

# Soluble Silicon

## Its Role in Crop and Disease Management of Greenhouse Crops

Silicon (Si) is one of the most abundant elements on the surface of the earth, but its essentiality in plant growth has not been clearly established (12). While its physiological and nutritional role in plants appears limited, there is accumulating evidence that increased Si absorption offers protection against fungal diseases (6). However, the extent of its prophylactic properties has varied from one study to another and from one species to another. Despite this lack of scientific uniformity, the use of soluble Si has become increasingly popular in the greenhouse industry, where it is amended directly to the nutrient solution (32). Currently, it is mostly applied for cucumber (*Cucumis sativus* L.) and rose (*Rosa* spp.) production, where growers are reporting better protection against powdery mildew and other diseases, along with greater yield (4,30,32). These observations were obtained primarily from the European industry, since registration of soluble Si for horticultural purposes has yet to be approved in North America. However, confusion and conflicting reports abound concerning the spectrum of plant species that benefit from Si feeding, plant pathogens affected by the treatment, optimal concentrations, the fate of Si in the plant, and precise mode of action. This situation has left many North American growers and companies inquiring about the benefits of using soluble Si, and many scientists are investigating its properties.

This paper gives an overview of the current status of soluble Si in horticulture, primarily in relation to plant protection against fungal diseases. We will present a synopsis of the known and reported beneficial properties of soluble Si

in horticultural crops, particularly long English cucumber, including a summary of the current commercial situation and use of the product. Finally, the latest developments in learning the mode of action of Si in plants will be described. Many of these developments were obtained through an ongoing collaboration between the Pacific Agriculture Research Centre of Agriculture and Agri-Food Canada at Agassiz, B.C., and the Département de phytologie at Laval University, Qc.

### Physiological Role

**Effects on growth.** There now appears to be good evidence for the promotive effects of Si on the growth of monocotyledonous plants. Much of this information has been carefully reviewed by Epstein (12). A direct role for Si in the growth of horticultural crops is much less clearly established, even though it has been demonstrated that dicots as diverse as cucumber, *Citrus* spp., black raspberry (*Rubus occidentalis* L.), and strawberry (*Fragaria* spp.) accumulate Si in shoot tissues (13,14,16,35). Silicon is well-known to affect plant mineral nutrition, and at least in some cases, may promote plant growth through this interaction (15). In other cases, interpretation of the data may be confounded by the fact that Si reduces the incidence of diseases such as powdery mildew (*Sphaerotheca fuliginea* (Schlechtend.:Fr.) Pol-lacci), which would improve crop growth irrespective of any direct growth effects of Si on the crop. In this regard, studies that claim a beneficial effect of Si on cucumber growth and yield do not clearly state whether or not the effects of Si on powdery mildew were taken into account (1,4,20,29-31,33). A study in which powdery mildew was controlled, either by fungicides or with a resistant variety, showed no relationship between Si in the nutrient feed and the growth of the crop (28). Since Si appears to alleviate both abiotic and biotic stress (12), it may be that the effects of Si on plant performance are evident only when some form

of stress is imposed. Clearly, further research is required to determine whether a physiological role for Si exists in commercially important vegetable crops, particularly since most of these crops are grown in soilless culture where the SiO<sub>2</sub> concentration is usually less than 0.17 mM (10 ppm) (D. L. Ehret, *unpublished*). This becomes especially important in recirculating nutrient systems, where Si levels in the nutrient solution can become extremely low because of uptake by the crop.

**Fruit quality.** In cucumber, supplementation of nutrient solutions with Si can also influence the fruit, with the development of a bloom being reported by several workers (4,28). A relatively detailed analysis of the fruit surface using scanning and transmission electron microscopy showed that on fruit from plants treated with Si, the trichomes had a coarser appearance than those from plants without Si (25). Energy dispersive X-ray analysis also showed that Si in the peel was confined to the trichomes (Fig. 1).

### Prophylactic Role

**History.** Whether or not we acknowledge the prophylactic properties of Si in plants, it is interesting to look back into history and find that our ancestors may well have relied on Si, albeit unknowingly, to protect their crops against fungal attacks. While one may argue that ancient concoctions of plant extracts are more related to alchemy than science, our present knowledge of such concoctions reveals that they contain some of the same active ingredients currently used in plant protection. For instance, it has been known for centuries that extracts of horsetail (*Equisetum arvense* L.), when applied as a drench or as a spray, protect against diseases such as damping-off and powdery mildew. Interestingly, horsetail is a plant with one of the highest silicon contents in its tissues (over 15% dry weight). When ground in water, the liquid extracts contain sodium silicate. Specific recipes for horsetail prepara-

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tions can be found in books dealing with organic and/or biological agriculture (27). It is remarkable that reported properties of plant extracts containing sodium silicate have been corroborated by recent scientific experiments with commercial products of soluble silicon (Fig. 2; 5,17).

The earliest reported scientific work on the role of Si in plant disease control was done in the 1920s and the 1930s. For the most part, this work dealt with cereal and grass pathosystems, including studies involving rice blast and powdery mildew pathogens. Wagner (34) was the first to report an interaction between Si fertilization and cucumber powdery mildew. He found that Si fertilization of cucumber increased the latent period and reduced the level of infection by the powdery mildew pathogen.

**Current situation.** In Europe, potassium silicate (or metasilicate) is available commercially and is marketed for the

greenhouse industry. The extent of the market appears to be large enough to justify competition among several companies. To our knowledge, there are currently four commercial products offered by as many companies. All products contain Si in the soluble form as potassium metasilicate. It is usually sold to growers in drums of 185 liters (300 kg). The retail price ranges between \$700 and \$800 US per drum.

Soluble Si products are promoted for cucumber and rose production. While it has been impossible to learn the exact proportion of growers using potassium silicate, companies estimate that more than 60% of cucumber growers and over 30% of rose growers use it on a regular basis. When questioned about Si properties, company representatives claim that it improves the vigor of the plants and offers disease protection against powdery mildew. (We have been unable to obtain

data from the companies that supports such claims.) Companies attribute the effects to the presence of silicon in the apoplast of leaf cells, which makes the leaves harder and more erect, creating a physical barrier to pathogens and enhancing light interception. Recommended concentrations for the nutrient feed range from 1.7 to 2.0 mM SiO<sub>2</sub> (approximately 100 ppm) for roses and from 0.75 to 1.0 mM (approximately 50 ppm) for cucumber. Based on our experience, the latter concentration for cucumber (50 ppm) is too low to offer optimal protection against powdery mildew and root rot caused by *Pythium* spp., 100 ppm being optimal in both cases (8,16). However, 50 ppm is apparently critical for avoiding the presence of a bloom on cucumber fruit, a situation that Dutch growers want to avoid even if they have to settle for reduced disease protection.

To our knowledge, the beneficial effects of soluble silicon amendments in commercial greenhouses are corroborated only by empirical observations. Most growers will claim that they have reduced fungicide applications and improved yield as a result of using Si (32). However, in absence of a reliable control, it is hard to assess the economic benefits of using soluble Si. Considering the increasing number of growers who use Si in their production management every year, one has to assume a general level of satisfaction among users.

While greenhouse growers in Europe have been using soluble Si for several years, North American growers are still waiting for approval of its use by governmental agencies. Attempts to register potassium silicate as a fertilizer in Canada have failed because supportive data showing its nutrient properties are lacking (and probably always will be). The cost of registering potassium or sodium silicate as a fungicide would be higher than registering it as a fertilizer. However, growers and several agrochemical companies have expressed interest in commercializing a Si product.

## Recent Developments

**Research with cucumber.** Recent investigations on the role of Si in growth and control of diseases of cucumber began in the 1980s with work in Japan (20,21) and the United Kingdom (1). The two research teams examined the role of Si in growth and development of cucumber plants. Using hydroponic culture, the two groups noted that when nutrient solutions were amended with 100 ppm of SiO<sub>2</sub>, the Si-treated plants remained almost free of powdery mildew, while Si-untreated plants suffered natural outbreaks of the disease. In field experiments with plants growing in soil, Miyake and Takahashi (21) also noted that Fusarium wilt of cucumber was reduced by Si treatment.

Research programs examining the dis-

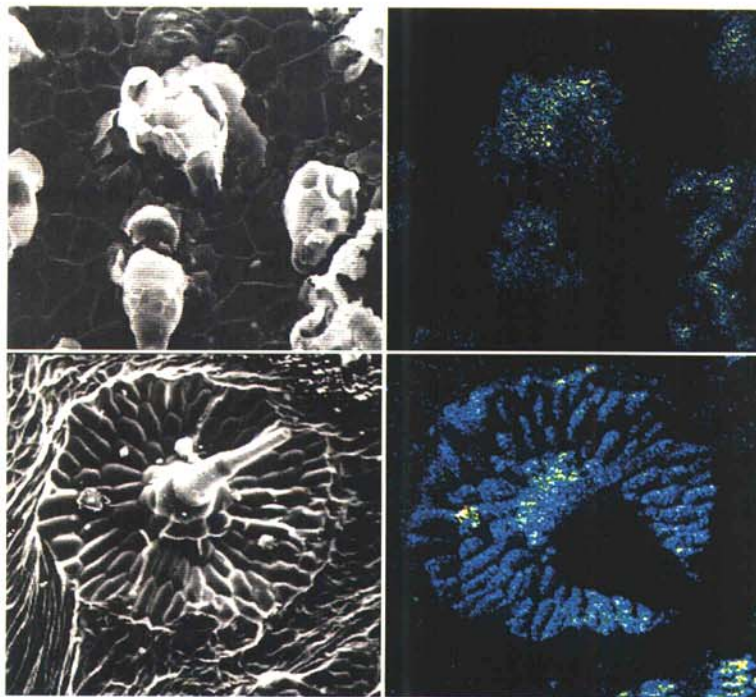


Fig. 1. Scanning electron microscope (SEM) image (top left) of a fruit trichome from a Si-fed cucumber plant with the Si distribution on the right. The bottom left figure is a SEM image of a leaf trichome from a Si-fed cucumber plant with the Si distribution on the right.

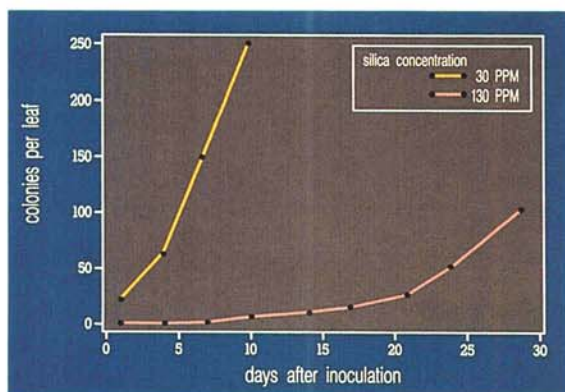


Fig. 2. The number of colonies of *Sphaerotheca fuliginea* produced over time on cucumber plants treated with nutrient solutions amended (1.75 mM) or unamended (0.05 mM) with Si under greenhouse conditions.

ease-suppressive effect of soluble silicon on hydroponically grown long English cucumber plants were initiated at the P.A.R.C. (Agassiz) and Laval University in the late 1980s. The program at Agassiz was initiated to further examine the role of Si fertilization in reducing cucumber powdery mildew. At Laval University, the work focused on the role of Si fertilization in reducing the effects of *Pythium* root rot. In the powdery mildew experiments, young cucumber plants were treated with nutrient solutions containing from 3 to 230 ppm of SiO<sub>2</sub> as soluble sodium silicate. Selected leaves were inoculated with conidia of *S. fuliginea*, and the plants were monitored over 2 weeks to determine the severity of powdery mildew under greenhouse conditions. The Si treatment reduced the area of the leaves covered with colonies of *S. fuliginea* by up to 98% (Fig. 3). Optimum disease control was achieved with concentrations of SiO<sub>2</sub> in the nutrient solutions of 100 ppm or higher (16). In agreement with the findings of Wagner (34), colony number and size decreased as Si in the nutrient solution was increased. Further, Menzies et al (16) found the disease-suppressive effect was the same when potassium silicate was substituted for sodium silicate, and control could not be attributed to the modification of the hydroponic solution's electrical conductivity because of the addition of the sodium silicate, or to the addition of Na or K to the solutions. Only Si influenced the susceptibility of the cucumber plants to *S. fuliginea*.

In order to monitor the effectiveness of Si in controlling powdery mildew

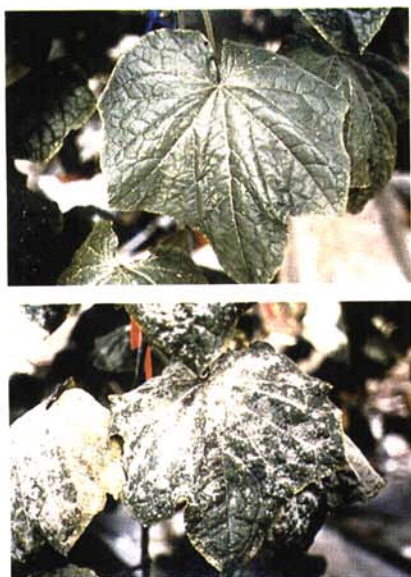


Fig. 3. The effect of treating cucumber plants with nutrient solutions amended (1.75 mM) or unamended (0.05 mM) with Si on the development of *Sphaerotheca fuliginea* on leaves. The upper leaf is on a plant treated with a Si-amended nutrient solution, while the lower leaf is on a plant treated with a nutrient solution unamended with Si. Both leaves were inoculated with equal amounts of conidia of *S. fuliginea*.

under conditions close to those in a commercial greenhouse, a larger experiment was conducted using cucumber crops in 6 × 5 m greenhouse compartments. Plants in one greenhouse received a nutrient solution amended with 100 ppm Si, while plants in a neighboring greenhouse received an unamended nutrient solution. Approximately 6 weeks after seeding, one leaf on each plant was inoculated with conidia of *S. fuliginea*. The number of colonies that developed on the top seven leaves of each plant was then monitored over the next 4 weeks. By that time, the silicon had delayed the development of severe powdery mildew on the leaves (the point when 100 colonies per leaf was recorded) by 3.5 weeks (Fig. 2; J. G. Menzies and D. L. Ehret, unpublished). Although complete control of the pathogen was not achieved, development of the disease epidemic was slowed considerably.

In the *Pythium* root rot experiments conducted at Laval University, cucumber plants were grown in recirculating nutrient solutions amended with 0, 100, or 200 ppm of SiO<sub>2</sub> in the form of potassium silicate. The Si amendment of the nutrient solutions significantly reduced plant mortality (Fig. 4), root decay, and yield losses attributable to *Pythium ultimum* Trow (8). Interestingly, no differences were observed between the 100 and 200 ppm SiO<sub>2</sub> treatments, corroborating results by Menzies et al (16), which showed a similar optimum concentration for disease control. On uninfected plants, feeding Si did not increase fruit yield, which suggests that the yield increase on infected plants was attributable to better disease control rather than to nutrient properties. Further experiments at Laval University and the Agassiz Research Station demonstrated that amending nutrient solutions with 100 ppm of SiO<sub>2</sub> also reduced the detrimental effects of

*Pythium aphanidermatum* (Edson) Fitzp. on cucumber (Fig. 5; 11).

Additional work done by A. Schuerger at the EPCOT Center (2) on the effects of Si against cucumber powdery mildew revealed that the beneficial properties of Si were independent of light intensity but greatly reduced when the temperature rose above 24 C.

In Europe, research demonstrated that the addition of potassium metasilicate to nutrient solutions will reduce the incidence of powdery mildew (4,22,30) and stem lesions caused by *Botrytis cinerea* Pers.:Fr. (22,30) and *Didymella bryoniae* (Auersw.) Rehm (22) on cucumber plants.

#### Research with other horticultural crops.

The success in reducing the severity of cucumber diseases with Si-amended nutrient solutions stirred growers to question whether Si would similarly benefit other crops. It is not surprising, therefore, that research has also occurred on the range of plants that will respond to Si treatment.

Treatment of muskmelon and zucchini squash with Si-amended nutrient solutions reduced the infection severities of powdery mildew caused by *S. fuliginea* and *Erysiphe cichoracearum* DC. when inoculated onto the leaves (17). Research results also suggest that feeding Si to roses growing in rock wool reduces the incidence of powdery mildew (32). Interestingly, Si feeding drastically reduced powdery mildew of dandelion (R. R. Bélanger, unpublished). There are also reports that a Si treatment reduces *Pythium* root rot on hydroponically grown lettuce, but our greenhouse experiments did not confirm this (R. R. Bélanger and J. G. Menzies, unpublished). Treatment of grape with Si-amended nutrient solutions did not affect the severity of disease caused by *Uncinula necator* (Schwein.)



Fig. 4. Effect of soluble silicon (Si) on control of *Pythium ultimum* infections on long English cucumber plants grown in a recirculating nutrient solution system. Plants on the left (Si-P+) were grown in a basic nutrient solution inoculated with *P. ultimum*; plants on the right were grown in a nutrient solution inoculated with *P. ultimum* and amended with 1.7 mM (100 ppm) Si.

Burrill on subsequently inoculated plant leaves (5). Finally, Miyake and Takahashi (19) reported generalized beneficial effects of a Si treatment on tomato plants but our greenhouse trials were inconclusive (J. G. Menzies, *unpublished*).

**Foliar applications.** The interest in the prophylactic role of Si on horticultural crops sparked an interest in exploring not only the range of plants that respond to Si treatment, but also different application methods, allowing Si to be applied to nonhydroponic crops or those unable to transport Si through their vascular systems from roots to leaves.

Foliar sprays containing 100, 500, 1,000, and 2,000 ppm of  $\text{SiO}_2$  were applied to leaves of cucumber, muskmelon, and zucchini squash plants, and 1 day later the leaves were inoculated with the respective powdery mildew pathogens (Fig. 6). Control treatments included plants untreated with Si and plants treated with Si-amended nutrient solutions. Foliar applications of 1,000 ppm of Si were found to be equally effective to a 100-ppm Si amendment in reducing the severity of powdery mildew on the different host leaves (17). Also of interest was the fact that a foliar application of 1,000 ppm of Si onto grape leaves reduced the severity of powdery mildew, whereas treating grapes with Si-amended nutrient solutions did not (5).

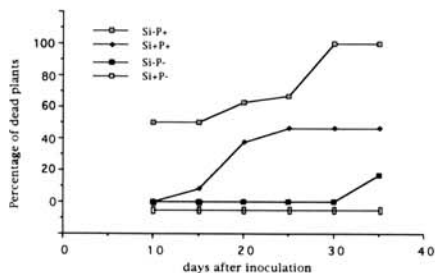
### Mode of Action

**Root uptake.** Wagner (34) was the first to speculate on the mode of action of Si supplied as a fertilizer amendment in reducing disease severity. He noted that since there was a positive correlation between the degree of mildew resistance and the concentration of silicic acid deposits at the sites of powdery mildew infection, it was likely that powdery mildew infection was prevented by the increased silicification of the epidermal cells. He hypothesized that the initial penetration of the germ tubes was impeded by Si, and that consequently that a smaller percentage of the spores germinating on the epidermis of Si-treated plants succeeded in infecting plants. He also observed noticeable differences in the further development at

the sites of infection. Although, Miyake and Takahashi (20) and Menzies et al (16) did not speculate on the mode of action of Si in reducing powdery mildew infection on cucumber, their initial findings did not contradict the hypothesis of Wagner. Indeed, these workers observed a negative correlation between the severity of powdery mildew on cucumber leaves and the amount of Si in the leaf tissue. The mode of action of Si in reducing the severity of powdery mildew on cucumber was initially examined by Samuels et al (23,24). Using scanning electron microscopy and energy dispersive X-ray analysis, they found that Si-treated cucumber leaves had low Si in epidermal cells and trichome hairs, but had highly silicified trichome bases (Fig. 1). When Si-deprived plants were exposed to nutrient solutions containing Si, the element was rapidly deposited in an insoluble polymerized form in the trichome bases (24). This suggests that trichome bases differ from the surrounding epidermal cells, which did not become silicified, and that silicification is not necessarily concomitant with cell wall deposition. Examination of powdery mildew infected leaves of Si-treated cucumber plants revealed that Si is deposited not only in the trichome bases, but also at points of attempted penetration of *S. fuliginea* (Fig. 7; 23,24). A high Si content of the host cell wall was observed at regions where the pathogen appeared to be attempting to penetrate the host, i.e., at points along fungal germ tubes or hyphae where the host cell wall had become modified into a region of smooth texture. Si was also observed to accumulate in germinating fungal conidia (23), suggesting Si movement from the cucumber leaf tissue to the germinating conidia. Germinating conidia had significantly shorter germ tubes on Si treated plant leaves (18,23); however, Si treatment did not affect the number of germinating conidia that formed haustoria (18). As colonies of *S. fuliginea* developed from initial points of infection,

measurements of total hyphal length per colony showed that colonies on Si-treated plants were significantly smaller than those on control plants (18,23). The presence of high Si surrounding *S. fuliginea* colonies was correlated with less hyphal growth (23), and the number of haustoria produced per colony was significantly reduced over time by Si treatment (Fig. 8). Samuels et al (26) did not observe any difference in the ultrastructure of haustoria but noticed deposits within cell walls of infected cells or cells around the trichome base, which were electron opaque in both Si-treated and Si-untreated plants. In Si-treated plants, the cell walls often shattered when sectioned, and there were extensive electron-dense deposits within the host cell wall, the papillae region between the host cell wall and the plasma membrane, and the host collar around the haustorial neck. No Si was detected in the extra-haustorial membrane, haustoria, fungal mycelium, or uninfected epidermal cells, with the exception of the trichome bases. Samuels et al (26) were unable to determine the nature of the electron-dense deposits, but in light microscopic studies, the most striking difference between the Si-treated and untreated plants was the accumulation of phenolic materials in infected host epidermal cells (18). Si treatment significantly hastened the accumulation of phenolic materials in these cells and increased the number of infected cells that accumulated phenolic materials (Fig. 9). It is likely that the electron-dense deposits observed by Samuels et al (26) were deposits of phenolic materials used for defense by the plant.

Chérif et al (9,10) also conducted studies on the mode of action of soluble Si using the cucumber-*P. ultimum* pathosystem. The examination of Si-treated and untreated plants using scanning electron microscopy and energy dispersive X-ray analysis revealed that in uninfected plants, Si deposits were detected only in the base cells of trichomes on the



**Fig. 5.** Percent mortality over time of long English cucumber plants grown in a standard nutrient solution (Si-) or in a solution amended with 1.7 mM soluble silicon (Si+) and inoculated with *P. aphanidermatum* (P+) or sterile potato-dextrose agar (P-).



**Fig. 6.** Cucumber leaf sprayed with a 17 mM (1,000 ppm) Si solution. Note the deposits of Si on the cucumber leaf surface.

hypocotyl or leaf tissue of Si-treated plants (Fig. 10). In a tangential section, no detectable Si accumulation in the epidermal, cortical, or stelar tissues of the root was found on either Si-treated

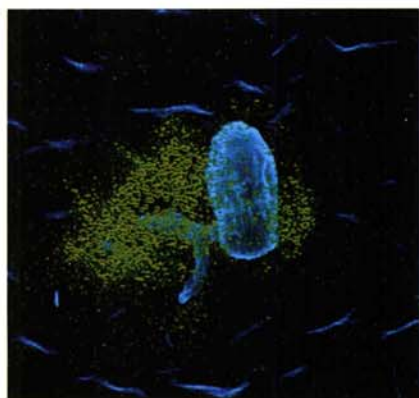


Fig. 7. Fixed, critical-point dried, germinating conidia on Si-treated cucumber leaf 24 hours after inoculation, with silicon distribution shown with green dots (X-ray dot map overlay; 24).

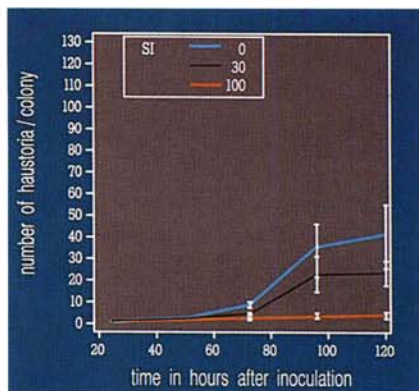


Fig. 8. The number of haustoria per colony produced by *Sphaerotheca fuliginea* on leaf pieces from cucumber treated with nutrient solutions containing low (0.05 mM), medium (0.50 mM), and high (2.30 mM) concentrations of Si.

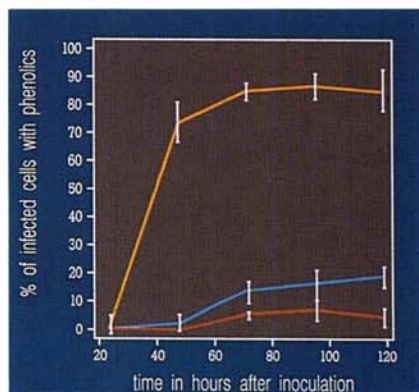


Fig. 9. Percentage of cells that stained green in toluidine blue in leaf pieces of cucumber treated with nutrient solutions containing low (0.05 mM), medium (0.50 mM), and high (2.30 mM) concentration of Si infected with *Sphaerotheca fuliginea*. The stain indicates deposition and/or accumulation of phenolics.

or untreated plants. They did not find Si accumulation in the roots of infected plants, but the Si treatment did reduce the severity of the disease caused by *P. ultimum* (8,10). Interestingly, no Si was detected at points of fungal penetration on the leaf surface when plants were grown in 100% relative humidity (Fig. 11). On the other hand, the Si-treated and untreated plants responded to *P. ultimum* infection by occlusion of stelar cells with an amorphous material (Fig. 12). The main difference between Si-treated and untreated plants was the extent and timing of this reaction. They found that defense reactions of root cells in the Si-treated plants were faster and more extensive than in untreated plants, providing effective pathogen restriction. Seventy-two hours after inoculation with *P. ultimum*, approximately 22% of the area of transverse sections of Si-treated



Fig. 10. Secondary electron image of cucumber hypocotyl grown in direct contact with soluble silicon (Si); Si distribution shown with white dots (X-ray dot map overlay). Si is concentrated at the bases of the trichomes and on the surface of the hypocotyl. Bar = 25  $\mu$ m.



Fig. 11. Secondary electron image of silicon (Si) distribution (Si distribution shown with white dots; X-ray dot map overlay) on a leaf surface inoculated with *Pythium ultimum*. Cucumber plants were grown in presence of Si under conditions of saturated humidity. No Si is associated with fungal penetration sites.

plant roots was composed of cells containing the amorphous material, compared to 2% in untreated plants (Fig. 12). They also noted that this amorphous material was more than just a physical barrier to pathogen ingress into the cell. Mycelium of the fungus that grew through the amorphous material collapsed and became extensively damaged (Fig. 13). Chérif et al (9) suggested that the amorphous material filling the stelar cells of the root may be composed of polyphenolics, especially fungitoxic phenolic compounds. Although the work with the powdery mildew-cucumber pathosystem demonstrated that Si accu-

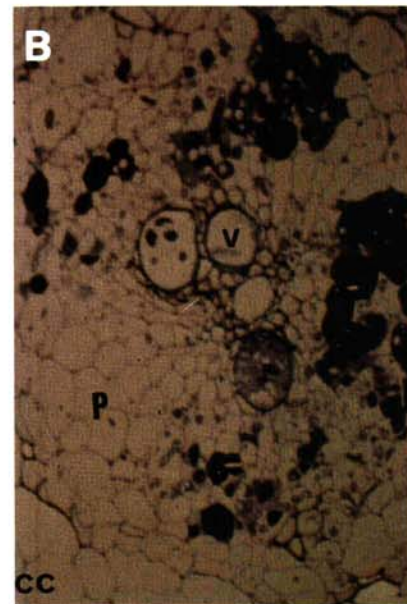
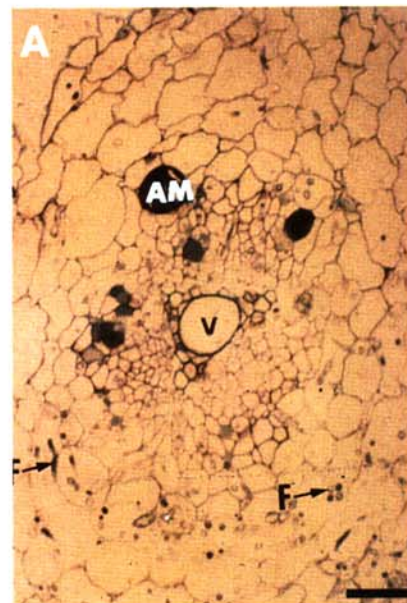


Fig. 12. Transverse sections of roots of cucumber plants inoculated with *Pythium ultimum* (F) and grown (A) without or (B) with soluble silicon. Root section from plants grown with Si have stained heavily following incubation with toluidine blue, indicating deposition of amorphous material (AM). Bar = 10  $\mu$ m. CC, cortex; P, pericycle; V, vessel.

mulation always occurred at points of pathogen penetration, Samuels et al (24) also concluded that the Si of importance in this reaction was the Si available in the plant's transpiration stream, not the cell wall bound Si. In both pathosystems, the major difference between Si-treated and untreated plants appeared to be in the rapidity and extent of phenolic accumulation in infected host cells. Chérif et al (7) demonstrated that phenolics extracted from Si-treated plants displayed a strong fungistatic activity against *P. ultimum* and *P. aphanidermatum* (Fig. 14). They further showed that a Si treatment resulted in a more intense and rapid activation of peroxi-

dases and polyphenoloxidases after infection with *Pythium* spp.

While the role of silicified cell walls in protecting plants against pathogens may not be completely discarded, recent results suggest that Si is acting in the cucumber host tissue by affecting the signals between the host and pathogen, resulting in a more rapid and extensive activation of the plant defense mechanisms (7,9,10,24).

**Foliar sprays.** When Si is applied as a foliar spray, its mode of action in reducing powdery mildew severity may be different from when it is fed through the roots. In a greenhouse study of grape infection by *U. necator*, feeding plants

1.7 mM Si had no effect on disease severity, whereas spraying leaves with 17.0 mM Si one day before inoculation substantially reduced development of the disease (5). Scanning electron micrographs with X-ray analysis showed that both methods of application resulted in Si being translocated in the leaf and deposited around the fungal appressoria. Si accumulations around *U. necator* penetration sites has also been found in leaves from field-grown grapevines not supplemented with Si (3). In the former study, the scanning electron micrographs and X-ray analysis also revealed that the fungal hyphae did not develop on sprayed leaf surface areas where dry Si deposits were present. To test whether Si was an inhibitor of conidia germination or germ tube development, conidia of *U. necator* were cultured on an agar medium to which 0–17 mM Si was added. In that range, the presence of silica weakly promoted conidia germination and germ tube development. Whether Si spray created a physical barrier to hyphal penetration or induced accumulation of phenolics and/or other defense mechanisms is not known.

## Conclusion

Despite the fact that silicon has been used in agriculture for centuries as a disease-preventing agent, its properties and mode of action in plant biology remain poorly understood. The recent market introduction and expanding use of Si-based products in Europe support its beneficial effects for horticultural applications. Several independent studies confirm the prophylactic role of Si against powdery mildew of greenhouse cucumber, and this application remains the main target of commercialization. However, recent experiments have highlighted the preventive role of silicon against a wider array of pathogens affecting different crops.

While the prophylactic properties of Si are now acknowledged, the exact mechanisms by which it protects the plants are still debated. This inability to decipher the biochemistry of Si in planta has hurt the North American horticultural industry by preventing the commercialization of Si-based products. The hypothesis associating root-fed Si with the formation of a mechanical barrier is slowly being abandoned in light of recent results showing that Si would trigger the plant's defense mechanisms. From a scientific point of view, the latter hypothesis appears more stimulating, but it may delay even further the commercialization of Si products. Indeed, the putative mode of action is reminiscent of the activity exerted by certain fungicides (e.g., fosetyl Al), which would classify Si as a fungicide in terms of registration regulations. Unfortunately, the current status of Si prevents North American growers from

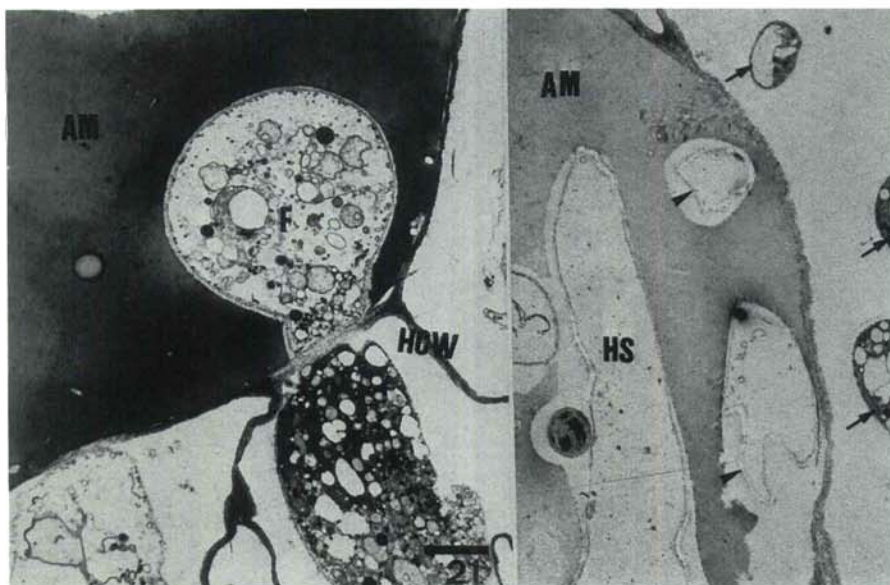


Fig. 13. *Pythium ultimum* hyphae trying to invade cucumber root cells filled with amorphous material (AM) are damaged and appear mostly as empty hyphal shells (HS) compared to hyphae invading an adjacent cell (arrows) not plugged by amorphous material. HCW, host cell wall.

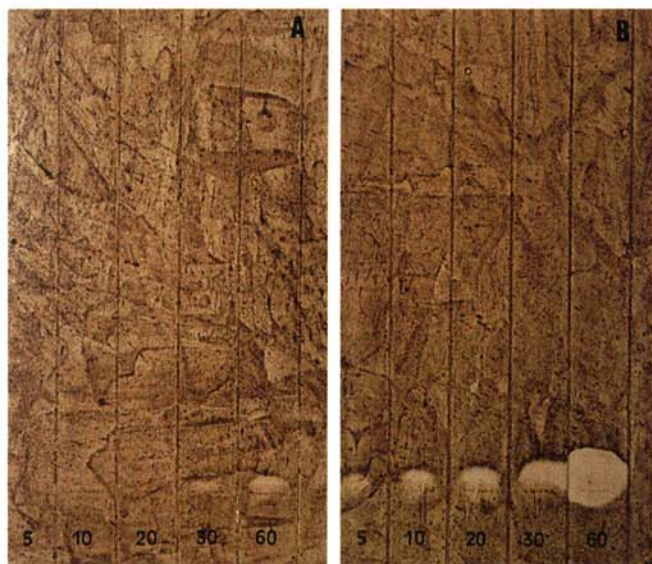


Fig. 14. Fungitoxic activity of glycosidically bound phenolics following acid hydrolysis, as revealed by a bioassay with *Cladosporium cucumerinum* on thin-layer chromatography plates. (A) Antifungal activity of different concentrations (5–60  $\mu$ l) of aglycones extracted from control cucumber plants, and (B) aglycones extracted from cucumber plants challenged with powdery mildew and grown in presence of soluble Si.

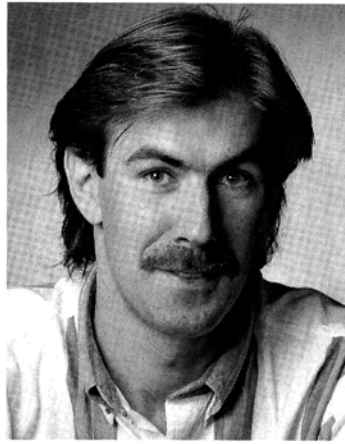
competing on equal footage with their European counterparts. At the same time, several potential applications of this natural product that could replace or at least reduce the use of pesticides are being left unexplored.

### Acknowledgments

We thank the following organizations for financial contributions: National Science and Engineering Research Council of Canada, British Columbia (B.C.) Greenhouse Vegetable Research Council, Science Council of B.C., Department of Energy Mines and Resources, Canada, and le programme d'entente auxiliaire Canada-Québec sur le développement agro-alimentaire. We thank numerous collaborators who contributed in one way or another in the preparation of this manuscript. Contribution 145 from the Horticulture Research Center, Laval University, and 527 from P.A.R.C. (Agassiz).

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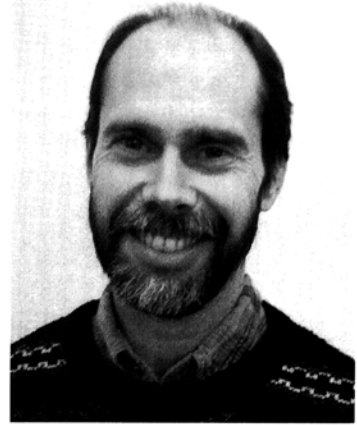
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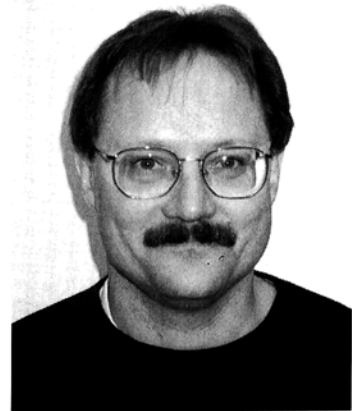
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