Effects of Silicon Applications on Soybean Rust Development Under Greenhouse and Field Conditions

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Abstract

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Soybean rust (SBR), caused by *Phakopsora pachyrhizi*, is one of the most destructive fungal diseases affecting soybean production. Silicon (Si) amendments were studied as an alternative strategy to control SBR because this element was reported to suppress a number of plant diseases in other host-pathogen systems. In greenhouse experiments, soybean cultivars inoculated with *P. pachyrhizi* received soil applications of wollastonite (CaSiO_3) (Si at 0, 0.96, and 1.92 t ha⁻¹) or foliar applications of potassium silicate (K_2SiO_3) (Si at 0, 500, 1,000, or 2,000 mg kg⁻¹). Greenhouse experiment results demonstrated that Si treatments delayed disease onset by approximately 3 days. The area under disease progress curve (AUDPC) of plants receiving Si treat-

ments also was significantly lower than the AUDPC of non-Si-treated plants. For field experiments, an average 3-day delay in disease onset was observed only for soil Si treatments. Reductions in AUDPC of up to 43 and 36% were also observed for soil and foliar Si treatments, respectively. Considering the natural delayed disease onset due to the inability of the pathogen to overwinter in the major soybean production areas of the United States, the delay in disease onset and the final reduction in AUDPC observed by the soil Si treatments used may lead to the development of SBR control practices that can benefit organic and conventional soybean production systems.

Soybean rust (SBR), caused by *Phakopsora pachyrhizi* Syd. & P. Syd. (Urediniomycetes, Uredinales), also known as Asian soybean rust, is a potentially devastating fungal disease that threatens commercial and organic soybean (*Glycine max* (L.) Merr.) production worldwide (35). Severe SBR damage on soybean is a consequence of windborne urediniospores, susceptible host plants with conducive environmental conditions at the time of infection, and the subsequent crop and pathogen development (13,14,16). A minimum of a 6-h dew period and temperatures ranging from approximately 15 to 29°C are necessary for urediniospore infection (21,27,28). The main effects of *P. pachyrhizi* on soybean development are a reduction in photosynthetic leaf area, early plant maturation, and premature defoliation, with low individual seed weight and overall yield reductions (49). Related to this, high levels of SBR infection result in plants with fewer pods and poor seed quality (5); specifically, lower protein (34).

Breeding single-gene resistance to control SBR in soybean has not proven durable (20); therefore, the most adequate option in managing an SBR epidemic is through the application of fungicides, such as triazoles and strobilurins, which substantially increase overall production costs. However, even with chemical control, in years of high SBR pressure, yield reductions of approximately 50% were observed (52).

An alternative approach to manage plant disease and reduce the extensive use of fungicides is through nutrient management strate-

gies. Mineral nutrition plays an important role in the physiological functioning of plants, and has been shown to be an important component for managing plant disease (8). Silicon (Si), supplied as H_4SiO_4 , has been reported to increase plant resistance to biotic stresses (disease and insects) and improve plant tolerance against abiotic disturbances (8,10,23,25,26,40).

Yield gains in plants supplied with Si have been attributed to several factors, such as increased plant growth, improved mineral nutrient balance, and mechanical strength. These benefits also provide the plant some resistance to various environmental stresses (8,10,42). Elevated Si content in plants known to accumulate Si, such as rice (*Oryza sativa* L.), sugarcane (*Sacharum* spp. L.), and wheat (*Triticum aestivum* L.), is associated with higher yields (6). Si fertilization also has reduced fungal disease susceptibility for a number of monocotyledonous and several dicotyledonous plant species (8,29,49). Rice fields amended with Si had lower incidences of neck blast (*Magnaporthe grisea* (T.T. Hebert) M.E. Barr) that, in turn, reduced or eliminated fungicide applications (44–46). The application of foliar Si sprays reduced the number of powdery mildew (*Uncinula necator* (Schwein.) Burrill) colonies on grape (*Vitis vinifera* L.) leaves and considerably increased yield (4,38). In greenhouse studies with cucumber (*Cucumis sativus* L.), soluble potassium silicate (K_2SiO_3) applications showed positive correlations with resistance to powdery mildew (*Sphaerotheca fuliginea* (Schltdl.) Pollacci) (3,29). Liang et al. (24) found that root or foliar Si applications reduced disease severity and that only the root Si application enhanced the activity of pathogenesis-related proteins in cucumber.

Studies including soybean and Si fertilization are scarce. Some studies evaluated nutrient toxicity (Al and Mn) and physiological effects and showed that soybean responded positively to Si amendments (1,18,22,30). Under Si-free conditions, soybean plants displayed malformations such as leaf curling of newly developed leaves (seventh and eighth leaves) during flowering (30). They also reported necrotic spots on soybean leaves and low pollen fertility in cases of severe Si deficiency. In other studies, the use of potassium silicate sprays against SBR on soybean was tested with

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considerable success, and up to 70% reduction in SBR severity was observed in some cases (32,41). In comparison, Nolla et al. (33), based on only one disease evaluation, reported that soil Si applications were not effective in suppressing SBR development. However, they found that Si applications reduced the incidence of frog eye (*Cercospora sojina* Hara) and downy mildew (*Peronospora manshurica* (Naumov) Syd.).

Because Si amendments have been demonstrated to enhance resistance to a number of plant diseases, and some research suggests that Si may suppress SBR development in soybean, the objective of this study was to evaluate the efficacy of Si via soil (CaSiO_3) or foliar (K_2SiO_3) applications as a means to reduce SBR severity in two soybean maturity groups under greenhouse and field conditions in Florida.

Materials and Methods

Treatments and cultural conditions. *Greenhouse experiments.* Two greenhouse experiments were conducted in summer 2007 and 2008. Greenhouse temperatures and humidity averages for both experiments were 28°C and 80%. Two soybean cultivars were tested in the first greenhouse experiment: DP5634RR, which is glyphosate (Roundup-Ready) resistant, maturity group 5; and Hinson Long Juvenile, which is a forage soybean, maturity group 8. In the second greenhouse experiment, only the DP5634RR cultivar was tested.

Free-draining plastic pots were filled with 0.85 kg of a potting mix (Hyponex potting soil; Hyponex Corp., Maryville, OH) for the first greenhouse experiment. In the second experiment, free-draining plastic pots were filled with 1.5 kg of an Ultisol soil (fine-loamy, kaolinitic, thermic Plinthic Kandiudult, Tifton series). The potting mix and soil chemical compositions are presented in Table 1. Three soybean seeds were sown per pot and thinned to one plant per pot at 10 days after planting (DAP). The plants were watered as needed, typically once per day.

Soil-applied Si. Vansil W-50 (Vanderbilt Co., Norwalk, CT) is a fine-grade (talc-like) form of the naturally occurring mineral ore, wollastonite (CaSiO_3), with a median particle diameter of 2.8 μm . It contained approximately 24% Si and 34% Ca. The Vansil W-50 wollastonite in slurry (10% wt/wt) had a pH of 10 to 11. Dry Vansil W-50 was mixed with the potting substrate at rates of Si equivalent to 0 (control), 0.96, and 1.92 t ha^{-1} or W-50 at 0, 4, and 8 t ha^{-1} (wollastonite at 0, 2, and 4 g pot^{-1}) for the first greenhouse experiment. For the second greenhouse experiment, the soil was amended with Si rates of 0 (control) and 1.92 t ha^{-1} (W-50 at 0 and 8 t ha^{-1}), which equated to Si at 0 and 0.96 g pot^{-1} (wollastonite at 0 and 4 g pot^{-1}).

A $\text{Ca}(\text{OH})_2$ control treatment was included in both greenhouse experiments to account for liming and Ca effects of the wollastonite treatments. Four grams of hydrated lime ($\text{Ca}(\text{OH})_2$; Lime &

Cement Co., Allgood, AL) were added per pot ($\text{Ca}(\text{OH})_2$ at 8 t ha^{-1} or Ca at 4.3 t ha^{-1}). The hydrated lime had a pH of 12.4 (saturated solution at 25°C).

Foliar-applied Si. A foliar solution of potassium silicate, (K_2SiO_3 ; AgSil 25; PQ Corp., Valley Forge, PA) was also tested. AgSil 25 is a readily soluble silicate used as a foliar spray and containing approximately 9.7% Si, with a pH of 11.3. An atomizer with propellant cartridge (Sprā-tool; Arvoe Industries Inc., Gardnerville, NV) was used to apply foliar Si treatments to both leaf surfaces until point of run-off (approximately 6 ml per plant), for both greenhouse experiments. In the first greenhouse experiment, three foliar Si rates were tested: 500, 1,000, and 2,000 mg kg^{-1} (pH 10, 10.1, and 10.4, respectively). In the second greenhouse experiment, only the Si rate of 2,000 mg kg^{-1} rate was tested. The manufacturer-recommended Si rate for foliar sprays is 1,000 mg kg^{-1} .

The foliar Si treatment solutions were applied twice in the first greenhouse experiment, at 38 and 48 DAP. These ages corresponded to soybean physiological stages V6 (sixth trifoliolate fully expanded) and R2 (full bloom, flower at top two nodes). In the second greenhouse experiment, the foliar Si treatment solutions were applied three times at 18, 23, and 28 DAP. This corresponded to physiological stages V3 (third trifoliolate fully expanded), V5 (fifth trifoliolate fully expanded), and V6 (sixth trifoliolate fully expanded). A foliar control treatment consisted of DI water with pH adjusted to 10.4 with KOH. This was to control for a possible pH effect (equivalent to the foliar solution pH for Si at 2,000 mg kg^{-1}). A control solution of DI water (Si at 0 mg kg^{-1} , pH 7.2) was used in both greenhouse experiments as a control for the spraying effect (i.e., spraying action may possibly wash urediniospores off of the leaf surfaces).

In the second greenhouse experiment, a combined treatment of soil-applied Si at 1.92 t ha^{-1} plus a foliar Si treatment at 2,000 mg kg^{-1} was included to test for potential additive effects (foliar- and soil-applied Si).

Field experiment. Repeated field experiments were conducted during 2007 and 2008 at the North Florida Research and Education Center in Quincy. The average monthly temperature for July, August, and September, when SBR disease evaluations were made, ranged from 24 to 27°C for both years (11), which is considered suitable for SBR development (21,27,28). Both soybean cultivars (DP5634RR and Hinson Long Juvenile) were tested. The study area used in the 2007 field experiment was comprised of two related soil series, with 60% of the area being a Tifton fine loam (fine-loamy, kaolinitic, thermic Plinthic Kandiudult) and 40% being a Norfolk fine loam (fine-loamy, kaolinitic, thermic Typic Kandiudult) (48). The primary difference between series was that Tifton had plinthite in the B horizon. The experimental area used in the 2008 experiment was a Norfolk series soil (48). In both years, the field experiment received standard commercial soybean cultural practices for soybean planted for hay or silage (50). Seeding rate was adjusted based on pure live seed, which was determined to be about 30 seeds m^{-2} . Each experimental unit (22.2 m^2) was comprised of four 6.1-m rows with 0.91 m between rows. Alleys (1.8 m) separated each experimental unit.

The soil Si treatments (Vansil W-50) were manually applied and raked into the upper 5 cm of soil within field plots with W-50 at 0, 4.44, 8.88, and 17.76 kg plot^{-1} (W-50 at 0, 2, 4, and 8 t ha^{-1} or Si at 0, 0.48, 0.96, and 1.92 t ha^{-1}) 1 day prior to sowing in 2007 and 6 days prior to sowing in 2008. The $\text{Ca}(\text{OH})_2$ control treatment was equivalent to lime at 17.76 kg plot^{-1} ($\text{Ca}(\text{OH})_2$ at 8 t ha^{-1} or Ca at 4.3 t ha^{-1}). To apply the foliar treatments (K_2SiO_3 solutions with Si at 500, 1,000, or 2,000 mg kg^{-1}), a backpack sprayer (D. B. Smith Field King, Mills, NY) was used. The center two rows of each plot were sprayed until leaf runoff at 1.1 liter plot^{-1} , which was proportional to 1,000 liters ha^{-1} . A DI H_2O (Si at 0 mg kg^{-1}) and pH-adjusted water (10.4 with KOH) controls were also tested. All foliar treatments were applied three times, at 39, 53, and 67 DAP for 2007 and at 29, 42, and 53 DAP for 2008. This corresponded to physiological stages V5 (fully expanded fifth trifoliolate), R2 (full bloom), and R3 (beginning pod).

Table 1. Soil analysis of the potting mix and soil used in the first and second greenhouse experiments, respectively

Parameter	Potting mix ^y	Ultisol ^z
P	137 mg kg^{-1}	...
K	469 mg kg^{-1}	...
Ca	3,163 mg kg^{-1}	1,221 mg kg^{-1}
Mg	233 mg kg^{-1}	117 mg kg^{-1}
S	142 mg kg^{-1}	...
B	0.9 mg kg^{-1}	...
Zn	7.9 mg kg^{-1}	...
Fe	153 mg kg^{-1}	...
Cu	2 mg kg^{-1}	...
Mn	9.5 mg kg^{-1}	...
Water pH (1:2, vol/vol)	6.8	6.7
Organic matter	4%	...
Cation exchange capacity	18.9 meq 100 g ⁻¹	...
Soil Si	12 mg kg^{-1}	29 mg kg^{-1}

^y Mehlich-1 method was used to extract potting mix nutrients.

^z Acetic acid (0.5 N) was used to extract Ca and Mg from the soil and Si from both substrates.

Inoculum procedures. *Greenhouse experiments.* The procedures to obtain the urediniospore suspensions were the same for both greenhouse and field experiments. Urediniospores of *P. pachyrhizi* were collected from greenhouse plants, using leaves with approximately 35% disease as the inoculum source (15). Excised leaves were gently washed with deionized water and blotted dry with absorbent paper towel. Subsequently, the leaves were placed in a sealed transparent plastic box containing Whatman no. 1 filter paper (Whatman, Piscataway, NJ) saturated with DI water. Following a 48-h incubation at 23°C, fresh urediniospores were collected with a brush and placed into a 0.05% surfactant solution (Tween-20; Sigma-Aldrich, St. Louis). A hemacytometer was used to adjust the resulting urediniospore suspension (1×10^4 cells mL^{-1} for the first greenhouse study and 3×10^4 cells mL^{-1} for the second greenhouse study).

The soybean plants were inoculated on the day after the first foliar Si application, which was 39 and 19 DAP for the first and second greenhouse experiments, respectively. The urediniospore suspensions were sprayed using an atomizer containing a propellant cartridge (Sprā-tool; Aervoe Industries Inc.). Each plant was sprayed on both leaf surfaces until run-off (approximately 6 ml per plant). The pots with the inoculated plants were sealed in 50-liter white plastic bags (Glad Tall Kitchen Bag, Oakland, CA) for 24 h. The first greenhouse experiment received a second application of urediniospore suspension (1×10^4 cells mL^{-1}) 9 days after the first inoculation because no infection symptoms were observed as of that date.

Field experiment. Due to low rainfall (which inhibits natural SBR infection) in the 2007 field experiment, the middle rows of each experimental unit were artificially inoculated (3×10^3 cells mL^{-1}) in the evening at 47 DAP with a backpack sprayer (D. B. Smith Field King). The center two rows of each experimental unit were sprayed with the inoculum suspension until leaf runoff at 1.1 liter plot^{-1} , which was proportional to 1,000 liters ha^{-1} . Artificial inoculations were not needed in the 2008 experiment year because environmental conditions were conducive to SBR disease infection.

Disease ratings. Disease severity ratings were recorded based on the Horsfall-Barrett scale (15). In all, 7 SBR disease evaluations were made from 12 through 31 August in the first greenhouse experiment and 15 disease evaluations were made from 28 June through 12 July in the second greenhouse experiment. In the field experiment, the two center rows of each experimental unit were used for SBR disease evaluation, thereby avoiding border effects. In all, 5 SBR disease evaluations were conducted from 8 September through 6 October 2007 and 17 disease evaluations were conducted from 13 August through 16 September 2008. Midpoint values of the disease rating scale were used to plot disease progress curves. The area under the disease progress curve (AUDPC) used to determine treatment effectiveness (17) was calculated as:

$$\text{AUDPC} = \sum_{i=1}^{n-1} [(y_i + y_{i+1}) \div 2] (t_{i+1} - t_i)$$

where y_i = disease proportion (percentage severity) at the i th observation, t_i = time (days), and n = total number of observations (47).

Plant and soil sampling. All soybean leaves from each pot were collected at 69 and 34 DAP for the first and second greenhouse experiments, respectively. They were gently rinsed with distilled water for approximately 10 s and oven dried at 70°C for 48 h. In the repeated field experiment at soybean development stage R7 (80 and 101 DAP for DP5634RR and Hinson Long Juvenile cultivars, respectively, in 2007 and 84 and 98 DAP for DP5634RR and Hinson Long Juvenile, respectively, in 2008), six plants were randomly removed from each experimental unit and all leaves were used for Si analysis. Oven-dried leaf samples from both greenhouse and field experiments were ground separately and sieved through a 2-mm² stainless steel screen. Leaf Si concentration was determined following the methodology described by Elliott and Snyder (9), with subsequent automated colorimetric analysis at 670 nm.

At the conclusion of each experiment, air-dried soil samples of all treatments from the greenhouse studies and soil (0 to 15 cm depth) from the field experiment were analyzed for soil water pH (1:2, vol/vol) and soil-extractable Ca, Mg, and Si concentrations using a 0.5 N acetic acid extraction method (43) at the University of Florida, Belle Glade EREC soil test laboratory.

Statistical analyses. The first greenhouse experiment was a two-by-nine factorial design with two soybean cultivars, nine Si treatments, and three replications ($n = 54$), while the second greenhouse experiment was a randomized complete block design with seven Si treatments and four replications ($n = 28$). The field experiment was a 2×10 factorial design with two soybean cultivars, 10 Si treatments, and four replications ($n = 80$), repeated in the second year. Analysis of variance was used to determine significant treatment effects (SAS for Windows, version 9.1; SAS Institute, Cary, NC). Treatment means were compared ($P \leq 0.05$) using Fisher's protected least significant difference. SigmaPlot (version 10.0; Hearne Scientific Software, San Rafael, CA) was used to plot disease severity over time.

Results

Soil and tissue composition. The soil and leaf Si concentrations from the first greenhouse experiment are given in Figure 1. The soil Si values were similar among soybean cultivars. The soil Si concentration from the Si at 1.92 t ha^{-1} treatment was 63% greater than the 0.96 t ha^{-1} treatment and 673% greater than the control (Fig. 1A). The average leaf Si concentration of cv. DP5634RR was about 45% greater than for cv. Hinson Long Juvenile in the first greenhouse experiment (Fig. 1B). Regardless of cultivar, the average leaf Si concentration of the Si at 1.92 t ha^{-1} treatment was 29% greater than the 0.96 t ha^{-1} treatment and 277% greater than the control treatment (Fig. 1B). Leaf Si concentrations from the foliar Si treatments (Si at 500, 1,000, and 2,000 mg kg^{-1}) were not significantly different from each other but were about 33% signifi-

Fig. 1. A, Soil silicon (Si) concentration and **B,** leaf Si concentration at 69 days after planting for cvs. DP5634RR and Hinson Long Juvenile in the first greenhouse experiment. Vertical bars = standard deviation of the mean. Soil treatments: Control (Si at 0 t ha^{-1}), Lime (8 t ha^{-1}), 0.96 (Si at 0.96 t ha^{-1}), and 1.92 (Si at 1.92 t ha^{-1}); foliar treatments: Water (Si at 0 mg kg^{-1}), pHKOH (pH adjusted with KOH), 500 (Si at 500 mg kg^{-1}), 1000 (Si at 1,000 mg kg^{-1}), and 2000 (Si at 2,000 mg kg^{-1}).

cantly greater than the foliar controls receiving either water or pH-adjusted water (Fig. 1B).

The soil and leaf Si concentrations from the second greenhouse experiment are given in Figure 2. The soil Si concentrations of treatments containing Si at 1.92 t ha⁻¹ and 1.92 t ha⁻¹ + Si at 2,000 mg kg⁻¹ were not significantly different from each other (Fig. 2A). The average soil Si concentration of the Si at 1.92 t ha⁻¹ and 1.92 t ha⁻¹ + Si at 2,000 mg kg⁻¹ treatments were 387% greater than the control treatment. The average leaf Si concentration of the combined (Si at 1.92 t ha⁻¹ + Si at 2,000 mg kg⁻¹) treatment was 43% greater than the 2,000 mg kg⁻¹ foliar treatment and 76% greater than the 1.92 t ha⁻¹ treatment (Fig. 2B). No significant differences were observed among the various Si control treatments (Si at 0 t ha⁻¹, lime at 8 t ha⁻¹, Si at 0 mg kg⁻¹, and KOH pH-adjusted water foliar treatment).

Fig. 2. A, Soil silicon (Si) concentration and **B,** leaf Si concentration at 34 days after planting in the second greenhouse experiment. Vertical bars = standard deviation of the mean. Soil treatments: Control (Si at 0 t ha⁻¹), Lime (8 t ha⁻¹), and 1.92 (Si at 1.92 t ha⁻¹); foliar treatments: Water (Si at 0 mg kg⁻¹), pHKOH (pH adjusted with KOH), 2000 (Si at 2,000 mg kg⁻¹), and 1.92+2000 (Si at 1.92 t ha⁻¹ + 2,000 mg kg⁻¹ foliar).

Soil pH and 0.5 N HOAc-extractable Si, Ca, and Mg from the repeated field experiments are presented in Table 2. The soil pH from both years usually increased as the soil Si rate increased. No significant differences were observed between the soil control (Si at 0 t ha⁻¹) and the foliar Si treatments. Also, the soil pH from the Ca(OH)₂ control treatment was comparable with the soil pH of Si at 1.92 t ha⁻¹. In both years, Si-amended soil treatments had greater extractable soil Si than nonamended soil treatments. Silicon at 1.92 t ha⁻¹ was 363 and 464% greater than the control (Si at 0 t ha⁻¹) for 2007 and 2008, respectively. There were no significant differences between the control soil Si concentration and the five foliar treatments (pH KOH-adjusted solution and Si at 0, 500, 1,000, and 2,000 mg kg⁻¹) for either year.

Final soil Ca concentration from the lime (8 t ha⁻¹) and Si at 0.96 and 1.92 t ha⁻¹ treatments were 62, 25, and 35% greater than the control treatment for 2007, and 595, 71, and 253% greater than the control treatment for 2008. The soil Ca concentration from the Si at 0.48 t ha⁻¹ treatment was not significantly different from the control treatment in either year (Table 2). The greater soil Ca concentration from 2007 might be due to residual Ca from past land management at this field site. Soil Mg concentrations increased with treatments receiving lime, which were 133 and 31% greater than the control treatment for 2007 and 2008, respectively. There was a trend of increasing soil Mg with increasing wollastonite application but it was not significant (Table 2). Wollastonite contains about 1.5% MgO.

Leaf Si concentration from the field studies are found in Figure 3. The average leaf Si concentration for cv. Hinson Long Juvenile was 56% greater than for cv. DP5634RR in both years. Leaf Si concentrations from the highest soil application rate (Si at 1.92 t ha⁻¹) and the highest foliar rate (Si at 2,000 mg kg⁻¹) were comparable, while the moderate soil rate (Si at 0.96 t ha⁻¹) resulted in leaf Si similar to that in the low and moderate foliar rates (Si at 500 and 1,000 mg kg⁻¹; Fig. 3). In comparison, the average leaf Si from the Si at 0.48 t ha⁻¹ soil rate was the lowest among all Si application rates. No significant differences were observed in leaf Si concentration among the non-Si treatments.

SBR disease progression. Disease onset was delayed an average of 3 days for soil treatment receiving Si at 1.92 t ha⁻¹ in both greenhouse and field experiments and for the foliar Si treatment (Si at 2,000 mg kg⁻¹) of the second greenhouse experiment (Table 3). The delay in disease onset of SBR is presented for only the second of the two greenhouse experiments in Figure 4. The foliar Si treatments were less effective in delaying disease onset under field conditions. In the repeated field experiment, the average 3-day delay for disease onset was clearly evident when Si was supplied via soil (Fig. 5B and E).

The AUDPCs from the greenhouse experiments are presented in Table 3, and the AUDPCs from the field experiments are presented in Table 4. In the first greenhouse experiment, the AUDPCs from

Table 2. Final soil pH and 0.5 N HOAc-extractable Si, Ca, and Mg (mg kg⁻¹) at 80 and 84 days after planting for 2007 and 2008 field experiments, respectively^z

Treatments	2007				2008			
	Si	Soil pH	Ca	Mg	Si	Soil pH	Ca	Mg
Soil Si (t ha ⁻¹)								
Lime (8 t ha ⁻¹)	31 d	7.3 ab	2,236 a	293 a	49 d	8.2 a	2,046 a	131 a
0	32 d	6.8 cde	1,382 d	126 cd	25 e	6.6 e	295 d	100 bc
0.48	48 c	6.6 e	1,377 d	126 cd	75 c	7.2 d	503 cd	96 c
0.96	99 b	7.2 ab	1,733 bc	130 cd	120 b	7.6 c	740 c	102 bc
1.92	148 a	7.5 a	1,874 b	135 bcd	141 a	7.9 b	1,040 b	120 ab
Foliar Si (mg kg ⁻¹)								
KOH (pH 10.4)	30 d	6.7 de	1,398 d	124 d	22 e	6.5 e	349 d	98 bc
0 (DI water)	34 d	6.8 cde	1,534 cd	136 bcd	22 e	6.5 e	339 d	99 bc
500	32 d	6.9 cd	1,527 cd	138 bcd	24 e	6.5 e	312 d	100 bc
1,000	33 d	7.0 bc	1,675 bc	148 bc	26 e	6.6 e	357 cd	113 abc
2,000	35 d	7.0 bc	1,747 ab	154 b	25 e	6.6 e	254 d	99 bc

^z Values sharing the same letter, within the same column, did not differ significantly at $P \leq 0.05$ as determined by the Fisher's protected least significant difference test.

treatments that included Si amendments (Si at 0.96 and 1.92 t ha⁻¹ and 500, 1,000, and 2,000 mg kg⁻¹) were not significantly different from one another, but all were 89% lower than the Si at 0 t ha⁻¹ soil control (Table 3).

The second greenhouse experiment resulted in greater AUDPC values (Table 3). In the first greenhouse experiment, the soybean plants were inoculated at 39 DAP compared with 19 DAP in the second experiment which, together with the three times greater (3×10^4 cells ml⁻¹) urediniospore suspension applied to plants in the second greenhouse experiment, were probably the major factors contributing to the AUDPC value differences observed between the two experiments. Although no significant AUDPC differences were observed among the Si at 1.92 t ha⁻¹, 2,000 mg kg⁻¹, and combined treatments (1.92 t ha⁻¹ + 2,000 mg kg⁻¹) for the second greenhouse experiment, their AUDPC values were 55% lower when compared with control plants (i.e., Si at 0 t ha⁻¹, lime at 8 t ha⁻¹, Si at 0 mg kg⁻¹ foliar, and pH KOH).

In field studies, the Si at 1.92 t ha⁻¹ soil treatment and 2,000 mg kg⁻¹ foliar treatment resulted in the lowest AUDPC values among all treatments (Table 4), while the non-Si controls, particularly foliar water treatments, resulted in the highest AUDPC values. Although not as obvious as in 2007, the data from 2008 suggested that, as Si application rates increased, final AUDPC values decreased (Table 4).

Discussion

SBR disease development. This is the first known reported study that compared foliar- and soil-applied Si concurrently on SBR development under greenhouse and field conditions. High leaf Si concentrations compared with the control were constantly associated with reduced SBR development across all experiments, as shown by the lower AUDPCs with those treatments (Tables 3 and 4). The time delay for SBR onset with soil Si treatments, in conjunction with the greater AUDPCs of the non-Si treatments, suggested that Si may have affected urediniospore direct leaf penetration and consequently, slowed SBR development, especially at the initial stages of the epidemic (7,29). The effects of Si treatments on AUDPC of SBR showed that Si applications in the

greenhouse experiments, whether soil or foliar, were not significantly different, regardless of Si application rates, and all AUDPC values were significantly lower than the AUDPC values from non-Si treatments. It is possible that disease pressure under greenhouse conditions was not as severe as in the field and, therefore, even low Si rates were effective against SBR.

Under field conditions, the results suggested that Si soil amendments were more effective than foliar-applied Si for suppressing SBR development because the soil treatments resulted in both a

Table 3. Integrated area under disease progress curve (AUDPC) for soybean rust from the greenhouse experiments^z

Treatments	AUDPC per experiment	
	First	Second
Control (Si at 0 t ha ⁻¹)	49.3 ab	86.6 a
Lime (8 t ha ⁻¹)	53.3 a	85.4 a
Si at 0.96 t ha ⁻¹	25.3 cd	NA
Si at 1.92 t ha ⁻¹	22.8 cd	55.4 b
KOH (pH 10.4)	50.8 ab	85.4 a
Si at 0 mg kg ⁻¹	36.6 bc	83.1 a
Si at 500 mg kg ⁻¹	32.9 cd	NA
Si at 1,000 mg kg ⁻¹	31.1 cd	NA
Si at 2,000 mg kg ⁻¹	18.5 d	58.1 b
Si at 1.92 t ha ⁻¹ + 2,000 mg kg ⁻¹	NA	54.4 b

^z Values sharing the same letter, within the same experiment, did not differ significantly at $P \leq 0.05$ as determined by the Fisher's protected least significant difference test. NA = not applicable. Si in t ha⁻¹ is soil applied, Si in mg kg⁻¹ is foliar applied.

Fig. 3. Leaf silicon (Si) concentrations of **A**, 2007 and **B**, 2008 field experiments at the R7 (beginning maturity) soybean physiological stage. Vertical bars = standard deviation of the mean. Soil treatments: Control (Si at 0 t ha⁻¹), Lime (8 t ha⁻¹), 0.48 (Si at 0.48 t ha⁻¹), 0.96 (Si at 0.96 t ha⁻¹), and 1.92 (Si at 1.92 t ha⁻¹); foliar treatments: Water (Si at 0 mg kg⁻¹), pHKOH (pH adjusted with KOH), 500 (Si at 500 mg kg⁻¹), 1000 (Si at 1,000 mg kg⁻¹), and 2000 (Si at 2,000 mg kg⁻¹).

Fig. 4. Greenhouse experiment 2 disease progress of soybean rust treated with soil applied wollastonite – **A**, silicon (Si) at 1.92 t ha⁻¹ or **B**, potassium silicate at Si at 2,000 mg kg⁻¹ foliar and the combined treatment (Si at 1.92 t ha⁻¹ soil-applied + 2,000 mg kg⁻¹ foliar) as compared with the controls: Control (no Si), Lime (8 t ha⁻¹), Water, and pHKOH (pH adjusted with KOH) treatments. Vertical bars = standard deviation from the mean. Foliar Si treatments were applied the day before urediniospore inoculation and at 4 and 9 days after inoculation.

delay in disease onset and a reduction in AUDPC. The overall low AUDPC values observed in 2007 were probably due to unusually dry weather conditions that occurred that year. Nolla et al. (33) tested different soil Si rates to determine whether Si could suppress a number of soybean diseases, including SBR. Although they observed suppression to frogeye leaf spot and downy mildew, they observed no effect against SBR. Unlike the current study, the authors evaluated the effects of their Si treatments one time, 79 DAP, hence missing any potential delay in disease onset as well as reduction in disease over time.

The lime (8 t ha⁻¹) control and the pH-adjusted water control foliar treatments were intended to discriminate pH effects from Si effects in SBR control across all experiments. The AUDPCs for these treatments were significantly greater than the AUDPCs for soil and foliar Si treatments (Tables 3 and 4), indicating that

neither Ca or pH was a possible contributing factor in SBR development. Comparatively, the Si at 0 mg kg⁻¹ foliar treatment was designated to mimic washing leaves of urediniospores caused by the foliar treatment applications.

Soil versus foliar Si treatments. The mechanisms responsible for the delay of SBR onset may include a Si physical barrier, similar to the double Si layer reported beneath the cuticle of Si-amended rice leaves and sheaths (51), or an expression of pathogenesis-induced host defense responses (physiological barrier; 7). The subcuticular Si layer appears to be more prominent when plants absorb Si by the roots than from a foliar application (12,24,39), because foliar Si absorption is likely very low, if at all. Guével et al. (12) also found that foliar Si applications were not as effective as root-applied Si in controlling powdery mildew (*Blumeria graminis* f. sp. *tritici*) on wheat. Liang et al. (24) found

Fig. 5. Disease progress of soybean rust in 2008 for **A, B, and C**, cv. DP5634RR and **D, E, and F**, cv. Hinson Long Juvenile treated with **A, B, D, and E**, soil applied wollastonite – silicon (Si) at 0.48, 0.96, and 1.92 t ha⁻¹ or **C and F**, foliar applied potassium silicate – Si at 500, 1,000, and 2,000 mg kg⁻¹ and controls: Control (Si at 0 t ha⁻¹), Lime (8 t ha⁻¹), Water (Si at 0 mg kg⁻¹), and pH KOH (pH adjusted with KOH) solution treatments. Vertical bars = with standard deviation of mean bars. Foliar Si treatments were applied the 29, 42, and 55 days after planting. The first days of soybean rust progression from the soil Si treatments are magnified to show the delayed in disease onset (**B and E**).

analogous results for powdery mildew (*S. fuliginea*) on cucumber when Si was applied foliarly. The authors also reported that no enhancement of pathogenesis-related protein activity was observed for foliar Si applications, indicating that disease control promoted by the foliar treatments was likely a physical effect of the Si being deposited on the cucumber leaf or an osmotic or pH effect of the Si solutions on the leaf surface. The application of foliar Si may physically coat the leaf surface after drying, interfering with urediniospore germination and penetration and, as a consequence, controlling SBR development (19).

Si and SBR resistance. Another mechanism proposed to explain the role of Si in mediated disease resistance is that Si can modulate resistance within the plant. Studies of different pathosystems showed that plants amended with Si increased production and accumulation of phytoalexins and phenolic compounds that are toxic to pathogen development (2,42). Together with the Si physical barrier, the production of pathogen-toxic compounds mediated by the presence of soluble Si increases the plant's natural defense mechanisms, thereby reducing disease damage. However, Pereira et al. (36) reported that foliar application of potassium silicate reduced SBR severity when compared with the control but did not increase the activity of soybean defensive enzymes. The fact that greater concentrations of leaf Si retarded SBR onset does not necessarily prove a cause-and-effect relationship between a physical protection and reduced disease; therefore, further studies are necessary to confirm the actual mechanism of soybean resistance against SBR initial development.

In another study where Si and a sugarcane rust disease were investigated, mixed results were observed (37). Raid and his colleagues (37) observed that Si had no influence on sugarcane brown rust development. They proposed that, because *Puccinia melanocephala* infects via stomates and not directly through the cuticle, this may be why Si did not effectively suppress brown rust development. However, the levels of brown rust severities observed in this 2-year study were 13% or less and perhaps disease levels were not high enough to detect treatment differences. In a more recent study (31), both foliar- and soil-applied Si were tested to determine their efficacy in suppressing sugarcane brown rust development in South Africa, where brown rust severity was found to be reduced from 85% in the control plants to 64% in sugarcane plants treated via soil (CaSiO_3) and foliar (K_2SiO_3) applications.

Si accumulation in soybean. Dicotyledonous plants, like soybean, can take advantage of the benefits that Si provides against many biotic and abiotic stresses, even though it may be accumulated in relatively low concentrations (8,42). In the field studies, the soybean leaves accumulated Si to approximately $3,500 \text{ mg kg}^{-1}$, while leaf accumulation was as great as $6,000 \text{ mg kg}^{-1}$ in the first greenhouse study. Our values (Tables 1, 2, and 3) agree with Miyake and Takahashi (30), who observed leaf Si values as great as

$8,400 \text{ mg kg}^{-1}$ in hydroponic culture, depending upon solution Si concentration and the period of Si supply.

In the first greenhouse study, both soybean cultivars had approximately twice the leaf Si concentration compared with the second greenhouse study or field studies. The first greenhouse study differed from the others in that an inert, soilless potting mix was used and yet the extractable soil Si was similar among studies, thereby suggesting that bioavailable Si was similar between potting mix and soil. When comparing between the two greenhouse studies, the first study was terminated at 69 DAP whereas the second one lasted only until 34 DAP. The longer growing period in the first greenhouse study probably contributed to the observed greater Si uptake. In contrast, the repeated field experiment lasted at least 80 days but had leaf Si concentrations below $3,500 \text{ mg kg}^{-1}$ over both years. Crops grown in the field typically go through a transpiration depression (stomatal closure) during early afternoon (period of greatest solar radiation and vapor pressure deficit). This likely can result in less Si movement through plants grown in the field (25). Additionally, under well-watered conditions (such as with the greenhouse experiments), positive substrate turgor pressure will pump nutrients through plants during the night (i.e., guttation). In soils that are below field capacity (i.e., the field studies in 2007 and 2008), this was much less likely to occur.

Another unusual result from these studies is that cv. DP5634RR demonstrated greater leaf Si concentrations than cv. Hinson Long Juvenile in the greenhouse study but had relatively lower concentrations in the field. Because the field studies lasted through full maturity and DP5634RR matures at least 2 weeks earlier than Hinson Long Juvenile, the discrepancy may simply be a matter of DP5634RR having less time to accumulate Si. In contrast, the greenhouse experiments were terminated prior to full maturity. These preliminary data warrant additional research into the effect that cultivar–environment may have on Si accumulation.

Conclusions. The use of Si amendments, such as wollastonite and potassium silicate, is an environmentally friendly strategy for sustainable crop production. However, further research on control of SBR that includes Si application timings or combinations of Si amendments with other fungicides or organic approved products, such as copper sulfate, needs to be performed. Si has been shown to improve host plant resistance and suppress other diseases as effectively as some fungicides (44–46). In these reported studies, Si was able to reduce both the number and rate of application of fungicides, and the combination of Si and fungicides always was the most effective in suppressing disease development. Therefore, a combination of disease control strategies may be the best approach to reduce production costs and optimize control practices in locations where soil Si is inherently low.

Since SBR discovery in North America in 2004, the late onset of disease experienced in the major soybean production areas has resulted in reduced economic impact. Any further delay in disease during the growth cycle of the soybean will benefit both organic and conventional soybean producers.

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Table 4. Integrated area under disease progress curve (AUDPC) for soybean rust in the 2007 and 2008 field experiments^a

Treatments	AUDPC	
	2007	2008
Soil Si (t ha^{-1})		
Lime (8 t ha^{-1})	280 abc	387 c
0	315 a	384 c
0.48	214 de	357 d
0.96	227 cde	340 e
1.92	181 e	324 f
Foliar Si (mg kg^{-1})		
KOH (pH 10.4)	295 ab	417 ab
0 (DI water)	297 ab	418 a
500	247 bcd	412 b
1,000	211 de	382 c
2,000	189 de	337 e

^a Values sharing the same letter, within the same year, did not differ significantly at $P \leq 0.05$ as determined by the Fisher's protected least significant difference test.

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