SILICON EFFECTS ON LOBLOLLY PINE SEEDLING GROWTH AND WATER STATUS

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Abstract.--Silicon (Si) is found deposited within various tissues of many plants, including gymnosperms. The objectives of this investigation were: 1) to quantify Si accumulation in loblolly pine (*Pinus taeda* L.), and 2) to determine the effects of Si on growth, seedling water loss and water status concurrent with an induced water stress.

Silicon was administered to potted seedlings growing in a growth chamber as K2SiO3 (Si concentration = 0, 130, 389, and 648 nM) as a nutrient solution. Applications were either once or twice a week. Atomic absorption analysis revealed a three-fold accumulation for the fascicles of Si-treated seedlings compared to their controls.

Water stress was induced by withholding the water/nutrient solution. Silicon treatment stimulated: 1) increases in fascicle diffusive resistance, 2) decreases in transpiration rates, and 3) increases in fresh weight in water-stressed seedlings. Pressure-volume isotherm analysis showed that Si increased tissue elasticity in both water-stressed and non-stressed seedlings and symplastic weight of water in stressed seedlings. It was concluded that Si-induced increases in loblolly pine seedling growth may be the result of reduced water loss and increased tissue elasticity during water stress.

Additional keywords: silicon, growth, diffusive resistance, transpiration, elasticity.

Silicon (Si) deposition in plants has been reported for both herbaceous and woody species, in epidermal and endodermal tissue and within the vessels of shoots and roots (Yoshida and Kitagishi 1962, Jones and Hendreck 1967, Scurfield et al 1974). Silicon enters plants as a component of water-soluble monosilicic acid, H4SiO4, which is transported subsequently through the root, stem and leaves (Barber and Shone 1966). Aston and Jones (1976) noted that the sites and pathways of transpiration were sites of Si accumulation. They observed large amounts of Si around guard cells and subsidiary cells.

Werner and Ross (1983) reported that gymnosperms accumulate large quantities of Si. Other researchers have suggested a beneficial role for Si relative to growth (Lewin and Reiman 1969, Yoshida and Kitagishi 1962, Miyake and Takahashi 1978, Adatia and Besford 1986), water economy and/or drought resistance (Yoshida and Kitagishi 1962). Adatia and Besford (1986) observed increased fresh and dried weights of cucumber plants grown hydroponically in a Si-amended nutrient solution. Yoshida and Kitagishi (1962) found that

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transpiration in Si-sufficient rice plants was 30% less than in Si-deficient plants.

The physiological role of Si is not well established. Its function in plant growth and transpiration, especially for gymnosperms, needs clarification.

The objectives of this study were: 1) to measure Si in fascicle tissue of loblolly pine (*Pinus taeda* L.) which was absorbed from the nutrient media, and 2) to relate Si deposition in fascicles to growth, seedling water loss and tissue water status.

MATERIALS AND METHODS

BA3R13-41 originated from a typically xeric habitat in Texas, and M-2-C was selected from a mesic habitat in Mississippi. Seeds were first stratified for 30 to 45 days and planted either in 25 cm Ray-Leach containers containing medium-textured sand and located in a greenhouse, or in 7.5 x 7.5 x 25 cm Marx-5, Spenser Lamier single containers, containing fritted clay, and located in a growth chamber. Distilled water was applied to the containers every day until the seedlings produced their primary fascicles; thereafter, a nutrient solution was applied every day for five days. On the remaining two days of the weeks, distilled water was applied to avoid accumulation of mineral salts in the growing media. Seedlings in the sand medium were maintained in a greenhouse in this manner for nine months, and then transferred to the growth chamber. Seedlings in the fritted clay medium were maintained in the growth chamber from the beginning. The growth chamber had a photoperiod of 12 hours and a constant temperature of 25°C. Light intensity was 350 uE m^{-2} sec^{-1}

After four to six weeks in the growth chamber, Si treatments were initiated. Silicon, as K2SiO3 was added to the nutrient solution in concentrations of: 0, 130, 389, and 648 nM. Seedlings were treated once or twice a week at the respective concentrations prior to induction of water stress. Silicon applications were continued until experiments were concluded. Water stress was induced by withholding water for a period of either 4 days (for seedlings growing in sand) or 12 to 14 days (for seedlings growing in fritted clay). Each drying cycle was terminated when predawn fascicle water potential (TO of the representative seedlings reached -1.2 MPa. Fascicle T_w was determined using a pressure chamber. Drying cycles were repeated for a period of 5 to 26 weeks. At the end of each drying cycle, all seedlings were watered with nutrient solution, with or without the addition of Si, until the growth medium was fully saturated and the predawn $_{ww}$ reached -0.2 MPa.

Growth was determined by measuring turgid-fresh weight (W_o) of shoots and roots immediately before pressure-volume (P-V) analysis. Shoot and root dry weight (Wd) was determined by oven drying at 105°C. Diffusive resistance (r_w) and transpiration rates (T) were determined using a Li-Cor Steady State Porometer (Model LI-1600). Four seedlings with two fascicles/seedling were used for both r_w and T measurements. Measurements were begun 4 hours after initiation of the photoperiod and were taken at 1, 2, 3, and 4 days after watering. The weight-averaged bulk modulus of elasticity () and the symplastic weight of water (W_s) were determined by analyzing P-V isotherms (Emadian 1987). Silicon content in whole fascicles was determined using an atomic absorption spectrophotometer (Perkin Elmer, Model 603).

RESULTS AND DISCUSSION

Electron microscopy and x-ray analysis revealed that Si was deposited, exclusively within the epidermal cells of Si-treated fascicles, as clusters of small dark particles (Emadian 1987). Similar deposits were not observed in comparable tissues of control seedlings. Atomic absorption analysis revealed that the Si-treated fascicles accumulated 1.6 mg/gDW of Si, about three times more Si than did controls (0.5 mg/gDW) (Table 1). Presumably, the Si in fascicles of control plants was due to Si released from the sand, the media used for growing the seedlings.

Table 1. Silicon content (mg/g dry weight) in fascicles' free 18-month old loblolly pine seedlings.

Paired Sample	648 nM Si	Control (Si)
1	1.7	0.6
2	1.4	0.5
3	1.8	0.5
4	1.3	0.5
Mean	1.6a	0.5b

¯Each sample consisted of 1 g dried tissue. p — 0.05 using Duncan's Multiple Range Test. Treatments with the same letter in common are not significantly different.

Silicon increased both W_o and Wd of loblolly pine seedlings (Table 2). Although growth increases were only 6% for well watered seedlings, growth increased 32 to 36% when Si-treated seedlings were water-stressed.

Table 2. Growth parameters' for 5-month old loblolly pine seedlings grown in a Si-amended fritted clay medium and subjected to water stress.

Treatment	Fresh shoot weight (W_o, g)	Dry shoot weight (W_d, g)	Dry root weight (W_d, g)
+Si -WS	17.1a	4.6a	1.8a
-Si -WS	15.5a	4.1a	1.7a
+Si +WS	11.0b	3.0b	1.1b
-Si +WS	8.1c	2.2c	0.8c

'Values are means of 10 replicates. p = 0.5 using Duncan's Multiple Range Test. Treatments with the same letter in common are not significantly different. All comparisons are within columns.

Diffusive resistance was increased for all concentrations of Si and frequency of its application, and such increases were more pronounced as water stress developed further in the seedlings. An opposite pattern was observed

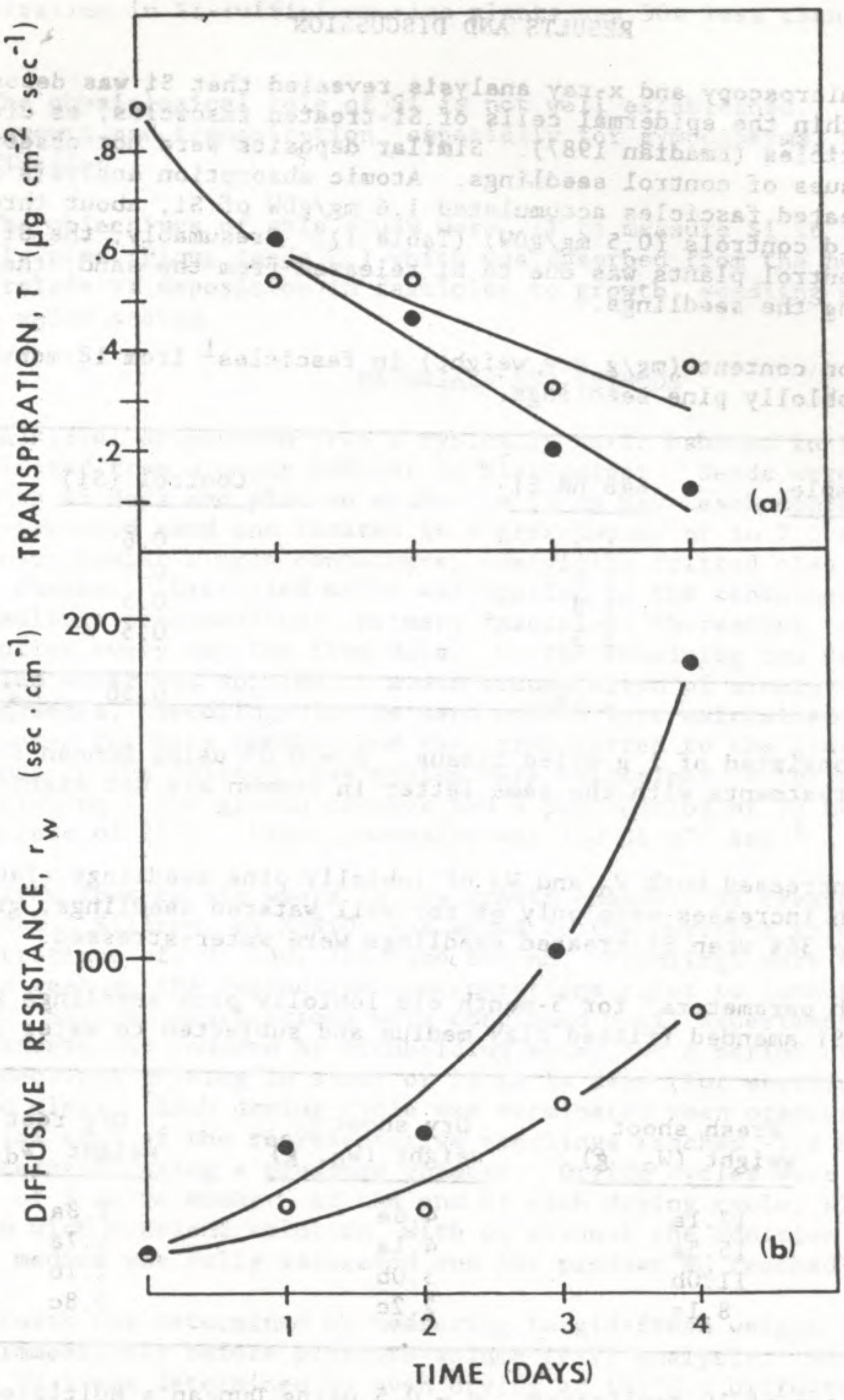

Figure 1. (a) Relationship between fascicle transpiration rate (T) of loblolly pine seedlings and time after watering with Si-amended nutrient solution for six months. (b) Relationship between fascicle diffusive resistance (r_w) of loblolly pine seedlings and time after watering with Si-amended nutrient solution for six months. 648 nM Si, twice per week; o----o control, 0 nM Si, twice per week. Seedlings growing in a sand medium.

with T (Figure 1). By the fourth day after watering, T was decreased more than 75% and r_w was increased 125% compared to controls.

Silicon at 648 nM, applied twice per week, increased shoot elasticity (reduced g) compared to controls (Table 3). This occurred under both stressed and non-stressed conditions. Oppositely, water stress decreased shoot elasticity (increased E) in the presence or absence of Si (Table 3). Silicon increased the symplastic weight of water (W_s) only in stressed seedlings whereas, water stress decreased W_s in both Si-treated and control seedlings (Table 3).

Table 3. Seedling water status parameters derived from pressure-volume isotherms after treatment with Si and/or water stress.

Treatment	Weight-average bulk modulus of elasticity ($\bar{\epsilon}$, MPa)	Symplastic weight of H_2O (W_s, g)
+Si -WS	3.9c	5.2a
-Si -WS	5.3b	5.2a
+Si +WS	4.7bc	4.0b
-Si +WS	6.4a	3.1c

p - 0.05 using Duncan's Multiple Range Test. Treatments with the same letter are not significantly different; all comparisons made within columns.

Although Si has not been conclusively established as an essential element, it is clearly beneficial to the growth of loblolly pine. Under an induced water stress, in a Si-amended soil, seedlings are better able to retain a greater propensity for increases in fresh weight growth. Increased seedling fresh weight appears to be related to increases in symplastic weight and reduced fascicle water loss during stress. Silicon-induced increases in shoot elasticity may also be one of the mechanisms by which increased symplastic weight of water is accomplished. More elastic tissues coupled with reduced water loss could result in larger cell volumes and larger overall fresh weight. Therefore, the long established preference of loblolly pine for sandy soils may well be due in part to the physiological role of Si. Furthermore, this study suggests that Si treatment of seedlings might provide enhanced survivability on drought-prone sites.

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