OUSL Journal (2016)
Vol. 11, (pp. 135 -162)

Role of Silicon on Enhancing Disease Resistance in Tropical Fruits and Vegetables: A Review

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Abstract

Silicon (Si) has proven to enhance disease resistance in a wide range of tropical fruits and vegetables. It has been used in controlling various diseases: mildews, rots, moulds, wilt, blight, anthracnose and leaf spots. However, the highest number of records was available on reducing diseases of powdery mildews on fruits and vegetables belonging to the family Cucurbitaceae. Silicon-mediated defense responses in plant pathosystems are mainly attributed to the physical resistance, which involves reduced penetrability and/or increased hardness and abrasiveness of plant tissues because of silica deposition. The main mechanism is the chemical resistance, which involves chemical defenses to pathogen attack through the enhanced production of defensive enzymes and the production of antifungal compounds such as phenolic metabolism products, phytoalexins and pathogenesis related proteins. Silicon has been applied as soluble silicates to the substrate or to soilless media at pre-harvest level on reducing disease susceptibility. Post-harvest dips of fresh produce in silicate solutions and use of Si combined with a biocontrol agent are other aspects of silicon application in controlling diseases in fruits and vegetables.

Keywords: Silicon application, plant pathogens, defense responses

Introduction

Silicon (Si) is taken up by plants at concentrations similar to the

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essential nutrients. However, persistent chemical fertilization and crop removal from the field tend to the depletion of Si availability for plants. As a result, Si has been identified as a limiting factor for Si-accumulating plants, as well as for the plants grown in soils deficient with Si (Epstein, 1999). The beneficial effects of Si have been observed in a wide variety of plant species including enhanced insect and disease resistance, reduced mineral toxicity, increased photosynthetic activity, superior nutrient imbalance, and enhanced drought and frost tolerance (Ma, 2004). Though silicon has not been recognized as an essential element for plant growth, plants deprived of Si are often weaker structurally and more prone to abnormalities of growth, development and reproduction. Silicon is considered as the only nutrient element which is not detrimental when collected in excess in plants (Ma and Takahashi, 2002).

Silicon is absorbed to plants from the soil solution with concentrations ranging from 0.1 to 0.6 mM as monosilicic acid, H_4SiO_4 (Ma and Takahashi, 2002). The Si concentrations vary widely in above ground plant parts, ranging from 0.1 to 10.0% on dry weight basis (Liang *et al.*, 2005). Plant species are considered as Si 'Accumulators' when the concentration of Si of its dry weight is greater than 1%. 'Intermediates' have Si amounts less than 0.1% in their biomass. Plants containing Si concentration below 0.5% of the bio mass are considered as 'Excluders' (Ma and Takahashi, 2002).

Silicon has been found to effectively control many of the diseases found in tropical fruits. However, diseases, such as blue mould and gray mould were reduced in fruits grown in temperate countries.

Silicon has been applied as a form of pre-harvest or post-harvest application, or root or foliar application. The research has also been done on silicon application in combination with yeast or phosphorus acid or hot water treatment. Different sources of silicon i.e. sodium silicate, calcium silicate, calcium silicate, rice hull (raw or partially burnt) have been used as sources for providing Si to the fruits and vegetables.

The following sections describe the disease control by application of silicon in tropical fruits and vegetables. Some records were available on reducing anthracnose disease in tomato and capsicum grown in

Sri Lanka.

Silicon and mildew diseases

Powdery mildew

A noticeable inhibitory effect against powdery mildew has been reported by silicon application in cucurbits. A majority of the alleviative effects studies has been accounted in cucumber powdery mildew caused by *Sphaerotheca fuliginea* (Samuels *et al.*, 1993; Menzies *et al.*, 1991; 1992; Fawe *et al.*, 1998; JungSup *et al.*, 2000; Schuerger and Hammer, 2003; Wei *et al.*, 2004; Liang *et al.*, 2005; QiuJu *et al.*, 2009; Buttaro *et al.*, 2009; Wolff *et al.*, 2012) and by *Sphaerotheca fuliginea* (Liang *et al.*, 2005). Effective suppression of the disease could be observed in some other cucurbits such as melons caused by *S. fuliginea* and/or *Erysiphe cucurbitacearum* (Menzies *et al.*, 1992; Yurong *et al.*, 2005; Guo *et al.*, 2005; Chen *et al.*, 2010). Root applied Si induced the resistance against *Podosphaera xanthii* reducing the disease severity in melon. Supplying silicon in nutrient solutions reduced the severity and incidence of powdery mildew in two varieties of melon, carosello and barattiere (Buttaro *et al.*, 2009). Furthermore, powdery mildew in zucchini squash caused by *E. cichoracearum and Podosphaera xanthii* pumpkin caused by *P. xanthii* (Heckman *et al.*, 2003) was lessened by pre-harvest silicon application.

Palmer *et al.* (2006) reported that powdery mildew caused by *Sphaerotheca aphanis* in strawberry can effectively be suppressed by foliar application of potassium silicate. Silicon had beneficial effects on strawberry plants and may serve as an alternative to fungicides for controlling powdery mildew when supplied as a foliar spray of potassium and sodium silicate. Kanto *et al.* (2004, 2007) and Wang and Galletta (1996) have recorded similar results about the strawberry- powdery mildew patho-system. However, root application of silicon could not reduce the disease severity in strawberry (Bowen *et al.*, 1992). Similar suppressive effects of Si against *Uncinula necator* were stated by Reynolds *et al.* (1996) and Blaich and Grundhofer (1998) in grapes. Foliar applied potassium silicate was found to exhibit inhibitory effects on *Leveillula taurica*, the powdery mildew causing fungi in tomato (Yanar *et al.*, 2013).

Downy mildew

Foliar application of Si suppressed cucumber downy mildew caused by *Pseudoperonospora cubensis* (Yu and Du, 2009; Yu *et al.*, 2010). Garibaldi *et al.* (2012) discovered that electrical conductivity and potassium silicate together significantly influenced downy mildew (*Bremia lactucae*) incidence and severity on lettuce in hydroponic system. The best results, in terms of disease control, were given by the addition of potassium silicate to the 0.95 g l^{-1} NaCl solution.

Silicon and rot diseases

Fruit rots

Alternaria fruit rot

The synergistic effects of biocontrol yeasts *Cryptococcus laurentii* and *Rhodotorula glutinis* combined with silicon against Alternaria fruit rot (*Alternaria alternate*) have been investigated in jujube fruit (Chinese date: *Zizyphus jujuba*). Combinations of *C. laurentii* and *R. glutinis* with Si were found to be most effective in controlling the diseases caused by *A. alternata* in jujube fruit (Shiping *et al.*, 2005). Post harvest sodium silicate treatments could resist the growth of *A. alternate* in pingguoli pear (Guo *et al.*, 2003).

Other fruit rots

The susceptibility to pink rot caused by *Trichothecium roseum* was shown to be decreased by postharvest Si application in muskmelon (Li *et al.*, 2012), Chinese cantaloupe (Yurong *et al.*, 2003; Guo *et al.*, 2007) and hami melon (Bi *et al.*, 2006). Yang *et al.* (2010) have revealed synergistic effects of silicon on disease control in apple brown rot (*Monilinia fructicola*). Foliar application of Si was effective in controlling tomato fruit rot caused by *Phytophthora capsici* (Mersha *et al.*, 2012)

Root rots

Pythium root rot

It was stated that Si is effective in controlling root rot in cucumber caused by *Pythium ultimum* and *P. aphanidermatum* (Cherif and Belanger, 1992; Chérif *et al.*, 1994a, 1994b). However, Heine *et al.* (2007) revealed that the incidence of root rot in cucumber, tomato and bitter gourd caused by *P. aphanidermatum* could not be controlled by Silicon application.

Phytophthora root rot

Silicon was effective in controlling cucumber root rot caused by *Phytophthora melonis* (Mohaghegh *et al.*, 2011). In hydroponic experiments, Khoshgoftarmanesh *et al.* (2012) have demonstrated that Phytophthora root rot (*P. drechsleri*) in cucumber could be alleviated by Si application. Bekker *et al.* (2007) found the efficacy of root application of potassium silicate on controlling the disease (*P. cinnamomi*) in avocado.

Fusarium root rot

Due to the application of Si to tomato seedlings, the disease severity of root rot caused by *Fusarium oxysporum* f.sp.*radicis-lycopersici* was reduced. This inhibitory effect was due to the delaying in onset and initial infection of roots and the movement of the pathogen from roots to stems (Huang *et al.*, 2011). Silicon was also reported to be effective to suppress the disease resulted by *F. solani* in tomato (El-Samman *et al.*, 2000). *Fusarium oxysporum* f.sp.*radicis-cucumerinum*, the causative fungi of cucumber root rot, could be effectively controlled by soil applied Si (Safari *et al.*, 2012). The alleviative role of Si on the disease was also recorded in other cucurbits in fact hamimelon: *F. semitectum,* cantaloupe: *Fusarium spp.* and rock melon: *F. oxysporum f. Sp. Melonis* (Bi *et al.*, 2006; Liu *et al.*, 2009; Kumar and McConchie, 2010)

Pink rot

Si application has also been shown to decrease susceptibility to pink rot caused by *Trichothecium roseum* in muskmelon (Li *et al.*, 2012), Chinese cantaloupe (Guo *et al.*, 2007; Yurong *et al.*, 2003) and hami melon (Bi *et al.*, 2006).

Banana root rot

Using the image analysis program WinRHIZO, Vermeire *et al.* (2011) exhibited that root-rot fungi *Cylindrocladium spathiphylli* infection in banana could be mitigated. The Si amendment also alleviated growth reduction caused by the pathogen.

Silicon and mould diseases

Blue mould

Ebrahimi *et al.* (2012) explained that postharvest silicon application was more effective in reducing the lesion diameter of blue mould decay of apples caused by *Penicillium expansum* in combination with the yeast, *Torulaspora delbrueckii* than using Si or *T. delbrueckii* alone. In a consequent study, Ebrahimi *et al.* (2013) discovered the efficacy of controlling the disease triggered by applying Si together with the yeast, *Metschnikowia pulcherrima*. Farahani *et al.* (2012) suggested that the yeast, *Candida membranifaciens* combined with different concentrations of silicon, improved the effectiveness of yeast in controlling the disease in apple. Similar results have been observed by Farahani *et al.* (2013) by dual application of silicon and the yeast, *Pichiaguillier mondii* in apples. Postharvest dips of apples in potassium silicate solution (Moscoso-Ramírez and Palou, 2014) and in Si added hot water (Etebarian *et al.*, 2013) were other means of suppressing the disease. Combinations of the yeast species, *Cryptococcus laurentii* and *Rhodotorula glutinis* along with Si was more successful in controlling blue mould caused by *P. expansum* on jujube fruit (Shiping *et al.*, 2005).

Green mould

Silicon has been reported to prevent the incidence of green mould caused by *Penicillium digitatum* in a number of citrus fruits (Abraham, 2010; Liu *et al.*, 2010). Mkhize *et al.* (2013) revealed that pre- and post-harvest Si amendments could upsurge the resistance of lemon to *P. digitatum*. Postharvest dips of potassium silicate before inoculation the same pathogen on oranges significantly reduced the severity of green mould (Moscoso-Ramírez and Palou, 2014).

White mould

In bean, disease incidence and severity of white mould (*Sclerotinia sclerotiorum*) were significantly reduced by 52% and 73%, respectively, via applying Si as calcium silicate together with calcium chloride (PaulaJúnior *et al.*, 2009).

Gray mould

On increasing the quality of organically grown strawberry, Prokkola and Kivijärvi (2008) found that silicon is effective in controlling gray mould (*Botrytis cinerea*), when applied as a combination with *Trichoderma* spp. in two weeks interval until harvested. Soil application of liquid potassium silicate to cucumber plants notably reduced the incidence of gray mould caused by *B. cinerea* (O'Neil, 1991). In contrast, post-harvest Si application was found to be ineffective for controlling gray mould (*B. cinerea*) in strawberry (Lopes *et al.*, 2014).

Silicon and wilt disease

Bacterial wilt

Soil supplied silicon enhanced the resistance in tomato plants against *Ralstonia solanacearum,* the causing agent of bacterial wilt (Ghareeb *et al.*, 2011). Silicon amendments were also reported to reduce the disease incidence in tomato when applied to soil (Dannon and Wydra, 2004; Diogo and Wydra, 2007; Kiirika *et al.*, 2013). However, dual application of silicon and a rhizobacteria strain *Bacillus pumilis* against the disease was not effective as same as application of silicon alone in tomato (Kurabachew and Wydra, 2014).

Recently, it was revealed that Si mediated resistance in tomato against *R. solanacearum* was associated with the changes of soil microorganism amount and soil enzyme activity (Wang *et al.*, 2013). The uptake of Si was significantly increased in the Si-treated tomato plants, where the Si content was higher in the roots than that in the shoots. The results showed that exogenous 2.0 mM Si treatment reduced the disease index of bacterial wilt by 19.18 % to 52.7 %. Si supply significantly increased soil urease and soil acid phosphatase activity under pathogen-inoculated conditions. After *R. solanacearum* inoculation, Si amendments significantly increased the amount of soil bacteria and actinomycetes and reduced soil fungi/soil bacteria ratio. The results suggested that Si amendment is an effective approach to control *R. solanacearum,* and Si-mediated resistance in tomato against *R. solanacearum* is associated with the changes of soil microorganism amount and soil enzyme activity (Wang *et al.*, 2013). Silicon amendment significantly reduced bacterial wilt incidence of tomato grown in peat substrate (Diogo and Wydra, 2007) and hydroponic culture (Dannon and Wydra, 2004).

Fusarium wilt

Fortunato *et al.* (2012) revealed that supplying Si to banana plants at seedling stage had a great potential in reducing the intensity of Fusarium wilt caused by *Fusarium oxysporum.* The suppressive effect of Si on the disease in cucumber caused by *Fusarium oxysporum*f.sp.radicis- *cucumerinum* was also reported by Safari *et al.* (2012).

Silicon and blight

Phytophthora blight

In cucumber, root applied liquid potassium silicate notably reduced the incidence of stem blight caused by *Didymella bryoniae* (O'Neil, 1991). Silicon accumulation in roots followed by Si supply could potentially reduce the severity of Phytophthora blight caused by *Phytophthora capsici* while enhancing the plant development in bell pepper (French-Monar *et al.*, 2010) as well as in pepper (Lee *et al.*, 2004). Foliar application of soluble silicon could efficiently control the disease in tomato caused *P. capsici* (Mersha *et al.*, 2012). In addition, silicon nutrition enhanced the resistance to stem blight caused by *Phomopsis asparagi* in two asparagus cultivars, UC157 and Gynlim (Lu *et al.*, 2008).

Stem blight

Application of liquid potassium silicate through a separate set of drip lines to cucumbers grown on rockwool slabs significantly reduced the incidence of stem blight caused by *Didymella bryoniae,* and appeared to reduce that of those caused by *B. cinerea* (O'Neil, 1991).

Silicon and anthracnose

Yang *et al.* (2008) have revealed that it could control the occurrence of anthracnose (*Colletotrichum higginsianum*) of flowering Chinese cabbage (*Brassica campestris* L.) on Si application. Injecting soluble silicon into trees prior to harvest significantly decreased the severity and incidence of postharvest anthracnose in avocado while, a combination of soluble silicon and phosphorous acid was not that effective in controlling of anthracnose (Anderson *et al.*, 2005). The disease in avocado could similarly be controlled effectively by postharvest application of soluble silicon (Bosse *et al.*, 2011). The susceptibly to the disease (*C. gloesporioides*) in tomato was mitigated by soil application of sodium silicate (David and Weerahewa, 2012; Weerahewa and David 2015), and application of partially burnt rice hull (Somapala *et al.*, 2015). Root and shoot applied Si was proven to be an effective way of reducing the disease severity caused by *C. gloesporioides* in *Capsicum annuum* L. 'Muria F1' (Jayawardana *et al.*, 2014, 2015). The significant reduction of anthracnose disease was observed in capsicum grown in simplified hydroponics system incorporated with raw rice hull as a supplement of silicon(Jayawardana *et al.*, 2016).Moreover, Si induced the resistance against *Fitopatologia Brasileira* and *C. lindemuthianum* in bean (Moraes *et al.,* 2006; Polanco *et al.*, 2012, 2014).

Silicon and Leaf spot

Foliar application of potassium silicate, as a source of soluble silicon, decreased angular leaf spot (*Pseudocercospora griseola*) severity on beans at more alkaline pH (Rodrigues *et al.*, 2010).

Banana sigatoka

The effect of silicon uptake on the susceptibility of banana to *Mycosphaerella fijiensis*, the causative pathogen of black sigatoka disease was investigated by Kablan *et al.* (2012). It was revealed that Si supply could alleviate the disease in the plants grown both in hydroponic culture system and in pots filled with compost.

Underlying mechanism/s of disease resistance mediated by silicon

There are mainly two methods by which Si induces the resistance in plants against infections. It is either by the chemical defense owing to the physical defense developed due to Si deposition on plant tissues preventing the pathogen penetration and/or by synthesis of anti-pathogenic compounds. In addition, systemic acquired resistance (SAR) was found to be induced upon silicon application in fruits and vegetables.

Mechanical Resistance

Silicon has been shown to be effective in mitigating biotic stress by means of mechanical resistance in fruits and vegetables in a number of studies. Pre-harvest or post-harvest silicon application had shown a great potential in controlling diseases by inhibiting or delaying the growth and development of the mycelium of the pathogen (Samuels *et al.*, 1993; Bowen *et al.*, 1992; Hu *et al.*, 2008; Yu and Du, 2009; Abraham, 2010) due to silicon deposition at infection sites and hyphae (Reynolds *et al.*, 1996)

Si application strongly inhibited spore germination, germ tube formation and development of appresoria and possibly the penetration of fungi were hindered. It was hypothesized that Si inhibits fungal disease by physically inhibiting fungal penetration peg dispersion of the epidermis (Menzies *et al.*, 1991a, 1991b; Bowen *et al.*, 1992; Yurong *et al.* 2005; Kanto *et al.*, 2007; Liu *et al.*, 2010). Si was translocated laterally through the leaf and surrounded the appressoria of *U. necator* upon foliar application of Si. Plant leaves that were fed with Si via roots showed a similar deposition of Si surrounding the appressoria making a rigid physical barrier for penetration (Bowen *et al.*, 1992).

It has also been found that the trichome bases on the epidermis tend to become silicified (Belanger *et al.*, 1995; Samuels *et al.*, 1993; Chérif *et al.*, 1994a) changing their morphology against infections. Si deposition in leaf hairs suppressed the fungal penetration as a result of increased density and length (Fatema *et al.*, 2011). Penetration peg incursion was found to be constrained by rapid Si deposition at the external openings like stomata of the leaves (Guo *et al*, 2007). A fast silicification at intercellular spaces, cuticle layer (Kanto *et al.*, 2007) and along the space between the exocarp and mesocarp (Guo *et al.*, 2007) made it more difficult for pathogen penetration and dispersion. Powdery mildew infected leaf cells of silicate treated plants were exhibited to have extensive silica polymerization enhancing the thickness against the fungi in the halo region surrounding the site of fungal penetration (Menzies *et al.*, 1991b). Altered surface morphology of the host cell walls was observed adjacent to the germinating hyphae (Samuels *et al.*, 1993). Deposition of silicon in host cell walls, papillae, around the haustorial neck and in-between the host cell wall and plasma membrane enhanced induced structural defense reactions (Samuels *et al.*, 1994) against *S. fuliginea.*

Changes in the pectic polysaccharide structure, is another aspect of silicon-induced mechanical defense. In particular, arabinan side chains of rhamnogalacturonan I increased in some vessel walls and galactan side chains of rhamnogalacturonan I increased in the xylem parenchyma, increasing the mechanical strength of the host against infection (Diogo and Wydra, 2007). Si application increased the cell wall lignin content which made it hard for dispersion of fungal mycelium (Polanco *et al.*, 2012). Silicon-treated plants increased resistance against infections by forming electron-dense layers along primary and secondary cell walls as well as over pit membranes of xylem vessels (Chérif *et al.*, 1994b) making it harder for fungal permeation and dispersion within the plant body.

Biochemical resistance

Silicon-mediated defense reaction is induced in fruits and vegetables by synthesis of secondary metabolites. Secondary metabolites influence the interactions between plants and the organisms that inhabit their environment: insects and other animals, microbes and fungi. They are obnoxious, repellent or downright toxic to biotic attackers of plants (Delhaize *et al.,* 1993). Antioxidant enzymes, phenolic compounds, chitinases and phytoalexins are the common secondary metabolites found related to chemical defense in fruits and vegetables.

Acquired resistance through antioxidant enzymes

Several studies showed that lowering disease severity in the Si-treated plants was in line with higher activity of antioxidant defense enzymes in particular, superoxide dismutase, catalase, peroxidase, ascobate peroxidase, guaiacol peroxidase, *β*-1, 3-glucanase and glutathione reductase. Plants protect cell and sub cellar systems from the cytotoxic effects of the active oxygen radicals using antioxidant enzymes. Silicon was said to be effective in controlling pre harvest diseases of fruits and vegetables as a result of these antimicrobial enzymes (Wei *et al*., 2004; Cherif *et al*., 1994b; Liang *et al*., 2005). A significant reduction in postharvest diseases by silicon application was noted with respect to enhanced defensive enzyme activity (Qin and Tian, 2005; Bi *et al*., 2006; Guo *et al*, 2007; Liu *et al*., 2009, 2010; Kumar and McConchie, 2010; Li *et al*., 2012; Ebrahimi *et al*., 2012; Polanco *et al*., 2012; Farahani *et al*., 2013; Polanco *et al*., 2014; Kurabachew and Wydra, 2014). Root-applied Si significantly enhanced the activities of defensive enzymes, for example catalase, peroxidase, polyphenoloxidase and *β*-1, 3-glucanase in two asparagus cultivars, UC157 and Gynlim against stem blight caused by *Phomopsis asparagi* (Lu et al., 2008).

Synthesis

Silicon could be used to reduce many fungal diseases mildew (Powdery mildew and downy mildew), rots (fusarium root rot, phytophthora root rot, pink rot), mould (Blue mould, green mould, gray mould, white mould), blight (phytophthora blight and stem blight), and wilt (fusarium wilt, and anthracnose) in tropical fruits and vegetables. A few bacterial diseases (bacterial wilt) were also reduced by application of silicon. Many diseases observed in tropical fruits and vegetable were significantly reduced by silicon application. However, gray mould in strawberry and blue mould diseases in some fruits grown in temperate countries (sweet cherry, peach, Jujube, apple, pear, oranges etc) were reduced by application of Silicon.

When considering the types of diseases and resistance enhanced by application of silicon in tropical fruits and vegetables, many records (75% of the published records) were available on reducing the powdery mildew disease in cucumber, muskmelon, Zucchini squash, pumpkin and about 25% of the published findings were available on reducing powdery mildew in disease in strawberry and grapes.

Silicon has been applied as a form of pre or post-harvest to reduce diseases in green mould or gray mould. But the postharvest application was done for reducing blue mould disease.

Foliar application of silicon has been used most effectively to reduce powdery mildew disease. However, blight disease was controlled by application of foliar or root.

The possible mechanism/s on diseases reduced by silicon could possibly be due to the formation of physical barriers by silicon depositions or by biochemical compounds formed or antioxidant defense enzymes formed.

Pre-harvest or post-harvest silicon application had shown a great potential in controlling diseases by inhibiting or delaying the growth and development of the mycelium of the pathogen. Powdery mildew infected leaf cells of silicate treated plants were exhibited to have extensive silica polymerization enhancing the thickness against the fungi in the halo region surrounding the site of fungal penetration

Conclusions

Silicon has proven to be an effective means of reducing diseases in tropical fruits and vegetables. Therefore, the use of silicon could reduce the use of fungicides for controlling diseases.

The remarked alleviative effect of Si was recorded in controlling powdery mildew in cucurbits. Silicon might be effective in suppressing diseases in fruits and vegetables than bacterial diseases since preponderance of the findings were related to Si mediated fungal diseases than bacterial diseases. Silicon-induced resistance against infections is mainly attributed to the mechanical and chemical defense. In addition, SAR like mechanisms were involved in silicon induced defense in fruits and vegetables.

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Received: 01-03-2016 **Revised**: 30-06-2016 **Accepted**: 24-08-2016