

The Role of Silicon (Si) in Increasing Plant Resistance against Insect Pests

Review article

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Silicon (Si) is reported to improve plant resistance to a range of biotic and abiotic stresses, with consequent yield increases. Silicon plays an important role in providing defense for crops of great economic importance against insect pests attack. In this study, the interaction between plants treated with silicon and reduced insect damage was reviewed. The current review presents the agronomic importance of silicon in plants, the control of insect pests in different major crop plants by silicon treatment, the different mechanisms of silicon-enhanced resistance, and the absence of silicon effects on insect pests. By integrating the data presented in this paper, a good knowledge of the association between silicon treatment, increasing plant resistance, and decreasing insect pest damage could be attained.

Keywords: insect pest–plant interactions, insect pest damage, silicon application.

One of the restricting factors of plant crops is susceptibility to insect pest infestation. Chemical control is widely used, but due to limitations, such as high cost of pesticides, insecticide persistence in food and/or environment, possibility of selection of insecticide-resistant populations to the products traditionally used and increased probability of harmfulness to non-target insects (Denholm and Rowland, 1992), new control alternatives should be sought.

Nutrition management with silicon (Si) can improve plant resistance and protect against abiotic stresses and decreases the incidence of insects and diseases, with consequent yield and productivity increase (Ma, 2004; Reynolds et al., 2009, 2016; Liang et al., 2007, 2015a,b; Van Bockhaven et al., 2013; Sakr, 2016a,b). Therefore, the addition of silicon fertilizer is a potential strategy and alternative management method to chemical control of insect pest thought the reduction in insect performance and plant damage. Silicon enhances plant resistance to a wide range of insect pests including borers and sap-feeding insects (Reynolds et al., 2009, 2016; Liang et al., 2015a).

Applications of silicon treatments have many agricultural benefits including improved plant growth, photosynthetic capacity, tolerance to frost, plant architecture, tolerance to water stress, quality of raw materials and productivity, yield and positive interactions with applied N, P and K fertilizers (Jones and Handreck, 1967; Savant et al., 1997,

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1999). The effects of silicon on the reduction in the incidence and severity of phytopathogenic fungi, bacterial and viral pathogens, and insect pest attack have been widely reported in several crop plant species (Ma, 2004; Reynolds et al., 2009, 2016; Van Bockhaven et al., 2013; Liang et al., 2015a,b; Sakr, 2016a,b). 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, 2004; Ma and Yamaji, 2006; Epstein, 2009; Van Bockhaven et al., 2013; Liang et al., 2015b).

Based on the literature, two major defense mechanisms due to silicon application against insect pest damage have been documented: physical defense and biochemical defense (Reynolds et al., 2009, 2016; Liang et al., 2015a). Physical defense is associated with an accumulation of absorbed silicon in the epidermal tissue as a mechanical barrier in leaf epidermis cells, increasing hardness that causes wear to insect mandibles and reducing digestibility. Biochemical defense is related to soluble silicon being involved in induced biochemical defense to insect pest attack through the enhanced production of defensive enzymes and phenolic compounds. Also, silicon can induce both types of defense mechanisms by causing decreased digestibility capacity, increased abrasiveness of plant tissues, and enhanced production and accumulation of chitinases, peroxidases, lignin and phenolics (Reynolds et al., 2009, 2016; Liang et al., 2015a).

To date, numerous studies have documented the ability of silicon application to improve resistance of plants to insect attack and reduce insect growth and reproduction in several plant crops (Table 1). Physical and/or biochemical protection systems due to silicon treatments against pest infestation have been shown for all insect feeding guilds: lepidopteran borers, phloem-feeding insects and xylem-feeding insects (Reynolds et al., 2009, 2016; Liang et al., 2015a). In order to understand the complex interaction between silicon applications and insect pest resistance in plants, this review aims to present the agricultural importance of silicon in plants, to underline the control of insect pests in different major crop plants by silicon treatment, to refer to different mechanisms of silicon-enhanced resistance, and to explain the presence of nil effects of silicon on insect pests.

Silicon uptake and accumulation in plants in relation with plant resistance to insect pests

Silicon is the second most abundant element in the earth's crust mass (27.70%), and is considered as the most important secondary mineral in the formation of soils (Lowenstam, 1981). In soil solution, silicon occurs mainly as monosilicic acid (H_4SiO_4) at concentrations ranging from 0.1 to 0.6 mM and is taken up by plants in this form (Epstein, 1994; Savant et al., 1997; Ma and Takahashi, 2002). After its uptake, it is transported via xylem to all parts of the plant and deposited in the form of silica gel or biogenetic opal as immobile amorphous $\text{SiO}_2 \cdot n\text{H}_2\text{O}$ in cell walls, intercellular spaces of root and leaf cells as well as in bracts (Aston and Jones, 1976). The amorphous silica, deposited below the cuticle, forms a physical barrier called double-layer silicon-cuticle. It maintains the leaves erect, reduces the transpiration and digestibility, increases hardness and abrasiveness and protects the plants against insects and fungal attacks (Ma, 2004; Liang et al., 2015a).

Table 1

Plant–insect associations on which the role of silicon in decreasing pest preference and growth rates has been observed

Host plant	Insect pest	Reference
Wheat	Hessian fly <i>Phytophaga destructor</i> Say (Diptera: Aphelinidae)	McColloch and Salmon (1923); Miller et al. (1960)
	Rose-grain aphid <i>Metopolophium dirhodum</i> Walker (Hemiptera: Aphididae)	Hanisch (1981)
	English grain aphid <i>Sitobion avenae</i> Fabricius (Hemiptera: Aphididae)	Hanisch (1981); Dias et al. (2014)
	Green bug <i>Schizaphis graminum</i> (Rondani) (Hemiptera: Aphididae)	Gomes et al. (2005); Goussain et al. (2005); Costa et al. (2011)
Maize	Stalk-borer <i>Chilo zonellus</i> Swinhoe (Lepidoptera: Pyralidae)	Sharma and Chatterji (1972)
	European corn borer <i>Ostrinia nubilalis</i> Hubner (Lepidoptera: Pyralidae)	Rojanaridpiched et al. (1984)
	Stem borer <i>Sesamia calamistis</i> Hampson (Lepidoptera: Noctuidae)	Setamou et al. (1993)
	Fall armyworm <i>Spodoptera frugiperda</i> Smith (Lepidoptera: Noctuidae)	Goussain et al. (2002); Neri et al. (2005)
	Asian corn borer <i>Ostrinia furnacalis</i> Guenee (Lepidoptera: Crambidae)	Hornig and Chu (1990)
	Leaf corn aphid <i>Rhopalosiphum maidis</i> Fitch (Hemiptera: Aphididae)	Almeida et al. (2015)
	Asian rice stem borer <i>Chilo suppressalis</i> Walker (Lepidoptera: Crambidae)	Sasamoto (1961); Djamin and Pathak (1967); Ma and Takahashi (2002); Hou and Han (2010)
Rice	Yellow stem borer <i>Scirpophaga incertulas</i> (Walker) (Lepidoptera: Pyralidae)	Panda et al. (1975); Rajamani et al. (2013)
	Brown plant-hopper <i>Nilaparvata lugens</i> Stal (Hemiptera: Delphacidae)	Yoshihara and Sogawa (1979); Rajamani et al. (2013); He et al. (2015)
	White-backed plant-hopper <i>Sogatella furcifera</i> Horvath (Hemiptera: Delphacidae)	Kin and Heinrichs (1982); Salim and Saxena (1992)
	African striped borer <i>Chilo zacconius</i> Bleszynski (Lepidoptera: Pyralidae)	Ukwungwu (1990)
	Leaf rice roller <i>Cnaphalocrocis medinalis</i> (Guenee) (Lepidoptera: Pyralidae Satyridae)	Ramachandran and Khan (1991); Nakata et al. (2008); Ye et al. (2013); Han et al. (2015)
	Stem-borer <i>Chilo agamemnon</i> Bleszynski	Soliman et al. (1997)
	Leaf miner <i>Hydrellia prosternalis</i> Deeming (Diptera: Ephydriidae)	Soliman et al. (1997)
	Green rice caterpillar <i>Naranga aenescens</i> Moore (Lepidoptera: Noctuidae)	Nakata et al. (2008)
	Gall midge <i>Orseolia oryzae</i> Wood-Mason (Diptera: Cecidomyiidae)	Rajamani et al. (2013)
	Green leaf hopper <i>Nephotettix virescens</i> Distant (Hemiptera: Cicadellidae)	Rajamani et al. (2013)

Table 1 continued

Host plant	Insect pest	Reference
Sugarcane	Sugarcane stem borer <i>Diatraea saccharalis</i> Fabricius (Lepidoptera: Crambidae)	Sidhu et al. (2013)
	Sugarcane shoot-borer <i>Chilo infuscatelus</i> Snell (Lepidoptera: Crambidae)	Rao (1967)
	Sugarcane scale <i>Melanaspis glomerata</i> (Green) (Homoptera: Coccidae)	Agarwal (1969)
	Sugarcane top borer <i>Scirpophaga excerptalis</i> Walker (Lepidoptera: Crambidae)	Gupta et al. (1992)
	Sugarcane stem borer <i>Diatraea saccharalis</i> Fabricius (Lepidoptera: Crambidae)	Anderson and Sosa (2001)
	African sugarcane borer <i>Eldana saccharina</i> Walker (Lepidoptera: Pyralidae)	Keeping and Meyer (2002); Meyer and Keeping (2005); Kvedaras et al. (2007a,b); Kvedaras and Keeping (2007); Keeping et al. (2014)
	Sugarcane spittlebug <i>Mahanarva fimbriolata</i> Stal (Hemiptera: Cercopidae)	Korndorfer et al. (2011)
Ryegrass	Argentine stem weevil <i>Listronotus bonariensis</i> Kuschel (Coleoptera: Curculionidae)	Barker (1989)
Sorghum	Central shoot fly <i>Atherigona indica infuscata</i> Malloch (Diptera: Anthomyiidae)	Ponnaiya (1951)
	Green bug <i>Schizaphis graminum</i> (Rondani) (Hemiptera: Aphididae)	Carvalho et al. (1999)
Sweet potato	Sweet potato weevil <i>Cylas formicarius</i> Fabricius (Coleoptera: Curculionidae)	Singh et al. (1993)
Cucumber	Whitefly <i>Bemisia tabaci</i> Gennadius (Hemiptera: Aleyrodidae)	Correa et al. (2005)
<i>Agrostis capillaries</i> , <i>Brachypodium pinnatum</i> , <i>Festuca ovina</i> , <i>Lolium perenne</i> , and <i>Poa annua</i> grass plants	African armyworm <i>Spodoptera exempta</i> Walker (Lepidoptera: Noctuidae)	Massey et al. (2006)
Cotton	Desert locust <i>Schistocerca gregaria</i> Forskal (Orthoptera: Acrididae)	
	Leaf-worm <i>Alabama argillacea</i> Hubner (Lepidoptera: Noctuidae)	Tomquelski et al. (2007)
Potato	Green peach aphid <i>Myzus persicae</i> Sulzer (Hemiptera: Aphididae)	Gomes et al. (2008)
	Cucurbit beetle <i>Diabrotica speciosa</i> Germar (Coleoptera: Chrysomelidae)	Gomes et al. (2009); Assis et al. (2012)
	Leaf-beetle <i>Diabrotica</i> spp. (Coleoptera: Chrysomelidae)	da Silva et al. (2010)
	Leaf-miners <i>Liriomyza</i> spp. (Diptera: Agromyzidae)	da Silva et al. (2010)
<i>Deschampsia caespitosa</i> , <i>Festuca ovina</i> , and <i>Lolium perenne</i> grass plants	African armyworm <i>Spodoptera exempta</i> Walker (Lepidoptera: Noctuidae)	Massey and Hartley (2009)

Table 1 continued

Host plant	Insect pest	Reference
Soybean	Whitefly <i>B. tabaci</i>	Ferreira et al. (2011)
Peanut	Silvering thrips <i>Enneothrips flavens</i> Moulton (Thysanoptera: Thripidae)	Dalstra et al. (2011)
Sunflower	Sunflower caterpillar <i>Chlosyne lacinia saundersii</i> Doubleday and Hewitson (Lepidoptera: Nymphalidae)	Assis et al. (2013, 2015)
Lemon	Mediterranean fruit fly <i>Ceratitis capitata</i> Wiedemann (Diptera: Tephritidae)	Mditshwa et al. (2013)
<i>Portulaca grandiflora</i> plants	Mealy-bug <i>Phenacoccus solenopsis</i> Tinsley (Hemiptera: Pseudococcidae)	Huang et al. (2014)
Tomato	Tomato leaf-miner <i>Tuta absoluta</i> Meyrick (Lepidoptera: Gelechiidae)	dos Santos et al. (2015)
Mandarin orange	Citrus black-fly <i>Aleurocanthus woglumi</i> Ashby (Homoptera: Aleyrodidae)	Vieira et al. (2016)

Epstein (1994) reported that the absorption of silicon by plants from the soil at differing rates depend on genotype, its concentration in the soil and environmental conditions. In plant tissues, silicon content varies considerably with the species, ranging from 0.1 to 10% silicon on a dry weight basis (Ma and Takahashi, 2002). Generally, plants can be classified as silicon accumulators, silicon non-accumulators or silicon excluders (Ma and Yamaji, 2006). Plants require large quantity of silicon (concentrations greater than 1% of dry weight) are considered accumulators (Epstein, 1999). In this category belong plants in Poaceae family, such as corn, oats, rye, wheat, and rice which accumulates silicon at rates up to 10% of dry weight (Takahashi et al., 1990). Plants are considered neutral of silicon at concentrations less than 0.1% of dry weight (Epstein, 1999). Most dicotyledons are unable to accumulate high levels of silicon in their shoots, such as tomatoes, soybeans and cucumber.

Plant resistance in restricting pest feeding may not be simply related to the total quantity of silicon *per se*, but due to the site, arrangement and organization of silicon in the plant. Sorghum resistance to central shoot fly *Atherigona indica infuscata* Malloch (Diptera: Anthomyiidae) did depend upon the early formation of irregularly shaped silica deposits in the epidermis of the leaf sheath (Ponnaiya, 1951). Miller et al. (1960) found that the level of resistance to the Hessian fly *Phytophaga destructor* Say (Diptera: Aphelinidae) depends mainly on the distribution of silica bodies in leaf sheaths of wheat and oat cultivars. In susceptible cultivars, larvae of *P. destructor* can feed in spaces between rows with rod-shaped masses, however, in resistant ones, dense and grainy shapes ranging from round to oblong did not provide suitable spaces for *P. destructor* feeding (Miller et al., 1960).

Lower levels of sugarcane scale *Melanaspis glomerata* (Green) (Homoptera: Coccidae) infestation were recovered on sugarcane clones with higher numbers of silica cells in the wax band of the inter-node (Agarwal, 1969). Hindered of oviposition rates by the Argentine stem weevil *Listronotus bonariensis* Kuschel (Coleoptera: Curculionidae) was positively correlated with high densities of silica deposits (inclusive of trichomes) in the sheath epidermis of ryegrass cultivars (Barker, 1989). Greater protection in resistant sugarcane cultivars to the African sugarcane borer *Eldana saccharina* Walker (Lepidoptera:

Pyralidae) was due to silica bodies scattered over the pseudostem than these deposited in discrete rows in susceptible cultivars (Kvedaras et al., 2007b). Also, the authors observed that small increases in plant silicon fertilization led to significantly reduce the number of larvae found.

Silicon in controlling insect pests

The association between silicon treatment and reduced insect damage has been the object of several studies on plant–insect interactions (Ma, 2004; Reynolds et al., 2009; Liang et al., 2015a). Silicon application has been shown to decrease development, reproductive period, longevity, and fecundity of insect pests (Reynolds et al., 2009; Liang et al., 2015a).

Traditionally, two sources of silicon have been used to deliver silicon to the plant in deficient agricultural soils: solid treatment incorporated into the soil in the form of calcium silicate (Ca_2SiO_4) and silicate solutions applied as a soil drench or as a foliar spray in the form of sodium silicate (Na_2SiO_3) (Savant et al., 1999; Reynolds et al., 2009; Heckman, 2013). The ideal characteristics considered for a good source of silica to pest insect control could be presented as follows: high concentration of soluble silicon available to plants, physical properties that will facilitate storage ability, easy to mechanical application, uncontaminated with heavy metals, and low cost (Reynolds et al., 2009; Heckman, 2013).

Furthermore, it has been demonstrated that the elicitors (biocompatible molecules) can exhibit remarkable resistance against insect pest damage in combination with silicon, for example, the insect growth regulator lufenuron in affecting the preference of the fall armyworm *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae) on maize (Neri et al., 2005), fungicide acibenzolar-S-methyl (ASM) in reducing the larval period and pupal weight and increased the pupal period of the leaf-worm *Alabama argillacea* Hubner (Lepidoptera: Noctuidae) (Tomquelski et al., 2007) on cotton, ASM in reducing weight of the sunflower caterpillar *Chlosyne lacinia saundersii* Doubleday and Hewitson (Lepidoptera: Nymphalidae) larvae on sunflower (Assis et al., 2015), and systemic insecticide imidacloprid in decreasing the mealy-bug third-instar *Phenacoccus solenopsis* Tinsley (Hemiptera: Pseudococcidae) nymphs and adult females on *Portulaca grandiflora* plants (Huang et al., 2014).

In spite of the wide difference between borers and sap-feeding pest insects regarding reproductive and feeding behaviour on crops of great economic importance, silicon can improve plant resistance to insect attack and infestation for the two guilds (Reynolds et al., 2009, 2016; Liang et al., 2015a), and it plays a role in pest resistance in most cultivated crops (Reynolds et al., 2009, 2016; Liang et al., 2015a).

Wheat (Triticum aestivum L.) resistance to pest infestation

Evidence indicated that the resistance of different varieties of plant to the Hessian fly *P. destructor* is due to high silica content (McColloch and Salmon, 1923). Increased silicon content in plant stems reduced largely damage caused by the larvae of Hessian fly, and greater protection was observed in susceptible cultivars treated with a solution containing sodium silicate (Miller et al., 1960).

Foliar Na_2Si_2 (1% concentration) treatment increased resistance in plants to two important aphids, the rose-grain aphid *Metopolophium dirhodum* Walker (Hemiptera: Aphididae) and the English grain aphid *Sitobion avenae* Fabricius (Hemiptera: Aphididae) through enhancing silicon solubility within the leaves (Hanisch, 1981). Dias et al. (2014) observed that reduced fecundity, reproductive period, longevity, intrinsic rate of increase, and net reproductive rate of apterous *S. avenae* was due to induction of antibiotic resistance in plants treated with silicon.

Positive effects of silicon treatment were evident as reduced preference, longevity and fecundity rates, nymph production and feeding times by nymphs of green bug *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae) (Gomes et al., 2005; Goussain et al., 2005; Costa et al., 2011).

Maize (Zea mays L.) resistance to pest infestation

Enhanced plant resistance by reducing the stalk-borer *Chilo zonellus* Swinhoe (Lepidoptera: Pyralidae) damage was due to increased silicon rates (Sharma and Chatterji, 1972). Higher levels of soluble silicon in the sheath and collar tissue enhanced plant resistance to the second generation of the European corn borer *Ostrinia nubilalis* Hubner (Lepidoptera: Pyralidae) (Rojanaridpiched et al., 1984). Setamou et al. (1993) noted that increased sodium metasilicate fertilization reduced larval stem borer *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) survival from 26.0% (control) to 4.0% at 0.56 g Si/plant.

High silicon application increased mortality levels of the fall armyworm *Spodoptera frugiperda* Smith (Lepidoptera: Noctuidae) (Goussain et al., 2002). By using artificial diets containing silica at different concentrations, Horng and Chu (1990) found that the mortality of larvae and pupae of the Asian corn borer *Ostrinia furnacalis* Guenee (Lepidoptera: Crambidae) increased as silica content increased, and they observed that the fecundity, net reproductive rate and intrinsic rate of increase were negatively correlated with diet silica content. Almeida et al. (2015) found that the silicon fertilization contributed to an increase in the induction of non-preference of corn leaf aphid *Rhopalosiphum maidis* Fitch (Hemiptera: Aphididae).

Rice (Oryza sativa L.) resistance to pest infestation

Sasamoto (1961) found that the increase in silicon content of plants grown in silicon supplied soils decreased their susceptibility to the Asian rice stem borer *Chillo suppressalis* Walker (Lepidoptera: Crambidae). High silicon application reduced the bore and faeces rates of *C. suppressalis* larvae *in vitro* (Ma and Takahashi, 2002). Moreover, Hou and Han (2010) noted that silicon treatment decreased penetration *C. suppressalis*, weight gain, and stem damage.

High silicon deposits in stems of resistant varieties inhibited larvae attack of the yellow stem borer *Scirpophaga incertulas* Walker (Lepidoptera: Pyralidae) (Panda et al., 1975). Growth inhibition of the brown plant-hopper *Nilaparvata lugens* Stal (Hemiptera: Delphacidae) was due to silicic acid at the concentration < 0.01 mg Si/ml (Yoshihara and Sogawa, 1979). High silicon content in plant lines had significant antibiotic and an-

tixenotic effects on *N. lugens* by reducing survival rate, settled insect number, fertility and honeydew excretion (He et al., 2015). Kin and Heinrichs (1982) observed that silicon application in seedlings reduced the adulthood level of nymphs of the white-backed plant-hopper *Sogatella furcifera* Horvath (Hemiptera: Delphacidae) and increased the male proportion.

High silicon content decreased the rates for bored stem and number of living larvae per plant of the African striped borer *Chilo zacconius* Bleszynski (Lepidoptera: Pyralidae) (Ukwungwu, 1990). The resistance of 11 rice cultivars to the stem-borer *Chilo agamemnon* Bleszynski (Lepidoptera: Crambidae) and to the leaf miner *Hydrellia prosternalis* Deeming (Diptera: Ephydriidae) increased due to higher levels of silicon application (Soliman et al., 1997).

Silicon concentration at 373 mg g⁻¹ dry weight in leaves increased plant resistance to the green rice caterpillar *Naranga aeneascens* Moore (Lepidoptera: Noctuidae) and leaf rice roller *Cnaphalocrocis medinalis* (Guenee) (Lepidoptera: Pyralidae) (Nakata et al., 2008). Moreover, low and high silicon levels applied to susceptible variety reduced larval survival rate and pupation rate in the *C. medinalis* (Han et al., 2015).

Sugarcane (Saccharum officinarum L.) resistance to pest infestation

Silicon increased plant resistance and decreased borer recovery, against the sugarcane shoot-borer *Chilo infuscatelus* Snell (Lepidoptera: Crambidae) (Rao, 1967), the sugarcane top borer *Scirpophaga excerptalis* Walker (Lepidoptera: Crambidae) (Gupta et al., 1992), and the sugarcane stem borer *Diatraea saccharalis* Fabricius (Lepidoptera: Crambidae) (Anderson and Sosa, 2001). Pan et al. (1979) also noted a reduction in the incidence of borer damage in silicon-treated plants by stem borers as compared with untreated control, following application of bagasse furnace ash and silica slag.

In both field and greenhouse trials, the silicon treatment significantly increased plant resistance by reducing damage, larval weight, and numbers of borers recovered from stalks to the African sugarcane borer *E. saccharina* (Keeping and Meyer, 2002; Meyer and Keeping, 2005; Kvedaras and Keeping 2007). Increased nymphal mortality and decreased the longevity of males and females of the sugarcane spittlebug *Mahanarva fimbriolata* Stal (Hemiptera: Cercopidae) was due to high silicon absorption and accumulation (Korndorfer et al., 2011).

Silicon induced resistance of other crops to pest infestation

Sodium silicate fertilization to sorghum affected preference and reduced feeding and number of nymphs produced by the green bug *S. graminum* (Carvalho et al., 1999). Singh et al. (1993) found that the incidence of the sweet potato weevil *Cylas formicarius* Fabricius (Coleoptera: Curculionidae) was negatively correlated with silica content of all the tested plant cultivars. Calcium silicate application in cucumber plants decreased the whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) population by reducing oviposition and increasing cycle length and mortality at the nymphal stage (Correa et al.,

2005). Silicon fertilization to potato reduced preference and growth rates of green peach aphid *Myzus persicae* Sulzer (Hemiptera: Aphididae) (Gomes et al., 2008).

Reduced potato leaf palatability due to silicic acid foliar or soil-treatments reduced feeding injury of the cucurbit beetle *Diabrotica speciosa* Germar (Coleoptera: Chrysomelidae) (Gomes et al., 2009; Assis et al., 2012). Ferreira et al. (2011) determined that silicon combined with soybean plant caused significantly mortality in whitefly *B. tabaci* nymphs.

A single silicon spraying to peanut governed a greater protection by reducing the number of the silvering thrips *Enneothrips flavens* Moulton (Thysanoptera: Thripidae) adults and nymphs (Dalastra et al., 2011). Assis et al. (2013) reported that the levels of injured leaves and leaf area consumption of the sunflower caterpillar *C. lacinia saundersii* were decreased due to silicon application combined with artificial mechanical injuries which negatively affect leaf palatability. Calcium silicate concentration at 50 mg L⁻¹ reduced the occurrence of Mediterranean fruit fly *Ceratitidis capitata* Wiedemann (Diptera: Tephritidae) injury symptoms in lemon plants (Mditshwa et al., 2013).

Mechanisms of silicon-enhanced resistance

Regardless of the numerous scientific studies about silicon effects on insect pest infestation, the characteristics, spectrum of efficacy and mode of action of silicon is not entirely understood (Ma 2004; Reynolds et al., 2009, 2016; Liang et al., 2015a). Under optimum conditions, silicon does not affect plant growth or development (Ma and Yamaji, 2006). However, beneficial and useful effects only manifest under stress conditions (Ma 2004; Liang et al., 2007, 2015b). The mechanisms by which silicon is likely to affect insect pest development, reproductive period, longevity, and fecundity characteristics are not fully understood and need further research (Reynolds et al., 2009, 2016; Liang et al., 2015a). Generally, the effect of silicon on resistance of plants to insect pest is considered to be due to either a deposition of silicon on cell walls acting as a mechanical barrier difficult the insect-pests attack, or biochemical changes related to plant defense (Reynolds et al., 2009, 2016; Liang et al., 2015a).

Physical defense

The hypothesis of silicon-physical enhanced resistance is based on two mechanisms by which silicon deposition acts as a physical barrier; however, both currently lack good experimental support (Reynolds et al., 2009; Liang et al., 2015a). First, silicon decreases the efficiency with which insect pests can digest plant leaves. Second, enhanced hardness and abrasiveness of plant tissues due to silicon may increase the wear on insect pest mouthparts, both of which could potentially impact on insect pest performance. It seems that the physical defense due to silica deposition, mainly as opaline phytoliths in association with cell walls, is the most widely accepted mechanism for the action of silicon in increasing plant resistance to insect pest infestation (Reynolds et al., 2009; Liang et al., 2015a).

Silicon reduces digestibility of plant tissues

Increased silicon plant content via silicate fertilization and/or silicon-rich diets may decrease insect pest growth and performance rates by reducing: (1) the consumption, (2) the efficiency of food utilization by decreasing the ingestion of sufficient quantities of nutrient and water, (3) the digestive efficiency by decreasing the conversion of ingested food to body mass, (4) by altering and deterring insect pest feeding, and (5) by counteracting the effects of high plant nitrogen rates in promoting insect pest performance (Reynolds et al., 2009, 2016; Liang et al., 2015a).

Chu and Horng (1991) observed that increased hardness level in stems to Asian corn borer *O. furnacalis* was due to calcium silicate slag applied to corn plants, and tissue hardness rates decreased the consumption of the leaves by pest, indicating that leaf hardness and abrasiveness due to high silica deposition may be associated with the resistance to the borer. The *O. furnacalis* larvae fed on artificial diets containing high silicon content resulted in increasing mortality of larvae and pupae, prolonging pre-oviposition period and shortening the oviposition period (Horng and Chu, 1990).

Salim and Saxena (1992) found that increased levels of silicon content in susceptible rice cultivars reduced plant consumption by *S. furcifera*, in addition to decreased number of nymphs becoming adults, adult longevity, female fecundity, growth and population increases. The rate of both conversion ingested food into body mass, and the amount of nitrogen absorbed from their food of the African armyworm *Spodoptera exempta* Walker (Lepidoptera: Noctuidae) was decreased due to silicon-rich diets (Massey and Hartley, 2009).

Increased leaf abrasiveness due to silicon uptake altered and deterred the desert locust *Schistocerca gregaria* Forskal (Orthoptera: Acrididae) and *S. exempta* fed on grass species (Massey et al., 2006). Under free-choice conditions, Chu and Horng (1991) reported reduced growth rates of Asian corn borer for silicon-treated plants but enhanced preference criteria for high-nitrogen-treated plants. Meyer and Keeping (2005) and Keeping et al. (2014) showed that silicon application via soil treatment can diminish the increased infestations of *E. saccharina* due to nitrogen fertilization. Moreover, rice plants received higher dose of silicon 600 kg/ha in combination with nitrogen fertilization recorded the lower incidence of yellow stem borer, gall midge *Orseolia oryzae* Wood-Mason (Diptera: Cecidomyiidae), brown plant hopper and green leaf hopper *Nephotettix virescens* Distant (Hemiptera: Cicadellidae) (Rajamani et al., 2013), thus ensuring that recommended rates of nitrogen could be applied for sugarcane and rice plants without limiting crop productivity. However, Keeping et al. (2014) found that silicon treatments with high nitrogen treatments did not significantly influence the exotic sugarcane thrips *Fulmekiola serrata* Kobus (Thysanoptera: Thripidae) infestation.

Nil effect of silicon artificial diets on insect pest has also been highlighted. Stanley et al. (2014) found that silicon artificial diets did not reduce larval growth for two cotton bollworms *Helicoverpa armigera* Hubner and *H. punctigera* Wallengren (Lepidoptera: Noctuidae), so results of this test do not corroborate the hypothesis that silicon is directly antibiotic to *Helicoverpa* spp. via ingestion (Stanley et al., 2014). Silicon applied to tomato leaves caused a detachment of the basal membrane in the midgut epithelium in

larvae of the tomato leaf-miner *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) (dos Santos et al., 2015).

Silicon causes mandible wear

In larval Lepidoptera, mandible wear due to increased hardness and abrasiveness of silicon in plant cell walls was correlated with reduced preference rates, so that feeding ability is compromised and impaired growth or starvation ensues (Raupp, 1985; Massey and Hartley, 2009). Mandibles replacement at each moult makes silicon effect is indefinite. However, increased mandible wear forced larvae fed on plants high in silicon to moult sooner than usual, which could be associated with decreased body weight in insect pests. Several studies have indicated augmented mandible wear in lepidopteran larvae fed on plant cultivars with high silicon content (Reynolds et al., 2009, 2016; Liang et al., 2015a).

Djamin and Pathak (1967) observed significant mandible damage in larvae of the stem-borer *C. suppressalis* fed on rice plants with increased silicon content. Artificial diets containing silicon at elevated concentrations caused high mandible wear in leaf rice roller larvae *C. medinalis* (Ramachandran and Khan, 1991). Goussain et al. (2002) reported that the applications of sodium silicate to corn plants caused wearing out in the incisory region of the mandibles of fall armyworm *S. frugiperda*. Rapid increasing in mandible wear of *S. exempta* was due to silicon fertilization to grass species (Massey and Hartley, 2009).

Negligible effect of silicon amendment on mandible wear has been shown in some studies. Calcium silicate fertilization to 'Penncross' creeping bentgrass caused a little mandible wear of the black cutworm, *Agrotis ipsilon* Hufnagel (Lepidoptera: Noctuidae) and the root-feeding masked chafer grubs, *Cyclocephala* spp. (Redmond and Potter, 2007). Kvedaras et al. (2009) observed that the sugarcane cultivars treated with silicon caused a slight mandible wear in *E. saccharina* larvae.

Biochemical defense

The soluble silicon in plant tissue may induce plant defense against insect pest attack via (1) increased activity of defensive enzymes, such as polyphenoloxidase, peroxidase, phenylalanine ammonia-lyase in leaves, and (2) increased production of defensive chemicals, such as tannins, lignin and phenols. Biochemical changes due to silicon absorption could diminish the quality of phloem sap and affect pest insect development criteria (Reynolds et al., 2009, 2016; Liang et al., 2015a). Many biochemical mechanisms of defense to insect pest infestation are shared with those against plant pathogenic fungi (Van Bockhaven et al., 2013; Sakr 2016b). Regarding all studies demonstrating the positive effect of silicon on insect pest preference, it is evident that the role of biochemical resistance was less important than physical defense (Reynolds et al., 2009, 2016; Liang et al., 2015a). Further research should be carried out on several pest insects to reveal the importance of biochemical defense to reduce insect pest damage.

Induced resistance to the green bug *S. germanium* generated by biochemical changes because of the absorbed silicon by wheat plants may be of greater importance than physical impediment, as the stylet eventually did reach phloem resulting in reduction

of probing time (Goussain et al., 2005). In the same association between *S. germanium* and wheat plants, increased activities of three defensive enzymes, polyphenoloxidase, peroxidase, and phenylalanine ammonia-lyase due to soluble silicon negatively affected pest growth and preference (Gomes et al., 2005). Indeed, induced resistance to the white-fly *B. tabaci* in cucumber due to silicon absorbed by plants was expressed by synthesis of defense chemicals that cause stylet withdraw (Correa et al., 2005).

Induced resistance by way of defensive chemicals including silica and phenols due to organic fertilizers applied to eggplant plants reduced preference and growth rates, feeding rate, oviposition, longevity and population buildup and prolonged the nymphal duration of eggplant insect pests (Zadda et al., 2007). Silicon fertilization increased lignin and tannins concentration in the leaves of potato plants to aphid *M. persicae* attack, and it seems that the silicon acted as a resistance inducer to insect pest by reducing fecundity and the rate of population growth (Gomes et al., 2008). da Silva et al. (2010) showed that the spray fertilization with solution of silicic acid acted as inducer of the tannin synthesis in the potato leaves and consequently, decreased the number of aphid and leaves injuries caused by the leaf-beetle *Diabrotica* spp. (Coleoptera: Chrysomelidae) and the number of mined leaves by leaf-miners *Liriomyza* spp. (Diptera: Agromyzidae).

Increased peroxidase and polyphenoloxidase activity in seedlings of mandarin orange due to potassium silicate application reduced development of citrus black-fly *Aleurocanthus woglumi* Ashby (Homoptera: Aleyrodidae); and both factors: feeding time of *A. woglumi* and silicon concentration induced synthesis of plant defense compounds (Vieira et al., 2016).

Indirect effects of silicon nutrition

Several indirect effects of silicon may be caused by delaying insect pest establishment and thus an increased probability of exposure to natural enemies, unfavorable climatic conditions or control procedure that target exposed insects (Reynolds et al., 2009, 2016).

The accumulation of silicon in sugarcane plants increases the difficulty of penetration by the African sugarcane borer *E. saccharina*, and it augments the exposure time of young larvae to natural enemies, abiotic conditions, or control practices that target such larvae (Kvedaras and Keeping, 2007). Also, Kvedaras et al. (2007a) observed an interaction between silicon-enhanced sugarcane resistance to African sugarcane borer *E. saccharina* and water stress. In sugarcane plants treated with silicon, water-stressed cane showed more reduction in borer numbers and stalk damage than non-stressed cane, particularly for susceptible cultivars (Kvedaras et al., 2007a). These results are in accordance with other studies, where lower fungal disease intensity in the silicon-treated plants is more obvious under conditions of abiotic stress than non-stressed conditions (Ma, 2004; Liang et al., 2015b). Such observation hypothesis shows that silicate fertilization could augment insect pest resistance of plants exposed to a multitude of a range of abiotic stresses, including salinity stress and heavy metal toxicity.

Feeding damage decrease for the sugarcane borer *D. saccharalis* due to silicon application increased exposure to unfavorable climatic conditions and natural enemies

arising from reduced boring success (Sidhu et al., 2013), and this provides evidence that silicon fertilization may contribute to the management of this pest.

Augmentation of plant resistance due to silicon application could be associated with increased production of plant hormones including jasmonate (JA) and salicylate (SA) (Reynolds et al., 2009, 2016). When damaged with insect pest attack, many plants released hormones attracting beneficial natural enemies into silicon-treated plants (Dicke et al., 2003; Reynolds et al., 2009, 2016). The application of potassium silicate with a subsequent *Helicoverpa armigera* Hubner (Lepidoptera: Noctuidae) larvae infestation augmented cucumber plants' ability to mount an induced response by attracting natural enemy, adult predator *Dicranolaius bellulus* Guerin-Meneville (Coleoptera: Melyridae) (Kvedaras et al., 2010).

Amplification of JA mediated defense responses in rice to *C. medinalis* was due to silicon application (Ye et al., 2013), and the authors suggest that silicon acted as a priming agent in pathogenesis-mediated host defense signaling pathway. Increased silicon content in grapevine plants infected by the light brown apple moth *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) significantly attracted the predatory beetle *Dicranolaius bellulus* (Guerin-Meneville) (Coleoptera: Melyridae) (Reynolds et al., 2014). By using solid-phase micro-extraction (SPME)/gas chromatography-mass spectrometry (GC-MS) analysis, the grapevine plant infected with the Australian grapevine moth *Phalaenoides glycinae* (Lewin) (Lepidoptera: Noctuidae) released seven volatile compounds, and higher amounts of *n*-heptadecane were detected only in plants treated with silicon (Reynolds et al., 2014).

Cases of non-effect of silicon on plant resistance to insect pests

There are studies on the failure of silicon to reduce pest performance and growth for the two main insect feeding guilds (Reynolds et al., 2009). However, no convincing evidence has been proposed in identifying any trend in how silicon plant content may differentially affect insect pests (Keeping and Kvedaras, 2008). Regarding some plant species, it seems that the insufficient accumulation of quantities of silicon do not protect them against pest insect attack (see the previous section on agricultural importance of silicon in plants).

Silicon content of soybeans had no significant effect on pupal weight of the Mexican bean beetle *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae) (Mebrahtu et al., 1988). In rice plants, no significant relationship has been established between silicon content and both: percentage white-heads and percentage dead-hearts caused by stem borers (mainly *C. suppressalis*) (Sunio et al., 2000). Corn plants treated with sodium silicate did not affect preference and growth rates of the corn leaf aphid *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae) compared to the control without silicon (Goussain, 2001).

Potassium silicate application at a concentration up to 800 ppm to poinsettia plants did not provide protection to greenhouse whitefly *Trialeurodes vaporariorum* Westwood

(Hemiptera: Aleyrodidae) developing on leaves (Hogendorp et al., 2010). On *Zinnia elegans* plants, pre-reproductive period and survivorship of the green peach aphid *Myzus persicae* Sulzer (Hemiptera: Aphididae) was not affected by potassium silicate solutions (Ranger et al., 2009). Potassium silicate solutions did not alter the proportion of pepper leaves that sustained chilli thrips *Scirtothrips dorsalis* Hood (Thysanoptera: Thripidae) damage, insufficient silicon accumulation level in leaf tissues did not govern protect against pest insect infestation (Dogramaci et al., 2013).

The probing behavior of the citrus mealy-bug *Planococcus citri* Risso (Hemiptera: Pseudococcidae) was not affected by soil calcium silicate treatment to coffee plants (Santa-Cecilia et al., 2014). Amado and Rizental (2015) found that the silicon application caused no significant differences for population size of cotton aphid *Aphis gossypii* (Hemiptera: Aphididae) and whitefly *B. tabaci* on cotton plants.

Conclusion

Silicon-induced plant resistance to insect pest infestation via physical and biochemical mechanisms represents a critical strategy, which provides an active and long lasting solution to maintain low levels of insect pest populations, and primary reduces yield losses. Enhanced resistance to insect attacks and infestation of lepidopteran borers and sap-feeding insects following artificial silicon applications have been observed in a wide variety of plant species. Physical defense due to silica deposition is more acceptable in explaining plant resistance to insect pests than a biochemical resistance because of silicon absorption. New approaches to understand silicon biochemical effects on plants and insect pests should be carried on induced resistance by silicon. Nil effect of silicon application against some pest insects, including the two main insect feeding guilds, is not limited to low silicon-accumulators, but it has been noticed in high accumulators, too. Silicon could be potentially of great benefit for non-insecticide pest management. Complete understanding of the biological role of silicon in plants improves the effective use of silicon to increase crop productivity and enhance insect pest resistance.

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