

SHORT COMMUNICATION

The ameliorative effect of silicon on soybean seedlings grown in potassium-deficient medium

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- **Background and Aims** Crop yield and nutritional quality are significantly reduced when potassium (K) in soil is deficient. As a beneficial element for plants, silicon (Si) is effective in alleviating the toxic effects of mineral nutrients. However, the roles played by Si in mediating deficiency in essential mineral nutrients in general and K in particular have not been investigated.
- **Methods** To evaluate the role of Si in K deficiency-induced inhibition of growth of soybean (*Glycine max*) seedlings, the effects of K deficiency on shoot and root growth, hydrogen peroxide accumulation, K contents, lipid peroxidation and activities of antioxidant enzymes in the absence and presence of 2 mM sodium silicate (Na_2SiO_3) were investigated.
- **Key Results** Both shoot and root biomass of soybean seedlings were markedly reduced when grown in K-deficient medium (1 mM K) compared with those grown in K-sufficient medium (5 mM). Addition of Na_2SiO_3 significantly ameliorated the K deficiency-induced reductions in shoot and root growth. Sodium silicate enhanced K concentrations in leaf, stem and root of K-deficient seedlings by 105.4, 83.4 and 58.8 %, respectively. Hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) contents in soybean seedlings were increased by 25 and 97 %, respectively, when exposed to K-deficient medium. These increases in accumulation of H_2O_2 and MDA were removed by addition of Na_2SiO_3 . Addition of Na_2SiO_3 reduced the K deficiency-induced increases in activities of superoxide dismutase, catalase and peroxidase.
- **Conclusions** Application of Si to soybean seedlings grown in K-deficient medium markedly enhanced K use efficiency. Therefore, Si not only increases tolerance to nutrient toxicity, but also ameliorates symptoms associated with deficiency in essential nutrients in plants.

Key words: Antioxidant enzyme activities, oxidative stress, potassium deficiency, silicon, soybean, *Glycine max*.

INTRODUCTION

Potassium (K) is the most abundant cation in plants, and plays important roles in many physiological processes such as photosynthesis, assimilate transport and enzyme activation. Potassium is essential for high-yield crop production, and can be a limiting factor for such crops under certain environmental conditions, for example drought (Liebersbach *et al.*, 2004) and salinity (Qi and Spalding, 2004; Rus *et al.*, 2004). Therefore, elucidation of the mechanisms underlying responses and adaptation of plants to K deficiency is of key importance. Although application of K fertilizers is an effective way to minimize K deficiency-induced loss of crop production, the economic burdens associated with the use of fertilizers, particularly in developing countries, are a limiting factor. Therefore, a better understanding of the mechanisms by which plants cope with K deficiency would provide a physiological basis for selecting crops with high K use efficiency (Rengel and Damon, 2008).

K deficiency reduces mechanical stability, nutritional quality and crop resistance to pathogens (Pettigrew, 2008). In this context, application of silicon (Si), which is one of the most abundant elements in the Earth's crust, has been shown to enhance lodging resistance through increased breaking strength and increased pushing tolerance (Uchimura *et al.*,

2000). In addition, Si is capable of increasing plant tolerance to pests and diseases by acting as a physical barrier to protect plants from attack by insects and pathogens, and/or acting as a modulator of host resistance to pathogens (Ma and Yamaji, 2008). Although there has been no consensus regarding whether Si can be defined as an essential element for plant growth and development (Epstein and Bloom, 2003), ample evidence indicates that Si plays an important role in protecting plants from abiotic and biotic stresses (Liang *et al.*, 2007; Ma and Yamaji, 2008). For instance, Si is effective in alleviating abiotic stresses, including salinity (Liang *et al.*, 2003), drought (Gong *et al.*, 2005), low temperature (Liang *et al.*, 2008), and nutrient toxicity such as from magnesium (Iwasaki and Matsumura, 1999), cadmium (Liang *et al.*, 2005; Vaculik *et al.*, 2009), aluminium (Hodson and Evans, 1995) and boron (Gunes *et al.*, 2007). The ameliorative effect of Si on plants suffering from abiotic stresses often occurs through counteracting oxidative stress by modulating antioxidant enzymes (Liang *et al.*, 2007). Deficiency in macronutrients including K also leads to oxidative stress, as evidenced by accumulation of reactive oxygen species (ROS) and membrane lipid peroxidation (Cakmak, 1994; Shin and Schachtman, 2004; Tewari *et al.*, 2004, 2007; Cakmak, 2005). ROS are strong oxidizing

agents that cause oxidative damage to critical molecules such as lipids and proteins, leading to cell lesion. Malondialdehyde (MDA) is a decomposition product of polyunsaturated fatty acids, and has been widely used as a parameter for lipid peroxidation (Mittler, 2002). Given that Si can alleviate oxidative damage induced by various abiotic stresses (cf. Liang *et al.*, 2007), it is conceivable that application of Si may mitigate K deficiency-induced inhibition of crop growth and development. However, there have been few studies to evaluate the role of Si in nutrient deficiency in general (Wallace *et al.*, 1976) and of K deficiency in particular. The present study investigated the effect of Si on soybean seedlings suffering from K deficiency with emphasis on lipid peroxidation and activities of major antioxidant enzymes, including superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD). To rule out the contributions of Na to the observed effect on soybean seedlings treated with Na₂SiO₃, the effect of NaCl on K-deficient soybean seedlings was also investigated.

MATERIALS AND METHODS

Plant materials

Soybean, *Glycine max* (L.) Merrill 'Tiefen 35' seedlings were grown in glasshouse conditions with maximum photosynthetic photon flux density (1200 h) of 1120–1330 mol m⁻² s⁻¹, and daily maximum and minimum temperatures of 32–38 and 20–30 °C, respectively. The average photoperiod was approx. 11 h. The seedlings were planted in pots (diameter 15 cm and height 30 cm) filled with vermiculite and watered with both K-sufficient and K-deficient solutions with and without 2 mM Na₂SiO₃ and 4 mM NaCl, respectively. The Si concentration (2 mM) used was comparable with those widely used in other studies investigating the ameliorative role of Si in abiotic stress (Hodson and Evans, 1995; Gong *et al.*, 2005; Gunes *et al.*, 2007; Kaya *et al.*, 2006; Liang *et al.*, 2003, 2005). The K-sufficient solution was half-strength Hoagland solution with 5 mM K and the K-deficient solution was half-strength Hoagland solution with K reduced to 1 mM. To maintain concentration of NO₃⁻ equal between the K-sufficient and K-deficient solutions, NO₃⁻ in K-deficient solution was reduced to 1 mM and supplemented with 4 mM NaNO₃, and an additional 4 mM NaCl was added in the K-sufficient solution to cancel the potential effect of Na. Each pot with three seedlings was watered with 100 mL K-sufficient and K-deficient solutions with and without Na₂SiO₃ and NaCl every 3 d during the experimental period. The initial pH of the nutrient solution after addition of Na₂SiO₃ was approx. 7.8, and the pH was adjusted to 6.0 with HCl prior to irrigation. Each treatment had four pots. After the seedlings were grown in the two K regimes in the absence and presence of Na₂SiO₃ and NaCl for 60 d, physiological parameters such as root length, lateral root density, biomass, K contents and enzyme activities were determined. Lateral root density was determined by counting total visible lateral root number and was normalized on the basis of primary root length.

Determination of K contents

The 60-d-old soybean plants were harvested and separated into leaves (the third fully expanded), stems and roots for

analysis of K contents in these organs. After thorough rinsing with distilled water, leaves, stems and roots were oven-dried for 4 d at 70 °C and digested with nitric acid. K contents were measured by atomic absorption spectrophotometry. Measurements were repeated four times.

Determination of hydrogen peroxide and lipid peroxidation

Hydrogen peroxide concentration was determined by the peroxidase-coupled assay protocols described by Veljovic-Jovanovic *et al.* (2002). Briefly, approx. 0.5 g of young soybean leaves (the third fully expanded) were ground in liquid N₂ and the powder was extracted in 2 mL 1 M HClO₄ in the presence of insoluble polyvinylpyrrolidone (PVP) (5 %). The homogenate was centrifuged at 12 000g for 10 min and the supernatant was neutralized with 5 M K₂CO₃ to pH 5.6 in the presence of 100 µL 0.3 M phosphate buffer (pH 5.6). The solution was centrifuged at 12 000g for 1 min and the sample was incubated for 10 min with 1 U ascorbate oxidase to oxidize ascorbate prior to assay. The reaction mixture comprised 100 mM phosphate buffer (pH 6.5), 3.3 mM DMAB (*p*-dimethylaminobenzaldehyde), 70 µM MBTH (3-methylbenzthiazolinone-2-hydrazone) and 0.3 units peroxidase. The reaction was initiated by addition of 200 µL sample. The absorbance change at 590 nm was monitored at 25 °C.

Lipid peroxidation was determined by measuring the MDA content via thiobarbituric acid reaction. The amount of MDA-equivalent TBA-reactive substance (TBARS) was derived from the difference in absorbance at 532 and 600 nm using an extinction coefficient of 155 mm cm⁻¹ as described by Tewari *et al.* (2007).

Electrolyte leakage

Electrolyte leakage was assessed as described by Lutts *et al.* (1996). Leaf 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 2 h; subsequently, electrical conductivity of the solution (*L_t*) was determined. Samples were then autoclaved at 120 °C for 20 min and the final electrical conductivity (*L₀*) was obtained after equilibration at 25 °C. Electrolyte leakage was defined as:

$$\text{Electrolyte leakage(\%)} = (L_t/L_0) \times 100.$$

Enzyme assays

SOD (EC 1.15.1.1) activity was measured as described by Giannopolitis and Ries (1977). Briefly, young leaves (approx. 0.60 g) were ground thoroughly with a cold mortar and pestle in 50 mM potassium phosphate buffer (pH 7.0) with 0.1 mM EDTA. The homogenate was centrifuged at 15 000g for 20 min at 4 °C. The supernatant was crude enzyme extraction. Activity of SOD was measured by the photochemical method with nitro-blue tetrazolium (NBT). One unit of SOD activity was defined as the amount of enzyme required to give 50 % inhibition of the rate of NBT

reduction at 560 nm. Activities of SOD were represented on soluble protein bases.

POD (EC 1.11.1.7) activity was assayed following the protocols used by Liang *et al.* (2003). Briefly, fresh young soybean leaves (approx. 1 g) were homogenized in an ice bath in 5 mL 50 mM borate buffer (pH 8.7) containing 5 mM sodium hydrogen sulfite and 0.1 g PVP. Enzyme extract was obtained by centrifuging the homogenate at 10 000g at 4 °C for 25 min. A substrate mixture containing acetate buffer (0.1 M, pH 5.4), ortho-dianisidine (0.25 % in ethyl alcohol) and 0.1 mM 0.75 % H₂O₂ was added to the enzyme extract (0.1 mL). POD activity was determined based on the change in absorbance of the brown guaiacol at 460 nm.

CAT (EC 1.11.1.6) activity was determined by monitoring the decrease in absorbance at 240 nm for 1 min following the decomposition of H₂O₂. The reaction mixture contained 50 mM phosphate buffer (pH 7.0), 15 mM H₂O₂ and 0.1 mL enzyme extract. CAT activity was calculated from the extinction coefficient (40 mm⁻¹ cm⁻¹) for H₂O₂.

RESULTS AND DISCUSSION

Root growth, dry mass of root and shoot

Previous studies have shown that deprivation of K leads to marked decreases in lateral root length, but not primary root length, and lateral root density in *Arabidopsis thaliana* (Shin and Schachtman, 2004). In contrast, in soybean both primary and lateral root length of seedlings was markedly inhibited when seedlings were grown in K-deficient medium (1 mM K) for 60 d in comparison with those grown in K-sufficient (5 mM K) medium (Fig. 1A, B). The K deficiency-induced reductions in length of primary and lateral roots were significantly ameliorated by the addition of 2 mM Na₂SiO₃ such that the length of primary and lateral roots was significantly longer than that in K-sufficient solutions (Fig. 1). In addition to root growth, lateral root density in seedlings grown in K-deficient medium was also significantly reduced under conditions of K deficiency and the decrease in lateral root density was enhanced substantially in the presence of Na₂SiO₃ (Fig. 1C). To test whether the ameliorative effect of Na₂SiO₃ on root growth of K-deficient seedlings had resulted from contributions of Na⁺ ions, the effect of equivalent Na⁺ ions on K-deficient root growth was also investigated by adding 4 mM NaCl to the K-deficient medium. As shown in Fig. 1, addition of NaCl to K-deficient solutions significantly enhanced growth of both primary and lateral roots and lateral root density of K-deficient seedlings. However, the ameliorative effect of NaCl on root growth and lateral root density was significantly less than that of Na₂SiO₃ (Fig. 1), suggesting that both Na and Si play a role in amelioration of root growth and development under K-deficient conditions with Si being more effective than Na. That Na⁺ alleviated K deficiency-induced inhibition of root growth implies that Na⁺ may partially substitute K⁺ for root growth under K-deficient conditions. In this context, it has been observed that K deficiency promotes accumulation of Na⁺ in maize (Jordan-Meille and Pellerin, 2008) and *Trifolium repens* (Henning, 2003). Because addition of NaCl alleviated K

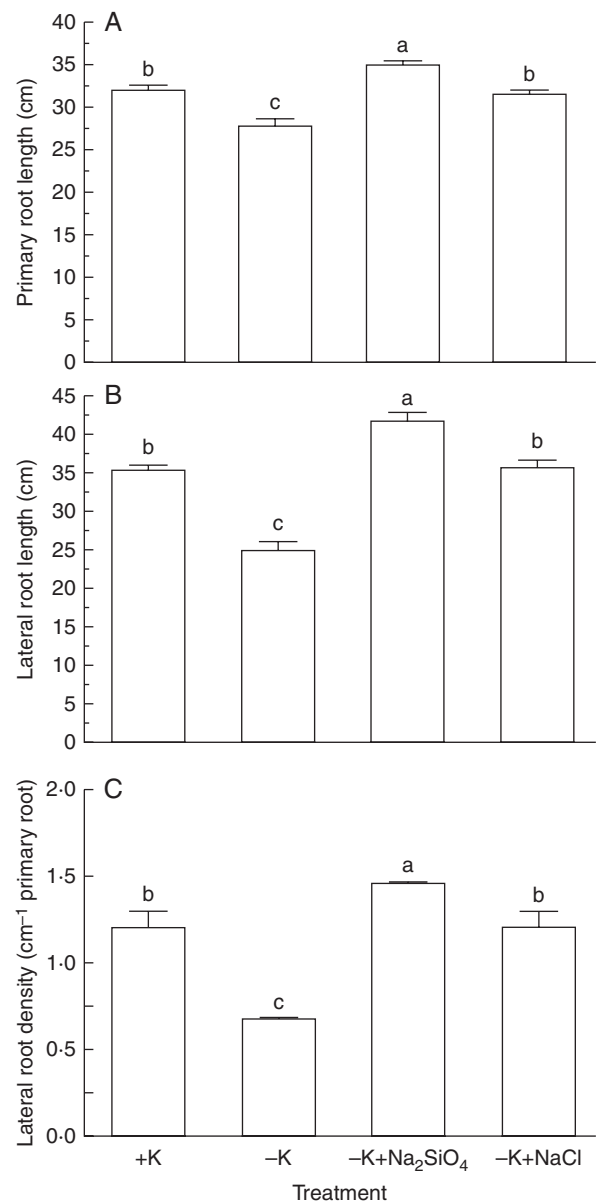


FIG. 1. Effects of K deficiency on (A) primary root length, (B) lateral root length and (C) lateral root density of soybean seedlings in the absence and presence of Na₂SiO₃ and NaCl. Soybean seedlings were grown in 5 mM (+K) and 1 mM K (-K) supplemented with 2 mM Na₂SiO₃ or 4 mM NaCl for 60 d. Data are the mean \pm s.e. of seven individual seedlings for each treatment. Different letters shown in the error bars indicate significant differences among control and treatments at $P < 0.05$.

deficiency-induced root growth, treatment with NaCl under conditions of K deficiency were included throughout the study.

In addition to measurements of root length, the effect of K deficiency on dry mass of both root and shoot was also investigated, as well as root/shoot ratio in the absence and presence of Na₂SiO₃ and NaCl. Similar to root growth, addition of Na₂SiO₃ and NaCl to the K-deficient medium markedly enhanced the dry weight of root, stem and leaf, with the effect of Na₂SiO₃ being much greater than that of NaCl (Table 1). It is of interest that the dry weight of root, stem and leaf for soybean seedlings grown in K-deficient medium

TABLE 1. Effect of Na₂SiO₃ and NaCl on dry weight of soybean seedlings under K deficiency

Treatment	Root d. wt (mg plant ⁻¹)	Stem d. wt (mg plant ⁻¹)	Leaf d. wt (mg plant ⁻¹)	Root/shoot ratio
CK	1.701 ± 0.071 ^b	0.729 ± 0.062 ^b	0.781 ± 0.011 ^a	0.284 ± 0.024 ^b
-K	1.120 ± 0.090 ^c	0.546 ± 0.023 ^d	0.489 ± 0.014 ^c	0.195 ± 0.020 ^d
-K + Na ₂ SiO ₃	2.460 ± 0.068 ^a	0.894 ± 0.011 ^a	0.717 ± 0.016 ^a	0.318 ± 0.010 ^a
-K + NaCl	1.723 ± 0.072 ^b	0.629 ± 0.013 ^c	0.633 ± 0.040 ^b	0.245 ± 0.019 ^c

Data are the mean ± s.e. of four replicates with each replicate containing at least three seedlings. Soybean seedlings were grown in medium watered with full nutrient solution (5 mM K) (CK) and K-deficient solution (1 mM) (-K) in the absence and presence of 2 mM Na₂SiO₃ (-K + Na₂SiO₃) and 4 mM NaCl (-K + Na₂SiO₃) for 60 d. Values with different letters within each column are significantly different at $P < 0.05$.

were greater than those grown in K-sufficient medium when Na₂SiO₃ was added to the K-deficient solution (Table 1). K deficiency also reduced root/shoot ratio, and this decrease was markedly reversed by application of Na₂SiO₃ (Table 1). Although root/shoot ratio was also increased by addition of NaCl to the K-deficient medium, the magnitude of the increase was much less than that induced by application of Na₂SiO₃ (Table 1). In contrast to the K-deficient medium, addition of either NaCl or Na₂SiO₃ to the K-sufficient medium had no effect on shoot and root biomass (data not shown). These results suggest that Si can significantly ameliorate K deficiency-induced inhibition of both shoot and root growth.

Potassium contents

There were significant decreases in K⁺ contents in roots, stems and leaves of soybean seedlings when grown in K-deficient medium compared with those grown in K-sufficient medium, with the decreases in K⁺ contents being greater in roots and stems than in leaves (Table 2). When Na₂SiO₃ was added to the K-deficient medium, K⁺ contents in roots, stems and leaves were increased by 105.4, 83.4 and 58.8 %, respectively, leading to greater K⁺ contents in the three organs of K-deficient seedlings than those in K-sufficient seedlings (Table 2). In contrast to Na₂SiO₃, addition of NaCl had no significant effect on K⁺ contents in roots, stems and leaves for soybean seedlings grown in K-deficient medium (Table 2). One interesting finding was that Si can facilitate K⁺ accumulation in K-deficient soybean seedlings such that K⁺ contents became greater than K-sufficient seedlings, with K contents in roots being mostly enhanced by Si (Table 2). Previous studies have shown that Si can reduce accumulation of cations such as Na⁺ (Liang, 1999; Liang *et al.*, 2003), Cd²⁺ (Liang *et al.*, 2005), Mn²⁺ (Iwasaki and Matsumura, 1999) and Al³⁺ (Hodson and Evans, 1995) due to deposition of Si in the roots, thus ameliorating salinity and heavy metal toxicity to plants. Liang (1999) reported that treatment of barley seedlings with NaCl markedly reduced K⁺ concentrations in shoots, and this inhibitory effect on K⁺ accumulation was ameliorated by addition of Si. The Si-dependent K⁺ accumulation under saline conditions has been ascribed to the enhancement of H⁺-ATPase activity in the presence of Si (Liang, 1999; Liang *et al.*, 2003). A similar explanation may also account for the Si-induced increase in K accumulation under K-deficient conditions.

MDA and hydrogen peroxide contents

There was a significant increase in MDA concentrations in soybean leaves when grown in K-deficient medium, and the K

TABLE 2. Changes in K contents in roots, stems and the third fully expanded leaves of soybean under K deficiency in response to addition of 2 mM Na₂SiO₃ and 4 mM NaCl to K-deficient medium

Treatment	Root K (mg g ⁻¹)	Stem K (mg g ⁻¹)	Leaf K (mg g ⁻¹)
Control (CK)	18.92 ± 0.39 ^b	16.77 ± 1.13 ^b	20.49 ± 1.18 ^b
K deficiency (-K)	10.32 ± 0.82 ^c	10.49 ± 0.89 ^c	17.14 ± 0.72 ^c
-K + Na ₂ SiO ₃	23.50 ± 1.52 ^a	19.24 ± 0.95 ^a	27.21 ± 2.27 ^a
-K + NaCl	12.09 ± 1.01 ^c	11.60 ± 0.34 ^c	17.37 ± 1.72 ^c

Data are from seedlings grown under different treatments for 60 d and expressed as mean ± s.d. of four replicates. Values with different letters within each column are significantly different at $P < 0.05$.

deficiency-induced increase in concentrations of MDA was abolished in the presence of Na₂SiO₃ such that MDA concentrations in K-deficient leaves were lower than those in K-sufficient leaves (Fig. 2A). In contrast to treatment with Na₂SiO₃, addition of NaCl had no effect on MDA concentrations in K-deficient soybean leaves (Fig. 2A), suggesting that Si is responsible for alleviating the effect of Na₂SiO₃ on K deficiency-induced MDA accumulation. In addition to MDA, K deficiency also evoked accumulation of H₂O₂ in soybean leaves, and the increase in H₂O₂ concentrations was markedly reduced by Na₂SiO₃ (Fig. 2B). Although the K deficiency-induced elevation of H₂O₂ was reduced by addition of NaCl to the K-deficient medium (Fig. 2B), the reduction in H₂O₂ concentrations in K-deficient leaves by NaCl was significantly less than that caused by addition of Na₂SiO₃ (Fig. 2B). There was a significant increase in electrolyte leakage in soybean leaves when exposed to the K-deficient medium, and this increase was reversed by application of Na₂SiO₃ (Fig. 2C). Moreover, the K deficiency-dependent electrolyte leakage was attenuated by NaCl (Fig. 2C), but the effect of NaCl on electrolyte leakage was significantly less than that of Na₂SiO₃ (Fig. 2C). Similar ameliorative effects of Si on electrolytic leakage induced by salinity (Liang *et al.*, 2003), boron toxicity (Gunes *et al.*, 2007) and osmotic stress (Kaya *et al.*, 2006) have been reported. These results indicate that Si can stabilize the structure and integrity of plasma membranes by affecting the stress-dependent peroxidation of membrane lipids (Liang *et al.*, 2003). Similar to the present findings, Shin and Schachtman (2004) reported K deficiency-induced accumulation of H₂O₂ in *Arabidopsis* leaves. Potassium deficiency has been shown to elicit lipid peroxidation in mulberry (*Morus alba*) leaves, as evidenced by accumulation of MDA (Tewari *et al.*, 2007). Therefore, the present results indicate

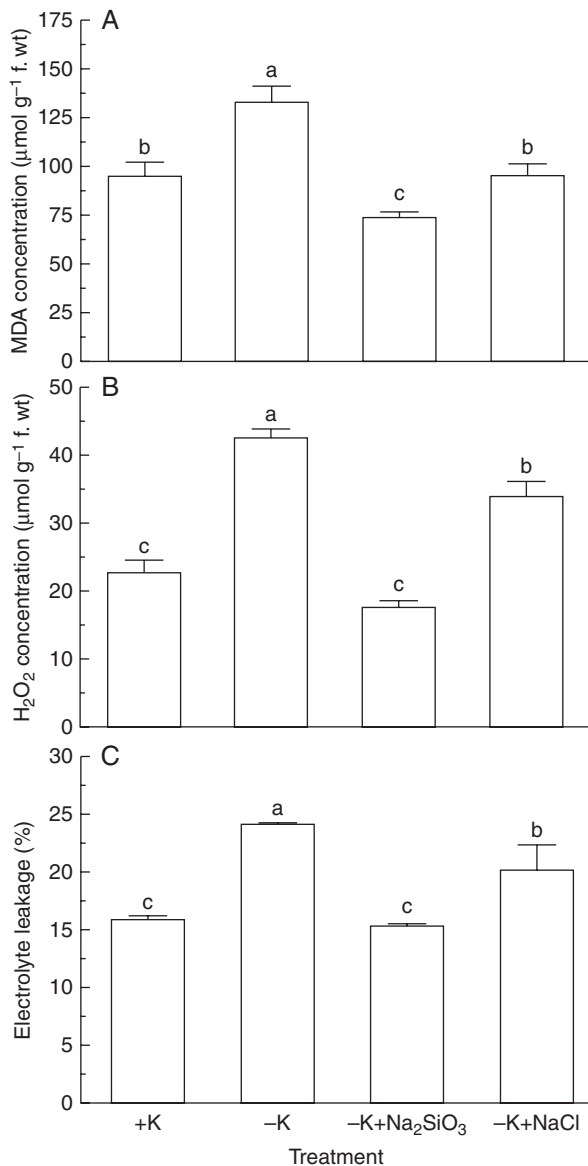


FIG. 2. Effects of K deficiency on accumulation of (A) malondialdehyde (MDA), (B) H₂O₂ and (C) electrolyte leakage of soybean seedlings in the absence and presence of Na₂SiO₃ and NaCl. Soybean seedlings were grown in 5 mM (+K) and 1 mM K (-K) supplemented with 2 mM Na₂SiO₃ or 4 mM NaCl for 60 d. Data are the mean \pm s.e. of four replicates. Different letters shown in the error bars indicate significant differences among control and treatments at $P < 0.05$.

that Si can effectively ameliorate membrane lipid peroxidation, thus protecting plants from oxidative stress.

Antioxidant enzyme activities

Previous studies have demonstrated that Si can reduce salinity-induced lipid peroxidation by regulating antioxidant enzymes in plants (Liang *et al.*, 2003). As Si reduced lipid peroxidation and H₂O₂ contents in K-deficient seedlings, the effect of K deficiency on activities of antioxidant enzymes in the absence and presence of Si was investigated. Activities of SOD, POD and CAT were increased substantially when

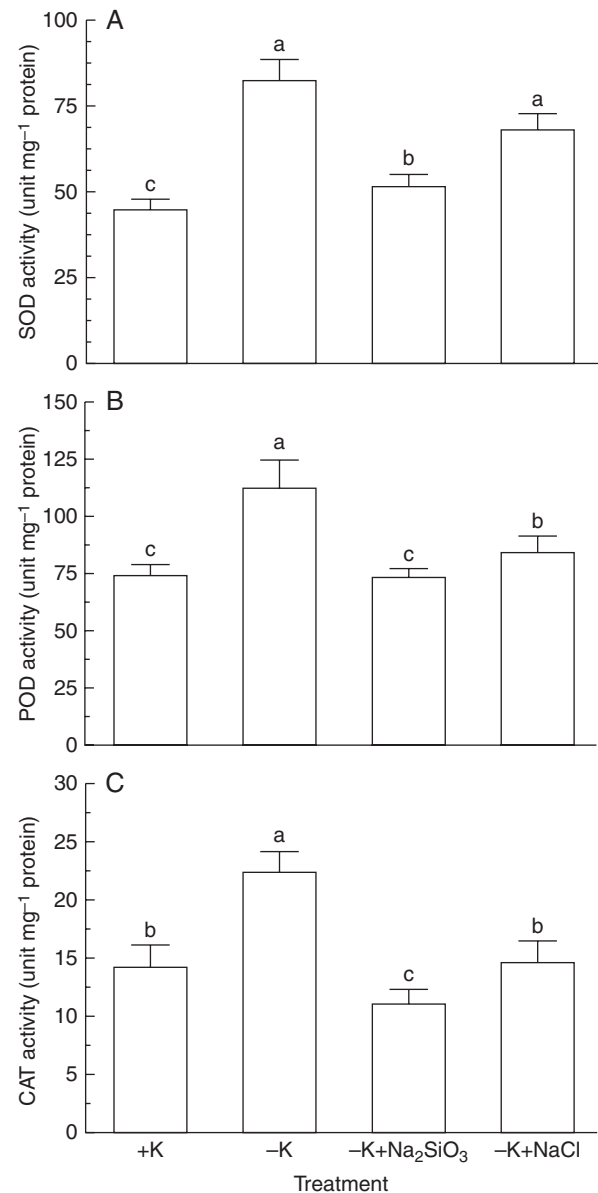


FIG. 3. Effects of K deficiency on activities of (A) superoxide dismutase (SOD), (B) peroxidase (POD) and (C) catalase (CAT) of soybean seedlings in the absence and presence of Na₂SiO₃ and NaCl. Soybean seedlings were grown in 5 mM (+K) and 1 mM K (-K) supplemented with 2 mM Na₂SiO₃ or 4 mM NaCl for 60 d. Data are the mean \pm s.e. of four replicates. Different letters shown in the error bars indicate significant differences among control and treatments at $P < 0.05$.

soybean seedlings were exposed to K-deficient medium (Fig. 3). The K deficiency-induced increases in activities of SOD, POD and CAT were inhibited markedly by addition of Na₂SiO₃ to K-deficient medium (Fig. 3A). In contrast to Na₂SiO₃, the K deficiency-induced increase in SOD activity was not affected by addition of NaCl to K-deficient medium (Fig. 3A). Activities of POD and CAT were reduced by addition of NaCl to the K-deficient medium, but the inhibitory effect of NaCl on K deficiency-induced increases in POD and CAT activities was significantly less than that of Na₂SiO₃ (Fig. 3B, C). Changes in antioxidant enzyme activities such as SOD,

POD and CAT have been widely reported in plants in response to deficiency in macronutrients, including K, to modulate toxic levels of ROS (Cakmak, 1994; Tewari *et al.*, 2004, 2007). For instance, a K deficiency-induced increase in SOD activity has been observed in mulberry (Tewari *et al.*, 2007) and maize leaves (Tewari *et al.*, 2004), while CAT was stimulated by K deficiency in maize leaves (Tewari *et al.*, 2004), but not in mulberry leaves (Tewari *et al.*, 2007). In contrast to the present findings, Tewari *et al.* (2004, 2007) noted that POD activity was not affected by K deficiency in both mulberry and maize. This discrepancy may be accounted for by the differences in plant species, K-deficient regimes and treatment periods. For instance, in the present study, soybean plants grown in 5 and 1 mM K medium were referred to as K-sufficient and K-deficient seedlings, respectively. In contrast, K deficiency was taken as removal of all K in the growth medium in both *Arabidopsis* (Shin and Schachtman, 2004) and mulberry (Tewari *et al.*, 2007). In addition, the relatively long-term effect of K deficiency on soybean seedlings (60 d) was investigated herein, whereas responses of *Arabidopsis* and mulberry to K starvation for 10 and 30 d were investigated, respectively (Shin and Schachtman, 2004; Tewari *et al.*, 2007). The longer treatment period with relatively high K concentrations employed here is of more physiological relevance, and thus the present findings may have important significance in farming practice. Moreover, the effects of Si on the K deficiency-induced changes in antioxidant enzyme activities, membrane lipid peroxidation and H₂O₂ concentrations are comparable with the effects of Si on those parameters evoked by boron toxicity (Gunes *et al.*, 2007). For instance, excess B-induced accumulation of H₂O₂ and MDA, and increased activities of SOD and CAT were markedly reduced by Si (Gunes *et al.*, 2007). The findings that Si alleviated K deficiency-induced oxidative damage to soybean plants by modulating antioxidant enzyme activities may underlie the observed ameliorative effect of Si on shoot and root growth (Table 1).

Conclusions

The present study demonstrates that application of Si to K-deficient medium markedly alleviated K deficiency-induced inhibition of both root and shoot growth in soybean seedlings. In addition, Si significantly enhanced K accumulation in soybean plants exposed to K-deficient medium, thus alleviating K deficiency-induced membrane lipid peroxidation and oxidative stress by modulating antioxidant enzymes. These results highlight that Si is not only involved in amelioration of nutrient toxicity, but can also improve nutrient use efficiency under nutrient-deficient conditions. These findings may also have important implications in agronomic practice to improve nutrient efficiency by application of Si fertilizer under nutrient-deficient conditions.

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LITERATURE CITED

- Cakmak I. 1994. Activity of ascorbate-dependent H₂O₂-scavenging enzymes and leaf chlorosis are enhanced in magnesium- and potassium-deficient leaves, but not in phosphorus-deficient leaves. *Journal of Experimental Botany* **45**: 1259–1266.
- Cakmak I. 2005. The role of potassium in alleviating detrimental effects of abiotic stresses in plants. *Journal of Plant Nutrition and Soil Science* **168**: 521–530.
- Epstein E, Bloom AJ. 2003. *Mineral Nutrition of Plants: Principles and Perspectives*, 2nd edn. New York: John Wiley & Sons.
- Giannopolitis CN, Ries SK. 1977. Superoxide dismutase in higher plants. *Plant Physiology* **59**: 309–314.
- Gong H, Zhu X, Chen K, Wang S, Zhang C. 2005. Silicon alleviates oxidative damage of wheat plants in pots under drought. *Plant Science* **169**: 313–321.
- Gunes A, Inal A, Baggi EG, Coban S, Pilbean DJ. 2007. Silicon mediates changes to some physiological and enzymatic parameters symptomatic for oxidative stress in spinach (*Spinacia oleracea* L.) grown under B toxicity. *Scientia Horticulturae* **113**: 113–119.
- Henning GH. 2003. The effect of potassium deficiency on growth and N₂-fixing in *Trifolium repens*. *Physiologia Plantarum* **129**: 440–449.
- Hodson MJ, Evans DE. 1995. Aluminum/silicon interactions in higher plants. *Journal of Experimental Botany* **46**: 161–171.
- Iwasaki K, Matsumura A. 1999. Effect of silicon on alleviation of manganese toxicity in pumpkin (*Cucurbita moschata* Duch cv. Shintosa). *Soil Science & Plant Nutrition* **45**: 909–920.
- Jordan-Meille L, Pellerin S. 2008. Shoot and root growth of hydroponic maize (*Zea mays* L.) as influenced by K deficiency. *Plant Soil* **304**: 157–168.
- Kaya C, Tuna L, Higgs D. 2006. Effect of silicon on plant growth and mineral nutrition of maize grown under water-stress conditions. *Journal of Plant Nutrition* **29**: 1469–1480.
- Liang YC. 1999. Effects of silicon on enzyme activity and sodium, potassium and calcium concentrations in barley under salt stress. *Plant Soil* **209**: 217–224.
- Liang YC, Chen Q, Liu Q, Zhang WH, Ding RX. 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 YC, Wong JWC, Wei L. 2005. Silicon-mediated enhancement of cadmium tolerance in maize (*Zea mays* L.) grown in cadmium contaminated soil. *Chemosphere* **58**: 475–483.
- Liang YC, Sun WC, Zhu YG, Christie P. 2007. Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: a review. *Environmental Pollution* **147**: 422–428.
- Liang YC, Zhu J, Li ZJ, *et al.* 2008. Role of silicon in enhancing resistance to freezing stress in two contrasting winter wheat cultivars. *Environmental and Experimental Botany* **64**: 286–294.
- Liebersbach H, Steingrobe B, Claassen N. 2004. Roots regulate ion transport in the rhizosphere to counteract reduced mobility in dry soil. *Plant Soil* **260**: 79–88.
- Lutts S, Kinet JM, Bouharmont J. 1996. NaCl-induced senescence in leaves of rice (*Oryza sativa* L.) cultivars differing in salinity resistance. *Annals of Botany* **78**: 389–398.
- Ma JF, Yamaji N. 2008. Functions and transport of silicon in plants. *Cellular and Molecular Life Science* **65**: 3049–3057.
- Mittler R. 2002. Oxidative stress, antioxidants and stress tolerance. *Trends in Plant Science* **7**: 405–410.
- Pettigrew WT. 2008. Potassium influences on yield and quality production for maize, wheat, soybean and cotton. *Physiologia Plantarum* **133**: 670–681.
- Qi Z, Spalding EP. 2004. Protection of plasma membrane K⁺ transport by the salt overly sensitive1 Na⁺-H⁺ antiporter during salinity stress. *Plant Physiology* **136**: 2547–2555.
- Rengel Z, Damon PM. 2008. Crops and genotypes differ in efficiency of potassium uptake and use. *Physiologia Plantarum* **133**: 624–636.
- Rus A, Lee BH, Munoz-Mayor A, *et al.* 2004. AtHKT1 facilitates Na⁺ homeostasis and K⁺ nutrition in planta. *Plant Physiology* **136**: 2500–2511.
- Shin R, Schachtman DP. 2004. Hydrogen peroxide mediates plant root cell response to nutrient deprivation. *Proceedings of the National Academy of Sciences USA* **101**: 8827–8832.

- Tewari RK, Kumar P, Tewari N, Srivastava S, Sharma PN. 2004.** Macronutrient deficiencies and differential antioxidant responses – influence on the activity and expression of superoxide dismutase in maize. *Plant Science* **66**: 687–694.
- Tewari RK, Kumar P, Sharma PN. 2007.** Oxidative stress and antioxidant responses in young leaves of mulberry plants grown under nitrogen, phosphorus or potassium deficiency. *Journal of Integrative Plant Biology* **49**: 313–322.
- Uchimura Y, Ogata T, Sato H, Matsue Y. 2000.** Effects of silicate application on lodging, yield and palatability of rice grown by direct sowing culture. *Japan Journal of Crop Science* **69**: 487–492.
- Vaculik M, Luxa A, Luxovac M, Tanimoto E, Lichtscheidle I. 2009.** Silicon mitigates cadmium inhibitory effects in young maize plants. *Environmental and Experimental Botany* **67**: 52–58.
- Veljovic-Jovanovic S, Noctor G, Foyer CH. 2002.** Are leaf hydrogen peroxide concentrations commonly overestimated? The potential influence of artefactual interference by tissue phenolics and ascorbate. *Plant Physiology and Biochemistry* **40**: 501–507.
- Wallace A, Romney EM, Muller RT. 1976.** Nitrogen–silicon interaction in plants grown in desert soil with nitrogen deficiency. *Agronomy Journal* **68**: 529–530.