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Silicon-Induced Changes in Viscoelastic Properties of Sorghum Root Cell Walls

Taiichiro Hattori [1, 5], Shinobu Inanaga [1], Eiichi Tanimoto [2], Alexander Lux [3], Miroslava Luxová [4] and Yukihiro Sugimoto [1]

[1] *Arid Land Research Center, Tottori University, 1390 Hamasaka, Tottori, 680-0001 Japan*
[2] *Division of Information and Biological Sciences, Graduate School of Natural Sciences, Nagoya City University, Nagoya, 467-8501 Japan*
[3] *Department of Plant Physiology, Faculty of Natural Sciences, Comenius University, Mlynská dolina B-2, SK-842 15 Bratislava, Slovak Republic*
[4] *Institute of Botany, Slovak Academy of Sciences, Dúbravská cesta 14, SK-842 23 Bratislava, Slovak Republic*

Silicon is deposited in the endodermal tissue in sorghum (*Sorghum bicolor* L. Moench) roots. Its deposition is thought to protect vascular tissues in the stele against invasion by parasites and drying soil via hardening of endodermal cells. We studied the silicon-induced changes in mechanical properties of cell walls to clarify the role of silicon in sorghum root. Sorghum seedlings were grown in nutrient solution with or without silicon. The mechanical properties of cell walls were measured in three separated root zones: basal, apical and subapical. Silicon treatment decreased cell-wall extensibility in the basal zone of isolated stele tissues covered by endodermal inner tangential walls. The silicon-induced hardening of cell walls was also measured with increases in elastic moduli (*E*) and viscosity coefficients (η). These results provided new evidence that silicon deposition might protect the stele as a mechanical barrier by hardening the cell walls of stele and endodermal tissues. In contrast to the basal zone, silicon treatment increased cell-wall extensibility in the apical and subapical zones with concomitant decrease in *E* and η. Simultaneously, silicon promoted root elongation. When root elongation is promoted by silicon, one of the causal factors maybe the silicon-enhanced extensibility of cell walls in the growing zone.

Keywords: Cell wall — Extensibility — Growth — Root — Silicon — Sorghum.

Abbreviations: AE, apical elongation; AM apical maturation; BM, basal maturation; ITW, inner tangential walls.

Introduction

Silicon is the second most abundant element in the earth's crust (e.g. Ilea 1979). Although it has not been generally listed among the essential elements of higher plants, it has been demonstrated to be beneficial for the growth of plants, especially to plants in the family Gramineae (Matoh et al. 1991, Jarvis 1987). Most of the silicon absorbed by rice is transported to the shoot with the transpiration stream and accumulates as an insoluble gel in the epidermal tissue of leaf, leaf sheath, stem and ear, which are the marginal positions of the stream (Yoshida 1965). Even though only 2–3% or less of silicon is retained in the root, it seems to play several important roles there. It has been reported that silicon is deposited on the inner tangential walls (ITW) of root endodermal tissue in rice, sorghum and other gramineous species (Parry and Kelso 1975, Sangster and Parry 1976a). Silicon is deposited on the endodermal ITW in roots in an amorphous form and is called "silicon deposition" or "silicon aggregation". This deposition is distinguished from gel-form silicon accumulated in the shoot. Silicon deposition in sorghum roots has been well investigated anatomically by Parry and Kelso (1975), Sangster and Parry (1976a), Sangster and Parry (1976b), Sangster and Parry (1976c), Hodson and Sangster (1989a), Hodson and Sangster (1989b), and Hodson and Sangster (1993). In sorghum, the mechanical strengthening of root endodermal cell walls by silicon deposition is documented as being related to resistance to invasion by root parasites (Maiti et al. 1984). Lux et al. (1999) found, by anatomical analysis, that the intensity of silicification in the roots of rice was higher in an upland rice cultivar than in a lowland rice cultivar. Lux et al. (2002) further demonstrated that the drought-tolerant sorghum cultivar accumulated more silicon in roots than a drought-susceptible sorghum cultivar. They suggested that silicon deposition might be related to drought tolerance through the increase of resistance to radial water leakage of roots or to protection of stele tissues from mechanical damage caused by drying soil. However, the analytical observations are insufficient to confirm the physiological and/or mechanical roles of silicon deposition in roots. Thus, in the present report, we investigated the mechanical roles of silicon deposition. We studied the effects of silicon on the viscoelastic properties of cell walls by creep extension analysis (Tanimoto et al. 2000) in roots of sorghum (*Sorghum bicolor* (L.) Moench).

Results

Silicon-enhanced cell-wall extensibility

Table 1 shows the root length of sorghum on the 5th day after transplantation. Sorghum seedlings grown in the presence of silicon (silicon-plus treatment) had significantly longer roots

[5] Corresponding author: E-mail, hat@alrc.tottori-u.ac.jp; Fax, +81-857-29-6199.

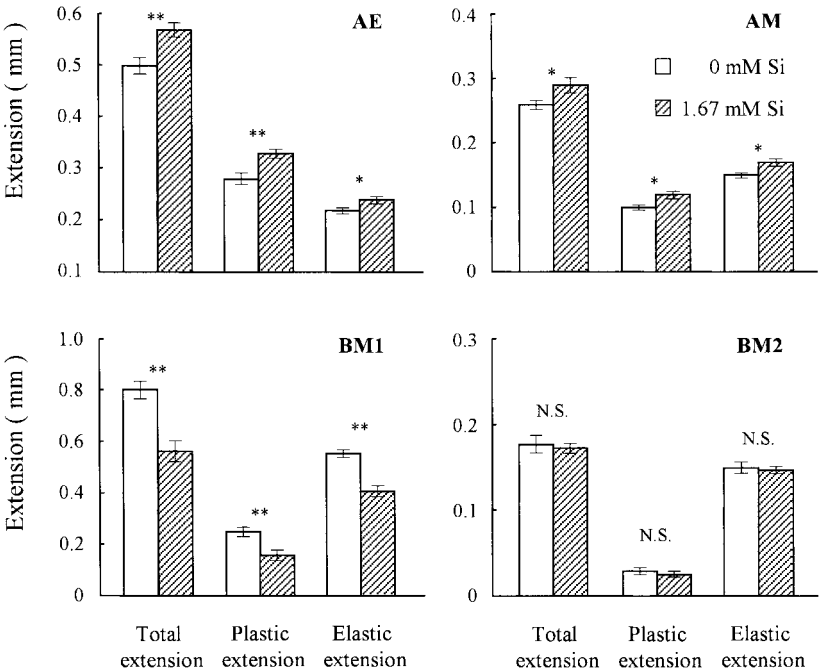

Fig. 1 Effects of silicon on cell-wall extensibility in different parts of a seminal root. Total extension was separated into plastic extension and elastic extension. The root zones and the load applied to each zone are as follows: AE, the apical elongation zone loaded 20 g mm^{-2} (n = 48 and 39 for the silicon-plus and -minus treatments, respectively); AM, the apical maturation zone of the root (20–30 mm from the tip) loaded 50 g mm^{-2} (n = 50 and 39, respectively); BM1, the basal maturation zone of stele covered by ITW endodermis loaded 50 g segment^{-1} (n = 24 and 23, respectively); BM2, the basal maturation zone without any tissue removed loaded 50 g segment^{-1} (n = 26 and 20, respectively). Data are means of 20–50 roots indicated by "n =" in each with vertical bars representing the standard error. N.S, Not significant by t-test; *, ** significant differences at 5% and 1% level by t-test, respectively.

(P<0.01) than those grown in silicon-free nutrient solution (silicon-minus treatment). Extensibilities of root cell walls in three different zones are shown in Fig. 1. The silicon-plus treatment increased the extensibility of cell walls in the apical elongation (AE) zone; reversible and irreversible extension increased about 9% and 15%, respectively, resulting in a 12% increase in the total extension (P<0.01). In the apical maturation (AM) zone, likewise, cell-wall extensibility increased with the silicon-plus treatment (P<0.05). In contrast to these apical zones, the silicon-plus treatment significantly decreased the cell-wall extensibility of stele tissues in the basal maturation (BM) zone; total extension decreased by 23% as a result of decreases in reversible and irreversible extensions (26% and 21%, respectively (P<0.01)). When whole BM segments with peripheral tissues were measured, no significant differences were observed between silicon-plus and silicon-minus treatments.

Comparison of physical parameters of cell walls

The extensibility of cell walls is described by physical

Table 1 Effect of silicon application on root length of sorghum grown in nutrient solution containing 0 and 1.67 mM SiO_2 on the 5th day after transplantation

SiO_2 concentration (mM)	Root length (mm)
0	166.6±3.4
1.67	180.5±3.8
	**

Data are means ± S.E. (n = 45 and 55 for silicon-plus and -minus treatment, respectively).
** Significant at 1% level by t-test.

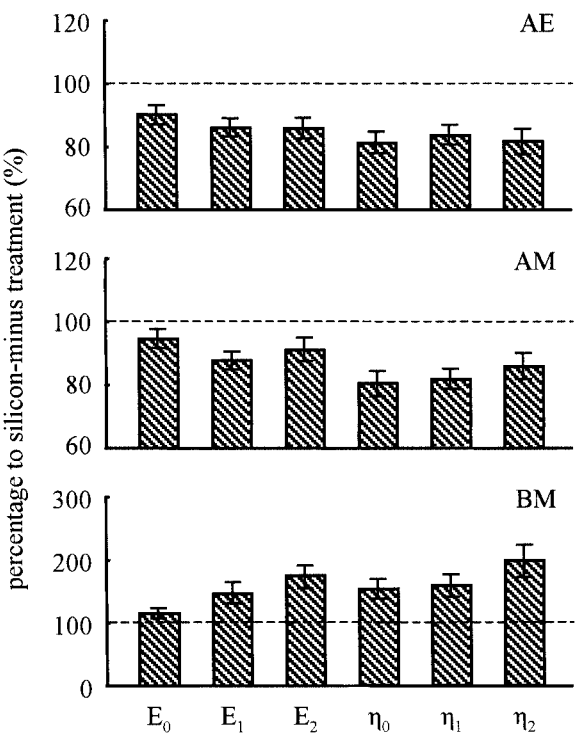

Fig. 2 Effects of silicon on the six viscoelastic parameters in different root zones. AE, Apical elongation zone; AM, apical maturation zone; BM, basal maturation zone. The extension curve of each root was analyzed by the six-element model shown in Fig. 4. The reciprocal values of six parameters were calculated to show that the greater the values the higher the extensibility of cell walls. The relative values (% of control in the silicon-minus treatment) were indicated. Data are means of 20–50 roots with the vertical bars representing the standard error.

Table 2 Effects of silicon application on distribution of six viscoelastic parameters in the AE zone (apical part of root) and the AM zone (subapical part, 20–30 mm from root tip)

Zone	SiO_2 concentration (mM)	E_0 ($\times 10^6$ N m^{-2})	E_1 ($\times 10^7$ N m^{-2})	E_2 ($\times 10^7$ N m^{-2})	η_0 ($\times 10^{10}$ pa s)	η_1 ($\times 10^8$ pa s)	η_2 ($\times 10^8$ pa s)
AE	0	2.63±0.11	2.12±0.08	2.39±0.10	1.18±0.06	8.02±0.33	1.01±0.05
	1.67	2.38±0.08	1.83±0.06	2.05±0.08	0.96±0.04	6.71±0.25	0.83±0.04
		*	**	*	**	**	**
AM	0	12.68±0.40	11.12±0.53	13.62±0.81	8.61±0.63	45.69±2.54	6.60±0.42
	1.67	11.97±0.39	9.76±0.31	12.41±0.51	6.93±0.34	37.63±1.47	5.62±0.27
		N.S.	*	N.S.	*	**	*

Data are means ± S.E. (n = 39–50).
N.S., Not significant; *, ** significant at 5% and 1% level by t-test, respectively.

parameters of the cell wall, namely elastic moduli (E_0, E_1 and E_2) and viscosity coefficients (η_0, η_1 and η_2). These parameters of the AE and AM zones are shown in Table 2 and those of the BM zone are shown in Table 3. The effects of silicon treatment on those parameters are shown in Fig. 2. Since all elastic moduli and viscosity coefficients are parameters of rigidity, the decrease in these values corresponds to the loss of rigidity or the increase in extensibility of cell walls.

Apical elongation zone (2.5–7.5 mm behind the tip) and apical maturation zone (22.5–27.5 mm behind the tip)—The silicon-plus treatment significantly decreased all six parameters in the AE zone (Table 2, Fig. 2). The effect of the silicon-plus treatment was relatively weaker in the AM zone. Four parameters were significantly decreased but the decreases in E_0 and E_2 were not significant at the 5% level. The effect of silicon treatment seemed to be clearer in η than in E. The differences of η_0 values between silicon-plus and silicon-minus treatments, especially, were higher than those of E_0, the former decreased about 20%, and the latter decreased 5–10%, respectively. The effects of silicon on values of E seemed to become weaker with the increase of the distance from the base.

Basal maturation zone (22.5–27.5 mm from root–stem junction)—In the case of the BM zone (stele tissues covered by endodermal ITW with cortex and epidermis removed), the silicon-plus treatment increased both η and E in contrast to those of the AE and AM zones (Table 2, 3, Fig. 2). The effect of the silicon-plus treatment on η_0 was clearer than on E_0 with 52% and 14% increases, respectively. On the other hand, effects of silicon on E_1 and η_1, E_2 and η_2 were almost the same.

Discussion

The role of silicon deposition in the root

It has been known that application of silicon increases resistance to diseases and keeps leaf blades erect in rice, wheat and other gramineous species. Mechanical hardening caused by silicon accumulation in shoot epidermal tissues provides crops with many beneficial effects. Silicon is also deposited on the

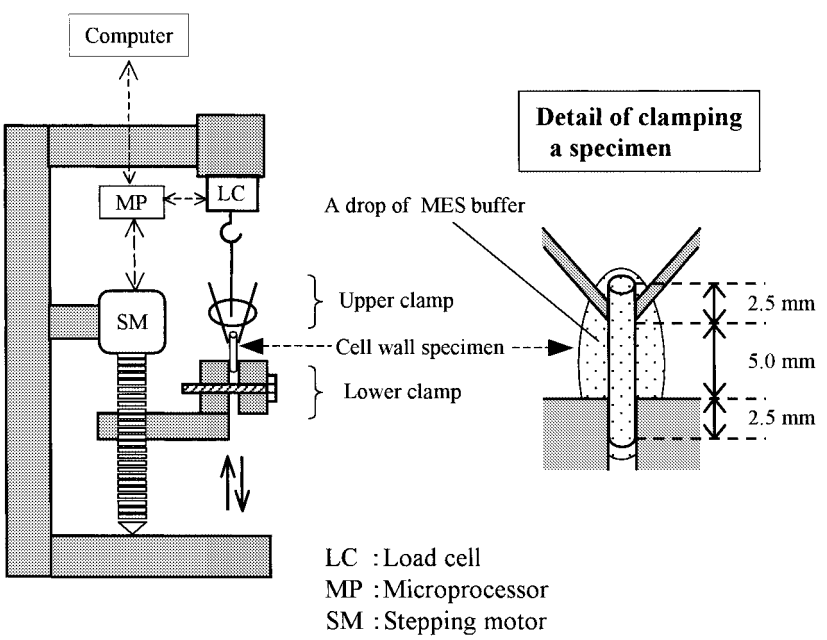

Fig. 3 Schematic illustration of the Rheoner creep meter and the clamping position of the cell-wall specimen. The microprocessor (MP) controls the up and down movement of the lower clamp which is driven by a stepping motor (SM). The movement is regulated by reading the digitized signal from the load cell (LC). The mode of these feed-back movements and the creep analysis of the data obtained are conducted by a computer system connected to the creep meter. The apical and basal 2.5-mm zones were pinched by the upper and lower clamps of a creep meter, respectively. The cell-wall specimen was kept in a drop of MES buffer during the measurement. (Modified from Tanimoto et al. 2000).

Table 3 Effects of silicon application on the distribution of six viscoelastic parameters in theBM1 segments (stele covered by the ITW of the endodermal cells)

Zone	SiO_2 concentration (mM)	E_0 ($\times 10^7$ N m^{-2})	E_1 ($\times 10^8$ N m^{-2})	E_2 ($\times 10^8$ N m^{-2})	η_0 ($\times 10^{11}$ pa s)	η_1 ($\times 10^{10}$ pa s)	η_2 ($\times 10^9$ pa s)
BM	0	8.50±0.34	2.97±0.16	2.68±0.19	1.56±0.07	1.10±0.10	1.00±0.09
	1.67	9.68±0.49	4.30±0.35	4.63±0.48	2.36±0.24	1.73±0.19	1.96±0.25
		*	**	**	**	**	**

Data are means ± S.E. (n = 24 and 23 for the silicon-plus and -minus treatments, respectively).
*, ** Significant at 5% and 1% level by t-test, respectively.

ITW of root endodermal cells. The physiological role of such silicon deposits in root is not well known. Maiti et al. (1984) and Lux et al. (1999) suggested that depositions of silicon on the endodermal ITW might protect vascular tissues against invasion by parasites and the effects of drying soil via mechanical hardening of root endodermal cells. Maiti et al. (1984) demonstrated that penetration by the haustorium of a parasite was not prevented by the peripheral tissues but was prevented by endodermal tissue which is highly thickened and has dense silicon depositions. The primary purpose of this study was to reveal whether or not silicon deposition changes cell-wall mechanical properties. To evaluate the effects of silicon deposition in stele tissues, measurements in the BM zone were partly performed on isolated stele covered by endodermal ITW with epidermal and cortical tissues removed. Silicon application increased elastic moduli (E) and viscosity coefficients (η) in these samples (Table 3). It was suggested that silicon depositions made cell walls of stele and endodermal tissues more rigid in the basal part of the sorghum root. The remarkable increase in mechanical parameters by silicon indicates that silicon deposited on the ITW of the endodermis makes it harder by increasing the viscosity coefficient, which is known to regulate irreversible extensibility of cell walls (Tanimoto et al. 2000). These results are compatible with the previous anatomical investigation of silicon deposition on endodermal ITW (Sangster and Parry 1976a, Sangster and Parry 1976b, Sangster and Parry 1976c). When whole root segments, with cortex and epidermis intact, were examined at the base, no significant effect caused by silicon was observed. Since cortical tissues occupy about 80% of the root cross-section in sorghum, the change in endodermal tissues due to silicon might be hidden by outer tissues which did not accumulate silicon (Fig. 1). We found for the first time that the mechanical hardening, i.e. the increase in E and η, of endodermal tissues was caused by silicon application to sorghum seedlings. These results provided evidence for the idea that silicon deposition in roots might protect the stele from invasion by parasites by being a mechanical barrier, as suggested by microscopic observation (Maiti et al. 1984, Lux et al. 1999).

Silicon-enhanced root elongation

The previous findings of Yoshida (1965) and the present study (Table 3; BM1) showed silicon-induced hardening of tissues. In contrast to them the silicon-plus treatment promoted root elongation and increased cell-wall extensibility in the apical part of the roots (Table 1, Fig. 1; AE and AM). These are new findings and they are compatible with the recent finding of silicon-induced growth promotion in etiolated young leaves of rice (Hossain et al. 2002a). Since the cell-wall extensibility and elongation growth of roots are strictly correlated (Tanimoto 1994, Tanimoto and Yamamoto 1997, Tanimoto et al. 2000), the silicon-enhanced cell-wall extensibility in the growing zone of the roots is probably one of the causal factors promoting root elongation (Fig. 1).

In the case of leaves (Hossain et al. 2002a), silicon application to rice promoted the elongation of leaf blades with a concomitant increase in cell-wall extensibility in its basal elongating zone. Although the mechanism of these growth-promoting effects of silicon, including our results, remains to be uncovered, it is commonly recognized that the promotive effects of silicon are restricted to young and immature tissues such as the apical part of the root and the basal part of the leaf in plants in Gramineae. These young tissues have flexible primary cell walls that are free from secondary thickening caused by maturation or deposition of some materials including silicon (Sangster and Parry 1976a). Therefore, the increase in extensibility of young elongating cell walls by silicon might be brought about by a silicon-induced decrease in thickness of the primary cell wall itself (Hossain et al. 2002b), the physiological mechanism of which is unknown. In the present study, the silicon-induced increase in plastic (irreversible) extension of cell walls is more remarkable than that of reversible extension (Fig. 1). Since the irreversible extensibility of cell walls, as regulated by the viscosity coefficient (η), was found to be strictly related to the acid-induced loosening of cell walls of pea roots (Tanimoto et al. 2000), the present promotion of root elongation by silicon may be brought about partially by an acid-induced decrease in viscosity coefficients of the elongating cell walls. Although the mechanism of silicon-enhanced irreversible extensibility of cell walls is unknown, Hossain et al. (2002a) found that the alkali-soluble hemicellulose fraction contained most of the silicon compounds in rice leaves. Pectin is also reported to be able to bind with silicon (Schwarz 1973, Scurfield et al. 1974). Hemicellulose and pectin in Gramineae differ from those of dicots and other monocots in their amount

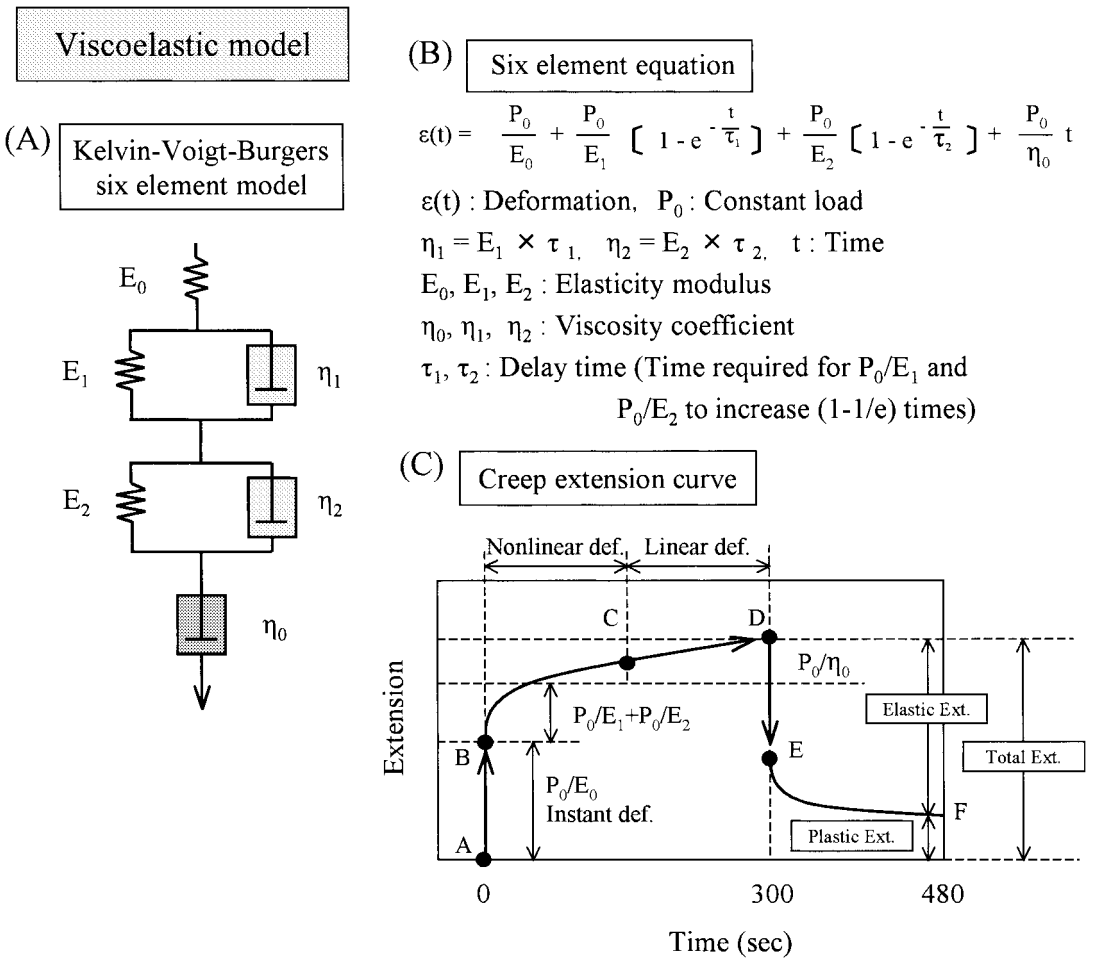

Fig. 4 A viscoelastic model and the equation for the creep extension analysis. (A) The Kelvin-Voigt-Burgers' six-element model is composed of one Hookean spring (E_0), one Newtonian dashpot (η_0) and two viscoelastic components (E_1, η_1 and E_2, η_2). (B) The equation for the six-element model. Deformation ($\varepsilon(t)$) of such a model under a constant load (P_0) is simulated by the equation of four members. (C) A typical creep extension curve during 300 s extension and 180 s shrinkage. The extension curve was analyzed using the method of Kamata et al. (1988). Linear instantaneous deformation (A to B), nonlinear deformation (B to C) and final linear deformation (C to D) were simulated with the equation (part B), and the physical parameters of the elastic moduli and viscosity coefficients were calculated. Total extension, plastic extension and elastic extension were also determined by reading the extensions at 300 and 480 s, respectively. (Modified from Tanimoto et al. 2000).

and chemical configuration. Cell walls of gramineous species are characteristically abundant in arabinoxylan, which is a heteropolymer composing hemicellulose, and have a smaller amount of polygalacturonic acid, which is a homopolymer-composing pectin (Carpita 1996). Since hemicellulose and pectin are major constituents of primary cell walls and their amount and molecular size change during root growth (Tanimoto and Huber 1997, Tabuchi and Matsumoto 2001), it is conceivable that silicon–hemicellulose and/or silicon–pectin conjugates cause the change in mechanical properties of root cell walls. The participation of pectin components to the mechanical properties of cell walls was also suggested by an in vitro model system (Chanliaud et al. 2002). Since gramineous species have an ability to absorb silicon actively from the rhizosphere, silicon concentration in plant sap rises drastically (Ma and Takahashi 2002). Such a silicon-concentrated condition in gramineous plants might facilitate the interaction of silicon molecules with cell-wall components and the formation of a silicon body. Although the physiological mechanisms remained to be uncovered, silicon plays two separate functions in root cell walls, strengthening the endodermal cell walls in the mature basal region and keeping the young expanding cell walls extensible in the apical region of the roots. By combining the two effects of silicon, our results may indicate that the application of silicon seems to be quite beneficial to plants grown under drought conditions by encouraging the development of a big root system and providing protection to roots against drying soil (Hattori et al. 2001).

Materials and Methods

Plant material and growth condition

Seeds of the drought-tolerant cultivar (*Sorghum bicolor* L. Moench, cv. Gadambalia) were provided by the Soil & Water Research Center, Agricultural Research Corporation, Sudan. Seeds were imbibed in distilled water for 24 h and allowed to germinate between filter papers for 3 days at 27°C in the dark. Seedling roots, 50–70 mm long, were selected and 10 seedlings each were transplanted into plastic containers with 3 liters of nutrient solution. Hydroponic culture was conducted in a controlled environmental chamber (type GC-A, Fuji Electric Co. Ltd., Tokyo Japan). Light and temperature conditions in the chamber were set to 14/10 h cycles of 35/25°C (day/night). Relative humidity was set at 30/40% (day/night). The photosynthetically active photon flux density was applied at 1,240 μmol m^{-2} s^{-1}.

Silicon treatment

Sorghum seedlings were grown hydroponically in half-strength Hoagland and Arnon nutrient solution with or without 1.67 mM SiO_2. Application of SiO_2 to the solution was conducted following the method of Okuda and Takahashi (1961). The pH of the solution was adjusted to 6.0 with 0.2 M KOH and 0.2 M HCl. To avoid the mechanical damage of sorghum root by agitation, a culture solution was replaced every day and kept without bubbling air through it. Seedlings with 170–220 mm long seminal roots were selected and harvested on the 5th day after transplantation. Then, three separate zones of the roots, each 10 mm long, were excised from the apical 10 mm zone (AE zone), from the 20–30 mm zone behind the root tip (AM zone) and from the 20–30 mm basal zone measured from the root–stem junction (BM zone). Epidermal and cortical tissues were removed by forceps from half of the BM segments to obtain stele tissues with the ITW of the endodermal tissues exposed. Excised root specimens were killed immediately in boiling methanol kept in a water bath at about 80°C for 300 s. Then root segments were washed twice with fresh methanol and stored in methanol at 4°C ready for measurement of cell-wall extensibility. Thirty to forty root segments were used for the measurements of mechanical properties and the experiments were duplicated.

Measurement of mechanical properties of root cell walls

Viscoelastic properties of cell walls—Creep extension analysis was carried out according to the method described by Tanimoto et al. (2000) to measure physical properties of cell walls. Methanol-killed root segments were rehydrated with MES buffer (pH 6.0) and extended in the Rheoner II creep meter (Yamaden RE-33005, Tokyo) (Fig. 3). The extension curve was measured for 300 s at a constant load and the shrinkage after removing the load was also recorded for 180 s. The extension of the cell wall was expressed as a non-linear creep extension curve (Fig. 4C). The dynamic nature expressed by this non-linear extension profile was simulated by a Kelvin-Voigt-Burgers' six-element model which is composed of three springs and three dashpots as shown in Fig. 4A. In this model, springs are ideal elastic bodies that extend in a moment by loading, and piston-like dashpots are ideal viscous bodies that extend at a constant rate under a constant load. The characteristics of these springs and dashpots decide the shape of the creep curve. Using this model, the non-linear extension profiles of cell wall are expressed by a mathematical equation (Six-element equation; Fig. 4B). Creep extension curves were able to be simulated by four-, six- and eight-element models in the Rheoner II creep meter. In the preliminary measurement of sorghum roots, most showed good fitting to the six-element model by the computer program installed in the creep meter, which analyzes the creep curve by four-, six- and eight-element models sequentially for detecting a linear portion of the curve on a logarithmically converted extension curve.

Measurement and analysis by a creep meter—The diameter of the root was measured in the extension zone under a stereomicroscope to obtain the cross area of the root. The root was fixed between two clamps of a creep meter. The extension zone of the root was kept in a drop of the MES buffer solution between two clamps to keep the cell-wall specimen wet during measurement (details in Fig. 3). The apical and basal 2.5-mm portions of the specimen were nipped by an upper and a lower clamp, respectively, leaving the central 5-mm zone for extension. The measurements were carried out at room temperature. A constant load was applied to the root by moving the lower clamp downward at a maximum speed of 0.5 mm s^{-1}. The movement of the lower clamp is controlled by communication of the load cell and stepping motor in a creep meter so that the load applied to roots was kept constant. The amount of load was determined based on the results of the preliminary experiment to test the breaking load of roots. The amounts of load applied to the AE and AM zones were 20 and 50 g mm^{-2}, respectively. For BM segments, a 50-g load was applied to all segments because cell walls of this zone were very hard compared with those of the AE and AM zones. Although this load corresponded to 800 g mm^{-2}, it was used to obtain suitable extension for determination of viscoelastic parameters of cell walls in the BM zone. The extension process was recorded by a computer at 0.5-s intervals for 300 s and then the load was released to record the shrinkage of the root for 180 s. The data were analyzed by a computer program using Kelvin-Voigt-Burgers' viscoelastic model to calculate the three elastic moduli (E_0, E_1 and E_2) and the three viscosity coefficients (η_0, η_1 and η_2) involved in the equation shown in Fig. 4B. These viscoelastic parameters corresponding to each element are shown in Fig. 4A. These parameters were calculated first by the program installed in the creep meter as described by Kamata et al. (1988) and by Tanimoto et al. (2000). In order to obtain the parameters with higher precision, they were then recalculated again with a non-linear least square method, using the first obtained value as the initial value for each calculation. The maximum length of the specimen at 300 s and the final length at 480 s were read to calculate the total extension, the reversible extension (elastic extension) and the irreversible extension (plastic extension). Data were analyzed statistically by using a *t*-test to evaluate the effects of applying silicon.

Acknowledgments

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