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Review Article

Silicon, the multifunctional element in reducing biotic and abiotic stress in plants

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Abstract

Despite the fact that Silicon (Si) is not considered a necessary ingredient for higher plants, however it is a typical beneficial element having a positive impact factor on the growth and production on the variety of plant species. Its beneficial effects are more expressed in plants under stressed conditions as it serves a protective component in plants resilience to both biotic and abiotic stress conditions. Availability of pure Si is rare, most of the Si in the earth's crust is bonded with oxygen. Plants have been shown to be more resistant to fungal and bacterial diseases when exposed to Si. In this review, we have discussed the consequence of Si in combating stress (biotic and abiotic) factors in plants and have focused on the physical, biochemical and molecular elements of the problem. As compared to the physical aspects of resistance, it has been found that in the majority of cases silicon induces biochemical and molecular resistance during plant pathogen system. Si forms an effective element thereby proving effectual resistance as defense related enzymes gets activated, antimicrobial substances are stimulated and defense signaling pathways are regulated. According to Taiz and Zeiger (2002), Si is found in found in various amounts throughout the plant tissue and increases plant growth and fertility.

Keywords: Silicon, Stress factors, Physical, Biochemical, molecular, Defense response.

INTRODUCTION

Plants are constantly subjected to various biotic and abiotic stress factors that make detrimental effects over the growth, development and production of plants. In order to combat these stress factors, plants have already developed innate defense mechanisms and Si is found to enhance those defense mechanisms in plants by regulating various defense pathways involving physical fortifications, enhancing biochemical and molecular parameter and regulating defense signaling pathways. Despite the fact that Si is not considered a necessary nutrient for plants, but being the second most plenteous element after oxygen and making about 70% of the soil mass is of great assistance for plant growth, production and disease resistance (Epstein, 1994; Savant et al., 1997; Ma & Yamaji, 2006). However, due to variances in root Si absorption capability, plants accumulate Si differently and monosilicic acid ($Si(OH)_4$) is most common type of Si available to the plants as a nutrient (Takahashi et al., 1990), Si availability to the plants is greatly influenced by various soil parameters including pH, clay, organic matter and iron (Fe) or aluminum (Al) oxides. In this review, the significance of Si in giving resistance to biotic and abiotic stress conditions is being investigated through physical, biochemical and molecular pathways.

Plants absorb Si, in the form of the uncharged molecule silicic acid ($Si(OH)_4$), is transported both passively and by silicon transporters (Ma & Yamaji, 2006). Si travels through the plasma membrane via two Si transporters, Lsi1 and Lsi2, which operate as influx and efflux transporters respectively in plants where Si is transported via Si transporters (Ma et al., 2006, 2007, 2008). Lsi1 is the only silicon influx transporter that is restricted to the root exodermis and endodermis. Lsi2 is a silicic acid efflux transporter that belongs to the nodulin-26 intrinsic protein III (NIP III) family (Ma et al., 2006, 2007).

Even though Si accretion varies widely amongst plant species, ranging from 0.1 percent to 10% of their dry weight, all plants contain Si (Epstein, 1999; Ma & Takahashi, 2002). Si accumulation in plants exerts various beneficial effects in them, it has been identified in gramineous plants such as rice and sugarcane, as well as various cyperaceous species (Epstein, 1994, 1999; Liang, 1999). Si imparts resistance to diseases produced by fungi, bacteria and pests. It has been demonstrated that Si has a significant function in increasing plant mechanical and physiological qualities as well as overcoming stress symptoms (Epstein, 1999; Richmond & Sussman, 2003., Fauteux et al., 2005; Marschner., 2012)

Silicon combating abiotic stress

Abiotic stress factors harshly effects the plants in every scenario and against these factors, silicon serves as supportive and beneficial element for plants to combating these stress factors as (drought, high temperature, freezing, radiation, UV, salt stress, nutrient imbalance, metal toxicity) (Ma, 2004., Shahnaz et al., 2011). Supporting to the above fact, Wheat plants grown in drought circumstances, Si treatment resulted in increased stomatal conductance, higher relative water content, and greater water potential as compared to plants that were not treated with Si fertilizer during drought stress, plants drought resilience and root development speed gets boosted when Si is applied (Mcginnity, 2015). Under salt stress condition, Si supplementation improves antioxidant enzyme activities as SOD (superoxide dismutase), APX (ascorbate peroxidase), GPX (guaiacol peroxidase), and CAT (catalase), as well as plant water status and water use efficiency (Coşkun et al., 2016). Improvement in chlorophyll content and photosynthetic activity in salt stressed maize and with drawl of injury laden by heat stress in Salvia on Si augmentation (Moussa, 2006; Soundararajan et al., 2014). Si reduces the deleterious effects of UV-B on soybean, wheat, and maize when administered exogenously (Yao et al., 2011; Shen et al., 2014). There is significant reduction in the uptake of heavy metals cadmium and copper by plants and prevents their root to shoot translocation (Figure 1). It was also established that there are events of various disease in plants, laden by the adsorption of heavy metals and uptake of some elements as Zn and Mn that affects the plants forms and form major threat to agricultural production. However, research suggests that heavy metal tolerance in plants is mediated by Si, and that their combined impacts at the plant and soil levels are significant (Rizwan, 2012).

Silicon combating biotic stress

Biotic stress factors laden by biotrophic, necrotrophic and hemi biotrophic pathogens have found to create detrimental effects on plants. To combat the stress, plants have developed various innate defense mechanisms and Si regulates these defense mechanisms by physical, molecular and biochemical pathways. Various studies have suggested that by boosting defense reactions, Si has a favorable effect on plant pathosystems and improves host resistance to a wide range of diseases. However, the actual mechanism of disease regulation mediated by silicon in higher plants is still poorly understood. (Remus-Borel et al., 2005; Cai et al., 2008; Ghareeb et al., 2011).

In diverse plant species, Si is an efficient strategy for controlling illnesses caused by both fungal and bacterial pathogens (Fauteux et al., 2005; Rodrigues & Datnof, 2015). By developing effective restrictions to the entry of pathogens to plants, silicon is found to be involved in the following pathways viz., strengthening the cells by physical fortifications (Epstein, 1999; Epstein, 2001; Rodrigues et al., 2015b), restricting the the passage of pathogens by stimulating systemic acquired resistance (SAR), by the production of antimicrobial compounds in plants and by activating the expression of multiple defense signaling pathways there by turning on of defense related genes (Fauteux et al., 2005; Datnoff et al., 2007; Fortunato et al., 2012b; Chen et al., 2014; Vivancos et al., 2015).

Physical barrier development

Silicon as an effective physical barrier is evidenced by the fact that Si provides structural fortification to cells by forming the physical barricade thereby preventing the pathogen penetrance into the cells (Figure 2). This improved resistance in plants is related to the enhanced epidermal tissue density of silicified long and short, mechanical strength in plants driven by the Si application via a thick layer of Si formation beneath the cuticle forming the double cuticle Si layer (Ma & Yamaji, 2006, 2008), thickening of the cellulosic membrane and coming in contact with organic substances in the epidermal cell wall through papilla formation thereby preventing enzyme degradation that have been resulted from the penetration of fungus into the membrane (Inanaga et al., 1995; Fauteux et al., 2005; Datnoff et al., 2007). Si gets cross linked with hemicellulose in the main cell wall thereby preventing pathogen access into the cells (He et al., 2015; Guerriero et al., 2016). Pectins and polyphenols form the primary constituents of the cell wall and gets complexed with Si, thereby increasing the flexibility of cell walls in plants as they grow (Emadian & Newton, 1989).

In case of rice plants, blast disease resistance against *M. grisea* is imparted when Si is applied on the leaf blades, as silicon forms physical barrier and restricts the entry of pathogen (Kim et al., 2002). Si prevents powdery mildew infection in cucumber and hypheal fungus *Pyricularia oryzae* in wheat plants by forming physical barrier (Souse et al., 2013). When Si is given through the roots, it causes plants to develop systemic acquired resistance (SAR) by preventing the progress of infection to the healthy plant parts (Liang et al., 2005a). Thus, by forming physical barrier, Si plays the preventative role in different ways by restricting the entry of pathogens to the plants. However, there develops complexity how Si provides defense mechanisms through biochemical and molecular mechanisms pathways in plants.

Biochemical Mechanism enhancement

Biochemical resistance in plants gets intensified after Si supplementation via boosting the activity of defense-related enzymes, antimicrobials, and systemic signals (Datnoff et al., 2007; Fortunato et al., 2012b). Si addition stimulates the activity of defense related enzymes as phenyalanineammonia-lyases, polyphenoloxidases, peroxidases, chitinases and gluconases, β-1,3 glucanase in plants while host pathogen

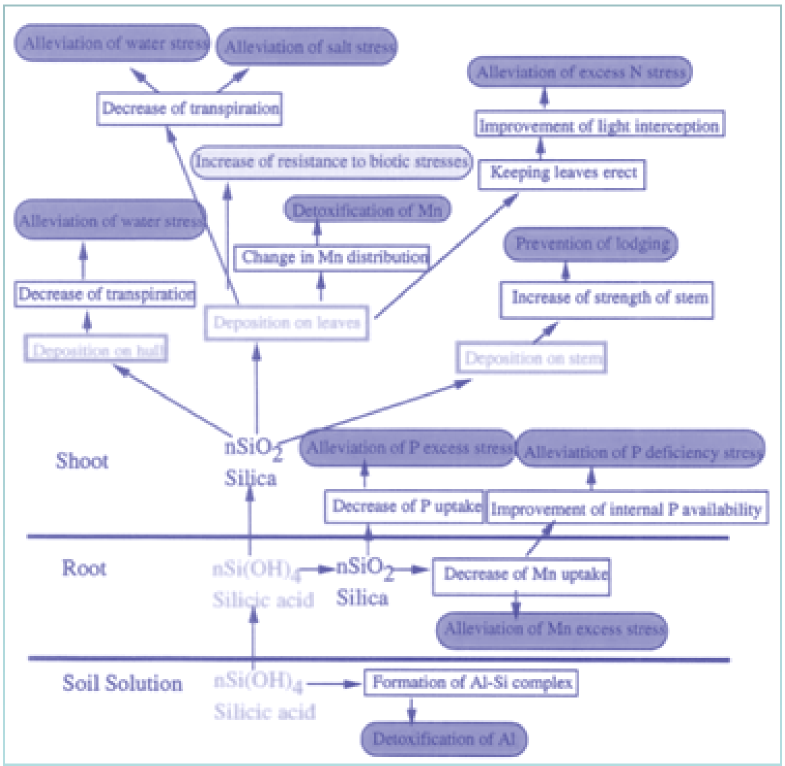


Figure 1. Effect of Si under multiple abiotic stresses

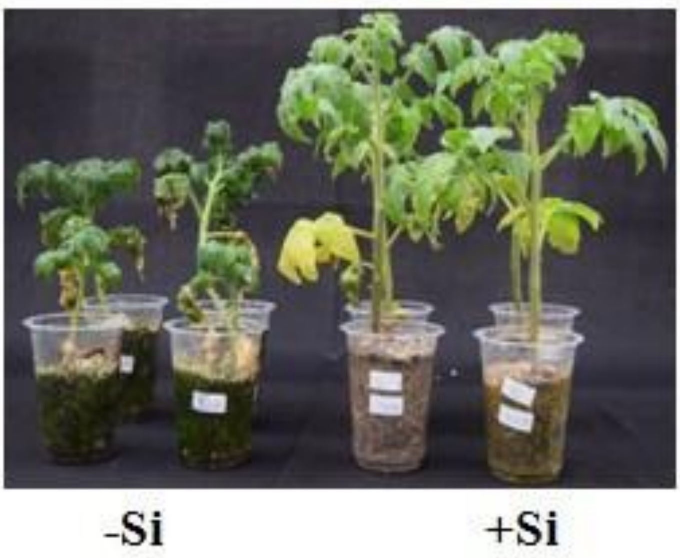


Figure 2. Early blight symptoms in Tomato after inoculated with *Alternaria Solani* for 10 days. Tomato plants were continuously treated with (+Si) or without silicon (–Si)

interaction (Fauteux et al., 2005; Datnoff et al., 2007; Van et al., 2013; Rodrigues et al., 2003, 2004, 2005; Cai et al., 2008). Si application boosts the activation of genes that control defense-related enzymes. After Si treatment, the leaves of banana, coffee and cucumber plants accumulate more defense-related enzymes, providing resistance to a wide range of diseases (Fortunato et al., 2012, Cherif et al., 1994; Liang et al., 2005). By controlling the activity of defense related enzymes such as phenylalanine ammonia-lyase (PALa and PALb) and lipoxygenase (LOXa). Sheath blight lesions in rice, gray leaf spot disease in perennial rye grass, and pink rot in Chinese melon are all suppressed by Si in the form of sodium silicate (Rahman et al., 2015, Guo et al., 2007, Schurt et al., 2014). The enzyme of phenolic oxidation i.e. Polyphenol oxidase identified in both free and bound form in the cytoplasm and chloroplast is primarily responsible for pathogen resistance in plants by increasing antibacterial activity, lignin biosynthesis and is involved in cell wall fortification by cross linking of cell wall proteins (Quarta et al., 2013, Song et al., 2016, Brisson et al., 1994). Chitinase enhances the resistance in plants to wide array of pathogens. It is involved in the hydrolysis of the cell wall of pathogenic fungi. Si application enhances chitinase activity when applied through the roots in pythum spp. (cherif et al., 1994. Liang et al., 2005). Higher activities of chitinases and peroxidases in Si treated wheat amplifies resistance to blast (*Pyricularia oryzae*) as reported by Xavier et al. (2011). By boosting chitinase and 1,3-glucanase activity after Si application as potassium silicate and sodium silicate, the incidence of *Mycosphaerella pinodes* and pink rot is reduced (Dann & Muir, 2002, Bi et al., 2006). Similarly, prevention of rice against herbivory and brown spot could be enhanced by Si addition in the form of potassium silicate solution (Ye et al., 2013, Dallagnol et al., 2011). The activity of defense-related enzymes is increased, which reduces the risk the powdery mildew (*Podosphaera xanthii*) by Si application, Chitinase, superoxide dismutase, peroxidase, and 1,3-glucanase are all activated as a result of Si treatment (Dallagnol et al., 2015). Similarly, increased activities of chitinases, 1,3glucanases, phenylalanineammonia-lyases, and other chitinases, in Si treated leaves of soyabeen, decreases the target spot infection (*Corynespora cassiicola*) (Fortunato et al., 2015).

Antimicrobial compound production

There is considerable increase in the activities of antimicrobial compounds on Si application thereby providing defense to plants against wide range of pathogens (Fauteux et al., 2005; Datnoff et al., 2007; Van et al., 2013). Phenols, flavonoids and phytoalexins form the antimicrobial compounds and their activities are stimulated by Si. Defense related enzymes play an important role in the production and accumulation of antimicrobial lignin, flavonoids and phytoalexins and their stimulation during plant pathogen interaction and their activity is enhanced by Si application (Chérif et al., 1994; Fawe et al., 1998; Rodrigues et al., 2004; Remus Borel et al., 2005). Lignin and flavonoid production is enhanced after Si supplementation that results in higher PAL activity (Dixon et al., 2002; Hao et al., 2011). Growth of the plant pathogens gets delayed after Si application during plant pathogen interaction by developing plant disease resistance (Dallagnol et al., 2011; Fortunato et al., 2015).

Si application results in the production of flavonoids that impart resistance to wide range of pathogens in multiple hosts. Through Si addition, there is prevention of *Podosphaera pannosa* in rose plant, *Pyricularia oryzae* in wheat and damping off of the Cucumber plants by *Pythium ultimum*i (Chérif et al., 1994, Shetty et al., 2012, Silva et al., 2015). Antimicrobial production by Si addition enhances resistance to powdery mildew (*Blumeria graminis*) in wheat and blast resistancein rice (*Pyricularia oryzae*) (Filha et al., 2011, Belanger *et al*., 2003), In case of model plant Arabidopsis, Si application results in the production of antimicrobial compounds thereby preventing powdery mildew infection (*Erysiphe cichoracearum*) in wheat (Ghanmi et al., 2004), Si application prevents the target spot development in soybean, brown spot and sheath blight development in rice (Fortunato et al., 2015, Dallagnol et al., 2011, Zhang et al., 2013). Incidence of powdery mildew caused by *Erysiphe cichoracearum* in Arabidopsis, *Podosphaera xanthii* in cucumber plants and blast in rice is reduced by phytoalexins (Ghanmi et al., 2004; Fauteux *et al*., 2005; Fawe et al., 1998; Rodrigues et al., 2004, 2005). Si application has found increase the accumulation of the flavonoids and phytoalexins in cucumber plants during *Podosphaera xanthii* infection (Fawe et al., 1998). Similar results were found in rice that stimulation of phytoalexin production after Si addition provides resistance to blast (Rodrigues et al., 2004, 2005). In perennial ryegrass pathosystems, Si supplementation results in the enhancement in phenolic acids, flavonoids and genes that encode PAL and lipoxygenase providing resistance against gray leaf spot disease (Rahman et al., 2015).

Si treated rice plants show decreased blast disease severity by regulating the activity of antimicrobial glycosylated phenolics and diterpenoid phytoalexins (Cai et al., 2008). Antimicrobial compounds as flavonoids, lignin, lignin-thioglycolic acid and soluble phenolics decreases the level of brown spot and blast in rice and wheat plants repectively (Dallagnol et al., 2011, Xavier et al., 2011, Rodrigues et al., 2014). Regarding the rice–*Rhizoctonia solani* pathosystem, Si induced enhancement of phenolic metabolism contributes to the improved resistance to sheath blight of a susceptible rice cultivar (Zhang et al., 2013). Fortunato et al., 2015 found higher activity of total soluble phenolics and ligninthioglycolic acid derivatives in leaves of soybean plants when supplied with Si led to reduced incidence of target spot (*Corynespora cassiicola).* In case of perennial ryegrass–*Magnaporthe oryzae* interaction, several phenolic acids including chlorogenic acid, flavonoids and relative levels of genes encoding phenylalanine ammonia lyase and lipoxygenase were significantly increased in Si amended plants compared with non-amended control plants (Rahman et al., 2015) and increased lignin concentration reduces the incidence of powdery mildew in melon plants (Dallagnol et al., 2015).

Systemic signal regulation

Plants are constantly subjected to a variety of biotic and abiotic challenges. Because of their sessile nature they have evolved complicated defense mechanisms to survive such stressful conditions. Various constitutive and inducible defense mechanisms regulated by an immune system that have been developed by plants against pathogen infection have been regulated by the network of signal transduction pathways (Grant et al., 2013). In systemic signaling pathway, SA, JA, and ET plays important role in plants, thereby enhancing their immunity to pathogen infection and makes adjustment in defense responses in plants (Clarke et al., 2000; Devadas et al., 2002). Si supplementation shows upregulation of these signaling molecules upon plant pathogen interaction. Biotrophic and hemi biotrophic pathogens are being actively affected by SA, whereas necrotrophic pathogens are predominantly affected by JA and ET (Pieterse et al., 2012). Si through JA accumulation in rice makes rice plant resistant against insect herbivores and regulates JA biosynthesis in plants that have been infected ((Ye et al., 2013, Kim et al., 2014). In case of Arabidopsis, application of Si leads to the biosynthesis of SA, JA, ET in leaves providing resistance against powdery mildew infection (*Erysiphe cichoracearum*) (Fauteux et al., 2006). Tomato plants infected with *Ralstonia solanacearum* and rice infected with *Magnaporthe oryzae* after Si application results in the activation of JA and ET signaling pathway, upregulation of defense signaling marker genes thereby providing resistance to disease (Zhang et al., 2004; Chen et al., 2009; Ghareeb et al., 2011, Iwai et al., 2006; De Vleesschauwer et al., 2008; Brunings et al., 2009, Van et al., 2015a).

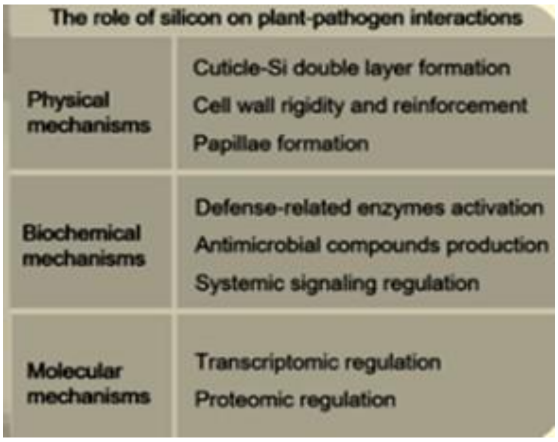
SA signaling pathway gets up regulated upon Si application through the positive regulation of genes EDS5 and SID2 while EDS1 and PAD4 are involved in SA biosynthesis (Shah, 2003). In case of model plant Arabidopsis, plants having higher concentration of Si were most resistant to pathogen infection than control as reported in the TaLsi *Golovinomyces cichoracearum* infection showing higher expression of EDS1, PAD, NPR1 and three SA-induced genes (PR1, PR2, and PR5) that are involved in defense pathway (Vivancos et al., 2015). PR genes are expressed significantly by NPR1 in response to SA and WRKY proteins positively up regulate the NPR1 expression as reported in tomato plant (Li et al., 2004, Ghareeb et al., 2011), WRKY1 expression was up regulated in Si treated tomato plants infected with *R. solanacearum.* NPR1 negatively regulates SA production in wild type plants. While herbivore attack suppress SA/ JA cross talk thus allowing beginning of JA- mediated defense against herbivore attack thereby demonstrating the regulatory role of NPR1 in cross talk. Si by serving as a priming agent for the JA pathway induces defense response expression and amplification of JA-mediated defense response.

Physical barrier formation through Si accumulation, upregulates JA signaling making overall leaf silicification and maturation of phytolith bearing silica cells (Fauteux et al., 2006; Ye et al., 2013). JA regulates the expression of Defensins (PDF1,2) in Arabidopsis or proteinase inhibitors I and II (PI I and PI I*I*) in tomato (Doares et al., 1995; Manners et al., 1998; Ryan and Moura 2002). The negative regulator of JA signaling pathway JAZ1 is found to be degraded by Ubiquitin-protein ligase and is found to be involved in fine modification of JA related genes (Thines et al., 2007). Ubiquitin protein ligase contribute to the defense response signaling and after Si application in pathogen infected plants, ubiquitin protein ligase activity gets up regulated (Dreher & Callis, 2007).

Ethylene signaling also plays profound role in disease defense response by up regulating the set of defense genes in plants. The three ethylene (ET) marker genes JERF3, TSRF1 and ACCO present in plants showed their response against various pathogens in plants. In ethylene biosynthesis, ACCO is concerned as TSRF1 form, an ET-responsive transcription factor (Pirrello et al., 2012). In case of tomato plant- *R.solanacearum* infection after Si treatment, there was found up regulation of JERF3, TSRF1 and ACCO genes showing that Si induced resistance were mediated via ET and JA pathways (Ghareeb et al., 2011). During *Botrytis cinerea* infection in Arabidopsis, the PDF1 expression was raised on Si application demonstrating its role as a modulator of signaling pathway involved in plant defense response against fungi (Cabot et al., 2013). After Si application to multiple crop plants, three classes of active defense mechanisms gets illustrated during plant pathogen interaction that involves the primary, secondary and tertiary responses. Primary response comes in cells infected with pathogens. Secondary response is restricted to cells near primary infection site and is induced by elicitors and the tertiary response is the systemic acquired response (SAR) that is transported to whole tissues of an infected plant hormonally (Hutcheson, 1998).

Molecular mechanism

Si application results in the prevention of diseases by enhancing resistance to wide range of pathogens in plants (Fauteux et al., 2005; Vivancos et al., 2015). To demonstrate the defense responses of Si in various pathosystems, transcriptomic and proteomic studies have been carried out (Fauteux et al., 2006; Chain et al., 2009; Majeed Zargar et al., 2010; Ghareeb et al., 2011). Si application to cucumber results in the mediation of systemic acquired resistance (SAR), resulting in enhanced expression of genes involved in encoding novel proline-rich protein that is associated in cell wall fortification at the sites where penetration of fungi is attempted into epidermal cells (Kauss et al., 2003). By utilizing molecular biology techniques such as subtractive cDNA libraries or microarrays, defense-related genes gets expressed in control or infected model Arabidopsis plants, their microarray results showed that Si-treated plants react to pathogen inoculation through the up regulation of defense and pathogenesis related genes, which confirms that Si plays an active role in enhancing host resistance to pathogen infection (Fauteux et al., 2005) (Figure 3). Various transcriptional changes that were induced by pathogen infection gets nullified after Si application as reported in case of *Arabidopsis-Erysiphe cichoracearum* pathogen infection, resulting in the alteration of gene expression of nearly 4000 genes and number and expression of up regulated defense related genes were not significantly changed in control and Si treated plants (Fauteux et al., 2005). Whereas on Si treatment the magnitude of the down-regulated genes that are involved in primary metabolism gets attenuated (Fauteux et al., 2006). Si supplementation to tomato plants inoculated with *R. solanacearum* readily changes 26 proteins thus signifying that the change in protein level in plants is correlated to the Si mediated resistance to diseases



The role of silicon on plant-pathogen interactions	
Physical mechanisms	Cuticle-Si double layer formation Cell wall rigidity and reinforcement Papillae formation
Biochemical mechanisms	Defense-related enzymes activation Antimicrobial compounds production Systemic signaling regulation
Molecular mechanisms	Transcriptomic regulation Proteomic regulation

Figure 3. Si mediated defense response in plants as physical, biochemical and molecular mechanisms.

(Chen et al., 2014). In both local and systemic resistance, Si plays an important role in providing resistance without being a second messenger (Fauteux et al., 2005; Bockhaven et al., 2013). Genome-wide studies on Arabidopsis, tomato and rice grown in soil amended with Si and compared to non-amended control plants have resulted in differential and unique expression of large number of defense related genes in host plants.

CONCLUSION

By combining the overall information on the stress factors affecting the host plants and defense through physical, biochemical and molecular mechanisms that can be characterized to Si mediated plant defense responses have been summarized in this review. Firstly, the Si provides resistance against pathogens by forming physical barriers involving cell wall reinforcement, silicification, cuticle-silica layer formations, papillae formation. Secondly, Si is involved in biochemical mechanisms for providing resistance against pathogens by activating defense related enzyme synthesis, antimicrobial compound productions and by systemic signaling pathways and finally, silicon in pathogen plant interactions involves the complex molecular mechanisms for providing resistance against biotic stress. Although numerous studies have elucidated the possible mechanism of Si mediated resistance at the physical, biochemical, and molecular levels, detailed mechanisms of Si regulated plant–microbe interactions, such as plant signaling transduction and transcriptome regulation of defense-related pathways, are needed for further study.

Conflict of interest

The authors declare that there is no conflict of interest.

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