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Silicon Suppresses Fusarium Crown and Root Rot of Tomato

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Abstract

Fusarium oxysporum f.sp. *radicis-lycopersici*, the causal agent of Fusarium crown and root rot (FCRR), is a serious soilborne disease of tomato. Soil fumigation and host resistance may reduce the impact of this disease, but other alternative management strategies are needed because these options may not always be available or effective. The purpose of this study was to determine the potential of silicon (Si) to reduce the disease severity of FCRR. Seven-day-old seedlings of Bonny Best tomato, susceptible to FCRR, were transplanted in sand culture amended with Hoagland's nutrient solution with (+Si) or without (−Si) 100 mg Si/l. At 3 weeks after transplanting, three inoculum concentrations 0, 10^6 and 10^7 conidia/plant were used to inoculate the seedlings. Disease severity and silicon concentration were evaluated at 4 weeks after inoculation. Disease progress over time was investigated using the seedlings amended with Si or without Si and inoculated with 0 or 10^6 conidia/plant. Disease severity was evaluated at 2, 3, 4 and 6 weeks after inoculation. After rating disease, evaluated plants were divided into shoots and roots for silicon concentration analysis. Si significantly reduced the severity of FCRR on the stem of tomato at 4 weeks after inoculation. Results of disease progress suggested that the decrease in the disease severity of FCRR by Si amendment was probably due to a delay in onset in initial infection of roots and the movement of the pathogen from roots to stems. Si contents of roots and shoots were significantly higher in tomato plants supplied with Si than in those without Si. Moreover, the increase in the Si content of roots was significantly correlated with the reduction of disease severity of root, crown and stem, indicating a silicon-mediated resistance. Supplying Si to tomato seedlings can reduce the disease severity of FCRR, providing an alternative disease management strategy.

Introduction

Fusarium oxysporum f.sp. *radicis-lycopersici*, the causal agent of Fusarium crown and root rot (FCRR), is an important soilborne pathogen of tomato (Jarvis and Shoemaker 1978; Katan et al. 1991). This pathogen has been found in many tomato production regions of the world, even though it is a relatively newly identified pathogen (Katan et al. 1991). No physiological races have been reported, but considerable genetic diversity in the pathogen population is revealed by the existence of many vegetative compatibility groups (VCGs) (Katan et al. 1991; Katan and Katan 1999). The pathogen can be introduced to new tomato-growing regions by means of infected seeds, transplants, soil and media (Jarvis 1988; Hartman and Fletcher 1991; Menzies and Jarvis 1994). Once introduced, this polycyclic pathogen can be disseminated via root-to-root contact, dispersal of airborne conidia, water flow and fungus gnats of the genus *Bradysia* (Rowe et al. 1977; Jarvis 1988; Hartman and Fletcher 1991; Gillespie and Menzies 1993; Rekah et al. 1999), resulting in a difficult challenge of controlling this disease.

The tomato production area in the world has been increasing as the tomato consumption increases at an average rate of 3% annually (Nicola et al. 2009). However, FCRR has become more common in both greenhouse and field tomato production, reducing the yield up to 15–65% (Ozbay and Newman 2004). Soil fumigation has been investigated to manage this disease (Marois and Mitchell 1981; McGovern et al. 1998; Hibar et al. 2007), but social and environmental concerns have caused the phaseout of certain chemicals such as methyl bromide. The disease may become more of a problem in tomato production with the adoption of organic and other low-input production strategies. Other management strategies may become more important for managing this disease. Biopesticides such as *Trichoderma harzianum*, *Fusarium equiseti* and *Glomus intraradices* have been evaluated for

controlling FCRR (Datnoff et al. 1995; Horinouchi et al. 2008). However, the efficacy of these microorganisms for biocontrol is affected by their ability to multiply rapidly in fumigated soils, to efficiently and effectively colonize roots, or establish their population in the rhizosphere, and to suppress the population reestablishment of *F. oxysporum* f.sp. *radicis-lycopersici* (Marois and Mitchell 1981). Further research in biological control needs to be conducted for application in the field, especially in non-fumigated soils (Datnoff et al. 1995). The use of resistance cultivars is effective for controlling FCRR. However, the *Frl* resistance gene conferring resistance to FCRR is only deployed in a few new cultivars (Scott 2008). Susceptible cultivars with satisfactory horticultural traits are still being used by tomato growers. Moreover, the potential exists that resistance might be matched by novel virulent races due to the evolutionary potential of the pathogen and environmental conditions (McDonald and Linde 2002). Based on the aforementioned, alternative and environment-friendly approaches for managing FCRR need to be evaluated.

Silicon (Si) has been used to moderate biotic and abiotic stresses on tomato (Peaslee and Frink 1969; Al-Aghabary et al. 2004; Dannon and Wydra 2004; Diogo and Wydra 2007), even though tomato is unable to accumulate a considerable amount of this element in comparison with rice, cucumber and a number of other crop species (Ma et al. 2001). Si may accumulate in the cytoplasmic fraction or cell walls of roots in tomato and other plant species (Heine et al. 2005). If so, the reinforcement of root cell walls caused by Si accumulation may affect the penetration of *F. oxysporum* f.sp. *radicis-lycopersici* because the pathogen penetrates the epidermis of tomato roots directly and afterwards produces intracellular and intercellular hyphae in the outer parenchyma of cortical tissues beneath the penetrated sites (Brammall and Higgins 1988). Likewise, resistant cultivars can form a defensive barrier in the parenchyma cells and prevent the pathogen from spreading towards the central vascular bundle (Brammall and Higgins 1988; Xu et al. 2006). As with the defensive barrier induced in the resistant cultivar, Si influences the creation of a physical barrier and also mediates other defence responses in the host (Datnoff et al. 2007; Cai et al. 2009).

Si-mediated resistance in tomato may not be located in the roots. For example, Si-mediated resistance in tomato against *Ralstonia solanacearum* is probably located in stem tissues due to changes in the pectic polysaccharide structure of stem cell walls, restricting the bacterial movement to the stems (Diogo and Wydra 2007). Interestingly, Si significantly decreased the bacterial population in roots and stems of the resistant cultivar, Hawaii 7998, in comparison with the cultivar without Si. These results suggested that Si-mediated resistance may also exist in tomato roots. Recently, Si has been shown to significantly suppress Phytophthora blight on pepper, a plant species closely related to tomato, as a result of increasing the concentration of Si in roots (French-Monar et al. 2010). However, it has not been previously established whether the Si content of roots in tomato has the potential to suppress FCRR disease severity development.

The objectives of this study were (i) to investigate effects of Si and inoculum concentrations on disease severity of FCRR, (ii) to evaluate the effect of Si on disease progress and (iii) to determine the relationship between disease development (on roots, crowns and stems) and the Si content of roots and shoots.

Materials and Methods

Plant growth and silicon amendment

Seeds of the tomato cultivar 'Bonny Best', susceptible to FCRR, were soaked in 1% (v/v) sodium hypochlorite (NaOCl) for 2 min for surface sterilization and then washed several times with sterile water. The sterilized seeds were sowed in a commercial growth medium (Metro Mix 300; Palmetto, FL). One week after sowing, seedlings at the cotyledon stage were transplanted to 150-mm-diameter plastic pots (Hummert International, Earth City, MO, USA) filled with 1.5 kg sand provided by the University of Florida Turfgrass Research Envirotron. Sand substrate was used as the growing medium because silicic acid in the soil solution is considerably so low that only very small amounts of silicon can be absorbed by plant roots (Whittenberger 1945). Two tomato seedlings were planted in each pot. The seedlings were grown in a growth chamber held at 20°C (12-h light photoperiod with photonflux of 70.7 μmol/m^2/s). Hoagland's nutrient solution (Hoagland and Arnon 1950) without (−Si) or with (+Si) 100 mg Si/l (3.56 mM) as sodium metasilicate nonahydrate ($Na_2SiO_3{\cdot}9H_2O$) (Epstein 1994) was adjusted to pH 5.0 using 36 N sulphuric acid (H_2SO_4) before applying it to tomato plants as lowering the pH of growing media increases the disease severity of FCRR (Jones et al. 1993). The nutrient solution contained N 224 mg, P 62 mg, K 235 mg, S 32 mg, B 0.5 mg, Mn 0.5, Zn 0.05, Cu 0.02, Mo 0.01 mg and Fe 1.56 mg/l and was prepared using deionized water. Tomato plants in each pot were fertigated with 50 ml of nutrient solution with and without Si every other day within 18 days after transplanting, and then the solution was applied daily 1–3 days later. Thus, a total of 600 ml of nutrient solution with or without Si was applied to the plants before inoculating with the pathogen for all experiments described elsewhere. Deionized water was used to irrigate tomato plants as needed.

Inoculum production and inoculation procedure

Isolate CL-0601, belonging to VCG 0098 of *F. oxysporum* f.sp. *radicis-lycopersici*, was used in this study due to its high virulence revealed by a previous study (Huang 2009). Depending on the experiment, 10 ml of a conidial and mycelial fragment suspension with 10^5 and/or 10^6 conidia/ml, recovered from 14-day-old cultures grown on carnation leaf agar (CLA),

was placed on crowns using a pipette with sterile tips at 3 weeks after transplanting. The inoculated plants were placed in a completely randomized design in an incubator at 20°C with 12-h light photoperiod (photonflux of 70.7 μmol/m^2/s).

Effects of silicon and inoculum concentration

A factorial design of six treatments with five replicates (10 plants) was arranged in a completely randomized design in the incubator: (i) plants with silicon, treated with sterile water (+Si − FORL), (ii) plants with silicon, inoculated with *F. oxysporum* f.sp. *radicis-lycopersici* at a concentration of 10^6 conidia/plant (+Si + FORL1), (iii) plants with silicon, inoculated with *F. oxysporum* f.sp. *radicis-lycopersici* at a concentration of 10^7 conidia/plant (+Si + FORL2), (iv) plants without silicon, treated with sterile water (−Si− FORL), (v) plants without silicon, inoculated with *F. oxysporum* f.sp. *radicis-lycopersici* at a concentration of 10^6 conidia/plant (−Si + FORL1), and (vi) plants without silicon, inoculated with *F. oxysporum* f.sp. *radicis-lycopersici* at a concentration of 10^7 conidia/plant (−Si + FORL2). At 4 weeks after inoculation, all plants were harvested, washed and rated for disease severity and then divided into shoots and roots for silicon quantification.

Effect of silicon on disease progress over time

To further investigate and confirm the effect of silicon on FCRR, another experiment was conducted on disease progress over time using partial treatments of the aforementioned factorial design: +Si − FORL, +Si + FORL1, −Si − FORL and −Si + FORL1. Ten plants of each treatment were evaluated for disease severity as well as divided into shoots and roots for silicon concentration analysis at 2, 3, 4 and 6 weeks after inoculation.

Disease assessments

Three disease severity ratings were used to independently evaluate roots, crowns and stems. Root infection was rated visually as the percentage of roots showing discoloration. Brown discoloration in crowns was scored according to a 0–4 scale: 0 = no symptom; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%; and 4 = 76–100%. Disease severity in stems was defined as the ratio of the lesion length divided by the stem length. The area under disease progress curve (AUDPC) was calculated as previously described (Shaner and Finney 1977) for studying the effect of silicon on disease progress over time. Diseased plants were sampled to confirm the presence of the inoculated isolate, CL-0601, using vegetative compatibility grouping (Correll et al. 1987).

Determination of dry root and shoot weight and silicon quantification

After rating for disease severity, plants were divided into shoots and roots, washed in deionized water and dried separately in paper bags for 72 h at 80°C (Isotemp Oven; Fisher Scientific, Pittsburgh, PA, USA). Dry roots and shoots were weighed, ground using a Cyclotec™ 1093 sample mill (FOSS, Denmark), passed through a 40-mesh screen and stored in 20-ml plastic scintillation vials (Fisher Scientific, Pittsburgh, PA, USA). Si analysis was conducted as previously described (Elliott and Snyder 1991) using a colorimetric analysis with a modification of the digestion procedure of plant tissues. One hundred milligrams of plant tissues was used for digestion in a 100-ml plastic high-speed polypropylene copolymer tube (Fisher Scientific, Pittsburgh, PA, USA) using 2 ml of 30% H_2O_2 and 3 ml of 100% NaOH. The tube was then placed in a 100°C water bath for one hour to initiate the tissue digestion before autoclaving for 20 min. If necessary, an additional amount of 30% H_2O_2 was added and the autoclave cycle was repeated until the tissues were completely digested.

Statistical analysis

All data collected were subjected to analysis of a factorial experiment in SAS v. 9.2 (SAS Institute, Cary, NC, USA) using PROC GLM to evaluate the effects of Si and inoculum concentration and their interaction. Standard analysis of variance (ANOVA) was also performed. Treatment mean comparisons were made using Fisher's protected least significant difference test (FLSD) at $P \leq 0.05$. Regression analysis was performed to determine the relationship between silicon content and disease severity using SIGMAPLOT version 10.0 (Systat Software, Chicago, IL, USA).

Results

Effects of Si and inoculum concentration

Compared to the −Si treatment, the application of Si significantly increased the concentration and uptake of Si in shoots and roots by 119–300% at the time of inoculation and by 101–144% at the time of harvest (Table 1). Si supply also significantly enhanced dry weight of roots by 20.8%, but no significant difference was detected for dry weight of shoots and total dry weight per plant between +Si and −Si treatments (Tables 1 and 2). The effect of inoculum concentration significantly affected dry weight, silicon uptake of roots and shoots and Si concentration in the shoots. Although no significant interaction was revealed between Si and inoculum effects for these plant components, a significant interaction was observed for Si uptake of the shoot (Table 2).

The application of Si significantly decreased disease severity of the stems at 4 weeks after inoculation, although disease severity of the root and crown was not significantly affected by Si supply (Tables 3 and 4). No significant interaction between Si application and inoculum concentration was detected, suggesting that the response to inoculum concentration was consistent between +Si and −Si treatments. At 4 weeks after inoculation, disease severity of both the root and crown was not significantly different between the two inoculum concentrations, 10^6 and 10^7 conidia/plant,

Table 1
Effect of silicon (Si) applications on Si concentration, dry weight and Si uptake of tomato inoculated with *Fusarium oxysporum* f.sp. *radicis-lycopersici* at the time of inoculation (week 0) and the time of harvest (week 4)

	Shoot			Root			
Treatments	Dry weight (g/plant)	Si concentration (mg/g dw)	Si uptake (mg)	Dry weight (g/plant)	Si concentration (mg/g dw)	Si uptake (mg)	Total dry weight (g)
Week 0							
Without Si	0.30	0.31	0.09	0.03	1.51	0.06	0.34
With Si	0.39	0.95	0.36	0.06	3.31	0.21	0.45
FLSD ($P \leq 0.05$)	0.16	0.25	0.11	0.02	0.43	0.09	0.17
Week 4							
Without Si	1.62	0.45	0.73	0.24	0.77	0.18	1.86
With Si	1.65	0.92	1.53	0.29	1.55	0.44	1.94
FLSD ($P \leq 0.05$)	0.14	0.11	0.17	0.04	0.13	0.06	0.17

FLSD, Fisher's least significant difference.

Table 2
Analysis of variance for effects of silicon (Si) supply and inoculum concentration (IC) on plant components

		F valuesa						
		Shoot			Root			
Source of variation	df	Dry weight (g/plant)	Si concentration (mg/g dw)	Si uptake (mg)	Dry weight (g/plant)	Si concentration (mg/g dw)	Si uptake (mg)	Total dry weight (g)
Si	1	0.15ns	74.3***	98.9***	5.69*	156***	78.1***	0.83ns
IC	2	18.5***	5.49*	26.7***	24.9***	1.37ns	15.5***	23.7***
Si × IC	2	0.84ns	2.05ns	6.75**	0.48ns	0.89ns	2.14ns	0.31ns

aLevels of probability: ns, not significant, *≤ 0.05, **≤ 0.01 and ***≤ 0.001.
df, degrees of freedom.

Table 3
Analysis of variance of effects of silicon (Si) supply and inoculum concentration (IC) on components of disease development

		F valuesa		
		Disease severity		
Source of variation	df	Root	Crown	Stem
Si	1	0.16ns	0.01ns	5.15*
IC	2	55.6***	146***	215***
Si × IC	2	0.10ns	0.01ns	2.26ns

aLevels of probability: ns, not significant, *≤ 0.05, **≤ 0.01 and ***≤ 0.001.
df, degrees of freedom.

Table 4
Disease severity of tomato plants amended with or without sodium metasilicate (Na_2SiO_3) at 4 weeks after inoculation with *Fusarium oxysporum* f.sp. *radicis-lycopersici*

	Disease severity[a]		
Treatments	Root	Crown	Stem
Without Si	44.7	1.80	27.7
With Si	42.3	1.80	23.7
FLSD ($P \leq 0.05$)	12.1	0.31	3.63

[a]Root infection was rated visually as the percentage of root system showing discoloration; disease severity of crown was evaluated using a 0-4 scale where 0 represents health and 4 means 100% discoloration; stem discoloration was defined as the ratio of the lesion length in stem divided by the stem length.
FLSD, Fisher's least significant difference.

but the latter significantly caused larger stem lesions (Table 5).

Effect of Si on disease progress

Similar positive effects of Si on plant components were observed as in the aforementioned experiment. For example, the application of Si significantly increased the dry weight of roots (23.8%) and the concentration and uptake of Si in shoots (283 and 372%, respectively) and in roots (251 and 334%, respectively) at the time of inoculation (Figs 1 and 2). However, the +Si treatment did not significantly affect the dry shoot weight at any investigation time (Fig. 1).

An apparent delay in disease onset was observed in roots, crowns and stems (Fig. 3). Root discoloration was not observed for the +Si treatment but was evident for the −Si treatment at 2 weeks after inoculation. Moreover, the +Si treatment significantly decreased root infection by 82.1% at 3 weeks after inoculation (Fig. 3). The onset of crown discoloration was delayed in tomato plants that received Si, and a significant decrease in the disease severity of the crown was observed in tomato plants amended with Si up to 4 weeks after inoculation. As with the other two disease ratings, stem discoloration was delayed in tomato

Table 5
Effect of inoculum concentration on disease severity of tomato plants at 4 weeks after inoculation with *Fusarium oxysporum* f.sp. *radicis-lycopersici*

Inoculum concentration (conidia/plant)	Disease severity[a]		
	Root	Crown	Stem
0	0	0	0
10^6	62.0	2.6	35.9
10^7	68.5	2.8	41.2
FLSD ($P \leq 0.05$)	14.8	0.38	4.46

[a]Root infection was rated visually as the percentage of root system showing discoloration; disease severity of crown was evaluated using a 0-4 scale where 0 represents health and 4 means 100% discoloration; stem discoloration was defined as the ratio of the lesion length in stem divided by the stem length.
FLSD, Fisher's least significant difference.

plants amended with Si and a significant decrease in the disease severity of the stems was observed at 4 weeks after inoculation. However, no significant difference was detected between −Si and +Si treatments at 6 weeks after inoculation (Fig. 3).

Si supply significantly lowered the AUDPC value for disease severity of the stem by 52.5%, although the value for disease severity of the root and crown was not significantly different between −Si and +Si treatments (Table 6). Regression analysis was used to further analyse the effect of silicon on FCRR development in the root, crown and stem. The results showed that a linear model best described the relationship between silicon content of roots and disease severities of roots, crowns and stems (Fig. 4). Regression analysis also suggested that disease severity decreased consistently with increasing silicon content of the roots. Interestingly, the linear model also best described the relationship between silicon content of shoots and disease severity of stems ($R^2 = 0.469$, $P = 0.029$, not shown), suggesting that disease severity of stem decreased consistently with increasing silicon content of shoots.

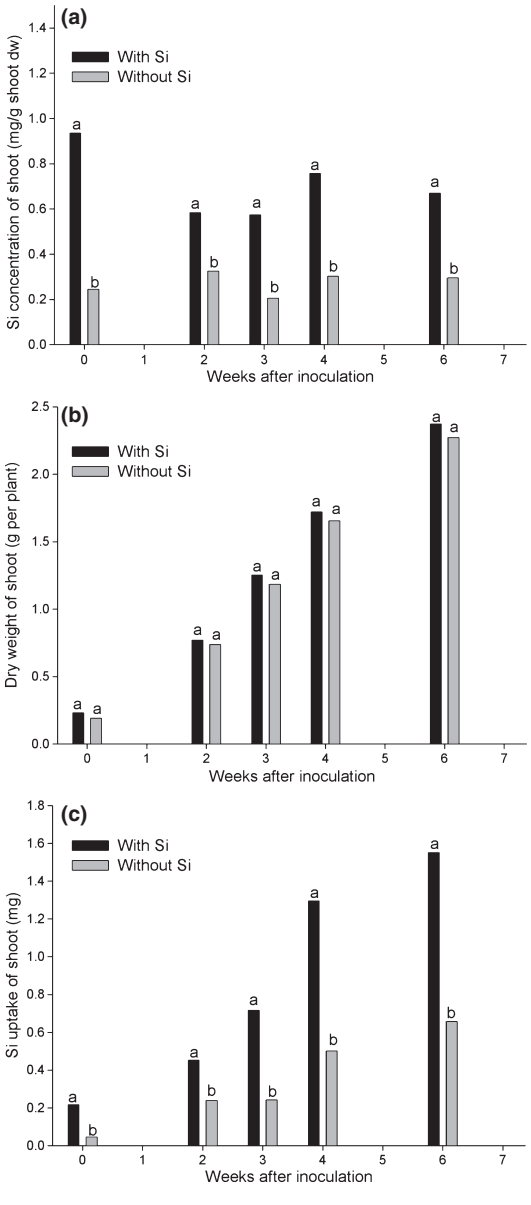

Fig. 1 Effect of silicon (Si) on Si concentration (a), dry weight (b) and Si uptake (c) of the tomato shoot. Bars with the same letter at each time period do not differ significantly at $P \leq 0.05$ as determined by Fisher's protected least significant difference test

Discussion

Because no conclusive effect of silicon on FCRR development was previously found due to inconsistent results from previous experiments (J. Menzies, personal communication; Menzies et al. 2001), to our knowledge, this is the first study to positively demonstrate that Si fertilization may suppress FCRR development. In our experiments, Si delayed disease onset, resulting in reduced disease severity at 4 weeks after inoculation (Fig. 3). As long as a Si fertilizer was being applied, a moderate level of control of FCRR was exerted up to 4 weeks. However, this protection disappeared at 6 weeks after Si fertilization stopped. Interestingly, regression analysis showed that the increase in the Si content of roots was significantly correlated with the reduction of disease severity of roots, crowns and stems (Fig. 4). These findings suggested that a silicon-mediated resistance and/or reduction of fungal colonization in tomato plants amended with Si occurred.

Formation of a physical barrier has been proposed to explain Si-mediated resistance (Yoshida et al. 1962; Datnoff et al. 2007; Cai et al. 2009). Si can accumulate and deposit beneath the cuticle to form a cuticle −Si double layer, preventing leaves from the penetration of pathogens (Samuels et al. 1991; Datnoff et al. 2007). Although physical barriers in roots may not be associated with silicon-mediated resistance in tomato to *Ralstonia solanacearum*, a vascular limited bacterial pathogen, Si fertilization was observed to trigger changes in the pectic polysaccharide structure of tomato stem cell walls (Diogo and Wydra 2007). The structural change induced by Si in the stem cell walls

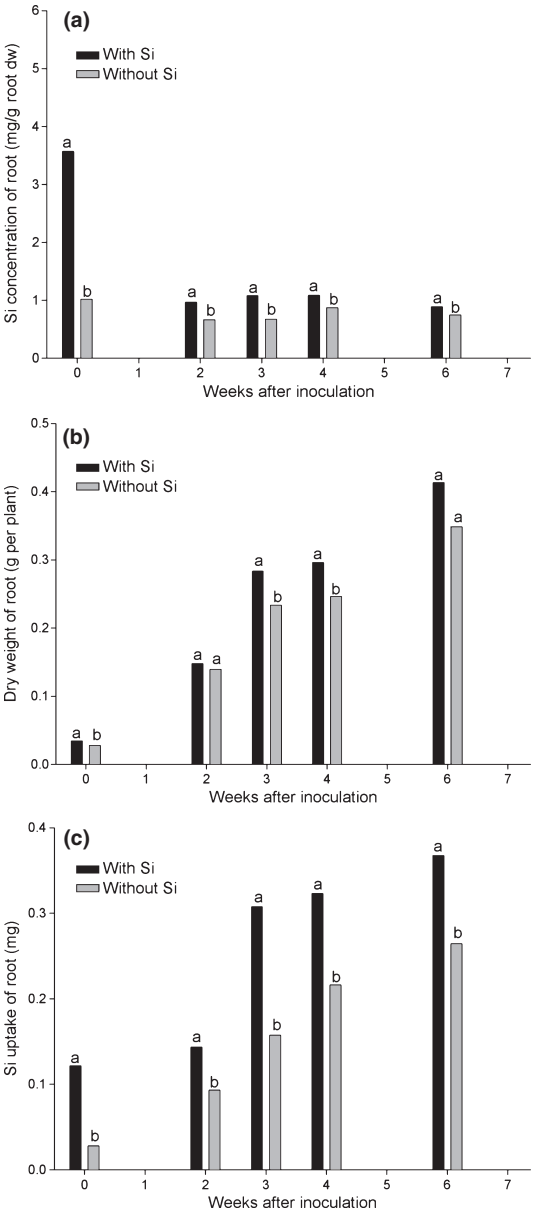

Fig. 2 Effect of silicon (Si) on Si concentration (a), dry weight (b) and Si uptake (c) of the tomato root. Bars with the same letter at each time period do not differ significantly at $P \leq 0.05$ as determined by Fisher's protected least significant difference test

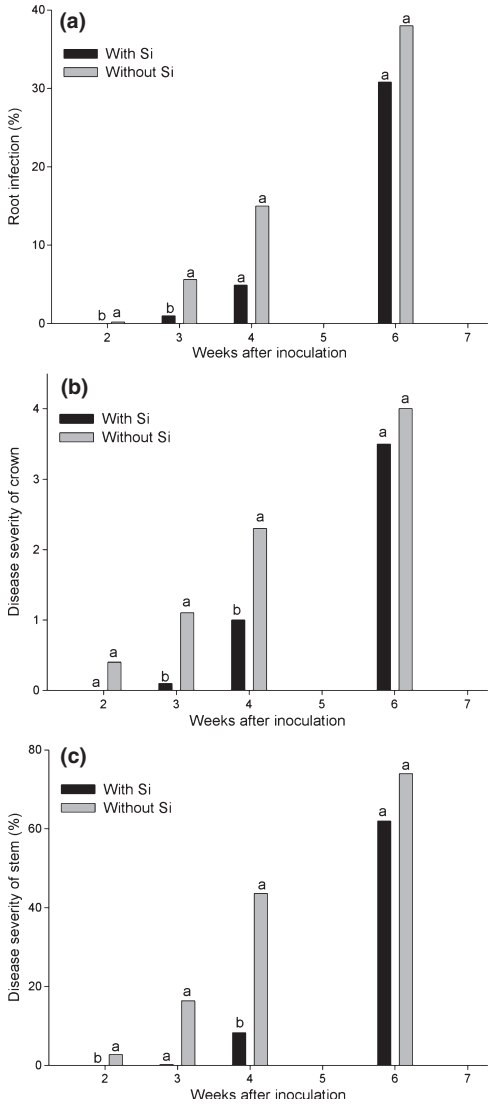

Fig. 3 Effect of silicon on symptom development of Fusarium crown and root rot expressed as root infection (a), disease severity of crown (b) and of stem (c) on tomato cultivar Bonny Best over 6 weeks after inoculation. Bars with the same letter at each time period do not differ significantly at $P \leq 0.05$ as determined by Fisher's protected least significant difference test

Table 6
Area under disease progress curve (AUDPC) of tomato plants amended with or without sodium metasilicate (Na_2SiO_3) and inoculated with *Fusarium oxysporum* f.sp. *radicis-lycopersici*

	AUDPC[a]		
Treatments	Root	Crown	Stem
Without Si	66.2	8.76	157
With Si	39.2	5.10	74.6
FLSD ($P \leq 0.05$)	49.1	4.47	78.3

[a]AUDPC was calculated using the formula: $\Sigma([(x_i + x_{i-1})/2](t_i - t_{i-1}))$ where x_i is the rating at each evaluation time and $(t_i - t_{i-1})$ is the time between evaluations.
FLSD, Fisher's least significant difference.

has been suggested to be associated with the capability of the plant to restrict the bacterial movement from roots to stems (Diogo and Wydra 2007). Our study also suggested that the +Si treatment likely limited the basipetal spread of *F. oxysporum* f.sp. *radicis-lycopersici* from infected roots (Fig. 3), although the reinforcement in cell walls of tomato roots was not evaluated. Interestingly, a significant relationship between silicon content of shoots and disease severity of stems was exhibited ($R^2 = 0.469$, $P = 0.029$, not shown), suggesting that Si concentration of the stem may be associated with the movement of the pathogen in stems. Due to Si accumulation mainly in the cell-wall fraction of tomato roots (Heine et al. 2005) and unclear mechanisms of Si-mediated resistance in tomato, it is pertinent to further investigate the physical barrier, biochemical and molecular mechanisms

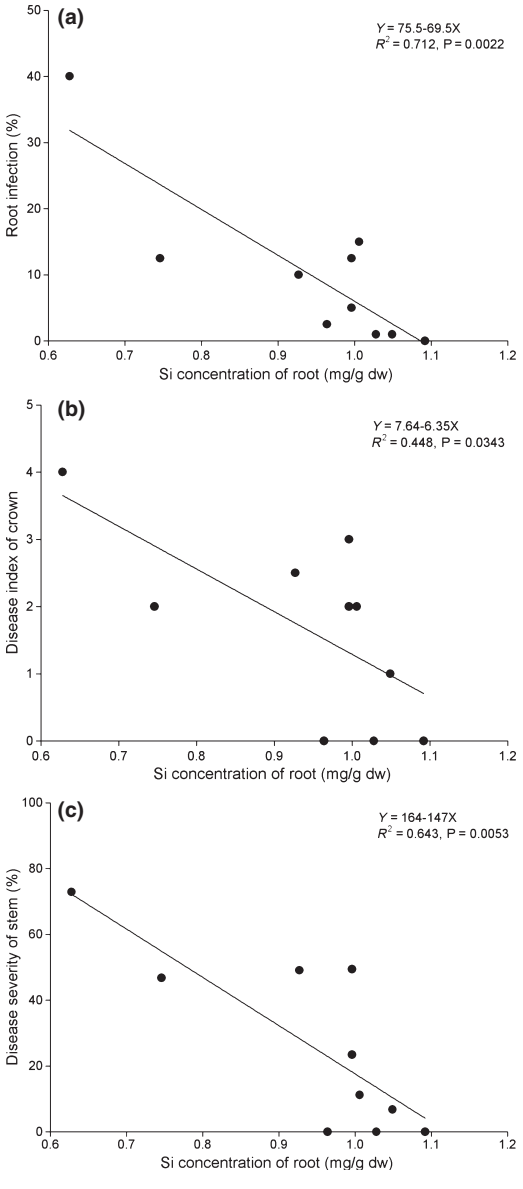

Fig. 4 Relationship between root infection (a), disease severity of crown (b) and stem (c) and silicon concentration of tomato root at 4 weeks after inoculation with *Fusarium oxysporum* f.sp. *radicis-lycopersici*

involved in silicon-mediated resistance (Datnoff et al. 2007; Cai et al. 2009) to *F. oxysporum* f.sp. *radicis-lycopersici*.

Inoculum concentration significantly affected the disease severity of the roots, crowns and stems, whereas no significant interaction was revealed between Si and inoculum levels (Table 3), suggesting that the response to inoculum concentrations was consistent between +Si and −Si treatments in this study. In other words, the effect of Si was not significantly impacted by the inoculum level. When the effects of Si and inoculum concentration were analysed separately for their individual impact on disease severity, the +Si treatment significantly reduced the disease severity of the stem but not the root or crown. This result suggested that disease progress already had reached the stem at 4 weeks after inoculation and that the pathogen had proliferated in roots and crowns overwhelmingly and was no longer affected by Si (Table 4). Levels of inoculum concentration also significantly affected disease progress. The disease severity of the stem in plants inoculated with 10^7 conidia/plant was significantly higher than in those inoculated with 10^6 conidia/plant, whereas no significant difference was shown for the disease severity of either roots or crowns between these two inoculum concentrations (Table 5). These results suggested that the inoculum concentration of 10^7 conidia/plant might have a greater infection rate compared with that of 10^6 conidia/plant.

Inoculum concentration of 10^6 conidia/plant was selected for studying disease progress to corroborate the effect of Si on FCRR as it was closer to initial inoculum density for disease onset under field conditions (Rekah et al. 2001). Results of the disease progress study suggested that the decrease in disease severity caused by the +Si treatment was due to delaying the onset in initial root infection and the subsequent movement of the pathogen from the roots to the stems (Fig. 3). Tomato plants treated with Si did not show any visible symptoms of discoloration in the roots, crowns and stems until 2 weeks after inoculation, while those without Si supply had very apparent brown lesions. The disease severity of roots showed a significant difference between −Si and +Si treatments at 3 weeks after inoculation as a result of significant variance in Si content of roots (Figs 2 and 3). These findings suggested that soilborne diseases may be reduced using Si fertilizers for Si low-accumulating plants with a limited capacity to accumulate Si in roots and inefficient translocation of this element to shoots.

Although tomato has a lower efficiency in the radial transport of Si, the presence of the transporter gene in roots has resulted in the concentration of Si in the root-cell symplast being higher than that of the external solution (Mitani and Ma 2005). The release of Si from the cortical cells to the xylem (xylem loading) is probably mediated by passive diffusion due to a defective or an absence of the transporter for the xylem loading in tomato (Ma and Yamaji 2008). These findings suggest that the Si concentration is higher in the root than that in the shoot of tomato. Results of this study found that Si is mainly accumulated in the tomato root (Table 1, Figs 1 and 2), which is in agreement with previous studies (Dannon and Wydra 2004; Heine et al. 2005; French-Monar et al. 2010). Si amendment significantly increased Si contents in both the roots and shoots, even though tomato is unable to uptake a large amount of Si compared with rice and cucumber (Ma et al. 2001). Infection by *F. oxysporum* f.sp. *radicis-lycopersici* did not increase the Si accumulation in tomato, whereas cucumber plants accumulated more Si around penetration sites (Chérif et al. 1991). In this study, tomato plants were pretreated with Si, but Si application was discontinued after inoculation, resulting in a rapid decrease in Si contents of roots and shoots during incubation (Figs 1 and 2).

A rapid decline of Si-mediated resistance to *Sphaerotheca fuliginea* was observed after transferring cucumber plants treated with Si to Si-free solution (Samuels et al. 1991), and this was also found in the *Pythium aphanidermatum*/bitter gourd system (Heine et al. 2007). The availability of soluble silicic acid, but not the total Si concentration in roots, at the time of infection has been suggested as the main contributor to Si-mediated resistance (Chérif and Belanger 1992). Although Si accumulates in the cell-wall fraction of roots in tomato (Heine et al. 2005), it is not clear whether the continual application of Si after inoculation may increase the availability of soluble silicic acid and enhance Si-mediated resistance to FCRR.

Although Si is not defined as being an essential nutrient for plants, it has been suggested that it is an essential element involved in the physiology of tomato growth through phytohormone synthesis (Ma and Takahashi 2002). In this study, 3.56 mM Si was added to Hoagland's nutrient solution, whereas 1 mM Na_2SiO_3 was previously recommended to maintain normal plant biology (Epstein 1994). Si significantly increased dry root weight, whereas no significant difference was shown for dry shoot weight between −Si and +Si treatments. In addition to Si-mediated resistance, the dry weight of roots was increased by amending the plant with Si, suggesting that Si application may also benefit tomato plants by enhancing normal physiology (Epstein 1999). For example, root biomass enhanced by Si amendment may affect the release of exudates to the rhizosphere in which beneficial microorganisms can use them as a primary food source. Consequently, these exudates may enhance the population density and activity of these microorganisms, reducing the ability of the pathogen to infect the roots of the plant (Raaijmakers et al. 2009). Because Si has been reported to mitigate biotic and abiotic stresses on tomato (Peaslee and Frink 1969; Al-Aghabary et al. 2004; Dannon and Wydra 2004; Diogo and Wydra 2007), how to apply Si fertilizers for field-grown tomatoes is worthy of being further investigated. The results presented herein show that supplying Si to tomato seedlings can reduce the disease progress of FCRR, suggesting that Si may be integrated with other management strategies to reduce losses caused by this disease.

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