Silicon's Role in Plant Stress Reduction and Why This Element Is Not Used Routinely for Managing Plant Health

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Abstract

Numerous reviews and hundreds of refereed articles have been published on silicon's effects on abiotic and biotic stress as well as overall plant growth and development. The science for silicon is well-documented and comprehensive. However, even with this robust body of information, silicon is still not routinely used for alleviating plant stress and promoting plant growth and development. What is holding producers and growers back from using silicon? There are several possible reasons, which include: (i) lack of consistent information on which soil orders are low or limited in silicon, (ii) no universally accepted soil test for gauging the amounts of soluble silicon have been calibrated for many agronomic or horticultural crops, (iii) most analytical laboratories do not routinely assay plant tissue for silicon and current standard tissue digestion

procedures used would render silicon insoluble, (iv) many scientists still state that plants are either silicon accumulators or non-accumulators when in reality all plants accumulate some silicon in their plant tissues, (v) silicon is not recognized as being necessary for plant development, (vi) lack of economic studies to show the benefits of applying silicon, and (vii) lack of extension outreach to present the positive benefits of silicon to producers and growers. Many of these issues mentioned above will need to be resolved if silicon is to become a standard practice to improve agronomic and horticultural crop production and plant health.

Keywords: host defense responses, legislation, pests, plant diseases, plant nutrition, sustainable agriculture

Silicon (Si), the second most abundant element in the earth's crust after oxygen, helps plants to overcome various abiotic and biotic stresses (Debona et al. 2017). Unfortunately, the benefits from Si were mainly overlooked until the beginning of the 20th century, partly due to the element's abundance in nature and also due to the lack of visible symptoms of either deficiency or toxicity. As a result, plant physiologists have largely disregarded this element from any meaningful plant experiments. However, in field and greenhouse environments, plants are regularly exposed to different stresses, especially in soils that are deemed to be low or limited in soluble Si. An awareness of Si deficiencies in soils has become recognized as being a limiting factor in overall plant development, production, and health. Seven international conferences on Si in Agriculture (United States 1999, Japan 2002, Brazil 2005, South Africa 2008, China 2011, Sweden 2014, and India 2017) were held with the overarching theme of providing a forum where the benefits of Si were discussed among plant scientists, agricultural managers, and companies producing Si

materials. In 2015, an International Society of Silicon in Agriculture was established (<http://www.issag.org/home.html>). Even with these outcomes, the use of Si as a plant protectant or as a fertilizer in agricultural production by growers in many countries have been slow to materialize. The purpose of this review is to provide some general insights into what Si does and why it has not been adopted in plant management programs. We also provide an overview of the terms used in the discussion of Si in soil and plants, its status as an essential versus beneficial nutrient, and its role in ameliorating both abiotic and biotic types of stresses.

Terminologies Used for Si

Silicon refers to the chemical element Si in the periodic table of the elements under column IVA, directly beneath carbon (C). It has an atomic number 14 and is a tetravalent metalloid. Silica refers to silicon dioxide (SiO₂) and is the principal constituent of sand. Silicates are found in association with the cations Ca²⁺, K⁺, Mg⁺, and Na⁺ to form the most commonly known crystalline or amorphous compounds – CaSiO₃, K₂SiO₃, Na₂SiO₃, and MgSiO₃. Silicic acid, Si(OH)₄ (aka monosilicic acid or ortho-silicic acid) refers to the soluble form of Si that is readily available for absorption by plant roots. Silicene (R₂SiO, where R is an organic group) is used in the manufacture of plastic substances and other synthetic rubber-like compounds. The terms amorphous and crystalline silica are used to describe the lattice structure of the compound (Dixon and Schulze 2002). In general, crystalline silicates with lower impurities release

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more silicic acid than amorphous silicates with higher concentrations of contaminants.

Soil and Plant Si Concentrations

Soil solutions contain Si concentrations between 2.8 and 17.1 mg Si liter⁻¹ but lower and higher values may be encountered (Epstein 1994). Concentrations of this magnitude are typical for several other inorganic nutrients such as Ca, K, S, and are more than phosphorus concentrations in the soil solution. However, the dissolution of Si from soil minerals is slow, and its adsorption or resorption by the soil along with repeated cropping may reduce its levels to the point that supplementation is required for maximum crop yield (Savant et al. 1996, 1997). Some soils contain little soluble Si in their native state. Low-Si soils are typically highly weathered, leached, acidic, low in base saturation, and include large amounts of iron and aluminum sesquioxides. Thus, highly weathered soils such as Oxisols and Ultisols can be relatively low in soluble Si. Histosols (soils ≥30% organic matter), low in minerals, may also contain little Si. Further, soils composed mainly of quartz sand (silica [SiO₂]) (e.g., sandy Entisols) may be high in insoluble Si but low in soluble Si. Recently, Alfisols, Inceptisols, and Spodosols were found to be limiting in soluble Si (Tubaña et al. 2016). Many soilless mixes fall into this category as well. These low soluble Si soil conditions are found in many crop-producing areas of Africa, Asia, the Americas, and even Europe (Fig. 1).

All plants absorb measurable concentrations of Si in the range of 0.005 to 11.3% from the soil (Hodson et al. 2005), and 42 angiosperm orders, representing over 100 orders or families, have been reported to do so (Table 1). Based on their Si concentration in leaf tissues, plant species were initially classified as low, intermediate, and high accumulators, but without any mechanistic evidence supporting such classification (Handreck and Jones 1967).

This classification was later refined by categorizing high-, intermediate-, and low-accumulator plant species with active, passive, or rejective mechanisms for Si uptake, respectively (Takahashi et al. 1990). When determining whether a plant accumulates Si, past studies solely focused on measuring Si in the foliage and not in other plant organs such as roots (Hodson et al. 2005; Lewin and Reimann 1969). Recently, some plant species, such as tomatoes, peppers, and coffee, amended with Si, had root Si concentrations that are equal to or exceed Si levels in their shoots (Carré-Missio et al. 2009; French-Monar et al. 2010; Huang et al. 2011). Poaceae will tend to accumulate more Si in their tissue when compared with dicots (Epstein 1994; Hodson et al. 2005). In general, wetland grasses will average between 4.6 and 6.9%, dryland grasses from 0.5 to 1.4%, and dicots less than 0.23% on a dry matter basis. At the low end of the range (0.1%), Si corresponds on a dry matter basis with macronutrients such as Ca, Mg, P, and S. At the upper end of 10%, the tissue concentrations will exceed mineral nutrients such as N and K (Epstein 1994). Nutrients are designated as macro or micronutrients depending on whether the concentration is above or below 0.1%, respectively (Epstein and Bloom 2005). Clearly, Si is a principal mineral constituent of plants, which accumulate it within ranges to easily classify Si as either a macro or micronutrient.

The difference in Si accumulation between plant species is likely attributed to differential regulation of its absorption and distribution throughout the plant tissues. Roots and leaves are Si sinks as they contain higher concentrations of this element compared with stems, culms, petioles, and flowers. While roots of hyperaccumulators like rice tend to continually transport Si into leaves, resulting in concentrations up to 10%, plants that accumulate within the micronutrient range (less than 500 ppm), such as tobacco, maintain high root concentrations and restrict root to shoot translocation until being exposed to stress (Zellner et al. 2019). This could help explain the differences

Fig. 1. Soil orders in the world with different levels of sufficient and low soluble silicon available to plants (adapted from USDA-NRCS 2005).

between root and foliar Si concentrations. Silicon absorption from the soil solution is still unclear. However, the movement of Si into lateral and main roots through an NIP2 aquaporin located within the plasma membrane of root hairs has been reported to occur in rice (Ma et al. 2011). Homologous NIP2 proteins from barley (Chiba et al. 2009), corn (Mitani et al. 2009), crookneck squash (Mitani et al. 2011), cucumber (Sun et al. 2017), soybean (Deshmukh et al. 2015), tobacco (Zellner et al. 2019), and wheat (Montpetit et al. 2012) have also been demonstrated to transport silicon. Once Si is taken up, it can either move apoplastically or symplastically through the root tissues until it reaches the exodermal and/or endodermal cells. At this point, Si must move through a transport mechanism into the cells to be transported to shoots. Movement of Si into cells within the root can occur through pore channels such as the NIP2, where passive movement down a concentration gradient occurs or the active arsB-like pore that uses energy from ATP or a proton motive force Si to move against its concentration gradient (Ben Fekih et al. 2018; Dey and Rosen 1995; Yang et al. 2012). Also, endocytosis can occur where the apoplastic contents, including Si, can be absorbed into the cell. Both NIP2 and arsB-like pores have been functionally characterized from grains and squash (Chiba et al. 2009; Mitani et al. 2009, 2011; Yamaji and Ma 2007). The pattern of expression for the rice transporters at the distal and proximal side of cells for osNIP2;1 and Lsi2 (arsB-like protein) suggested a preferred symplastic movement for Si through their root systems. Wheat and corn have a less organized distribution of these two transporters, making it unclear if a symplastic versus apoplastic route is favored for Si transport. Once Si has moved into or past the endodermal layer, it then passes via transport mechanisms into the xylem vessels, leading to distribution throughout the plant tissues (Ma et al. 2011). In rice, other osNIP2 proteins localized at nodes are responsible for trafficking and unloading Si from xylem vessels into specific developing tissue such as the panicles during grain formation (Yamaji et al. 2008). Whether a similar mechanism is present for other grains or any dicots is unclear as no studies have yet been published for these species.

Some plants have mechanisms to deposit large amounts of Si as phytoliths into specialized cells through a dehydration reaction (Currie and Perry 2007). This type of biosilicification seems to be present within the Poaceae as no appearance of silica cells has been reported in other dicots. Some dicots do possess the ability to deposit large amounts of Si on the leaf surface and within specific organs. For instance, *Zinnia elegans* concentrates Si in subsidiary cells and trichome structures (Fig. 2). Other organs include Si-containing scales in New Guinea impatiens (Frantz et al. 2010). Recently, it

was shown to be distributed in the stinging hairs or trichome structures across many different plant species (Mustafa et al. 2018). These types of biosilicification or Si extrusion have not been demonstrated in many plant species, and it would be interesting to determine if plants that accumulate less than 0.2% Si foliarly have a mechanism to polymerize or store a high Si load safely.

Analysis of Si in Soil and Plant Tissues

Since plants take up Si in the form of monosilicic acid, $\text{Si}(\text{OH})_4$, from the soil solution, this is the most relevant form of Si in the soil solution for managing plant Si nutrition. Thus, the amount of soluble Si in the soil is an essential decision tool for Si fertilization. This is determined by quantifying the concentration of Si in soil extracts. While uncommon, plant Si is also used as the basis for a fertilizer recommendation. The adoption of soil and plant Si testing as tools for deriving Si fertilizer recommendation has been challenged mainly by the lack of agreement in procedures to use.

The two components of soil Si testing are the extraction procedure and the method of its quantification in the soil extracts. The establishment of different procedures for extracting Si from soil began in the 1960s. Since then, several procedures have been established, and almost all of these had several modifications made mainly to reduce the extraction time requirement (Table 2) (Tubañá and Heckman 2015). The quantity of Si extracted from the soil differs depending on the extraction procedure used (Babu et al. 2016; Paye et al. 2018; Tubañá et al. 2012; Wang et al. 2004). In addition to this, the method by which Si concentration in soil extracts is quantified, colorimetric versus inductively coupled plasma spectrometry (ICP), also affects the soil Si test values.

For this reason, both the critical soil Si and test interpretation, which is required for making fertilizer recommendation, become specific to the soil Si testing procedure used. This means that the work associated with the establishment of critical soil Si and test interpretation is essentially repeated every time a new testing procedure is developed. Considering the number of crops and soil classes across landscapes to cover, the amount of research work quickly multiplies. Even after more than five decades, soil Si testing has yet to be adopted as a tool for making its recommendation to growers. Hence to date, Si fertilization is an option rather than a routine agronomic or horticultural practice. Both the 0.5 M acetic acid and 0.01 M calcium chloride extraction procedures have shown some potential (Crusciol et al. 2018; Korndörfer et al. 1999; Paye et al. 2018; Snyder 2001); however, the database on critical Si levels and soil test interpretations for many economically important crops and major soil types across agricultural landscapes remains weak. Some examples of established critical soil Si levels based on 0.5 M acetic acid extraction procedure include the 32 g Si m^{-3} for sugarcane production in Florida (McCray et al. 2011) and different levels for rice at 19, 41, and 54 mg Si kg^{-1} (Korndörfer et al. 2001; Narayanaswamy and Prakash 2009; Paye et al. 2018).

Unlike soil Si determination, there have been no major disagreements among the studies carried out on digestion procedure nor quantification of Si in the digest for its determination in plant tissues. Most of the follow-up research revolves around validating and improving procedures in terms of efficiency and safety. Between the gravimetric method, solubilization, and digestion procedures, the selection is made based on precision, turnaround time, cost, and required instrumentation. The autoclave-induced digestion method developed by Elliott and Snyder (1991) became the most widely used method. Both the excessive foaming during digestion and unstable color development of the digest with reagents contributed to this method's low precision (Haysom and Ostatek-Boczynski 2006; Kraska and Breitenbeck 2010; Taber et al. 2002). Subsequently, it led to developing a modified procedure known as oven-induced digestion (OID) developed by Kraska and Breitenbeck (2010). Here, the addition of octyl-alcohol and 5 mM ammonium fluoride were included in the steps to address these issues. Instead of an autoclave, a bench-top oven is used to heat the solution during the digestion. While the hydrofluoric acid (HF) in a closed vessel microwave digestion followed by ICP is new and is considered a more robust procedure than

Table 1. Forty-four angiosperm clades containing plant species known to accumulate silicon in their plant tissues^a

Angiosperm clade

Acorales, Asparagales, Aquifoliales, Apiales, Alismatales, Asterales, and Arecales
Brassicales, Bromeliaceae, and Boraginaceae
Celastraceae, Cornales, Commelinales, Cucurbitales, and Caryophyllales
Dipsacales
Ericales
Fabales and Fagales
Geraniales, Garryales, and Gentianales
Liliales, Limiales, and Laurales
Myrtales, Malpighiales, Malvales, and Magnoliales
Nymphaeaceae
Pandanales, Proteales, Piperales, and Poales
Ranunculales and Rosales
Santalales, Solanales, Staphyleaceae, Sapindales, Schisandraceae, and Saxifragales
Vitaceae
Zingiberales

^a Data source: Hodson et al. (2005).

OID (Le Blond et al. 2011), the safety and HF-resistant setup requirement limit its adoption in soil/plant testing laboratories. Nondestructive and high-throughput methods using portable X-ray fluorescence and near-infrared reflectance spectroscopy have shown potential in terms of speed and accuracy (Reidinger et al. 2012; Smis et al. 2014). However, more calibration studies are needed to include a wide array of plant species. Perhaps, once

certified in the future, the required sophisticated instrumentation by these methods may also limit its adoption.

Sources of Si and Their Use

There are several solid and liquid sources of Si that have been used as soil conditioners, amendments, or as fertilizers for agronomic

Fig. 2. Scanning electron microscopy (A to D) and corresponding energy-dispersive X-ray (EDS) spectroscopy maps for silicon (A1, B1, C1, and D1) deposition on the adaxial leaf surface of zinnia plants grown in calcium silicate-amended substrate. Silicon was located throughout basal cells (bs), guard cells (gc), subsidiary cells (sc), and trichomes (tr). The EDS maps for oxygen (A2, B2, C2, and D2), potassium (A3, B3, C3, and D3), and carbon (A4, B4, C4, and D4) are shown as references for elemental distributions.

and horticultural crops grown in the field or greenhouses (Table 3). For these materials to be useful, they must meet many criteria that include a relatively high soluble Si content, a physical state that will facilitate storage ability and ease of application, and they must contain negligible soil contaminants such as heavy metals (Gascho 2001). Solid sources of Si that have been used successfully when incorporated into the soil include wollastonite (a naturally occurring mined calcium silicate), calcium silicate slag (a byproduct of the phosphate or steel industries of thermophosphate), and cement (Gascho 2001; Tubaña and Heckman 2015). Another Si material is the diatomaceous earth mined from sedimentary rocks. These deposits contain fossilized diatoms and can vary significantly in Si composition depending on the diatom species present due to differences in physical and morphological characteristics. However, some researchers question whether diatoms are a viable source of Si (Haynes 2017). Crop residues (e.g., miscanthus, rice hulls, and wheat straw) are also a potential source. Still, the Si composition and concentration from these plant types (e.g., phytoliths) may not release Si at the same rate for meeting the plant's demand for the element when needed (Frantz et al. 2010). Based on several field and greenhouse experiments, many of these solid materials were pre-plant applied at rates ranging from 300 to 800 kg elemental

Si ha⁻¹ (Datnoff et al. 1991; Korndörfer et al. 2001; Rodrigues et al. 2015a; Seebold et al. 2001). Liquid sources of Si include silica gel, monosilicic acid, and calcium-, potassium-, and sodium silicates that are used in hydroponic, greenhouse, and field plant production as a foliar spray or drench at concentrations of up to 100 ppm Si depending on the source. In many instances, these liquid sources have been used as a contact bio-pesticide to suppress plant diseases and/or insect pests as evidenced by their efficacy when applied foliarly and compared with root applied Si (Rodrigues et al. 2015a). However, some research with monosilicic acid suggests that a foliar application may increase rice yield (Prakash et al. 2011). Also, the use of these foliar-applied products has expanded to be used in vineyards as well as in the fields of blueberry, peanut, tomato, and tobacco aiming to control diseases and alleviating some abiotic stresses.

More recently, silica nanoparticles have been shown to promote plant growth (Suriyaprabha et al. 2012) or enhance disease resistance (El-Shetehy et al. 2021). Silica nanoparticles might prove to be another Si source for future use in agriculture, but further studies need to be conducted to understand what concentrations are beneficial, how the particles move through plant tissue, and how long particle integrity is maintained (Elmer and White 2018).

Table 2. Extraction procedures for estimating soluble silicon in the soil solution and adsorbed phase^a

Solution	Procedures
H ₂ O	10 g in 50 ml + 0.1% NaN ₃ to reduce biological activity; incubate 21 days at room temperature with manual shaking 2 times a day 10 g in 100 ml; 4 h shaking 10 g in 60 ml; incubate at 40°C for 2 weeks 10 g in 100 ml; 1 h shaking
CaCl ₂	0.01 M CaCl ₂ ; 1 g sample in 20 ml solution; 16 h shaking 0.01 M CaCl ₂ ; 10 g sample in 100 ml solution; 1 h shaking
Na acetate + acetic acid	0.18 N Na acetate + 0.87 M acetic acid, adjusted to pH 4; 10 g sample in 100 ml solution; 5 h occasional shaking at 40°C
NH ₄ acetate	0.18 N Na acetate + 0.87 M acetic acid, adjusted to pH 4; 10 g sample in 100 ml solution; 1 h shaking 5% (0.5 M) NH ₄ acetate, adjusted to pH 4.5–4.8 with 0.1 M acetic acid; 1 g sample in 20 ml solution; 1 h shaking 5% (0.5 M) NH ₄ acetate, adjusted to pH 4.8 with 0.1 M acetic acid; 1 g sample in 10 ml solution; 1 h shaking
Acetic acid	0.5 M acetic acid; 1 g sample in 10 ml solution; 1 h shaking with 12 h resting 0.5 M acetic acid; 1 g sample in 10 ml solution; 1 h shaking
Citric acid	0.5 M acetic acid; 10 g sample in 25 ml solution; overnight resting followed by 2 h shaking
Na citrate + NaHCO ₃	0.1 M citric acid; 1 g sample in 50 ml solution; 2 h shaking, resting overnight then 1 h shaking
NH ₄ citrate	80% 0.3 M Na citrate and 20% 1 M NaHCO ₃ ; 2 g sample in 50 ml solution; 5 min at 80°C
H ₂ SO ₄	1 M NH ₄ citrate; 10 g sample in 25 ml solution; 80 h shaking
Mehlich-3	0.005 M H ₂ SO ₄ ; 1 g sample in 200 ml solution; 16 h shaking 2 g soil in 10 ml Mehlich-3 solution; 5-min shaking

^a Data source: Tubaña and Heckman (2015).

Table 3. Some companies that sell potential solid and liquid sources of silicon^a

Company	Product name	Products description	Website
Agripower	Agripower Silica	Diatomaceous Earth	https://agripower.com.au/
CalSil Corp.	Sili-Cal	Calcium silicate	http://www.calsilcorp.com/
Dyna-Gro	Pro-Tekt	Potassium silicate solution	https://dyna-gro.com/
Harsco	CrossOver	Calcium and magnesium silicates	https://www.crossover-soil.com/
Montana Grow	Natural Si Fertilizer	Diatomaceous Earth	https://montanagrow.com/
Plant Tuff Inc.	Plant Tuff	Calcium and magnesium silicates	http://planttuff.com/
Privi Life Sciences Ltd.	Silixol	Orthosilicic acid	http://privilifesciences.com/
PQ Corp.	Sil-MATRIX	Potassium silicate	https://www.pqcorp.com/
Rexil Agro	OSAB ₃	Hydrated silicon dioxide, potassium chloride, polyethylene glycol, and boric acid	http://rexil-agro.com/
Vanderbilt Minerals, LLC	Vansil W-10	Calcium metasilicate	https://www.vanderbiltminerals.com/
Yara	ActiSil	Choline chloride and orthosilicic acid	https://www.yara.co.uk/

^a This list of silicon-containing products does not constitute a recommendation or endorsement by the authors.

Root Versus Foliar-Applied Si for Suppressing Plant Diseases

Different solid or liquid sources of soluble Si either applied to the roots or foliage have been used for suppressing plant diseases (Rodrigues et al. 2015a). As mentioned previously, the root application provides an efficient means of Si absorption and distribution in plant tissues. Foliar application of Si has also been used for disease control. When the foliar application of Si has been compared with root (soil) application, plants respond better to the latter (e.g., reduction in disease development) (Table 4). This comparison has been successfully demonstrated in the following different host-pathogen interactions: cucumber/powdery mildew, melon/powdery mildew, wheat/powdery mildew, rice/blast, rice/brown spot, and soybean/Asian soybean rust (Abed-Ashtiani et al. 2012; Cacique et al. 2013; Guével et al. 2007; Lemes et al. 2011; Liang et al. 2005; Rezende et al. 2009). The mechanism by which Si affects pathogen infection is dependent on whether it is applied via the roots or foliage. When roots take up Si, it moves continuously through the xylem vessels into the root endodermis and cell membranes leading to distribution throughout plant tissues. Only when Si is root absorbed will several defense responses be potentiated within the host plant. In contrast, foliarly applied Si will quickly polymerize on the leaf surface to form a chemical-physical barrier, and most likely, the changes in pH or the osmotic potential of the phyllosphere explain the reductions in the development of some foliar diseases (Rodrigues et al. 2015b). While small amounts of Si may migrate through the cuticular matrix, more plausibly, the osmotic shift in the epidermal environment could induce Si migration from the vascular tissues to other parts of the leaves.

Although root-applied Si is consistently more effective than foliarly applied to suppress foliar diseases, the efficiency will be intrinsically linked to the plant's ability to uptake Si from the soil solution and accumulate high amounts in the shoots. However, foliarly applied Si can still be used for many plant species infected by fungal or bacterial pathogens. Still, the efficacy for disease control may depend on the application frequency, the environmental conditions, the lifestyle of the pathogen and its level of aggressiveness, as well as the amount of inoculum produced during the infectious period (Andrade et al. 2013; Bowen et al. 1992; Yanar et al. 2011). For instance, liquid solutions are quickly depleted from the environment either due to plant absorption or leaching from the root zone. The phloem-limited movement of Si, similarly to Ca, requires a continual supply so that new plant growth tissues can be efficiently protected. This explains why liquid products need either continual or multiple applications throughout the plant's life cycle. With solid fertilizers, the continual release into the root zone occurs throughout the growing season. Some products, such as calcium silicate slags, may have a residual effect up to three years following the initial soil amendment.

Biotic Stress

Plant diseases. Many economically important plant species have benefited from the Si supply by showing a substantial decrease in

the intensities of diseases caused by pathogens of different lifestyles (Table 5) (Debona et al. 2017). Rice is one plant that benefits the most from Si supply because of its inherent ability to accumulate a high concentration of Si in shoots due to Si-transporter proteins located in the roots. As a consequence, the intensities of diseases such as bacterial blight, brown spot, grain discoloration, leaf scald, leaf and panicle blast, stem rot, and sheath blight were dramatically suppressed (Debona et al. 2017). The Si supply dramatically impacted some important components of host resistance (e.g., incubation period, latent period, colony or lesion size, lesion number per unit of leaf area, lesion expansion, and inoculum produced per infection site), therefore contributing to lower disease development for many diverse host-pathogen interactions (Debona et al. 2017; Fortunato et al. 2015; Rodrigues et al. 2015a). Interestingly, the level of resistance of some rice and sorghum cultivars susceptible to foliar diseases was raised to the resistance level of cultivars showing race-specific resistance (Debona et al. 2017; Resende et al. 2013; Rodrigues et al. 2001; Seebold et al. 2001). The most important soil-borne diseases known to date to be controlled by Si include *Phytophthora* root rot on avocado and soybean; *Phytophthora* blight on bell pepper; *Pythium* root rot on bitter melon; *Pythium* root rot and stalk rot on corn; *Pythium* root rot, dollar spot, and brown patch on creeping bentgrass; *Fusarium* wilt on cucumber and lettuce; *Fusarium* root rot on melon; basal stem rot on oil palm; root-knot nematodes on banana, coffee, and rice; *Fusarium* wilt and *Fusarium* crown and root rot of tomato; gummy stem blight on watermelon; and brown patch on zoysiagrass and tall fescue (Fortunato et al. 2015). Banana plants from cultivar Maçã, susceptible to Panama disease, showed no leaf chlorosis and less darkening of the rhizome-pseudostem when supplied with Si and infected by *Fusarium oxysporum* f. sp. *cubense* (Fig. 3A and C) (Fortunato et al. 2012). On the other hand, plants not supplied with Si showed early leaf chlorosis and intense darkening of the rhizome-pseudostem (Fig. 3B and D). Histochemical analyses of root sections of banana plants supplied with Si indicated intense deposition of flavonoids in the sclerenchyma and metaxylem vessels in response to *F. oxysporum* f. sp. *cubense* infection as indicated by the intense fluorescence in contrast to the roots of nonsupplied Si plants (Fig. 4) (Fortunato et al. 2014).

The intensity of grain husk discoloration, an important rice seed-borne disease, was shown to be greatly decreased for Si-supplied plants (Fortunato et al. 2015). In fact, the transmission of *Bipolaris oryzae*, the major causal agent of grain discoloration, from the seeds of plants supplied with Si was found to have a lower seedling discoloration, and seedling emergence was vastly improved (Fortunato et al. 2015). Although both foliar and root applied Si has proven effective in reducing many foliar diseases, root applied has been demonstrated to be more efficient because the element helps to potentiate the plant's defense responses. The supply of Si has also been shown to decrease certain diseases to the same level of intensity as fungicides (Brecht et al. 2004; Seebold et al. 2004). The application of Si undoubtedly would be well-suited for inclusion in an integrated disease management strategy. It would permit possible reductions in the

Table 4. Comparative efficiency of root versus foliar applications of silicon for plant disease management

Crop	Disease	Pathogen	Disease control efficiency ^a	
			Root	Foliar
Cucumber	Powdery mildew	<i>Podosphaera xanthii</i>	15 to 36%	Ineffective
Melon	Powdery mildew	<i>Podosphaera xanthii</i>	73%	65%
Rice	Blast	<i>Pyricularia oryzae</i>	80 to 95%	52 to 91%
Rice	Blast	<i>Pyricularia oryzae</i>	75%	53%
Rice	Blast	<i>Pyricularia oryzae</i>	76%	56%
Rice	Brown spot	<i>Bipolaris oryzae</i>	37%	Ineffective
Soybean	Rust	<i>Phakopsora pachyrhizi</i>	5 to 54%	33 to 89%
Soybean	Rust	<i>Phakopsora pachyrhizi</i>	16 to 43%	19 to 36%
Watermelon	Gummy stem blight	<i>Didymella bryoniae</i>	≈ 75%	≈ 30%
Wheat	Powdery mildew	<i>Blumeria graminis</i> f. sp. <i>tritici</i>	≈ 80%	≈ 40%

^a Variables evaluated included incidence, severity, and area under disease progress curve. Data source: Rodrigues et al. 2015a.

use of fungicides while enhancing host plant resistance. Based on these and other findings, this often-overlooked element has the potential to be a viable means of managing the occurrence of epidemics of important plant diseases.

How does Si slow down the development of disease symptoms? This challenging question may be explained by following two lines of thinking supported by the literature, especially using the rice-*Pyricularia oryzae* interaction as a model. One of the first hypotheses proposed to explain the lower number and smaller lesion sizes of blast developing on rice leaves was Si deposition and polymerization beneath the cuticle, in the cell wall, and inside the bulliform cells.

Table 5. Pathogens causing damping off, galls, leaf blights, leaf spots, powdery mildews, root rots, rusts, and wilts in plants reported to be suppressed by silicon^a

Pathogens	Genera
Fungi	<i>Bipolaris</i> , <i>Blumeria</i> , <i>Colletotrichum</i> , <i>Corynespora</i> , <i>Diplocarpon</i> , <i>Erysiphe</i> , <i>Fusarium</i> , <i>Leptosphaeria</i> , <i>Magnaporthe</i> , <i>Phaeosphaeria</i> , <i>Phakospora</i> , <i>Rhizoctonia</i> , <i>Septoria</i> , <i>Sphaerotheca</i> , <i>Sclerotinia</i> , and <i>Uncinula</i>
Oomycetes	<i>Phytophthora</i> and <i>Pythium</i>
Bacteria	<i>Acidovorax</i> , <i>Pseudomonas</i> , <i>Ralstonia</i> , and <i>Xanthomonas</i>
Virus	<i>Nepovirus</i>
Nematode	<i>Meloidogyne</i>

^aData source: Debona et al. 2017.

Fig. 3. Visual aspect of banana plants (A and B) and darkening intensity of the rhizome-pseudostem (C and D) when growing in a silicon-deficient soil amended (A and C) or nonamended (B and D) with calcium silicate and infected by *Fusarium oxysporum* f. sp. *cubense*.

Later, this same hypothesis was also put forth to explain the reductions in disease intensities occurring in other monocots as well as in some dicot species (Debona et al. 2017; Rodrigues et al. 2015b; Seebold et al. 2001). Since Si deposition beneath the cuticle is uneven, penetration by appressoria, as in *P. oryzae* on rice, can still occur despite an increase in the incubation and latent periods (Cacique et al. 2013; Debona et al. 2017; Rodrigues et al. 2015b). The role played by Si is more than just a physical barrier for increasing rice resistance to blast. Blast lesions were smaller on the leaves of rice plants supplied with Si (Fig. 5), indicating that some host defense responses could be affecting the colonization of leaf tissues by *P. oryzae* (Rodrigues et al. 2003; Seebold et al. 2001). For the *Arabidopsis thaliana*-*Erysiphe cichoracearum*, cucumber-*Colletotrichum lagenarium*, cucumber-*Podosphaera xanthii*, rice-*Monographella albescens*, rice-*Rhizoctonia solani*, wheat-*Bipolaris sorokiniana*, and wheat-*P. oryzae* interactions, the silicification of the epidermal cells delayed fungal penetration, leaf tissue colonization, and sporulation (Araujo et al. 2016; da Silva et al. 2015; Debona et al. 2017; Rodrigues et al. 2015b).

Although the physical barrier hypothesis is just the beginning of how to explain the role of Si in suppressing the development of some diseases, Coskun et al. (2018) recently proposed the apoplastic obstruction hypothesis. They suggested that the amorphous Si portion deposited in the apoplast interferes with the recognition process establishing the specificity between the pathogen and its host by altering the effector movement, and subsequently the establishment of infection by the pathogen. Undoubtedly, the view, as well as hypotheses, on how Si functions as a potential modulator of host defense will continue to advance as our knowledge of the element grows at the physiological, biochemical, and molecular levels.

Many biochemical mechanisms of defense potentiated by Si were reported to occur in different plant species in response to pathogen infection. In the leaves of rice plants not supplied with Si, hyphae of *P. oryzae* massively colonize the mesophyll cells, which showed intense disorganization and absence of amorphous material (Fig. 6A and C). By contrast, fungal hyphae colonizing the mesophyll cells in the leaves of Si-supplied plants were often surrounded by dense amorphous material and reduced to empty shells (Fig. 6B and D) (Rodrigues et al. 2003). Many empty hyphae of *M. albescens* were evenly surrounded or trapped in dense osmiophilic material that also partially occluded epidermal and mesophyll cells and the vascular bundle of rice plants supplied with Si (Araujo et al. 2016). High concentrations of flavonoids and phenolic acids occurred in the leaves of cucumber plants supplied with Si and infected by *P. xanthii* (Debona et al. 2017). There was a greater deposition of dopamine, flavonoids, lignin, and phenolics in the sclerenchyma cells as well as in the metaxylem and phloem vessels in the roots of banana plants supplied with Si and infected with *F. oxysporum* f. sp. *cubense* (Debona et al. 2017). Phenolic and flavonoid concentrations enhanced in leaves of Si-supplied wheat plants infected by *P. oryzae* (Cruz et al. 2015; da Silva et al. 2015).

In response to Si, the activities of chitinase (CHI), β -1,3-glucanase (GLU), phenylalanine ammonia-lyase (PAL), peroxidase (POX), and polyphenoloxidase, all involved either directly or indirectly on host defense responses, were higher for several host-pathogen interactions such as banana-*F. oxysporum* f. sp. *cubense*, banana-*Xanthomonas campestris* pv. *musacearum*, bitter melon-*Erysiphe* sp., cucumber-*Pythium ultimum*, cucumber-*P. xanthii*, coffee-*Meloidogyne exigua*, cotton-*Colletotrichum gossypii* var. *cephalosporioides*, cotton-*Phakopsora gossypii*, cotton-*Ramularia areola*, melon-*P. xanthii*, pea-*Mycosphaerella pinodes*, perennial ryegrass-*P. oryzae*, rice-*B. oryzae*, rice-*M. albescens*, rice-*P. oryzae*, rice-*R. solani*, rice-*Xanthomonas oryzae* pv. *oryzae*, sorghum-*Colletotrichum sublineolum*, soybean-*Phakopsora pachyrhizi*, and tomato-*Pseudomonas syringae* pv. *tomato* (da Silva et al. 2015; Dallagnol et al. 2011; Debona et al. 2017; Resende et al. 2013; Tatagiba et al. 2014). Anthocyanins, flavonoids, lignin-thioglycolic acid derivatives, momilactones, and phenolics originated from either primary or secondary metabolisms were of detrimental importance for the resistance of some plant species supplied with Si when challenged by pathogens (Debona et al. 2017; Resende et al. 2013; Rodrigues et al. 2015b). The up-regulation

Fig. 4. Histochemical characterization of flavonoids, lignin, and dopamine in the roots of banana plants from cultivar 'Maçã' nonsupplied with silicon (-Si) (A, C, E, G, and I) or supplied with Si (+Si) (B, D, F, H, and J) at 32 days after inoculation with *Fusarium oxysporum* f. sp. *cubense*. **A**, Strong yellow-orange autofluorescence (arrow) in the vascular bundles and in the sclerenchyma cells in the roots of -Si plants. **B**, Slight yellow-orange autofluorescence (arrow) near the phloem and metaxylem vessels in the roots of +Si plants. **C**, Absence of fluorescence in the vascular bundles, sclerenchyma, and endodermis cells in the roots of -Si plants stained with Neu's reagent. **D**, Strong yellow fluorescence in the roots of +Si plants stained with Neu's reagent (arrow). **E**, Slight orange-yellow fluorescence in the cells surrounding the phloem and metaxylem vessels and the sclerenchyma cells in the roots of -Si plants stained with Wilson's reagent. **F**, Strong orange-yellow fluorescence in the phloem vessels and in the sclerenchyma cells in the roots of +Si plants stained with Wilson's reagent (arrow). **G**, Absence of lignin deposition in the roots of -Si plants stained with phloroglucinol-HCl. **H**, Strong lignin deposition in the cortex of the roots of +Si plants stained with phloroglucinol-HCl (arrow). **I**, Absence of dopamine in the roots of -Si plants. **J**, Dopamine was strongly suspected to occur in the phloem and metaxylem vessels (arrow) of the roots of +Si plants as confirmed by orange-yellow fluorescence after staining with lactic acid + glyoxylic acid stain. c = cortex, e = endodermis, mx = metaxylem, p = phloem, and s = sclerenchyma. Bars = 50 µm. Reprinted from Fortunato et al. (2014) with permission.

of genes encoding for GLU, chalcone synthase, CHI, cinnamyl alcohol dehydrogenase, lipoxygenase, PAL, POX, and PR-1 potentiated by Si was of great importance for the increased resistance of perennial ryegrass to *P. oryzae*, rice to *P. oryzae*, rose to *Podosphaera pannosa*, and wheat to *P. oryzae* infections (Cruz et al. 2015; Debona et al. 2017; Rodrigues et al. 2015b). The antioxidant metabolism (high ascorbate peroxidase, catalase, glutathione reductase, and superoxide dismutase activities) of plants supplied with Si and infected by pathogens were more efficient in the removal of reactive oxygen species (Debona et al. 2014, 2017; Domiciano et al. 2015).

At the physiological level, the photosynthetic performance of plants infected by pathogens (e.g., common bean by *C. lindemuthianum*, cotton by *R. areola* and *C. gossypii* var. *cephalosporioides*, rice by *P. oryzae* and *M. albescens*, sorghum by *C. sublineolum*, and wheat by *P. oryzae*) was preserved by Si fertilization. For example, compared with nontreated controls, leaf gas exchange parameters and foliar temperature were not significantly different, healthy leaf area and concentration of photosynthetic pigments were only slightly reduced, with minor damage to the chloroplasts and less impairments in energy dissipation via chlorophyll *a* fluorescence (Aucique-Pérez et al. 2014; Debona et al. 2017; Domiciano et al. 2015; Tatagiba et al. 2016). Some photochemical parameters associated with chlorophyll *a* fluorescence such as the quantum yield of photosystem II (PSII) photochemistry (F_v/F_m), the photochemical quenching coefficient, and the electron transport rate, were greatly improved for rice plants infected with *P. oryzae* and *M. albescens* as well as for wheat plants infected with *P. oryzae* grown in the presence of Si (Aucique-Pérez et al. 2014; Domiciano et al. 2015; Tatagiba et al. 2016). The inefficiency of the *lsi1* (low Si; defective in active Si uptake) rice mutant, which originated from the wild-type cultivar Oochikara, to actively uptake Si resulted in greater brown spot severity and, consequently, reduced photosynthesis and lower foliar sugar concentration (Debona et al. 2017).

Insects and other pests. Although many insect herbivores, arthropods, and other pests have their behavior affected by plants

fertilized with Si, the mechanisms by which the Si-mediated antiherbivore defense remains to be determined (Table 6) (Debona et al. 2017; Reynolds et al. 2009, 2016). Interestingly, some mechanisms reported to explain the effect of Si to reduce disease development (e.g., physical barrier or the potentiation of antimicrobial compound production) might also explain the impact of Si against these pests.

Herbivore behavior of *Spodoptera exempta* exposure to high-Si diets was affected due to reduced leaf digestibility that resulted in mandible wear (Massey and Hartley 2009). A decrease in the third-instar's weight gain and pupal weight of the rice leaf folder (*Cnaphalocrocis medinalis*) at a high Si rate was linked to reduced food quality and food conversion efficiencies (Han et al. 2015). For rice supplied with Si, there were lower relative growth rates and reduced boring success of the sugarcane borer (*Diatraea saccharalis*) (Sidhu et al. 2013). High foliar Si concentration compared with the untreated control was associated with reduced sugarcane stalk larval penetration by the pyralid borer *Eldana saccharina* (Kvedaras and Keeping 2007). McNaughton and Tarrant (1983) reported that heavily grazed African grasses accumulated more Si in their leaf blades than did less heavily grazed plants, indicating that silicification was probably an inducible defense against mammalian herbivores. In another study, Si applied to the soil or foliage showed that the greenbug aphid's (*Schizaphis graminum*) stylet penetration into wheat was not affected, therefore challenging the physical barrier hypothesis (Goussain et al. 2005).

Furthermore, the biochemical analysis confirmed that Si enhanced wheat defense mechanisms against the greenbug aphid through increased POX, PPO, and PAL activities, especially when plants received Si before aphid infestation (Gomes et al. 2005). High concentrations of 5-caffeoylquinic acid, *p*-coumaroylquinic acid, and rutin in zinnia plants supplied with Si reduced the total cumulative fecundity and the intrinsic rate of increase of *Myzus persicae* (Ranger et al. 2009). Rice plants grown in Si-amended soil and infested with the leaf folder (*Cnaphalocrocis medinalis*) displayed higher CAT, PAL, POX, PPO, and SOD activities and lower

Fig. 5. Development of blast lesions on the adaxial leaves of rice plants nonsupplied (A) or supplied (B) with silicon at 96 h after inoculation with *Pyricularia oryzae*.

Fig. 6. Transmission electron micrographs of leaf samples obtained from rice plants nonsupplied (A and C) or supplied (B and D) with silicon at 72 (A and B) and 120 (C and D) hours after inoculation with *Pyricularia oryzae*. A and C, Fungal hyphae massively colonize the mesophyll cells, which showed signs of intense disorganization. B and D, Fungal hyphae invading the mesophyll cells were often surrounded by dense amorphous material and reduced to empty shells. Amorphous material (red asterisks [*]) and blue arrows) and fungal hyphae (f). Bars = 1 μ m (B and C) and 2 μ m (A and D).

malondialdehyde concentration than plants grown in nonamended soil (Debona et al. 2017). The level of transcripts for defense marker genes, jasmonic acid (JA) accumulation, POX, and PPO activities, as well as the level of a trypsin protease inhibitor, increased in rice plants supplied with Si being attacked by *C. medinalis* (Ye et al. 2013). Besides, JA was important in rice resistance against leaf borer attack because Si was not able to increase resistance against this insect in plants whose genes involved in JA biosynthesis or JA perception were silenced (Ye et al. 2013).

Interestingly, Si deposition was reduced when JA signaling was compromised, indicating a strong interaction between JA-mediated responses to insect herbivores and Si, as well as the promotion of Si accumulation and JA (Ye et al. 2013). Tritrophic (plant-herbivore-natural enemy) interactions were also affected by Si. In this scenario, Si may either reduce insect feeding by making them more vulnerable to their natural enemies or by changing the composition and concentration of herbivore-induced plant volatiles (HIPVs), thus attracting the insect's enemies (Gatarayiha et al. 2010; Kvedaras et al. 2010). Although potassium silicate applied at higher concentrations (0.08 and 0.16%) alone did not kill mites (*Tetranychus urticae*), *Beauveria bassiana*-induced mite mortality was enhanced for beans, cucumber, eggplant, and maize plants (Gatarayiha et al. 2010). Cucumber plants supplied with Si were more attractive to adults of the predator *Dicranolaius bellulus* when attacked by larvae of *H. armigera* in comparison with nonsupplied plants (Kvedaras et al. 2010). The number of eggs from *H. armigera* removed from potted cucumber plants and placed in a lucerne stand with numerous predatory arthropods was higher in the presence of Si (Kvedaras et al. 2010). The effects of herbivore-induced plant volatiles might not have become apparent because wheat plants were narrowly spaced, and a non-choice design was employed (Reynolds et al. 2009, 2016).

Table 6. Insects and other pests reported to be suppressed by silicon^a

Feeding guild	Pest
Chewing insects	Caterpillars and stem borers
	Locusts and grasshoppers
	Maggots
	Beetles and weevils
	Sawflies
Piercing-sucking insects	Planthoppers
	Leafhoppers
	Stink bugs
	Aphids
	Whiteflies
	Scales
Cell content pest feeder	Spider mites

^a Compiled from Reynolds et al. (2009, 2016) and Kvedaras et al. (2010).

Table 7. Chemical and physical types of stresses reported to be alleviated by silicon^a

Environmental factors	Stress
Chemical types of stresses	Toxicity by metals such as Al, As, Cd, Fe, and Mn
	Soil salinity
	Nutrient imbalance in plant tissues (e.g., excess of N or P deficiency)
Physical types of stresses	Lodging
	Low and high temperatures
	Drought stress
	Radiation

^a Compiled from Bhat et al. (2019) and Debona et al. (2017).

Abiotic Stress

Abiotic stress is any environmental factor, other than biological, that shifts homeostatic pathways (e.g., water and nutrient balance, temperature, light, and gas exchange) out of balance (Meena et al. 2017). When plants cannot adjust for these changes, a reduction in growth, vigor, and yield, as well as increased susceptibility to pathogen infections and pests may occur. The most pronounced use of Si by plants is for stress tolerance (Table 7). Regarding abiotic stress, Si acts either directly or indirectly, resulting in the modulation of plant defense responses. In essence, Si allows the plants to adjust or maintain internal balances more rapidly. Hormonal concentrations, transpiration rates, enzyme activities, changes in gene expression, and amino acid concentrations have been reported to occur for plants supplied with Si and exposed to stress (Zellner and Datnoff 2020). How and where Si fits into all of these specifically is still unclear.

While various external factors are involved in abiotic stress, two main internal results are water and nutrient imbalances. Abiotic stress that leads to water imbalances includes drought, heat, frost, salinity, and changes in the concentrations of nutrients, amino acids, and metabolites. The transpiration rate was altered in plants of different crops supplied with Si such as pistachio (Habibi and Hajiboland 2013), rice (Ma and Takahashi 2002), sorghum (Liu et al. 2014), tomato (Shi et al. 2016), and white lupin (Abdalla 2011) either in the absence or presence of stress conditions. In the roots of maize, onion, and rice, Si increased the formation of exodermis Casparian bands, which may explain how it protected the plants from water loss into the growing media (Fleck et al. 2015). Water use efficiency was also enhanced for alfalfa (Liu and Gang 2013), broccoli (Barreto et al. 2017), maize (Gao et al. 2005), and tomato (Romero-Aranda et al. 2006) plants supplied with Si. These examples suggest that Si is involved in water balance as a normal and stress response for both monocots and dicots.

Internal nutrient imbalances also are caused by various environmental factors, including water imbalances and the presence of pollutants or nutrients at toxic or deficient concentrations in the growing media (e.g., soil, soil-less mixes, and hydroponic solutions). Pollutants (e.g., Al, As, Cd, Cr, Hg, and Pb) and high concentrations of nutrients (B, Cu, Fe, and Mn) trigger plant defense pathways that reduce growth and yield (Singh et al. 2016). Plants alleviate heavy metal toxicity through the sequestration in the growing external media and internal apoplast as well as compartmentalization within cellular structures such as vacuoles (Gasic and Korban 2006; Sharma et al. 2016). Plants treated with Si have been protected against heavy metal stress (Bhat et al. 2019). Studies with Si show these responses for the toxicity of Al in potato (Dorneles et al. 2019), As and Cd in *Brassica chinensis* (Yao et al. 2017), As in *Brassica juncea* (Pandey et al. 2016) and maize (Tripathi et al. 2016), B toxicity in spinach and tomato (Gunes et al. 2007), Cd in *Brassica campestris* (Wu et al. 2016), Cr in *Brassica juncea* (Ashfaq et al. 2017) and *Pisum sativum* (Tripathi et al. 2015), Cu toxicity in *A. thaliana* (Fig. 7, Li et al. 2008), Mn toxicity in cucumber and rice (Che et al. 2016; Maksimović et al. 2012), and Ni in cotton (Khaliq et al. 2016).

In the case of nutrient deficiency, Si may also play a role in either nutrient availability in the media or remobilization in the plant (Hernandez-Apaolaza 2014). The deficiency of N in *Brassica napus* (Haddad et al. 2018), P in tomato (Zhang et al. 2019), K in soybean (Miao et al. 2010) and sorghum (Chen et al. 2016), Fe in barley (Nikolic et al. 2019), cucumber (Pavlovic et al. 2013), and soybean (Gonzalo et al. 2013), and Zn in soybean (Blanca Pascual et al. 2016) has been alleviated by Si.

Even when nutrients are available in the growing media, their distribution within the tissues of plants may lead to localized deficiencies that may predispose them to diseases. The availability of Ca for proper tissue development is vital to reduce diseases such as bitter pit in apple (Falchi et al. 2017), blossom-end rot in tomato (Hagassou et al. 2019), bract necrosis in poinsettia (McAvoy and Bible 1996), tip burn in *Brassica oleracea* (Lee et al. 2016), and cavity spot in carrots (Perry and Harrison 1979). These diseases are usually controlled by supplying Ca to the plants via foliar sprays even though this nutrient may not be limiting in the growth media. The disease occurs due to shifts in the transpiration rate or stream as

well as changes in internal protein or metabolite levels with a reduction in the apoplastic concentration of Ca in the infected tissues during plant development (Freitas et al. 2016; Gilliham et al. 2011; Hocking et al. 2016). The severity of blossom end rot decreased in Si-treated tomato plants (Stamatakis et al. 2003), but the role of this element in the mitigation of other calcium diseases, previously listed, has yet to be determined. Since Ca plays other roles in the development and cell signaling in plants, understanding the interaction of Si and Ca would be intriguing. Environmental conditions will change and become more extreme as global temperatures and CO₂ concentrations continue to rise. The intrinsic use of Si by plants to alleviate abiotic stress supports the need and application of this element for sustainable plant production and health.

Is Si an essential or a beneficial element? In the 1950s, Japan and Korea were the first countries to recognize the importance of Si in crop production, especially for rice. Researchers in these countries classified Si as being agronomically essential. Brazil, in 2004, was the third country to recognize Si formally. The Brazilian Ministry of Agriculture, which regulates commercial production of fertilizers, ruled that Si is an essential micronutrient. Nowadays, Si is still not recognized as an essential element, and in many countries, sources of Si are only sold as a soil amendment or conditioner as opposed to fertilizers. This is in part due to how essential plant nutrients are defined and is based on three criteria developed by Arnon and Stout (Epstein and Bloom 2005) that must be met: “(1) a deficiency of the element makes it impossible for the plant to complete its life cycle, (2) the deficiency is specific for the element in question, and (3) the deficiency is directly involved in the nutrition of the plant as for example as a constituent of an essential metabolite or required for the action of an enzyme system.”

Epstein and Bloom (2005) have argued that there are difficulties with this definition. For the first criterion, a plant can be quite severely deficient in an essential nutrient element and still be able to complete its life cycle. The second criterion implies that the element substituted for is “deficient”. Thus, this criterion merely reiterates the first one. Finally, the third criterion, that the element is directly involved in the plant nutrition, discounts correcting of unfavorable environmental conditions. This implicit disregard has not always

occurred during the discovery of other essential elements. When boron was discovered to be essential, no one had any evidence that “the element is directly involved in the nutrition of the plant” (Epstein and Bloom 2005). Based on these deficiencies in the Arnon-Stout definition, Epstein and Bloom (2005) have proposed the following: “An element is essential if it fulfills either one or both of two criteria: (1) The element is part of a molecule that is an intrinsic component of the structure or metabolism of a plant, and (2) the plant can be so severely deprived of the element that it exhibits abnormalities in its growth, development, or reproduction—that is, its ‘performance’—in comparison with plants not so deprived.” Since the essentiality of Si for diatoms and *Equisetum arvense*, “scouring rushes” is well established but has not been categorically demonstrated for other Si-accumulating plant species, Epstein and Bloom (2005) have proposed that Si is a “quasi-essential” element. However, the second criterion of Epstein and Bloom (2005) dealing with enhanced performance in the context of stress tolerance has been demonstrated in the literature for a broad range of plant species supporting the essentiality of Si for plant health (Frew et al. 2018; Guntzer et al. 2012; Lewin and Reimann 1969; Werner 1967).

Regulatory issues and the status of Si as a fertilizer or biopesticide. Regulatory agencies, along with the agricultural industry, are unsure how to define Si. Consequently, the debate about classifying this element as a biostimulant, fertilizer, or plant protectant is ongoing (Zellner and Datnoff 2020). The issue with only classifying Si as a biostimulant or fertilizer limits its marketing for use in alleviating abiotic stresses (e.g., drought and metal toxicities) and not for controlling plant diseases. In cases where Si is marketed for plant disease control, the EPA must register the product as a pesticide. Furthermore, in some countries such as Spain, new fertilizer regulations only allow for distribution of products with Si concentrations above 8%, eliminating many liquid Si products from the marketplace because of perceived low Si concentrations (Anna Botta Catala, Bio-Iberica S.A., personal communication).

In 2004, efforts were made by scientists from the University of Florida-IFAS and University of California-Davis to educate the Association of American Plant Food Control Officials (AAPFCO), the regulatory body that governs the labeling of fertilizers in the

Fig. 7. Significant reductions in shoot and root tissue of hydroponically grown *Arabidopsis thaliana* Col-0 treated with 30 μ M CuSO₄ (C, G) for 3 days. When 1.5 mM Si was added with 30 μ M CuSO₄ (D, H), there was a visible increase in both shoot and root growth. Addition of 1.5 mM silicon (B, F) to the nutrient media had no changes in shoot or root growth compared with the controls (A, E). Data source: Li et al. 2008.

U.S., about elevating the role of Si to a plant nutrient (AAPFCO 2017). Each state in the U.S. as well as Puerto Rico and Canada has its fertilizer regulatory program, and the laws and regulations for this program are based on AAPFCO's recommendations. This organization strives to gain uniformity by consensus considering consumer needs, protecting the environment, and maintaining fair competition among the industry. The AAPFCO, however, has a different definition for plant nutrients in comparison with Arnon and Stout, as well as Epstein and Bloom (2005). They placed nutrients into two categories as follows: (i) primary and (ii) secondary and micronutrients based on the needs and quantities of a required nutrient. Primary nutrients (term T8 by AAPFCO) include the following plant foods: N, available phosphate (P_2O_5), and soluble (K_2O), which are taken up in large quantities. Secondary are nutrients whose concentrations are less than primary, and micronutrients are needed in trace amounts (term T9 by AAPFCO), are those other than the primary nutrients that are essential for the normal plant growth that needs to be added to the medium. Secondary plant nutrients include Ca, Mg, and S, while plant micronutrients include boron, chlorine, cobalt, copper, iron, manganese, molybdenum, sodium, and zinc. This organization lacked a defined place for Si since this element does not fit the designated categories of primary, secondary, or micronutrient due to limited efficacy data.

As a consequence, the Labeling/Terms Committee of AAPFCO proposed a new category termed "Beneficial Substances or Compounds" (term T-73). This new term was defined as "any substance or compound other than primary, secondary, and micro plant nutrients that can be demonstrated by scientific research to be beneficial to one or more species of plants, when applied exogenously." However, Si was only given tentative approval by AAPFCO at that time because a method was not available to differentiate total Si content from soluble Si. A method had to be developed and validated for determining soluble Si from fertilizer sources. Based on earlier research (Buck et al. 2011), a 5-day method for determining the soluble Si concentrations in solid fertilizer products was developed using a sodium carbonate-ammonium nitrate extractant followed by visible spectroscopy with heteropoly blue analysis at 660 nm and was approved by AAPFCO after single-laboratory validation (Sebastian et al. 2013). This method was shown to correlate with plant Si uptake and can now be used for production quality control, label content compliance monitoring, and selecting an appropriate Si fertilizer source to meet crop production needs. Another aspect regarding this method is related to its initial development to be an indicator test to determine if a fertilizer source could provide soluble Si to plants, and the following Si recovery ranges for the sources tested were 0.2 to 8.4%. While the percentages of Si are reported with this method, the values obtained from the sources tested are not intended to provide a quantitative value to compare one potential Si source with another (Zellner and Datnoff 2020). Based on this method, the first Si fertilizer recognized was CrossOver ($CaMgSiO_3$, HARSCO), which is currently registered to contain the beneficial substance Si and is marketed in 44 U.S. states for use in the horticultural, turf, and general agricultural markets. Now, several other Si fertilizers are being labeled to contain beneficial substances and may be sold in the U.S. (Table 3).

In 2002, PQ Corporation submitted a petition to the Environmental Protection Agency (EPA) to allow the use of potassium silicate for disease control in crop production. The PQ Corporation conducted many field studies showing that potassium silicate would reduce the incidence and severity of powdery mildew. They also provided supportive data that potassium silicate could replace or be combined with other fungicides, including K bicarbonate and S. The PQ Corporation later amended their petition to include insecticide use based on data demonstrating reductions in mites and whiteflies with minor impacts on beneficial insects. In 2004, the Biochemical Classification Committee of the Biopesticides & Pollution Prevention Division of the EPA ruled that potassium silicate should be classified as a biochemical pesticide. This decision was based on evidence at that time that potassium silicate functioned as an inducer of systemic acquired resistance. As directed by the Pesticide Registration Improvement Act (PRIA), the registration was expected to be

completed by May 2006, but it did not happen until November 2007. At that time, scientists from PQ Corporation and the University of Florida-IFAS presented more in-depth data on the performance and potential mechanisms of Si for managing abiotic and biotic stress to the National Organic Standards Board (NOSB)/USDA National Organic Program (NOP). As a result, the NOSB and NOP approved the use of potassium silicate for plant disease control for organic farmers. Subsequently, potassium silicate (Si-MATRIX, PQ Corporation) was registered by the EPA in the U.S.A. and certified by Organic Materials Review Institute (OMRI) as the first Si organic pesticide for preventative control of powdery mildew and control of mites and aphids on high-value crops such as blueberries, strawberries, wine grapes, and others. In October 2014, NOSB re-evaluated potassium silicate based on more comprehensive information presented by scientists from PQ Corporation and the LSU AgCenter. As a consequence, the board ruled in favor of continuing its use for another 5 years.

Undoubtedly, Si is a crossover element that acts as both a plant protectant and a biostimulant/fertilizer because it affects both biotic and abiotic stress (Datnoff and Rodrigues 2015). Perhaps a new category should be created so that Si may achieve universal acceptance by regulatory agencies worldwide.

Some reasons why Si has not been used for plant health management. Currently, in the U.S., three groups (AAPFCO, ASA/CSSA/SSSA, and Si researchers) are awaiting the confirmation of Si as an essential nutrient. To begin, Si researchers refrain from using this descriptive term as it has not been accepted as such in the U.S. by regulatory bodies. The AAPFCO, however, is waiting for the triscientific societies, ASA, CSSA, and SSSA, to address Si as such. These societies do not view Si as an essential nutrient as the literature, and Si researchers have not made the essentiality argument. Furthering this problem is that as a few Si researchers try to break these barriers to justify Si as a nutrient for plant health, they are met with outdated, biased arguments by reviewers, using terms like "Si excluders" and "non-Si competent." These unjustified claims have only hurt the agriculture industry in the U.S. and other countries, depriving them of expanding these products. Scientific research is also affected as grant funding is limited in this field due to the misconceptions of Si's nutritional status for plant growth.

Nevertheless, some incremental progress has been made in recognizing Si. In 2012, the triscientific societies sponsored the first Silicon Symposium for soil fertility and nutrient management. The societies recognized that Si had not been given the same level of attention as a limiting factor in soil fertility and crop production as other nutrients. In 2015, the International Plant Nutrition Institute published an agronomic fact sheet entitled Nutri-Facts on Si that recognized it as either a "beneficial substance" or a "quasi-essential" nutrient (<http://www.ipni.net/nutrifacts-northamerican>). In 2017, *The Nature and Properties of Soils* published a section on Silicon in *Soil-Plant Ecology* (Weil and Brady 2017). In doing so, they stated this was the first edition that devoted a section to Si in more than 100 years of publishing this textbook. They further stated that "scientists studying soil-plant ecology have long treated Si as something of a neglected stepchild among the elements important to plants."

Effective, practical means of application, affordable Si sources, and methods for identifying conditions under which Si fertilization will be beneficial are still needed for use in disease and pest management (Datnoff and Rodrigues 2015). Research for using Si for plant disease suppression is still in its infancy since only a few large-scale field effects have been observed to date for rice, sorghum, and sugarcane. Soil tests for gauging the amounts of soluble Si have not been calibrated for many agronomic or horticultural crops, as previously mentioned. Furthermore, most analytical laboratories do not routinely assay plant tissues for Si. The current standard plant tissue digestion procedures, which use strong acids (e.g., nitric acid), would render Si insoluble, making an analysis of the digested material inaccurate and therefore meaningless. Thus, the two analytical tools most often used for determining the need for fertilization with plant nutrients are not widely available for Si.

There is also a paucity of economic studies to show the benefits of applying Si in agricultural or horticultural systems. Soil applications

of Si have demonstrated a minimum 1-year residual effect on disease control, thereby amortizing the cost of both the Si fertilizer and application (Alvarez and Datnoff 2001; Datnoff et al. 1991, 2007). In another study, a 2-year experiment showed that a 1995 residual soil Si application was not significantly different in suppressing rice blast development from a 1996 fresh Si soil application or full rates of fungicides (Seebold et al. 2004). More economic studies must be conducted to demonstrate to growers and producers the profitability of using Si.

Finally, there are only a few universities that have active Si research and extension field programs in the U.S. (Tubañá et al. 2016). The University of Florida-IFAS, located in the Everglades Agricultural Area, has a long-established program, over 30 years, in which soil Si levels have been well correlated with plant responses, including disease suppression and yields in both rice and sugarcane (Datnoff et al. 1991; Korndörfer et al. 2001; McCray et al. 2011). Since 2000, Rutgers Snyder Research and Extension Farm has established several trials on crops that include corn, pumpkin, turfgrass, and winter wheat (Heckman 2012). After two decades, they have demonstrated that the sources of Si used are as effective as liming materials for managing soil pH, and have quantified reductions in insect damage (e.g., European corn borer) and disease development (e.g., powdery mildew) along with increases in yields. In Louisiana, early Si research under field conditions demonstrated that this element could improve sugarcane yields (Viator et al. 2004) and suppress rice diseases (Bollich et al. 2001). Tubañá and her colleagues were the first to establish the critical soil Si levels for improving rice, sugarcane, and wheat production in Louisiana (Paye et al. 2018; Santos et al. 2015; White et al. 2017). All the aforementioned programs have had numerous field days and produced extension outreach materials to educate producers and growers about the positive benefits of Si. However, this is not the case in other parts of the U.S. or in other countries (Cairns et al. 2017; Laane 2017; Tewatia 2017). As a consequence, many Si manufacturers state that one of the biggest factors restricting the sale of their product is producers and growers having little understanding about the role of Si in agriculture (Cairns et al. 2017; Raugewitz 2017). Without more university or other public/private sector programs to provide research and extension outreach on Si, this will be a bottleneck to advancing the agronomic or horticultural practice of using Si for plant health management.

Conclusions

Without a doubt, Si is a vital and quantitatively major component of the soil-plant system that occurs in nature and agriculture (Epstein 1994). This element plays many important roles in a plant's life, especially in alleviating both abiotic and biotic stresses. On the basis of research conducted to date, with a few exceptions, the following generalizations about Si can now be made: (1) for any plant disease, a minimum Si concentration in plant tissues is needed to suppress it; (2) once that level of Si in plant tissues has been obtained, disease suppression will increase proportionally as the concentration of this element increases in plant tissues; (3) the Si supply to the plant roots must be continuous or the disease-suppressing effects will be reduced or disappear; (4) only when applying Si to roots will this element change plant responses against pathogen infection, pest attack, and even abiotic stress at the physiological, biochemical, and molecular levels; (5) many components of host resistance (e.g., incubation period, latent period, and lesion number) will be impacted by Si; (6) the level of resistance of some cultivars of rice and sorghum to foliar diseases may be increased by Si; and (7) disease suppression by Si can be as effective as fungicides (Datnoff and Rodrigues 2015).

The potential of Si has only begun to be realized commercially as a plant protectant in an integrated disease/pest management strategy or as a fertilizer for crop performance. Given the low Si content now being found in numerous soil orders as well as soilless potting mixes and the fact that many plant species contain macro and micronutrient concentrations of Si in their tissues, it seems prudent to consider soluble Si supplementation as a simple and inexpensive method to help maintain or enhance plant health especially in the context of sustainable agriculture.

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Wendy Zellner

Dr. Wendy Zellner received both her B.S. and Ph.D. in biology from the University of Toledo in 2005 and 2012, respectively. Her graduate research exclusively used low silicon-accumulating species to determine beneficial responses to viral infections with silicon supplementation and to identify silicon transporters present in their genomes. She then pursued a postdoctoral research opportunity with USDA-ARS from 2012–2016, where she continued characterizing silicon transporters in Solanaceae and focused on tomato and floriculture species to understand silicon release from different fertilizer sources and the effect of silicon supplementation on bacterial infection, drought, and heavy metal stress. Currently, she is with the University of Toledo as a research associate professor and is confirming the function of classical silicon transporters present in micro-accumulator silicon species, as well as working with manufacturers and distributors to develop or adjust current state-regulated efficacy and testing guidelines for the diverse silicon fertilizer industry. She has been actively studying the role of silicon as a plant nutrient for the past 16 years and hopes to see its status elevated from beneficial to essential due to its profound role in plant health.

Brenda Tubaña

Dr. Brenda S. Tubaña received a B.S. in agriculture in soil science from the University of the Philippines Los Banos (UP Los Banos) in 1992, an M.S. in soil science (soil fertility), UP Los Banos in 2002, and a Ph.D. in soil science (soil fertility) from Oklahoma State University in 2007. In 1993, Tubaña worked with the International Rice Research Institute in Los Banos, Laguna, Philippines, on nutrient management of upland/aerobic rice production. In 2004, she joined Oklahoma State University to pursue her Ph.D. Her project focused on developing a need-based nitrogen decision tool using remote sensing technology for corn and wheat. In 2007, she joined the School of Plant, Environmental, and Soil Sciences, Louisiana State University, as assistant professor of soil fertility. She conducts and coordinates statewide soil fertility research for major row-crop production in Louisiana. Her soil and crop science research on silicon is one of the few active research programs in the U.S. In 2015, she was awarded the Jack E. and Henrietta Jones Professorship. She is currently serving as the president of the International Society for Silicon in Agriculture, and head of the organizing committee for the 8th International Conference on Silicon in Agriculture. She has published more than 50 peer-reviewed articles and more than 150 conference abstracts/proceedings, trained many graduate students and post-doctoral fellows, and received numerous research and teaching awards.

Fabrício A. Rodrigues

Prof. Fabrício Ávila Rodrigues is an agronomist and received his Ph.D. in plant pathology from the University of Florida, Gainesville, in 2004. He is currently a full professor of plant pathology at the Plant Pathology Department at the Federal University of Viçosa, Brazil. Prof. Rodrigues is the author or co-author of more than 150 research articles and 15 book chapters, most of which are related to the control of plant diseases using inducers of resistance, understanding the infection process of several soilborne and foliar pathogens, how the pathogens affect the host physiology, as well as the defense mechanisms occurring in the host in response to pathogen infection. The current research projects under his supervision are: (i) metabolic and molecular alterations triggered by nutrients and silicon in several crops during the infection process of foliar and root pathogens, (ii) induced resistance in plants against foliar and root pathogens, (iii) mineral nutrition for plant disease control, (iv) biochemical, molecular, and physiological responses of crops infected by root and foliar pathogens, and (v) mechanisms associated with photosynthetic limitations in plants infected by pathogens.

Lawrence E. Datnoff

Dr. Lawrence E. Datnoff received a B.S. (horticulture and plant pathology) from the University of Georgia in 1976, an M.S. (plant pathology) from Virginia Tech in 1981, and a Ph.D. (plant pathology) from the University of Illinois in 1985. In 1986, Datnoff worked with USDA-ARS, and part of his research was conducted with CIMMYT in Mexico. In 1988, he joined the University of Florida focusing his research efforts on epidemiology and control of fungal plant pathogens that cause soilborne and foliar diseases in rice, turf, and vegetables. In 2008, he became professor and head of the Department of Plant Pathology and Crop Physiology, Louisiana State University. Datnoff pioneered early research efforts that highlighted the role of silicon in disease suppression, enhancement of host plant resistance, and the understanding of this resistance at both the physiological and molecular level. In the 1990s, Datnoff initiated silicon research programs with universities and other institutions in Brazil and Colombia with subsequent collaborations in Canada, India, and Japan. He conceived of and inspired a series of world conferences on silicon and agriculture. Datnoff has authored over 100 refereed publications, 34 book chapters, along with two groundbreaking books: *Silicon in Agriculture* and *Mineral Nutrition and Plant Disease*, and more recently, *Silicon and Plant Diseases*. He has been an invited speaker, visiting professor, and mentor in many countries. He also has received numerous awards for contributions to research, teaching, and professional leadership.

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