Resistance

Effects of Soluble Silicon on the Parasitic Fitness of *Sphaerotheca fuliginea* on *Cucumis sativus*

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ABSTRACT

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The effects of silicon treatment of cucumber on four components of parasitic fitness of *Sphaerotheca fuliginea* (a causal agent of powdery mildew of cucumber) were examined. Cucumber plants were treated with nutrient solutions amended with different concentrations of soluble silicon and selected leaves inoculated with known concentrations of conidia of the pathogen. Colony number per leaf, colony area per leaf, and the germination of conidia collected from inoculated leaves were significantly reduced with increasing silicon concentration in the nutrient solutions. The area of individual colonies was also reduced as silicon concentrations in the nutrient solutions increased from 0.05 to 4.10 mM. The decrease in receptivity of plants to mildew infection was apparently due to silicon accumulation in leaves and was not related to cation or ionic strength effects of the silicon treatments.

Silicon (Si) has been shown to decrease the receptivity of some plants to fungal pathogens. For example, the severity of disease incited by *Pyricularia oryzae* Cavara (the causal agent of rice blast) has been reported to decrease with an increasing Si content of rice tissue (3,16). A decreased severity of powdery mildew caused by *Erysiphe graminis* DC. f. sp. *tritici* Em. Marchal (13) and *E. g.* DC. f. sp. *hordei* Ém. Marchal (7) has also been associated with an increased Si content of wheat and barley tissues, respectively.

Miyake and Takahashi (14) and Adatia and Besford (2) reported a decrease in colony number per leaf and percentage of leaf area covered by powdery mildew in naturally infected cucumber treated with Si. The data are limited to the two concentrations of Si used in each experiment (0 and 1.7 mM and 0.17 and 1.7 mM, respectively). However, mildew observations were not a major focus of the work and only rough estimates of disease severity were made. To our knowledge, these are the only studies describing the effects of Si on mildew in a dicotyledonous plant.

The purposes of this study were to examine the effects of a range of Si concentrations on four components of parasitic fitness (colony number per leaf, colony area per leaf, individual colony size, and the germination of conidia collected from colonies produced on inoculated leaves) of *Sphaerotheca fuliginea* (Schlech.: Fr.) Poll. inoculated at known rates on cucumber; and to establish whether the effects of soluble silicon on parasitic fitness of *S. fuliginea* were attributable to Si per se, or to other aspects of the Si treatment.

MATERIALS AND METHODS

Long English cucumber (*Cucumis sativus* L. 'Corona') (DeRuiter Seeds Inc., Columbus, Ohio) was used in all experiments. Seeds were sown in rock wool cubes (Grodan, Roermond, Holland), watered with tap water, and grown for 2–3 wk (to the point of expansion of the first true leaf) under greenhouse conditions prior to being transplanted into horticultural grade sawdust. In British Columbia, the latter is a common growth medium for greenhouse cucumbers. This growth medium is composed of sawdust from Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (1). The plants were then grown under greenhouse conditions (average temperature of 20–25 C, average humidity of 50–75%) and watered daily with treatment solutions.

Experiment 1. Cucumber seedlings (10 per treatment) were grown in a base nutrient solution, typically used in sawdust culture, containing, in mM, 13.0 NO_3, 1.5 H_2PO_4, 7.0 K, 3.5 Ca, 1.0 Mg, 1.5 SO_4, and, in μM, 18.8 Fe, 5.5 Mn, 0.9 Zn, 0.2 Cu, 18.1 B, and 0.1 Mo. The nutrient solutions were prepared using tap water (0.5 mM of Si) and amended with 0, 0.45, 0.9, 1.35, and 1.8 mM of Si as Na_2SiO_3 (also amended with 0, 0.85, 1.7, 2.55, and 3.4 mM of Na, respectively). Final pH was adjusted to 6.0, with 10 N H_2SO_4 contributing from 1.5 to 3.3 mM of additional SO_4; the amount increased with Si concentration. Final ionic strength (measured as electrical conductivity) of the solutions ranged from 2.0 mS/cm at low Si concentration to 2.3 mS/cm at high Si concentration. In all experiments, the Si content of the nutrient solutions was monitored by spectrophotometric analysis (4).

Conidia of powdery mildew were collected from naturally infected leaves of cucumber plants and identified as *S. fuliginea* by using conidial characteristics (5). Infected leaves were shaken 48 hr prior to harvest of the conidia to dislodge old conidia and to ensure that the conidia used for inoculation had a high level of viability. The conidia were spray-inoculated onto the fully expanded second leaf of each plant as 1 ml per leaf of a 1,000 conidia per milliliter suspension in Fluorinert (FC-43; 3M Canada Inc.). The plants were arranged in a completely randomized design on a greenhouse bench. The leaves were harvested 10 days postinoculation and the following components of parasitic fitness of *S. fuliginea* were assayed: individual colony size, number of colonies per leaf, colony area per leaf, and the percent germination of conidia.

After determining colony number, the leaves were fixed to a sheet of paper and photocopied. The colonies highlighted on the photocopy were drawn onto acetate sheet overlays that were run through a Li-Cor 3000 portable area meter for an estimate of colony area per leaf. Leaf area was also measured with the area meter. Colony area divided by the colony number per leaf was used as an estimate of the individual colony size. Conidial germination was determined by inverting leaves with colonies of the pathogen over 2% water agar in petri dishes (one leaf per dish) and allowing the conidia to settle on the agar. The petri dishes were incubated for 24 hr at 20 C in the dark, and the germination of a minimum of 100 conidia per dish was determined using a light microscope at ×100 magnification. Conidia were considered to have germinated if a germ tube at least as long as the width of the conidium was produced.

The 10 leaves for each treatment were pooled and the Si content determined, after ashing, by gravimetric measurement of acid insoluble SiO_2 (Silica) (2).

This experiment was repeated using different plants, and leaf 4 was inoculated rather than leaf 2.

Experiment 2. Five seedlings per treatment were grown in nutrient solutions (as in experiment 1) of tap water (0.5 mM of Si) amended with 0, 0.45, 0.9, 1.35, 1.8, 2.7, and 3.6 mM of Si, added in the form of Na_2SiO_3 (contributing 0, 0.85, 1.7, 2.55, 3.4, 5.1, and 6.8 mM of Na, respectively). An additional treatment of five seedlings was included, using nutrient solution made with reverse-osmosis water containing 0.05 mM of Si, effectively zero Si for the purposes of this study. The pH was adjusted to 6.0 with 10 N H_2SO_4 contributing from zero (no acid added) to 5.3 mM of additional SO_4 and increasing with Si concentration. The electrical conductivity of the solutions increased from 2.0 to 2.6 mS/cm with increasing Si concentration. After full expansion, the fourth leaf of each plant was spray-inoculated with 1 ml of 1,000 conidia per milliliter of a Flourinert suspension, and the plants were arranged in a completely randomized design in the greenhouse. The inoculated leaves were sampled after 14 days of incubation, and the four components of parasitic fitness of *S. fuliginea*, the leaf area, and the Si content of the leaves were determined as in experiment 1.

Seven days after inoculation of the fourth leaf (before visual symptoms), the fifth leaves of the inoculated plants were also spray-inoculated with 1 ml per leaf of a 4,000 conidia per milliliter Fluorinert suspension. After 14 days of incubation in the greenhouse, the leaves and mildew colonies were assessed like the fourth leaf.

Experiment 3. An experiment was conducted to determine whether the effects of Si amendments on disease severity were due to Si, the accompanying cation, or to the increase in the ionic strength of the nutrient solutions resulting from silica amendments. Plants were grown in one of four solutions with electrical conductivities of 1.3, 2.6, 3.9, and 5.1 mS/cm achieved by either dilution or concentration of the base cucumber feeding formula. Cation effects were tested by growing plants in solutions of equal Si concentration, but varying in Na or K concentration using commercially available silicate products (N, Metso 200, and Kasil 6; National Silicates, Toronto, Ontario) (Table 1). Additionally, anion effects were tested by growing plants in the presence or absence of Si at constant Na (N or Na_2SO_4, respectively) or

TABLE 1. Concentration of K, Na, and Si in nutrient solutions used to determine the effects of Si amendments on severity of *Sphaerotheca fuliginea* (experiment 3)

Nutrient solution	Ion concentration (mM)		
	Si	Na	K
EC 2[a]	0.5	0.0	7.0
Na_2SO_4	0.5	1.0	7.0
K_2SO_4	0.5	0.0	7.5
N[b]	2.2	1.0	7.0
Metso 200[b]	2.2	6.8	7.0
Kasil 6[b]	2.2	0.0	7.5

[a] Base nutrient solution, containing (in mM) 13.0 NO_3, 1.5 H_2PO_4, 7.0 K, 3.5 Ca, 1.0 Mg, 1.5 SO_4, and (in μM) 18.8 Fe, 5.5 Mn, 0.9 Zn, 0.2 Cu, 18.1 B, and 0.1 Mo, with an electrical conductivity (EC) of 2.0 mS/cm.

[b] N and Metso 200 are commercially available sodium silicate products, and Kasil 6 is a commercially available potassium silicate product (National Silicates, Toronto, Ontario).

constant K (Kasil 6 or K_2SO_4, respectively) (Table 1). All solutions were prepared using tap water, adjusted to pH 6.0 with 10 N H_2SO_4, and unless otherwise stated, had an electrical conductivity of 2.6–2.8 mS/cm. The 10 seedlings used for each treatment were grown on a greenhouse bench in a completely randomized design. When fully expanded, the fourth leaf of each plant was spray-inoculated with 0.5 ml of a Fluorinert suspension of 2,000 conidia per milliliter. The plants remained on the greenhouse bench for 10 days, after which the number of colonies per leaf and the leaf area were assessed. The experiment was repeated.

Statistical analysis. All data were tested for homogeneity of variance using Hartley's test (15) and, if appropriate, transformed to log 10 or square root values. In experiments 1 and 2, the relationships between the concentrations of Si in the nutrient solutions and the leaf area, the parasitic fitness components of *S. fuliginea*, and the Si content of the leaves, were investigated using ANOVA for polynomial regression with a significance level of $P < 0.0001$, unless otherwise stated. In experiment 3, the data were analyzed using an ANOVA followed by a Student-Newman-Keuls procedure for means separation ($P < 0.01$).

RESULTS

Experiments 1 and 2. The area of leaf 2 in experiment 1 was not influenced by the Si treatments (Table 2), but leaf 4 in experiment 1 and leaf 4 and leaf 5 in experiment 2 showed significant reductions in leaf area when Si additions to the nutrient solutions were made. Increasing Si concentration from 0.5 to 2.3 mM decreased leaf area by 22% in leaf 4 of experiment 1 (Table 3), and by approximately 44% in leaves 4 and 5 in experiment 2 (Tables 4 and 5).

Colony number of *S. fuliginea* per leaf was negatively correlated with increasing Si amendments for all leaves in experiments 1 and 2. Increasing Si from 0.5 to 2.3 mM resulted in a 43% reduction in colony number per leaf for leaf 2 (Table 2) and an 85% reduction for leaf 4 (Table 3) in experiment 1. In experiment 2, the colony number per leaf decreased 97% for leaf 4 (Table 4), and 94% for leaf 5 (Table 5).

The individual colony size of *S. fuliginea* was not found to be significantly related to Si treatment for leaves 2 and 4 in experiment 1. However, increasing ambient Si was negatively correlated with individual colony size in experiment 2 as an increase in Si concentration from 0.05 to 4.10 mM reduced individual colony size by 72% on leaf 4 (Table 4) and by 84% on leaf 5 (Table 5).

Colony area was significantly reduced with increasing Si amendments (Figs. 1 and 2; experiment 1; leaf 4: $P < 0.04$). The colony area per leaf of leaf 2 in experiment 1 was reduced by 55%, and that of leaf 4 by 94% when Si was increased from 0.5 to 2.30 mM (Tables 2 and 3). In experiment 2, the colony area decreased 99% for both leaf 4 and leaf 5 when Si was increased from 0.02 to 4.10 mM (Tables 4 and 5).

The germination of conidia of *S. fuliginea* collected from leaves 2 and 4 in experiment 1 and from leaf 4 in experiment 2 ($P < 0.0057$) was significantly reduced by increasing Si amendments. Conidia germination ranged from 10.5 to 22.0% from plants grown in low Si solutions (Tables 2–4), to from 5.0 to 8.3% from plants grown in high Si solutions. Germination of conidia from leaf 5 in experiment 2 showed no relationship to the Si treatment and ranged from 7.6 to 1.4% (Table 5).

Since the leaves from individual plants in each treatment were pooled for Si determinations, leaves 2 and 4 were treated as replicates in experiment 1, and leaves 4 and 5 as replicates in experiment 2. There were significant relationships between the

TABLE 2. Effect of Na_2SiO_3 on leaf area and four components of parasitic fitness of *Sphaerotheca fuliginea* on leaf 2 in experiment 1

Silicon concentration in solution (mM)	Leaf area (cm^2)[a]	Colony number per leaf[a]	Individual colony size (mm^2)[a]	Colony area (cm^2)[a]	Conidial germination (%)[a]
0.50	304	481[b]	1.02	48.4[b]	10.5[b]
0.95	355	478	0.87	41.3	7.1
1.40	320	377	0.90	34.4	5.4
1.85	323	334	0.90	28.2	5.0
2.30	274	272	0.78	21.7	6.0

[a] Mean values, $n = 10$.
[b] There were significant negative correlations between the silicon concentration of the nutrient in solution and the colony number ($P < 0.0001$, $r^2 = 0.64$), colony area ($P < 0.0001$, $r^2 = 0.52$), and the conidial germination ($P < 0.0001$, $r^2 = 0.38$).

TABLE 3. Effect of Na_2SiO_3 on leaf area and four components of parasitic fitness of *Sphaerotheca fuliginea* on leaf 4 in experiment 1

Silicon concentration in solution (mM)	Leaf area (cm^2)[a]	Colony number per leaf[a]	Individual colony size (mm^2)[a]	Colony area (cm^2)[a]	Conidial germination (%)[a]
0.50	468[b]	173[b]	0.96	40.6[b]	16.4[b]
0.95	469	78	0.80	16.2	11.1
1.40	470	47	0.70	12.1	8.5
1.85	453	35	0.60	10.0	8.1
2.30	365	26	0.49	5.8	6.5

[a] Mean values, $n = 10$.
[b] There were significant negative correlations between the silicon concentration of the nutrient in solution and the leaf area ($P < 0.002$, $r^2 = 0.52$), colony number ($P < 0.0001$, $r^2 = 0.70$), colony area ($P < 0.04$, $r^2 = 0.81$), and the conidial germination ($P < 0.0001$, $r^2 = 0.55$).

TABLE 4. Effect of Na_2SiO_3 on leaf area and four components of parasitic fitness of *Sphaerotheca fuliginea* on leaf 4 in experiment 2

Silicon concentration in solution (mM)	Leaf area (cm^2)[a]	Colony number per leaf[a]	Individual colony size (mm^2)[a]	Colony area (cm^2)[a]	Conidial germination (%)[a]
0.05	890[b]	288[b]	1.70[b]	49.1[b]	14.4[b]
0.50	746	190	1.48	28.9	22.0
0.95	680	102	1.14	11.3	14.7
1.40	637	59	1.10	6.2	16.8
1.85	602	39	0.74	3.1	13.5
2.30	535	10	1.24	0.7	10.8
3.20	533	24	0.76	1.8	13.1
4.10	469	10	0.48	0.5	8.3

[a] Mean values, $n = 5$.
[b] There were significant negative correlations between the silicon concentration of the nutrient in solution and the leaf area ($P < 0.0001$, $r^2 = 0.91$), colony number ($P < 0.0001$, $r^2 = 0.63$), individual colony size ($P < 0.0001$, $r^2 = 0.36$), colony area ($P < 0.0001$, $r^2 = 0.85$), and the conidial germination ($P < 0.006$, $r^2 = 0.18$).

TABLE 5. Effect of Na_2SiO_3 on leaf area and four components of parasitic fitness of *Sphaerotheca fuliginea* on leaf 5 in experiment 2

Silicon concentration in solution (mM)	Leaf area (cm^2)[a]	Colony number per leaf[a]	Individual colony size (mm^2)[a]	Colony area (cm^2)[a]	Conidial germination (%)[a]
0.05	860[b]	568[b]	1.80[b]	103.4[b]	5.8
0.50	802	477	1.13	54.5	5.4
0.95	665	305	0.98	28.9	7.6
1.40	637	209	0.60	12.6	3.1
1.85	615	143	0.44	6.2	4.0
2.30	536	56	0.33	1.9	6.3
3.20	533	39	0.39	1.2	1.4
4.10	491	35	0.28	1.0	6.8

[a] Mean values, $n = 5$.
[b] There were significant negative correlations between the silicon concentration of the nutrient in solution and the leaf area ($P < 0.0001$, $r^2 = 0.88$), colony number ($P < 0.0001$, $r^2 = 0.93$), individual colony size ($P < 0.0001$, $r^2 = 0.84$), and colony area ($P < 0.0001$, $r^2 = 0.95$).

percentage of dry weight of Si in the leaves and the concentration of Si in the nutrient solutions in both experiments (experiment 1: $P < 0.0013$) (Fig. 3). The Si content ranged from 0.5 to 7.1% of leaf dry weight (Table 6).

Experiment 3. The electrical conductivity of the solution was found to have a significant effect on leaf area in both trials (Table 7). Leaf area was reduced at the lowest electrical conductivity (1.3 mS/cm) and in one instance, at the highest electrical conductivity (5.1 mS/cm). The Na_2SO_4, K_2SO_4, and Metso 200 treatments also significantly decreased leaf area compared to the unamended treatment at comparable electrical conductivity (2.6 mS/cm); N and Kasil 6 treatments had no effect. The electrical conductivity of the solution did not significantly affect colony number, nor did Na_2SO_4 or K_2SO_4 when compared to the unamended solution at an equivalent electrical conductivity (Table 7). Only the silica solutions N, Metso 200, and Kasil 6 significantly affected the number of colonies per leaf.

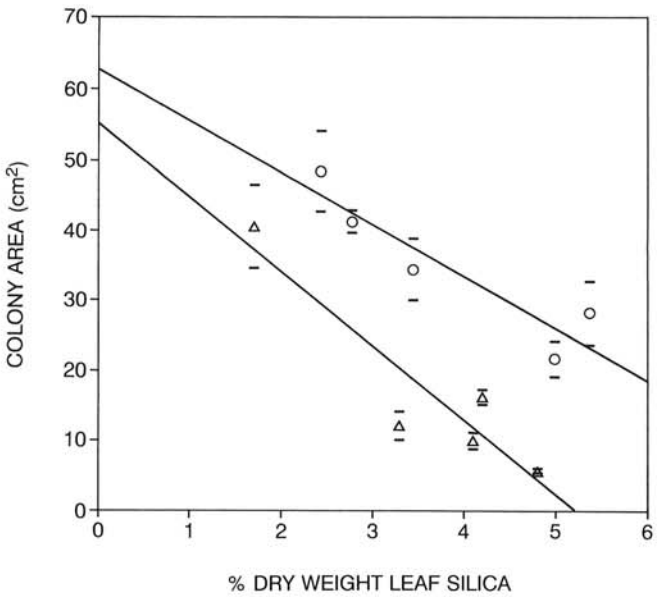

Fig. 1. The relationship between the silica content of the leaf of cucumber and the colony area of *Sphaerotheca fuliginea* (experiment 1). △ = leaf 2, $Y = 62.8 + (-7.4x)$, $r^2 = 0.85$, $n = 5$; ○ = leaf 4, $Y = 55.2 + (-10.6x)$, $r^2 = 0.85$, $n = 5$.

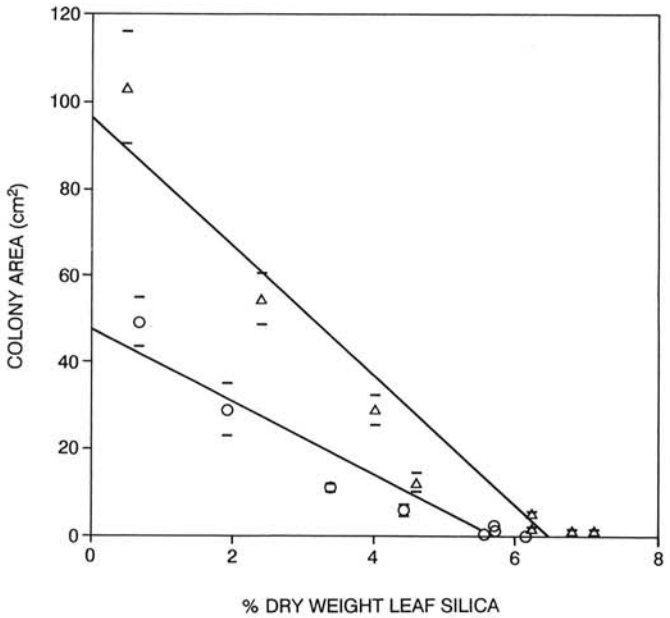

Fig. 2. The relationship between the silica content of the leaf of cucumber and the colony area of *Sphaerotheca fuliginea* (experiment 2). ○ = leaf 4, $Y = 47.6 + (-8.3x)$, $r^2 = 0.92$, $n = 8$; △ = leaf 5, $Y = 96.8 + (-14.9x)$, $r^2 = 0.92$, $n = 8$.

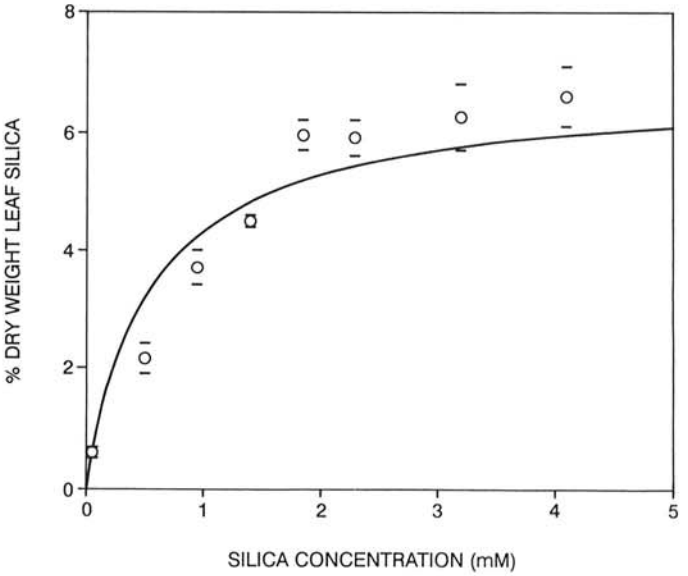

Fig. 3. The effect of feeding cucumber plants with different concentrations of soluble silicon on the silica content of the leaves (experiment 2). $Y = 0.6 + (3.6x) + (-0.5x^2)$, $r^2 = 0.96$, $n = 8$.

TABLE 6. Effect of Si solution concentration on Si content of leaves

Silicon concentration in solution (mM)	Silica content (% dry weight of the leaf)			
	Experiment 1[a]		Experiment 2[b]	
	Leaf 2	Leaf 4	Leaf 4	Leaf 5
0.05			0.7	0.5
0.50	2.4	1.7	1.9	2.4
0.95	2.8	4.2	3.4	4.0
1.40	3.4	3.3	4.4	4.6
1.85	5.4	4.1	5.7	6.2
2.30	5.0	4.8	5.6	6.2
3.20			5.7	6.8
4.10			6.1	7.1

[a] A total of 10 leaves were pooled per treatment.
[b] A total of five leaves were pooled per treatment.

TABLE 7. Effects of solution electrical conductivity, Na_2SO_4 or K_2SO_4, and silicon compounds on leaf area and colony number (experiment 3)

Treatment[a]	Experiment 3		Experiment 3 (repeated)	
	Colony number per leaf	Leaf area (cm^2)	Colony number per leaf	Leaf area (cm^2)
EC[b] 1.3	22.4 ab[c]	306 d	71.0 ab	226 d
EC 2.6	21.4 ab	570 a	88.5 ab	460 ab
EC 3.9	24.8 a	513 ab	104.1 a	537 a
EC 5.1	17.9 ab	388 c	86.3 ab	526 a
Na_2SO_4	16.7 b	420 bc	67.4 b	332 c
K_2SO_4	24.0 ab	460 bc	89.4 ab	329 c
N	4.0 c	497 ab	12.6 c	444 b
Metso 200	2.0 c	453 bc	19.8 c	330 c
Kasil 6	3.9 c	526 ab	17.5 c	417 b

[a] SO_4 in the nutrient solutions, in mM, was 4.0, 5.3, 6.9, 8.9, 8.2, 8.0, 6.5, 11.5, and 5.7, respectively.
[b] Base nutrient solution, containing (in mM) 13.0 NO_3, 1.5 H_2PO_4, 7.0 K, 3.5 Ca, 1.0 Mg, 1.5 SO_4, and (in μM) 18.8 Fe, 5.5 Mn, 0.9 Zn, 0.2 Cu, 18.1 B, and 0.1 Mo. EC = electrical conductivity (mS/cm).
[c] Values in the same column followed by different letters are significantly different as determined by ANOVA procedure and the Student-Newman-Keuls procedure for means separation ($P < 0.01$).

DISCUSSION

The amendment of nutrient solutions with soluble sodium silicate reduced the colony number and colony area of *S. fuliginea* on inoculated cucumber leaves, and reduced the percentage of germination of conidia produced on those leaves. Individual colony size was also reduced, but the relationship was significant only in experiment 2 in which a broader range of Si concentrations was used than in experiment 1. These results strengthen and extend the information available from the two previous studies of Si effects on mildew in naturally infected cucumber in which an increase from 0 to 1.7 mM in Si reduced colony number from >1.0 to <0.1 colony per cm^2 (14) and the percentage of leaf area covered by colonies was found to decline from 20 to 0% when Si was increased from 0.17 to 1.7 mM (2). The use of inoculated plants in the present study, however, permits a more accurate measure of the effects of Si on mildew at a specific time after introduction of the pathogen and eliminates the complications of secondary infection.

Previous studies with Si have not considered the potential influence of the Na or K cations associated with silicate, or the change in solution ionic strength, on disease susceptibility. The effects of sodium silicate on the parasitic fitness of *S. fuliginea* could not be attributed to Na or to the increase in the electrical conductivity of the solution which results from the addition of sodium silicate. The modification of the electrical conductivity of the solution, the substitution of K silicate for Na silicate, and the amendment of solutions with K_2SO_4 or Na_2SO_4 did not prove to be effective in reducing colony number (Table 7). Only Si influenced the receptivity of the plants to infection by *S. fuliginea*.

Increasing the concentration of Si in the nutrient solutions above 1.8 mM had little additional effect on the parasitic fitness components of *S. fuliginea*, possibly because of only minor increases in Si accumulation by leaves in those treatments (Table 6, Fig. 3). A relationship between the Si content of the plant tissue and the severity of a disease has previously been reported for *P. oryzae* on rice (3,16), *E. g. tritici* on wheat (13), *E. g. hordei* on barley (7) and for unspecified powdery mildew species on cucumber (14). The manner in which Si reduces the receptivity of the plants to disease is unknown. Silicon has been noted to accumulate at sites of penetration of *E. g. hordei* on barley leaves (8–12,18), of *E. g. tritici* on wheat leaves (8), and of *Uromyces phaseoli* (Pers.) G. Wint. var. *typica* (Soy) on French bean (6), which may be related to reduced disease susceptibility (6).

Reductions in leaf area noted in the Si treatment of experiment 3 do not appear to be due to Si per se, but may be due to the progressively higher levels of sulfate required to balance pH with increasing Si concentrations. At equivalent electrical conductivities of the nutrient solutions, leaf area was reduced to the greatest extent in those treatments with the highest sulfate concentrations (Na_2SO_4, K_2SO_4, and Metso 200) (Table 7). An excess of sulfate in cucumber nutrient solutions has been reported to cause a reduction in plant growth and yield (17). The concentration of SO_4 in the nutrient solutions did not significantly affect the colony number of *S. fuliginea* (Table 7).

The dramatic effects of Si on at least four parameters of parasitic fitness of *S. fuliginea* would suggest a potential use for Si in reducing the severity of this pathogen on greenhouse cucumbers. Further work is required to establish the effects of Si on other mildews (for example, *Erysiphe cichoracearum* DC.: Merat), and the extent of control of powdery mildew on cucumbers over time.

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