants and Soils*. San Deigo, CA: Academic Press, Inc.

Liang, Y. C., Q. Chen, Q. Liu, W. H. Zhang, and R. X. Ding. 2003. Exogenous silicon (Si) increases antioxidant enzyme activity and reduces lipid peroxidation in roots of salt-stressed barley (*Hordeum vulgare* L.). *Journal of Plant Physiology* 160: 1157–1164.

Liang, Y., J. Si, and V. Römheld. 2005. Silicon uptake and transport is an active process in *Cucumis sativus*. *New Phytologist* 167: 797–804.

Ma, J. 2004. Role of silicon in enhancing the resistance of plants to biotic and biotic stresses. *Soil Science and Plant Nutrition* 50: 11–18.

Mastrorilli, M., N. Katerji, and G. Rana. 1999. Productivity and water use efficiency of sweet sorghum as affected by soil water deficit occurring at different vegetative growth stages. *European Journal of Agronomy* 11: 207–215.

Maurel, C., J. Reizer, J. I. Schroeder, and M. J. Chrispeels. 1993. The vacuolar membrane-protein gamma-TIP creates water specific channels in *Xenopus oocytes*. *EMBO Journal* 23: 2241–2247.

Moore, S., and W. H. Stein. 1954. A modified ninhydrin reagent for the photometric determination of amino acids and related compounds. *Journal of Biological Chemistry* 211:907–931.

Morgan, J. M. 1984. Osmoregulation and water stress in higher plants. *Annual Review of Plant Physiology* 35: 299–319.

Ogawa, A., and A. Yamauchi. 2006. Root osmotic adjustment under osmotic stress in maize seedlings 1. Transient change of growth and water relations in roots in response to osmotic stress. *Plant Production Science* 9: 27–38.

Okuda, A., and E. Takahashi. 1961. Studies on the physiological role of silicon in crop plants. (Part 1). On the methods of silicon-free culture. *Japanese Journal of the Science of Soil and Manure* 32: 475–480 (in Japanese).

Premachandra, G. S., H. Saneoka, K. Fujita, and S. Ogata. 1992. Leaf water relations, osmotic adjustment, cell membrane stability, epicuticular wax load and growth as affected by increasing water deficits in sorghum. *Journal of Experimental Botany* 43: 1569–1576.

Salih A. A., I. A. Ali, A. Lux, M. Luxova, Y. Cohen, Y. Sugimoto, and S. Inanaga. 1999. Rooting, water uptake, and xylem structure adaptation to drought of two sorghum cultivars. *Crop Science* 39: 168–173.

Sharp, R. E., T. C. Hsiao, and W. K. Silk. 1990. Growth of the maize primary root at low water potentials. II. Role of growth and deposition of hexose and potassium in osmotic adjustment. *Plant Physiology* 93: 1337–1346.

Sonobe, K., T. Hattori, P. An, W. Tsuji, A. E. Eneji, K. Tanaka, and S. Inanaga. 2009. Diurnal variations in photosynthesis, stomatal conductance and leaf water relation in sorghum grown with or without silicon under water stress. *Journal of Plant Nutrition* 32: 433–442.

Steudle E., and C. A. Peterson. 1998. How does water get through roots? *Journal of Experimental Botany* 49: 775–788.

Yemm, E. W., and A. J. Willis. 1954. The estimation of carbohydrates in plant extracts by anthrone. *Biochemical Journal* 57: 508–514.