

Review

Silicon control of bacterial and viral diseases in plants

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Received: August 1, 2016

Accepted: October 20, 2016

Abstract: Silicon plays an important role in providing tolerance to various abiotic stresses and augmenting plant resistance against diseases. However, there is a paucity of reports about the effect of silicon on bacterial and viral pathogens of plants. In general, the effect of silicon on plant resistance against bacterial diseases is considered to be due to either physical defense or increased biochemical defense. In this study, the interaction between silicon foliar or soil-treatments and reduced bacterial and viral severity was reviewed. The current review explains the agricultural importance of silicon in plants, refers to the control of bacterial pathogens in different crop plants by silicon application, and underlines the different mechanisms of silicon-enhanced resistance. A section about the effect of silicon in decreasing viral disease intensity was highlighted. By combining the data presented in this study, a better comprehension of the complex interaction between silicon foliar- or soil-applications and bacterial and viral plant diseases could be achieved.

Key words: biochemical defense, foliar spray, physical defense, soil amendment

Introduction

Diseases caused by different bacterial pathogens are among the most potentially destructive and devastating diseases in all plant-growing areas of the world (Semal 1989). Yield losses reaching up to 100% and limiting crop production depend on bacterial causal agents, host plants and favorable environmental conditions. Control strategies using chemicals are unusable, not efficient or applicable according to host plant-bacterium pathosystems (Cooksey 1990). In some cases, breeding for host resistance is not available to growers, and a breakdown of usable resistance has frequently been reported due to genetic diversity of the strain as well as local environmental conditions (Lindgren 1997). Other bacterial control methods remain to be urgently investigated. Soil amendments that enhance host plant resistance were shown to have significant effects in reducing disease incidence (Datnoff *et al.* 2007). Therefore, silicon can contribute to the management of different crops by improving tolerance to environmental stress, giving lower intensity of diseases and pests, and enhancing crop growth, yield and quality (Fauteux *et al.* 2005; Cai *et al.* 2009; Van Bockhaven *et al.* 2013; Sahebi *et al.* 2014; 2015a,b; 2016). Moreover, silicon application has been gaining attention in the control of certain bacterial diseases (Chang *et al.* 2002; Diogo and Wydra 2007; Silva *et al.* 2010; Oliveira *et al.* 2012; Andrade *et al.* 2013; Conceico *et al.* 2014; Song *et al.* 2016).

Based on the literature, two mechanisms in which silicon can reduce the severity of bacterial diseases have been reviewed (Fig. 1). The first one is associated with an accumulation of absorbed silicon in the epidermal tis-

sue acting as a physical barrier (Gutierrez-Barranquero *et al.* 2012), and the second one is related to an expression of metabolic or pathogenesis-mediated host defense responses (Chang *et al.* 2002; Diogo and Wydra 2007; Silva *et al.* 2010; Oliveira *et al.* 2012; Conceico *et al.* 2014; Song *et al.* 2016). To date, a paucity of reports has documented the ability of silicon application to improve plant resistance to bacterial and viral diseases (Table 1). The beneficial effects of silicon in enhancing tolerance to a range of abiotic stresses and preventing plant diseases are not fully understood and need further research (Liang *et al.* 2015; Sahebi *et al.* 2016). In order to understand the complex interaction between silicon foliar- or soil-applications and bacteria resistance in plants, this review aims to explain the agricultural importance of silicon in plants, to refer to the control of bacterial pathogens in different crop plants by silicon application, and to investigate the different mechanisms of silicon-enhanced resistance. A section about the direct effect of silicon in decreasing viral disease intensity will be highlighted.

Agricultural importance of silicon in plants

According to the classical definition of essentiality (Arnon and Stout 1939), silicon has not been considered as an essential nutrient for plant growth and nutrition. However, it stands out for its potential as one of the most prevalent macro-elements, performing an essential function in augmenting plant resistance against abiotic and biotic stresses (Liang *et al.* 2007, 2015). The silicon-enhanced resistance mechanisms to biotic and abiotic

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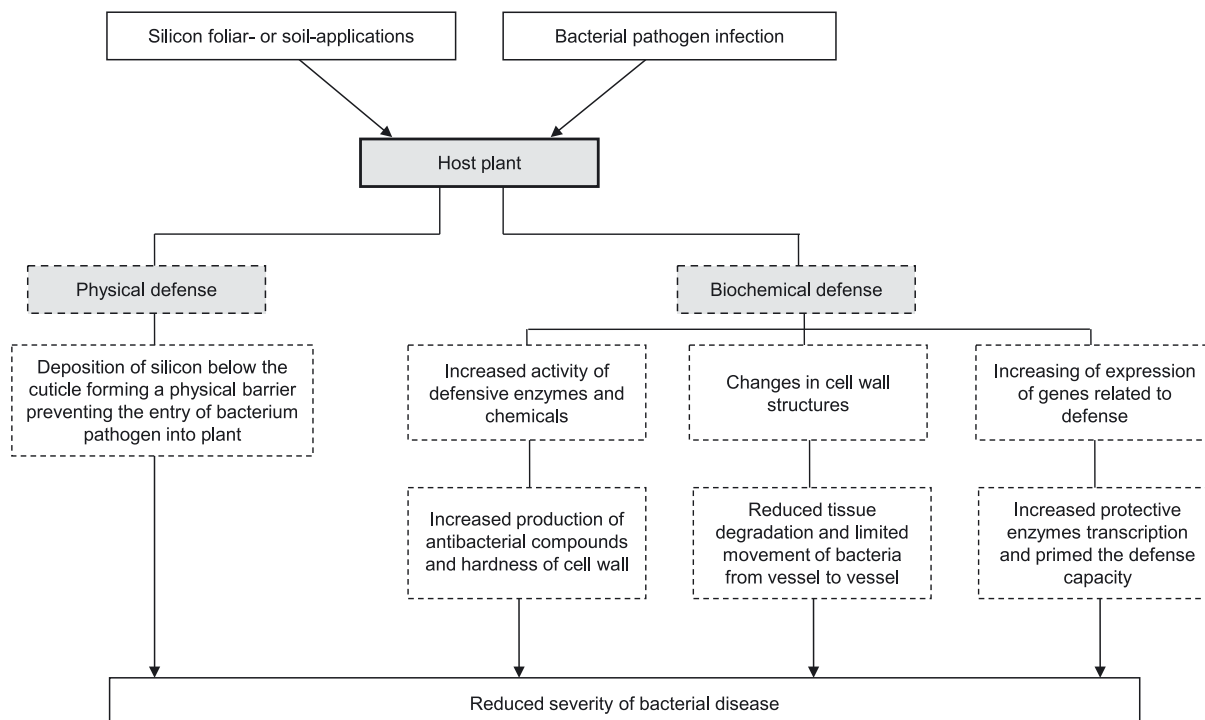


Fig. 1. Possible mechanisms of silicon enhanced resistance to bacterial pathogens

Table 1. Bacterial and viral diseases in affected crops on which the role of silicon in decreasing the incidence has been observed

Hosts	Pathogens	References
Rice	<i>Xanthomonas oryzae</i> pv. <i>oryza</i>	Chang <i>et al.</i> (2002); Xue <i>et al.</i> (2010); Song <i>et al.</i> (2016)
	<i>Ralstonia solanacearum</i>	Diogo and Wydra (2007); Ayana <i>et al.</i> (2011)
Tomato	<i>Pseudomonas syringae</i> pv. <i>tomato</i>	Andrade <i>et al.</i> (2013)
	<i>X. euvesicatoria</i> , <i>X. vesicatoria</i> , <i>X. gardneri</i> and <i>X. perforans</i>	Anjos <i>et al.</i> (2014)
Melon	<i>Acidovorax citrulli</i>	Ferreira (2009); Conceico <i>et al.</i> (2014); Ferreira <i>et al.</i> (2015)
Passion fruit	<i>X. axonopodis</i> pv. <i>passiflorae</i>	Brancaaglione <i>et al.</i> (2009)
Wheat	<i>X. translucens</i> pv. <i>undulosa</i>	Silva <i>et al.</i> (2010)
Cotton	<i>X. citri</i> subsp. <i>malvacearum</i>	Oliveira <i>et al.</i> (2012)
Mango	<i>P. syringae</i> pv. <i>syringae</i>	Gutierrez-Barranquero <i>et al.</i> (2012)
Sweet pepper	<i>R. solanacearum</i>	Alves <i>et al.</i> (2015)
Tobacco	<i>Tobacco ringspot virus</i>	Zellner <i>et al.</i> (2011)
Cucumber	<i>Cucumber mosaic virus</i>	Holz <i>et al.</i> (2014)
	<i>Papaya ringspot virus</i>	Elsharkawy and Mousa (2015)

stresses are misunderstood because of many intricacies surrounding silicon properties, absorption and efficiency (Liang *et al.* 2015).

Silicon is the second most abundant element in the earth's crust mass (27.70%). In soil solution, silicon occurs mainly as monosilicic acid (H_4SiO_4) at concentrations ranging from 0.1 to 0.6 mM. It is taken up by plant roots as noncharged monosilicic acid (Ma and Yamaji 2006), when the pH of the soil solution is below 9 (Ma and Takahashi 2002). After its uptake, monosilicic acid is polymerized into the form of silica gel or biogenetic opal as amorphous $SiO_2 \cdot nH_2O$ in cell walls, intercellular spaces of root and leaf cells as well as in bracts (Mitani *et al.* 2005).

Applications of silicon treatments have many agricultural benefits including enhanced yield, growth and plant production, structure design (height, stature, root penetration into the soil, photosynthetic capacity, resistance to environment, and tolerance to frost) (Datnoff *et al.* 2007). Silicon reduced transpiration and augmented plant resistance to drought stress, salinity and metal toxicity, and increased enzyme activity (Datnoff *et al.* 2007). On the other hand, the suppressive effects of silicon on the intensity of fungal, bacterial and viral pathogens, and insect pest infestation have been widely reported in crops of great economic importance (Fauteux *et al.* 2005; Reynolds *et al.* 2009; Silva *et al.* 2010; Zellner *et al.* 2011; Van

Bockhaven *et al.* 2013; Liang *et al.* 2015; Sakr 2016). Most importantly, silicon enhanced plant resistance against a multitude of stresses without the occurrence of resistance trade-offs and/or growth and yield penalties (Ma and Yamaji 2006; Epstein 2009; Liang *et al.* 2015).

Plant species and different genotypes of the same species differ significantly in their ability to absorb silicon. Also, silicon concentration in the soil and environmental conditions affect the ability of plant roots to absorb silicon (Epstein 1994, 1999, 2009). All terrestrial plants contain silicon in their tissues although its content varies considerably with the species, ranging from 0.1 to 10% silicon on a dry weight basis (Ma and Takahashi 2002). According to Ma and Yamaji's (2006) agricultural point of view, plants can be classified as silicon accumulators, silicon neutral or silicon-rejecters. In general, silicon uptake in graminaceous plants, such as wheat, oat, rye, barley, sorghum, maize, and sugarcane, is much higher than its uptake in dicotyledonous plants, such as tomatoes, beans, and other plant species (Epstein 1999; Ma and Yamaji 2006).

Role of silicon in controlling bacterial pathogens

A positive relationship between silicon and reduced severity of bacterial diseases has been reported in monocot and dicot host plants. Adding silicon fertilizers (solid and liquid) made plants more resistant to various bacterial pathogens. Solid calcium silicate (CaSiO_3) fertilizers incorporate into the soil. Liquid potassium silicate (K_2SiO_3) or sodium silicates (Na_2SiO_3) are applied as a soil drench or as a foliar spray (Datnoff *et al.* 2007).

It has been demonstrated that the elicitors (the bio-compatible molecules and biological agents) combined with silicon can exhibit remarkable resistance against bacterial pathogens. For example, the chitosan (Kiirika *et al.* 2013) and the rhizobacteria strain *Bacillus pumilis* (Kurbachew and Wydra 2014) reduces the severity of bacterial wilt (*Ralstonia solanacearum*) on tomato, and the antagonistic yeasts *Rhodotorula aurantiaca*, *R. glutinis* and *Pichia anomala* decreases the intensity of bacterial blotch (*Acidovorax citrulli*) on melon (Conceico *et al.* 2014).

Silicon does not inhibit the growth of bacterial pathogens *in vitro*. For example, Ferreria (2009) observed that silicon solutions (0.25, 0.50, 1.50, or 3.00 g CaSiO_2) did not affect *A. citrulli* growth *in vitro* (Ferreria 2009). Also, Ferreria *et al.* (2015) found that silicon did not affect *A. citrulli* directly. Oliveira *et al.* (2012) found that calcium silicate did not inhibit *Xanthomonas citri* subsp. *malvacearum* growth in culture medium at any of the tested silicon concentrations. However, a high pH of the silicon solution at rates of 0, 0.125, 0.25, 0.5 and 1 μl inhibited growth of *Pseudomonas syringae* pv. *tomato* *in vitro* (Andrade *et al.* 2013).

Regarding monocot host plants, Chang *et al.* (2002) treated four rice varieties with different degrees of resistance to bacterial blight (*Xanthomonas oryzae* pv. *oryza*) with silicon slag (0.2 to 0.4 t \cdot ha⁻¹) in the field, and they found that silicon application reduced significantly the length of the lesions by 5 to 22%. The severity index of *X. oryzae* pv. *oryza* in infected rice plants treated with silicon was decreased by 11.83–52.12% compared to the

control (Xue *et al.* 2010). Moreover, Song *et al.* (2016) found that the bacterial blight severity was 24.3% lower in the silicon-amended plants than in the non-silicon-amended plants. In the pathosystem of *Xanthomonas translucens* pv. *undulosa* and wheat plants, Silva *et al.* (2010) studied the resistance of plant to bacterial streak and observed a reduction of 50.2% in the chlorotic leaf area when 0.3 g \cdot kg⁻¹ of wollastonite (silicon source) was added to the soil.

As dicot host plants, Diogo and Wydra (2007) treated tomato genotypes with potassium silicate solution (K_2SiO_3) at the rate of 1 g \cdot l⁻¹ substrate against bacterial wilt (*R. solanacearum*), and they observed that the disease incidence was reduced by 38.1% and 100% in moderately resistant tomato and the resistant genotype grown under growth chamber conditions. In a field study, Ayana *et al.* (2011) reported that silicon fertilizer at a rate of 15 kg per 100 m² significantly reduced the mean wilt incidence caused by *R. solanacearum*. Silicon fertilizer as a soil amendment has been recommended under field conditions to augment resistance in moderately resistant cultivars where bacterial wilt disease problems prevail (Ayana *et al.* 2011). Potassium silicate at concentrations of 40 and 50 g \cdot l⁻¹ reduced tomato bacterial leaf spot disease caused by *Xanthomonas* spp. (Anjos *et al.* 2014). For bacterial wilt (*R. solanacearum*) of sweet pepper, Alves *et al.* (2015) found that 2.95 g silicon \cdot kg⁻¹ substrate increased the latent period (33.6%) and reduced the disease index (98%) and area under the disease progress curve (AUDPC) (93.7%) in comparison to the control. To study *A. citrulli* and melon plants, Ferreira (2009) treated plants with different doses of calcium silicate for the control of bacterial blotch (*A. citrulli*). The application of 3.0 g of $\text{SiO}_2 \cdot \text{kg}^{-1}$ of soil significantly reduced the disease index and the AUDPC and increased the incubation period. Also, Conceico *et al.* (2014) found that the incorporation of 1.41 g Si \cdot kg⁻¹ (calcium silicate) into the substrate and foliar spraying with 17 mM Si (potassium silicate) reduced severity of bacterial blotch and AUDPC compared to the control, and protected melon plants from infection by *A. citrulli* for 29 days. Also, Ferreira *et al.* (2015) found that the incorporation of 1.41 g Si \cdot kg⁻¹ into the soil reduced incidence (50%), the disease index (89%), and AUDPC (85%) and increased the incubation period (192%) in comparison to the control, and protected melon plants from infection by *A. citrulli* for 20 days. The severity of bacterial spot (*Xanthomonas axonopodis* pv. *passiflorae*) of passion fruit was reduced by silicate clay at concentrations between 1 and 2% by 70% (Brancaglione *et al.* 2009). The application of potassium silicate at a concentration of 1.50 g of $\text{SiO}_2 \cdot \text{kg}^{-1}$ of soil decreased the severity of angular leaf spot (54.9%) in cotton plants previously inoculated with *X. citri* subsp. *malvacearum* (Oliveira *et al.* 2012). In the pathosystem of *P. syringae* pv. *syringae* and mango plants, Gutierrez-Baranquero *et al.* (2012) found that trees treated with silicon gel showed significantly fewer necrotic buds and leaves. Andrade *et al.* (2013) found that the symptoms of bacterial speck (*P. syringae* pv. *tomato*) were reduced when tomato plants were sprayed with silicon at concentration of 2 ml \cdot l⁻¹.

Mechanisms of silicon enhanced resistance

The effect of silicon on the control of plant bacterial diseases, its mode of action, its properties, and its spectrum of efficacy in several pathosystems require more research both under farm conditions and as tissue culture (Sahebi *et al.* 2014, 2015a,b, 2016). Generally, the effect of silicon on plant resistance to bacterial pathogens is considered to be due to either a deposition of silicon on cell walls acting as a physical barrier making bacteria penetration difficult when soil amendment is applied, or biochemical changes related to plant defenses when a foliar spray or soil amendment is applied (Fig. 1).

Although foliar-applied silicon is effective in reducing bacterial blotch on melon and bacterial speck and bacterial leaf spot on tomato, applying silicon to the roots is more effective in decreasing several bacterial diseases (bacterial blight and bacterial streak on rice, bacterial streak on wheat, bacterial wilt on tomato and sweet pepper, bacterial spot on passion fruit, and bacterial blotch on melon) because it increases the plant's defense responses to both foliar and root infections.

Physical defense

In a study on of *P. syringae* pv. *syringae* and mango plants, silicon gel failed to reduce the bacterial populations on plant tissues, but it reduced disease levels, suggesting a non-bactericidal mode of action of this compound (Gutierrez-Barranquero *et al.* 2012). These authors proposed that the accumulation of absorbed silicon in the epidermal tissue forms a physical barrier preventing the entry of *P. syringae* pv. *syringae* into mango plants.

Biochemical defense

Soluble silicon in plant tissue may be associated with an increase in resistance to bacterial pathogens (Chang *et al.* 2002; Diogo and Wydra 2007; Silva *et al.* 2010; Ghareeb *et al.* 2011; Oliveira *et al.* 2012; Conceico *et al.* 2014; Song *et al.* 2016). In this model, the augmentation of resistance was due to (1) increased activity of defensive enzymes and chemicals, (2) changes in cell wall structures, and (3) increased expression of genes related to defense. Studies demonstrating the suppressive effect of silicon on bacterial pathogens make it evident that the role of increased plant defense response was more important than physical defense.

Chang *et al.* (2002) found that the decreased soluble sugar content in rice leaves applied with silicon increased field resistance to bacterial blight (*X. oryzae* pv. *oryza*). Enhanced β -1,3-glucanase, exochitinase and endochitinase activities in rice plants supplied with silicon decreased the intensity of *X. oryzae* pv. *oryza* (Xue *et al.* 2010). Song *et al.* (2016) found that the total concentrations of soluble phenolics and lignin, and activities of polyphenoloxidase and phenylalanine ammonia-lyase in rice leaves were higher in the plants treated with silicon. Among molecular features associated with reduction in bacterial blight symptoms in rice plants treated with silicon, silicon increased phenylalanine ammonia-lyase *Pal* transcription,

and inhibited catalase *CatA* expression in the earlier and later stages of bacterial inoculation, respectively (Song *et al.* 2016). In the pathosystem of *R. solanacearum* and tomato plants, Diogo and Wydra (2007) observed that silicon induced changes in the pectic polysaccharide structure in the cell walls of tomato plants after infection with *R. solanacearum*. Changes in cell wall structure may strengthen the pit membranes of the xylem vessels and the cell walls of parenchyma cells, reduce tissue degradation, limit movement of bacteria from vessel to vessel, and consequently decrease the severity of bacterial wilt on tomato (Diogo and Wydra 2007). Among molecular features associated with reduction in bacterial wilt severity in silicon-amended tomato plants, Ghareeb *et al.* (2011) found that silicon primed the defense capacity of the plant by changes in gene expression. A major role of the jasmonic acid/ethylene (JA/ET) signaling pathway, mediated by a cross-talk between reactive oxygen reaction (ROS), ET and JA signaling is involved in tomato defense capacity to *R. solanacearum* (Ghareeb *et al.* 2011). Alves *et al.* (2015) observed that the enhanced concentrations of total protein, catalase, ascorbate peroxidase, and chitinase decreased the severity of *R. solanacearum* on sweet pepper plants treated with calcium silicate. Increased chitinase activity and tissue lignification, and probably peroxidase activity with the highest concentration of the total soluble phenolics and lignin-thioglycolic acid derivatives in silicon-treated wheat plants decreased the severity of leaf streak (Silva *et al.* 2010). In the pathosystem of *X. citri* subsp. *malvacearum* and cotton plants, Oliveira *et al.* (2012) found that decreased levels of angular leaf spot in plants treated with silicon were due to enhanced accumulation of soluble proteins, superoxide dismutase, ascorbate peroxidase, guaiacol-peroxidase, phenylalanine ammonia-lyase and β -1,3-glucanase, and reduced levels of H_2O_2 . Possible cell wall lignification processes due to silicon gel application to mango plants reduced levels of bacterial apical necrosis caused by *P. syringae* pv. *syringae* (Gutierrez-Barranquero *et al.* 2012). Higher levels of polyphenol oxidase and ascorbate peroxidase in melon plants supplied with silicon decreased the severity of bacterial blotch by *A. citrulli* (Conceico *et al.* 2014).

Role of silicon in controlling viral pathogens

Up to now, the role of silicon in relation to viral pathogens has been attracting little attention. Zellner *et al.* (2011) found that the majority of tobacco plants treated with 0.1 mM K_2SiO_3 did not exhibit levels of systemic *Tobacco ringspot virus* symptoms to the same extent as the controls, and plants grown in elevated levels of silicon showed a delay in *Tobacco ringspot virus* systemic symptom formation. Zellner *et al.* (2011) noticed that the foliar accumulation of silicon may be part of a defense response in tobacco to *Tobacco ringspot virus*. Silicon supplementation in cucumber plants infected with *Cucumber mosaic virus* caused a shift in gene expression (Holz *et al.* 2014). Elsharkawy and Mousa (2015) found that silicon application to cucumber plants significantly reduced the severity of *Papaya ring spot virus* and its accumulation in leaves. The expression of the majority of various pathogen-re-

lated genes was mediated by silicon treatment. On the other hand, silicon was shown to increase viral incidence in tobacco infected with *Belladonna mottle virus* (Bengsch *et al.* 1989), and elevated levels of silicon did not alter *Tobacco mosaic virus* symptoms (Zellner *et al.* 2011). Data presented in this section suggested that the silicon effect may be virus-specific.

Conclusions

Supplying silicon to plants ideally fits in with environmental friendly strategies for sustainable crop production. In spite of a paucity of reports about the ability of silicon application to suppress bacterial and viral pathogens, economically important bacterial and viral diseases in wheat, rice, tomato, cucumber, tobacco, and melon are efficiently controlled by silicon treatments. The role of increasing plant defense response is more important than a physical barrier to bacterial pathogens. However, its effect in enhancing plant resistance against bacterial pathogens is not limited to silicon accumulators, and has been described in silicon neutral plants. Silicon does not seem to directly affect bacterial pathogens and therefore exerts no selective pressure. Silicon specifically reduces viral symptomatic area and delays systemic symptom formation. Recent progress in understanding the biological role of silicon in plants will be helpful in increasing crop yield and enhancing bacterial and viral pathogen resistance.

Acknowledgements

I would like to thank Professor Ibrahim Othman, Director General of Atomic Energy Commission of Syria and Professor Fawaz Kurdali the Head of the Agriculture Department for their support of this research.

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