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Effect of Silicon on Plant Growth and Mineral Nutrition of Maize Grown Under Water-Stress Conditions

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ABSTRACT

The effect of silicon (Si) on physiological attributes and nutritional status of maize (*Zea mays* cv. DK 647 F1) under water stress was studied in a pot experiment. Treatments were (1) well watered (WW): 100% of FC (soil field capacity), (2) WW + Si1: 100% of FC + 1 mM Si, (3) WW + Si2: 100% of FC + 2 mM Si, (4) water stress (WS): 50% of FC, (5) WS + Si1: 50% of FC + 1 mM Si and (6) WS + Si2: 50% of FC + 2 mM Si. In the control treatment, plants were irrigated to field capacity (100% FC). Water stress was imposed by maintaining a moisture level equivalent to 50% of field capacity, whereas the well-watered pots (control) were maintained at full field capacity. Water stress was found to reduce the total dry matter (DM), chlorophyll content, and relative water content (RWC), but to increase proline accumulation and electrolyte leakage in maize plants. Both Si treatments largely improved the above physiological parameters, but levels remained significantly lower than the control (WW) values except for electrolyte leakage and root:shoot ratios, which were higher. Only root DM appeared to show very little variation in any of the treatments. The concentration of Si in the plants was increased by Si addition into the nutrient solution. Water stress reduced leaf calcium (Ca) and potassium (K) of maize plants, but addition of Si increased these nutrient levels; Ca levels were similar to WW under the high-Si treatment, but K was lower. Root Ca and K were both increased by WS; root Ca was further increased by high Si (WS + Si2 treatment). Addition of Si to the WS treatments did not change root K. Results indicate that while application of Si may be one approach to improve growth of this crop and

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increase its production in arid or semi-arid areas where water is at a premium, this technique would not fully substitute for an adequate water supply.

Keywords: water stress, maize, silicon, membrane permeability, crop yield, chlorophyll

INTRODUCTION

Water supply is one of the environmental factors that control growth and development in plants. Water deficit adversely affects many physiological processes in plants. Plant growth and productivity are negatively affected by water stress and other environmental stresses (Shalhevet, 1993; Gadallah, 1995). In the whole plant, response to water stress involves different mechanisms, ranging from stomatal closure to root/shoot ratio increase, leaf area reduction, and osmotic adjustment (Nagy et al., 1995; Socias et al., 1997). In the physiological mechanism of drought avoidance, maintenance of favorable water status in plants is achieved through either efficient stomatal regulation (“water savers”) or high root activity (“water spenders”) (Levitt, 1980).

Maize (*Zea mays*) is grown all over the world under a wide range of climates. Of the relevant factors in maize establishment, drought is the main cause of severe yield reductions (Maiti et al., 1996). Genotypic differences have been identified for a range of morphological and physiological characteristics (Ackerson, 1983) as well as growth responses of maize to water stress (O’Regan et al., 1993; Sinclair et al., 1990).

Silicon (Si) has been regarded as an essential element in a number of species of the Poaceae and Cyperaceae, but it has not been possible to demonstrate that it is essential to all higher plants because direct evidence is still lacking that it is part of the molecule of an essential plant constituent or metabolite (Epstein, 1994, 1999). Recently, the role of Si in plant metabolism has received increasing attention. Liang et al. (2003) strongly suggest that Si may be involved in metabolic or physiological and/or structural activity in higher plants exposed to abiotic and biotic stresses. It has been reported that Si increases plant tolerance to high manganese (Mn) concentrations (Horst and Marschner, 1978), drought (Lux et al., 2002), heavy metals (Neumann and zur Nieden, 2001), and plant resistance to pests and pathogens (Belanger et al., 2003; Richmond and Sussman, 2003). However, the use of Si and its relationships with plant growth and with mineral nutrition of plants under water stress have not been studied in such detail.

A short-term experiment with maize was conducted to study the effectiveness of Si in mitigating the adverse effects of water stress and to investigate possible mechanisms of Si enhancement of drought tolerance in maize.

MATERIALS AND METHODS

Plant Culture and Treatments

A greenhouse experiment was conducted from the end of April to the middle of June 2004 with maize (*Zea mays* L. cv. DK 647 F1). After surface sterilization with 1% sodium hypochlorite for 10 min, seeds were rinsed thoroughly with distilled water and germinated on moist filter paper for 2 d in an incubator at 25°C. After germination, three seeds of maize were sown directly in plastic pots containing 8 kg of peat, perlite, and sand (1:1:1, v/v/v) mixture. They were thinned to one plant per pot seven days after sowing (DAS) and plants were then grown for a further five weeks under greenhouse conditions at average day/night temperatures of 25°C/15°C, maximum/minimum temperature of 32°C/12°C, and at ambient sunlight. Pots were covered with a black plastic to exclude light from the roots and to prevent evaporation.

Seedlings were irrigated at the full field capacity for one week in order to improve root development before initiating treatments. Treatments used in this experiment were (1) well watered (WW): 100% of FC (soil field capacity), (2) WW + Si1: 100% of FC + 1 mM Si, (3) WW + Si2: 100% of FC + 2 mM Si, (4) water stressed (WS): 50% of FC, (5) WS + Si1: 50% of FC + 1 mM Si, and (6) WS + Si2: 50% of FC + 2 mM Si. Silicon was added as Na₂SiO₃. Control plants were treated with an equivalent amount of NaCl. Water stress was imposed by maintaining a moisture level equivalent to 50% of FC, whereas the well-watered pots (control) were maintained at full field capacity (100% FC). The soil moisture content was monitored daily by weighing the pots. During water deficit, the degree of water stress was estimated gravimetrically by monitoring changes in the weight of the pot (plus plant). Weights of the plants were omitted because of their young development stage. The water-deficit treatment was applied for 35 d (from 10 to 45 DAP). The plants were harvested at 45 DAP. The total amount of nutrient solution applied to water-stressed and well-watered plants was the same, and well-watered plants also received additional water to reach the full pot capacity. Soil moisture at field capacity was 18%, while the permanent wilting percentage was c. 9%.

The basic nutrient solution used in this experiment was a modified Hoagland and Arnon formulation. All chemicals used were of analytical reagent grade, and composition of nutrient solution was (mg L⁻¹): 270 nitrogen (N), 31 phosphorus (P), 234 potassium (K), 200 calcium (Ca), 48 magnesium (Mg), 2.8 iron (Fe), 0.5 manganese (Mn), 0.5 boron (B), 0.02 copper (Cu), 0.05 zinc (Zn), and 0.01 molybdenum (Mo). The pH of nutrient solution was adjusted each time to 6.5 with 0.1 mM KOH. Each treatment was replicated four times in a randomized block design and each replicate included six plants (i.e., 24 plants per treatment).

Leaf Relative Water Content

Leaf relative water content (LRWC) was measured using the method of Yamasaki and Dillenburg (1999). Leaves were sampled from the midsection of each plant in order to minimize age effect on variability of results. Individual leaves were first removed from the stem and then weighed to obtain fresh mass (FM). In order to determine the turgid mass (TM), whole leaves were floated in distilled water inside a closed Petri dish. During the imbibition period, leaf samples were weighed periodically after the water was gently wiped from the leaf surface with tissue paper. At the end of the imbibition period, leaf samples were placed in a pre-heated oven at 80°C for 48 h to obtain dry mass (DM). All mass measurements were made using an analytical balance with precision of 0.0001 g. Values of FM, TM, and DM were used to calculate LRWC using the equation below:

$$\text{LRWC (\%)} = [(FM-DM)/(TM-DM)] \times 100$$

Chlorophyll Determination

One plant per replicate was used for chlorophyll determination. Prior to extraction, fresh leaf samples were cleaned with deionized water to remove any surface contamination. Chlorophyll extraction was conducted on fresh, fully expanded leaf material, a 1 g leaf sample was ground in 90% acetone using a pestle and mortar. The absorbance was measured with a UV/visible spectrophotometer (Pye Unicam SP6-550, UK) and chlorophyll concentrations were calculated using the equation proposed by Strain and Svec (1966).

$$\text{Chl.a (mg ml}^{-1}\text{)} = 11.64 \times (A663) - 2.16X(A645)$$

$$\text{Chl.b (mg ml}^{-1}\text{)} = 20.97 \times (A645) - 3.94X(A663)$$

(A663) and (A645) represent absorbance values read at 663 and 645 nm wavelengths, respectively.

Electrolyte Leakage

This parameter was included in order to gain more information on the membrane stability and thereby on the relative ion content in the apoplastic space. Electrolyte leakage was assessed as described by Lutts et al. (1996), using nine young leaf discs (diameters 10 mm) for each treatment. Samples were washed three times with deionized water to remove surface-adhered electrolytes. Leaf discs were placed in closed vials containing 10 mL of deionized water and incubated at 25°C on a rotary shaker for 24 h; subsequently, electrical conductivity of the solution (Lt) was determined. Samples were then autoclaved at 120°C for

20 min and the last electrical conductivity (L0) was obtained after equilibration at 25°C. The electrolyte leakage was defined as follows: Electrolyte leakage (%) = $(L_t/L_0) \times 100$.

Proline Determination

Proline was determined according to the method described by Bates et al. (1973). Approximately 0.5 g of fresh plant material was homogenized in 10 mL of 3% aqueous sulfosalicylic acid and filtered through Whatman No. 2 filter paper. Two mL of filtrate was mixed with 2 mL acid-ninhydrin and 2 mL of glacial acetic acid in a test tube. The mixture was placed in a water bath for 1 h at 100°C. The reaction mixture was extracted with 4 mL toluene and the chromophore containing toluene was aspirated and cooled to room temperature, after which the absorbance was measured at 520 nm with a Shimadzu UV 1601 spectrometer. Appropriate proline standards were included for calculation of proline in the sample.

Nutrient Analysis and Dry Weight

Three randomly selected plants per replicate were divided into leaves, stems, and roots, and dried in a forced-air oven at 70°C for 2 d to determine dry weights. The dried samples were ground to powder using a pestle and mortar and stored in polyethylene bottles. The sample was then microwave-digested in a mixture of 3 mL of 62% (w/w) HNO₃, 3 mL of 30% (w/w) hydrogen peroxide, and 2 mL of 46% (w/w) HF and the digested sample was diluted to 100 mL with 4% (w/v) boric acid. The Si concentration in the digest solution was determined by the colorimetric molybdenum blue method at 600 nm (Ma et al., 2002). Ground samples were dry-ashed at 550°C for four hours, mixed with 2 M hot HCl, filtered, and then brought to a final volume of 50 mL with distilled water. Potassium and Ca were determined in this sample solution using an ICP (Chapman and Pratt, 1982).

For statistical analysis, a two-way analysis of variance was performed and the LSD was calculated at $P \leq 0.05$ (Gomez and Gomez, 1984).

RESULTS AND DISCUSSION

Relative Water Content and Plant Growth

Relative water content (RWC) in leaves is known as an alternative measure of plant water status, reflecting the metabolic activity in tissues (Flower and Ludlow, 1986). In the present study, even well-irrigated (WW) plants showed

Table 1

Relative water content (RWC); total, shoot, and root dry weights; and root:shoot ratio of maize plants grown under water stress in the presence of silicon (Si)

Treatments*	RWC (%)	g/plant			Root:Shoot ratio
		Total DM	Shoot DM	Root DM	
WW	75.3 a	3.26 a	2.92 a	0.32 ab	0.110 d
WW + Si1	74.3 a	3.23 a	2.90 a	0.33 a	0.113 d
WW + Si2	76.4 a	3.25 a	2.94 a	0.31 a	0.105 d
WS	42.9 c	1.65 d	1.36 d	0.29 b	0.213 a
WS + Si1	62.5 b	2.08 c	1.78 c	0.30 ab	0.168 b
WS + Si2	69.4 b	2.39 b	2.08 b	0.31 ab	0.149 c

*WW: well watered; WS: water stressed; Si1: 1 mM and Si2: 2 mM Si as Na_2SiO_3 in nutrient solution.

Values followed by different letters, in the same column, are significantly different at $P \leq 0.05$.

a RWC significantly below 100%. Leaf RWC declined significantly with water stress (Table 1). Similar results have been reported for many plant species under water-stress conditions (Gadallah, 1995; Sairam, 1994; Ramanjulu and Sudhakar, 1997). This decrease in leaf RWC could be due to unavailability of water in the soil (Shalhevet, 1993) or root systems, which are not able to compensate for water lost by transpiration through a reduction of the absorbing surface (Gadallah, 2000). Addition of Si into nutrient solution did not cause further increases in RWC of WW plants. However, addition of Si into nutrient solution elevated water status in water-stressed plants. Silicon deposited in the tissues helps to alleviate water stress by decreasing transpiration and improves light interception characteristics by keeping the leaf blade erect (Epstein, 1999). Researchers have clearly shown that transpiration from leaves of some plants is considerably reduced by the application of Si (Agarie et al., 1998). This result has been explained by a well-thickened layer of silica gel associated with the cellulose in the epidermal cell walls, which may help to reduce water loss, while an epidermal cell wall with less silica gel will allow water to escape at an accelerated rate (Wong et al., 1972).

As shown in Table 1, the dry weights of both shoot and root were significantly reduced by water stress, and water stress appears to affect shoots more than roots and causes larger root:shoot ratios. Larger root:shoot ratios are usually due to a relatively greater decrease in shoot growth than in root growth under water stress. Water stress tends to increase biomass partitioning to roots, increasing root:shoot ratios (Klepper, 1991). Huck et al. (1983) observed an increase of root length in non-irrigated soybeans (*Glycine max*) when compared with irrigated ones. Inhibition in plant growth was significantly alleviated by Si supplement. Under water stress, Si significantly increased the dry weight of

shoots and total biomass of maize plants (Table 1). These results are in agreement with those reported by Lux et al. (2002), who noted that Si increased plant growth of sorghum (*Sorghum bicolor*) grown under water stress.

Proline, Chlorophyll, and Electrolyte Leakage

Water stress treatment resulted in significant accumulation in proline content (Table 2). Proline accumulation in response to stress has been reported widely, and may play a role in stress adaptation within the cell (Gilbert et al., 1998). Osmotic adjustment (OA) is part of drought-avoidance mechanisms to counteract the loss of turgor by increasing and maintaining a higher amount of intracellular compatible solutes in the cytosol and vacuole, and has been proven to be particularly significant among all the stress-adaptation mechanisms (Cushman, 2001). Proline is one of the key osmolytes contributing to OA (Hare and Cress, 1997). Both Si treatments reduced the proline accumulation in plants. This result could be due to the stimulation effect of Si on vegetative growth of maize plants grown under water stress.

Chlorophyll a and b content decreased in response to water stress (Table 2). The decrease may be due to the formation of proteolytic enzymes such as chlorophyllase, which is responsible for chlorophyll degradation (Sabater and Rodriguez, 1978) as well as damage to the photosynthetic apparatus (Yaseen, 1983). Addition of Si improved the chlorophyll levels in water-stressed plants compared with WS plants with no addition of Si, but the values were still lower than those for WW plants.

Table 2

Proline content, chlorophyll content, and electrolyte leakage of maize plants grown under water stress in the presence of Si.

Treatments*	Proline ($\mu\text{mol g}^{-1}$ FW)	mg mL ⁻¹		Electrolyte Leakage (%)
		Chl. a	Chl. b	
WW	17.4 d	1110 a	745 a	11.5 c
WW + Si1	18.2 d	1125 a	746 a	12.6 c
WW + Si2	18.4 d	1122 a	759 a	11.7 c
WS	25.3 a	780 c	475 c	32.3 a
WS + Si1	14.6 c	945 b	585 b	16.6 b
WS + Si2	12.6 b	935 b	605 b	14.0 b

*WW: well watered; WS: water stressed; Si1: 1 mM and Si2: 2 mM Si as Na₂SiO₃ in nutrient solution.

Values followed by the same letter, in the same column, are not significantly different at $P \leq 0.05$.

Electrolyte leakage was increased in the leaves of maize plants grown under water stress compared with the unstressed plants. Silicon treatments partially ameliorated this leakage, but values were still higher compared with WW plants (Table 2). It has been shown previously that Si reduces electrolytic leakage in leaves of barley (*Hordeum vulgare* L.) (Liang et al., 1996). This result could be due to Si affecting the structure and integrity of plasma membranes by influencing the stress-dependent peroxidation of membrane lipids (Liang 1999). Cell membranes are one of the first targets of many plant stressors, or and it is generally accepted that the maintenance of their integrity and stability under water-stress conditions is a major component of drought tolerance in plants. The degree of cell-membrane injury induced by water stress may be easily estimated by measuring electrolyte leakage from the cells (Bajji et al., 2002).

Mineral Nutrient Contents

As expected, addition of Si in nutrient solution increased the Si concentrations in both leaf and roots. These results are agreement with the findings of others (Gao et al., 2004; Rogalla and Römheld, 2002).

Concentration of Ca was significantly lower in leaves, but higher in roots of the water-stressed plants. Calcium plays a vital role in maintaining membrane stability and permeability (Mengel and Kirkby, 1987). Addition of Si increased both leaf and root Ca (Table 3). This could be why membrane permeability is impaired in leaves of water- stressed plants where Ca level is lower; addition of

Table 3

Calcium, potassium, and silicon in leaves and roots of maize plants grown under water stress in the presence of Si

Treatments*	mM/kg DW					
	Leaf			Root		
	Ca	K	Si	Ca	K	Si
WW	512 a	1397 a	7 c	330 c	185 b	4 d
WW + Si1	520 a	1412 a	124	345 c	198 b	27 b
WW + Si2	521 a	1394 a	221 a	354 c	187 b	43 a
WS	280 c	538 d	4 c	440 b	251 a	4 d
WS + Si1	380 b	825 c	114 b	485 b	249 a	14 c
WS + Si2	485 a	1038 b	200 a	580 a	238 a	25 b

*WW: well watered; WS: water stressed; Si1: 1 mM and Si2: 2 mM Si as Na₂SiO₃ in nutrient solution.

Values followed by the same letter, in the same column, are not significantly different at $P \leq 0.05$.

Si enhances Ca levels and partially restores the membrane integrity in water-stressed plants (Tables 2 and 3). Greater Ca concentrations in plant tissues may also help in achieving better crop survival, with improved plant growth under stress conditions (Cachorro et al., 1994). Knight et al. (1997) indicated that osmotic stress can mediate rapid elevations in cytosolic free Ca in *Arabidopsis* (*Arabidopsis thaliana*) seedlings, and that these changes in Ca²⁺ levels may mediate increases in the expression of drought-induced genes, which have protective functions.

Potassium concentration in leaf tissues was much lower in the water-stressed plants than in those under the WW treatments (Table 3). Under water-stress conditions, K concentration increased in the presence of Si. One possible mechanism for the stimulating effect of Si on K uptake could be the activation of H-ATPase in the membranes (Liang, 1999). Higher K levels in plants are beneficial in achieving better survival with improved growth under water stress (Umar, 2002; Sangakkara et al., 2001). Potassium is considered as one of the primary osmotic substances, which contribute to osmotic adjustment in many plant species (Ashraf et al., 2001; Iannucci et al., 2002).

The present results revealed that addition of Si improved the water-stress tolerance in maize seedlings by partially maintaining membrane permeability, and by enhancing chlorophyll, relative water content, leaf Ca and K, and shoot and total biomass. Therefore, application of Si may be one approach to improve growth of this crop and to increase its production in arid or semi-arid areas under water-stress conditions.

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REFERENCES

- Ackerson, R.C. 1983. Comparative physiology and water relations of two corn hybrids during water stress. *Crop Science* 23: 278–283.
- Agarie, S., H. Uchida, W. Qgata, F. Kubota, and P. B. Kaufman. 1998. Effects of silicon on transpiration and leaf conductance in rice plants (*Oryza sativa* L.). *Japanese Journal of Crop Science* 1: 89–95.
- Ashraf, M., A. Ahmad, and T. McNeilly. 2001. Growth and photosynthetic characteristics in pearl millet under water stress and different potassium supply. *Photosynthetica* 39: 389–394.
- Bajji, M., J. M. Kinet, and S. Lutts. 2002. The use of the electrolyte leakage method for assessing cell membrane stability as a water stress tolerance test in durum wheat. *Plant Growth Regulation* 36: 61–70.

- Bates, L. S., R. P. Waldren, and I. D. Teare. 1973. Rapid determination of free proline for water stress studies. *Plant and Soil* 39: 205–207.
- Belanger, R. R., N. Benhamou, and J. G. Menzies. 2003. Cytological evidence of an active role of silicon in wheat resistance to powdery mildew (*Blumeria graminis* f. sp. *tritici*). *Phytopathology* 93: 402–412.
- Cachorro, P., A. Ortiz, and A. Cerda. 1994. Implications of calcium on the response of *Phaseolus vulgaris* L. to salinity. *Plant and Soil* 159: 205–212.
- Chapman, H. D., and P. F. Pratt. 1982. *Methods of plant analysis. I. Methods of analysis for soils, plants and water*. Riverside, CA: Chapman Publishers.
- Cushman, J. C. 2001. Osmoregulation in plants: Implications for agriculture. *American Zoology* 41: 758–769.
- Epstein, E. 1994. The anomaly of silicon in plant biology. *Proceedings of the National Academy of Sciences of the United States of America* 91: 11–17.
- Epstein, E. 1999. Silicon. *Annual review in plant physiology and molecular biology* 50: 641–664.
- Flower, D. J., and M. M. Ludlow. 1986. Contribution of osmotic adjustment to the dehydration tolerance of water stressed pigeon pea [*Cajanas cajan* (L) Milsp] leaves. *Plant, Cell and Environment*. 9: 33–40.
- Gadallah, M. A. A. 1995. Effects of water stress, abscisic acid and proline on cotton plants. *Journal of Arid Environment* 30: 315–325.
- Gadallah, M. A. A. 2000. Effects of indole-3-acetic acid and zinc on the growth, osmotic potential and soluble carbon and nitrogen components of soybean plants growing under water deficit. *Journal of Arid Environment* 44: 451–467.
- 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.
- Gilbert, A. G., M. V. Gadush, C. Wilson, and M. A. Madore. 1998. Amino acid accumulation in sink and source tissues of *Coleus blumei* Benth. during salinity stress. *Journal of Experimental Botany* 49: 107–114.
- Gomez, K. A., and A. A. Gomez. 1984. *Statistical procedure for agricultural research*. New York: Wiley International Publishers.
- Hare, P. D., and W. A. Cress. 1997. Metabolic implications of stress induced proline accumulation in plants. *Plant Growth Regulation* 21: 79–102.
- Horst, W. J., and H. Marschner. 1978. Effect of silicon and manganese tolerance of bean plants (*Phaseolus vulgaris* L.). *Plant and Soil* 50: 287–303.
- Huck, M. G., K. Ishihara, C. M. Peterson, and T. Ushijima. 1983. Soybean adaptation to water stress at selected stages of growth. *Plant Physiology* 73: 422–427.
- Iannucci, A., M. Russo, L. Arena, N. Di Fonzo, and P. Martiniello. 2002. Water deficit effects on osmotic adjustment and solute accumulation in leaves of annual clovers. *European Journal of Agronomy* 16: 111–122.
- Klepper, B. 1991. Root-shoot relationships. In *Plant roots: The hidden half*, eds. Y. Waisel, A. Eshel, and U. Kafkafi, 265–286. New York: Marcel Dekker.

- Knight, H., A. J. Trewavas, and M. R. Kinght. 1997. Calcium signaling in *Arabidopsis thaliana* responding to drought and salinity. *Plant Journal* 12: 1067–1078.
- Levitt, J. 1980. *Response of plants to environmental stress*, Vol. 2. New York: Academic Press.
- Liang, Y. 1999. Effects of silicon on enzyme activity and sodium, potassium and calcium concentration in barley under salt stress. *Plant and Soil* 209: 217–224.
- 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. C., Q. R. Shen, Z. G. Shen, and T. S. Ma. 1996. Effects of silicon on salinity tolerance of two barley cultivars. *Journal of Plant Nutrition* 19: 173–183.
- Lutts, S., J. M. Kinet, and J. Bouharmont. 1996. NaCl-induced senescence in leaves of rice (*Oryza sativa* L.) cultivars differing in salinity resistance. *Annals of Botany* 78: 389–398.
- Lux, A., M. Luxova, T. Hattori, S. Inanaga, and Y. Sugimoto. 2002. Silicification in sorghum (*Sorghum bicolor*) cultivars with different drought tolerance. *Physiologia Plantarum* 115: 87–92.
- Ma, J. F., K. Tamai, M. Ichii, and G. F. Wu. 2002. A rice mutant defective in Si uptake. *Plant Physiology* 30: 2111–2117.
- Maiti, R. K., L. E. D. Amaya, S. I. Cardona, A. M. O. Dimas, and H. D. L. Castillo. 1996. Genotypic variability in maize cultivars for resistance to drought and salinity at the seedling stage. *Journal of Plant Physiology* 148: 741–744.
- Mengel, K., and E. A. Kirkby. 1987. *Principle of plant nutrition*. Berne, International Potash Institute.
- Nagy, Z., Z. Tuba, F. Zsoldos, and L. Erdei. 1995. CO₂-exchange and water relation responses of sorghum and maize during water and salt stress. *Journal of Plant Physiology* 145: 539–544.
- Neumann, D., and U. zur Nieden. 2001. Silicon and heavy metal tolerance of higher plants. *Phytochemistry* 56: 685–692.
- O'Regan, B. P., W. A. Cress, and J. Van Staden. 1993. Root growth, water relations, abscisic acid and proline levels of drought-resistant and drought-sensitive maize cultivars in response to water stress. *South African Journal of Botany* 59: 98–104.
- Ramanjulu, S., and C. Sudhakar. 1997. Drought tolerance is partly related to amino acid accumulation and ammonia assimilation: A comparative study in two mulberry genotypes differing in drought sensitivity. *Journal of Plant Physiology* 150: 345–350.
- Richmond, R. E., and M. Sussman. 2003. Got silicon? The non-essential beneficial plant nutrient. *Current Opinion in Plant Biology* 6: 268–272.

- Rogalla, H., and V. Römheld. 2002. Role of leaf apoplast in silicon-mediated manganese tolerance of *Cucumis sativus* L. *Plant Cell Environment* 25: 549–555.
- Sabater, B., and M. I. Rodriguez. 1978. Control of chlorophyll degradation in detached leaves of barley and oat through effect of kinetin on chlorophyllase levels. *Physiologia Plantarum* 43: 274–276.
- Sairam, R. K. 1994. Effect of moisture stress on physiological activities of two contrasting wheat genotypes. *Indian Journal Experimental Biology* 32: 594–597.
- Sangakkara, U. R., M. Frehner, and J. Nosberger. 2001. Influence of soil moisture and fertilizer potassium on the vegetative growth of mungbean (*Vigna radiata* L. Wilczek) and cowpea (*Vigna unguiculata* L. Walp). *Journal of Agronomy and Crop Science* 186: 73–81.
- Shalhevet, J. 1993. Plants under salt and water stress. In *Plant adaptation to environmental stress*, eds. L. Fowden, T. Mansfield, and J. Stoddart, 133–154. New York: Chapman and Hall.
- Sinclair, T. R., J. M. Bennet, and R. C. Machow. 1990. Relative sensitivity of grain yield and biomass accumulation to drought in field grown maize. *Crop Science* 30: 690–693.
- Socias, F. X., A. Pol, F. Aguilo, J. Vadell, and H. Medrano. 1997. Effects of rapidly and gradually induced water stress on plant response in subterranean clover leaves. *Journal of Plant Physiology* 150: 212–219.
- Strain, H. H., and W. A. Svec. 1966. Extraction, separation, estimation and isolation of chlorophylls. In *The chlorophylls*, eds. L. P. Vernon and G. R. Seely, 21–66. New York: Academic Press.
- Umar, S. M. 2002. Genotypic differences in yield and quality of groundnut as affected by potassium nutrition under erratic rainfall conditions. *Journal of Plant Nutrition* 25: 1549–1562.
- Wong, Y. C., A. Heits, and J. D. Ville. 1972. Foliar symptoms of silicon deficiency in the sugarcane plant. *Proc Cong Int Soc Sugarcane Technol* 14: 766–776.
- Yamasaki, S., and L. C. Dillenburg. 1999. Measurements of leaf relative water content in *Araucaria angustifolia*. *Revista Brasileira Fisiologia Vegetal* 11: 69–75.
- Yasseen, B. T. 1983. *An analysis of the effects of salinity on leaf growth in Mexican wheats*, PhD diss., University of Leeds.