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Silicon: A remedy to plant diseases

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Abstract

Silicon (Si) is the second most abundant element after oxygen on the earth's crust. The use of silicon in agriculture began in China more than 2000 years ago. Si is known to effectively mitigate various environmental stresses and enhance plant resistance against fungal, bacterial and viral pathogens. Even as early as 1917 there was report to suggest that Si was involved in rice's resistance against *Magnaporthe grisea*. Hence silicon is a great remedy to plant diseases and unlike pesticides its mode of action is not limited. Though a lot of research has been done in the use of silicon in reducing plant diseases, yet its use is limited, probably because the exact mechanism by which silicon mediates pathogen action remains a big question. In this review, the various plant diseases managed by silicon application and the effects of Si on plant-pathogen interactions are analyzed, mainly on physical and biochemical basis, and its role in inducing defense responses and activating the expression of defense related genes.

Keywords: Silicon, mechanical method, biochemical method and activating defense

Introduction

The use of silicon in agriculture probably began in China more than 2000 years ago. Probably the first researcher to suggest that Si was involved in rice's resistance to attack by the fungus *Magnaporthe grisea* [1]. Si is a good remedy to crop diseases and in the recent years a lot of research has been done on its use in controlling diseases. Silicon (Si) is the second most abundant element after oxygen in the earth's crust, and comprises up to 70% of soil mass [2, 3]. Generally, Si uptake takes place through plant roots as silicic acid [Si(OH)₄], an uncharged molecule [3], and passes through plasma membrane via two Si transporters, Lsi₁ and Lsi₂, which function as influx transporters and efflux transporters, respectively [4, 5]. Silicon may be applied as root or foliar application. 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, potassium silicate, calcium silicate, rice hull (raw or partially burnt) have been used as sources of silicon [6]. In its upward movement, via apoplast, from the roots to the leaves, silicon polymerization occurs in the extracellular spaces, accumulating on the walls of the epidermal cells of leaves and xylem vessels [7, 8, 9]. Accumulation rates of silicon in different plants vary between 1-10% [10, 11] and monocots store more silicon in comparison to dicots [12, 2]. The amounts of silicon accumulated in rice plants can be as much as 10% of plant dry weight. Si may also cause increased activity of enzymes involved in plant defense such asperoxidase, polyphenoloxidase, phenylalanine ammonia lyase and lipoxygenase [13, 14], which, in this case, is considered as a chemical barrier. Therefore, Si application can contribute in the management of plant diseases, among other practices. Si is helpful for improving the mechanical and physiological properties of plants and contributes to plants overcoming many biotic and abiotic stresses [1, 2].

More than 2000 years ago farmers in China incorporated rice straw along with manure as a fertilizer to enhance plant performance and yield. In the late 1950s, the first attempt to assess the possible uses of industrial by-products containing silicon as fertilizers was conducted in China. Subsequently, silicon application as fertilizers has increased steadily since 1970. As early as 1917 [1] suggested that Si was involved in rice's resistance to attack by the fungus *Magnaporthe grisea*, he showed the results of a comparative study of the chemical composition of rice plants from 13 different regions in western Japan, where infected plants always had lower concentrations of Si than healthy ones despite having grown under the same conditions. These results do not necessarily indicate that the incidence of disease was reduced by the concentration of Si or plants with lower concentrations were more susceptible but showed that there could be a relationship between concentrations of Si and the susceptibility of the rice plant to disease.

This study began a series of investigations into the possible relationship between Si and diseases of rice in Japan. Then [15], showed that, under controlled conditions, the application of Si to rice plants increased resistance to attack by the fungus *M. grisea* and that this increase in resistance was higher as the concentration of Si applied to the soil increased. The role of silicon in plant growth and potential disease reduction was first noted for dicots in 1939. As a result of research from the 1980s until today, silicon's potential to decrease the intensity of many diseases is now known for a large number of plant species.

Silicon can alleviate plant disease through (a) preventing pathogen penetration via structural reinforcement [2, 16], (b) through antimicrobial compound or biochemical production [17, 18, 19, 20], as well as (d) through increasing plant resistance by activating multiple signaling pathways and defense-related gene expression [21, 22]. In other words the beneficial effects of Si with regard to plant resistance to disease are attributed to Si accumulation in epidermal tissue, the formation of complexes with organic compounds in cell walls, the induction of phenolic compounds, phytoalexin/glucanase/peroxidase production, and regulating pathogenicity or stress-related gene expression to limit pathogen invasion and colonization [23]. Though a lot of research has been done in the application of silicon in plant disease control, the exact mechanism by which silicon acts is still a big question. Several authors have suggested different mode of action of silicon [24, 25, 26, 27].

Hence in this review the author after exhaustive study of the subject has given below some of the diseases managed by silicon application (Table 1) and the most appropriate mode of action of silicon.

Silicon a remedy to plant diseases

Plant diseases have been a major threat to agricultural production as they caused serious loss of crop yield and quality. Numerous studies have reported the effectiveness of Si in controlling diseases caused by fungal bacterial and viral pathogens in different plant species [17, 28]. The beneficial effect of Si was reported to reduce disease intensity, initially in monocots, including grasses or Poaceae, in the 60s [29]. In rice, it was associated with lower incidence and severity of rice blast, brown spot and sheath blight [30, 31, 32]. It was associated with rust (*Puccinia melanocephala*) in sugarcane [33], control of *Blumeria graminis* f. sp. *tritici* in wheat [34] and control of *Erysiphe graminis* in barley [35]. Then, promising results in reducing disease intensity were found in various pathosystems, also in dicots, including cercospora leaf spot and rust in coffee [36, 37], pestalotiopsis leaf spot and powdery mildew in strawberry [38], powdery mildew in melon, squash and cucumber [39, 7], rust in soybean [40, 41], anthracnose in common-bean and sorghum [14, 42] and root rot in tomato and avocado [43]. Some of the other diseases managed by silicon are tabulated below (Table 1).

Table 1: Effects of silicon on plant disease

Hosts	Diseases	Pathogens	Reference
Arabidopsis	Powdery mildew	<i>Erysiphe cichoracearum</i>	[44]
		<i>Agrobacterium tumefaciens</i>	[45, 22]
Banana	Black sigatoka	<i>Mycosphaerella fijiensis</i>	[46]
	Fusarium wilt	<i>Fusarium oxysporum</i> f. sp. <i>cubense</i>	[19]
	Root rot	<i>Cylindrocladium spathiphylli</i>	[47]
	Xanthomonas wilt	<i>Xanthomonas campestris</i>	[48]
Barley	Powdery mildew	<i>Blumeria graminis</i>	[49]
Bean	Angular leaf spot	<i>Pseudocercospora griseola</i>	[28]
Belle pepper	Phytophthora blight	<i>Phytophthora capsici</i>	[50]
Bent grass	Dollar spot	<i>Sclerotinia homoeocarpa</i>	[51, 52]
Bitter gourd	Powdery mildew	<i>Erysiphe</i> sp.	[53]
Capsicum	Anthracnose	<i>Colletotrichum gloeosporioides</i>	[54]
Cherry	Fruit decay	<i>Penicillium expansum</i> ,	[55]
Chinese cantaloupe	Fusarium root rot	<i>Fusarium</i> spp.	[56]
	Postharvest pink rot	<i>Trichothecium roseum</i>	[57]
Coffee	Leaf rust	<i>Hemileia vastatrix</i>	[37]
	Root-knot Nematode	<i>Meloidogyne exigua</i>	[58]
Common bean	Anthracnose	<i>Colletotrichum lindemuthianum</i>	[14, 16]
Cotton	Fusarium wilt	<i>Fusarium oxysporum</i> f. sp. <i>vasinfectum</i>	[59]
Creeping, turf grass	Brown patch	<i>Rhizoctonia solani</i>	[51, 52]
Cucumber	Crown and root rot	<i>Pythium ultimum</i>	[60]
	Fusarium wilt	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i>	[61]
	Powdery mildew	<i>Sphaerotheca fuliginea</i> , <i>Podosphaera xanthii</i>	[39, 62, 63, 64]
Gerbera daisy	Powdery mildew	<i>Erysiphe cichoracearum</i> , <i>Podosphaera fusca</i>	[65]
Hami melons	Decay	<i>Alternaria alternate</i> ,	[66]
Lettuce	Downy mildew	<i>Bremia lactucae</i>	[67]
Melon	Bacterial fruit blotch	<i>Acidovorax citrulli</i>	[68]
	Powdery mildew	<i>Podosphaera xanthii</i>	[69]
Muskmelon	Pink rot disease	<i>Trichothecium roseum</i>	[70]
	Powdery mildew	<i>Sphaerotheca fuliginea</i>	[62]
Oil palm	Basal stem rot	<i>Ganoderma boninense</i>	[71]
Pea	Brown spot	<i>Mycosphaerella pinodes</i>	[72]
Pearl millet	Downy mildew	<i>Sclerospora graminicola</i>	[73]
Perennial ryegrass	Fusarium patch	<i>Microdochium nivale</i>	[74]
	Gray leaf spot	<i>Magnaporthe oryzae</i>	[75]

Potato	Dry rot	<i>Fusarium sulphureum</i>	[76]
Pumpkin	Powdery mildew	<i>Podosphaera xanthii</i>	[77]
Rice	Blast	<i>Pyricularia oryzae</i> ,	[78]
		<i>Magnaporthe grisea</i> , <i>Magnaporthe oryzae</i>	[9]
	Brown spot	<i>Bipolaris oryzae</i> ,	[69, 83]
		<i>Cochliobolusmiyabeanus</i>	[32, 84]
	Grain discoloration	<i>Bipolaris oryzae</i>	[32]
	Leaf scald	<i>Monographella albescens</i> ,	[85]
		<i>Microdochium oryzae</i>	[86]
	Sheath blight	<i>Rhizoctonia solani</i>	[87, 88]
Rose	Powdery mildew	<i>Podosphaera pannosa</i>	[13]
Sorghum	Anthracnose	<i>Colletotrichum sublineolum</i>	[42]
Soybean	Phytophthora stem and root rot	<i>Phytophthora sojae</i>	[89]
	Rust	<i>Phakopsora sp</i>	[90]
St. Augustine grass	Gray leaf spot	<i>Magnaporthe grisea</i>	[91]
Strawberry	Powdery mildew	<i>Sphaerotheca aphans</i>	[38]
Sugarcane	Brown rust	<i>Puccinia melanocephala</i>	[92]
Tall fescue	Brown patch	<i>Rhizoctonia solani</i>	[93]
Tobacco	Viral infection	Tobacco ringspot virus	[94]
		Tobacco mosaic virus	[94]
	Bacterial speck	<i>Pseudomonas syringae</i>	[95]
	Bacterial wilt	<i>Ralstonia solanacearum</i>	[96, 21]
	Fusarium crown and root rot	<i>Fusarium oxysporum f. sp radices-lycopersici</i>	[97]
Tomato, bitter gourd	Root rot	<i>Pythium aphanidermatum</i>	[98]
Wheat	Blast	<i>Pyricularia grisea</i>	[99]
	Leaf blast	<i>Pyricularia oryzae</i>	[100]
	Leaf streak	<i>Xanthomonas translucens</i>	[58]
	Powdery mildew	<i>Blumeria graminis</i>	[101, 102, 103]
	Spot blotch	<i>Bipolaris sorokiniana</i>	[104]
Zucchini squash	Powdery mildew	<i>Erysiphe cichoracearum</i> ,	[62]

Mode of action of silicon in controlling plant diseases

Physical Mechanisms

The initial theory concerning the mode of action of Si in plants prophylaxis involved a mechanical barrier against penetration. The hypothesis of the physical barrier was proposed and supported by [105] who reported the existence of a silica layer about 2.5 mm thick below the cuticle of the leaves of rice and said the second layer formed by Si on the cuticle could prevent penetration of *M. grisea* and thus reduce damage on the leaves of the plant. Mechanical protection of plants caused by Si, a notable example of the protection of plants against pathogens due to Si acting as a physical barrier is the pathosystem rice-*Magnaporthe grisea*, wherein the increase in resistance has been associated with the density of silicified cells present in the epidermis of the leaves, which act as a physical barrier to prevent penetration of the fungus [18]. 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 has shown a great potential in controlling diseases by inhibiting or delaying the growth and development of the mycelium of the pathogen [106, 107] due to silicon deposition at infection sites and hyphae [108]. However, as early as 1965, the mechanical barrier theory was put into doubt by [109], citing [110] results of non-correlation between Si treatment and leaf toughness as measured by a needle-puncture method, from this result it seemed that Si protected the plants against disease, but the increase in mechanical toughness of the plant tissue resulting from absorbed Si is not sufficient to explain the mechanism of protection. Nevertheless, this theory was maintained over the years [9] investigated some of the cytological features that may be associated with resistance to pathogen attack provided by Si and observed that the thickness of the epidermal cell wall was not significantly affected by the presence of Si, but the

relationship between the thickness of the silica layer and the thickness of the epidermal cell wall was much higher in a cultivar which was identified as resistant than in one identified as susceptible. Si application strongly inhibited spore germination, germ tube formation and development of appressoria and possibly the penetration of fungi was hindered. It was hypothesized that Si inhibits fungal disease by physically inhibiting fungal penetration peg dispersion of the epidermis [111, 38, 112]. Upon foliar application Si was translocated laterally through the leaf and surrounded the appressoria. 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 [113]. Although these authors concluded that fortification of epidermal cell walls could be the main cause of the reduction of injuries sustained in the leaves by pathogen attack, they did not assume that this was sufficient evidence to explain the impediment of fungal penetration in the leaves. In its upward movement, via the apoplast, from the roots to the leaves, silicon undergoes polymerization in the extracellular spaces of the walls of leaf epidermal cells and xylem vessels [8, 35]. Upon the observation of Si accumulation in papillae stated that polymerized Si at attempted sites of penetration may provide an additional mean of resistance against penetration. Polymerization of potassium silicate on the leaf surface of cucumber, melon and pumpkin was also observed by [62] who reported that this physical barrier reduced the penetration of the fungus *Sphaerotheca fuliginea*. Powdery mildew infected leaf cells of silicate treated plants exhibited extensive silica polymerization enhancing the thickness against the fungi in the halo region surrounding the site of fungal penetration [39]. In general it is believed that the beneficial effects of Si on plant growth is attributed to improved overall mechanical strength and an outer protective layer [11, 2, 114]. Silicon-enhanced resistance is associated with the density of silicified

long and short epidermal cells, the thick layer of silica under the cuticle, the double cuticular layer, the thickened Sicellulose membrane, formation of papilla, and complexes formed with organic compounds in epidermal cell walls that strengthen plants mechanically [24]. Si is absorbed in roots, in the form of monosilicic acid, and is transported passively through transpiration stream and deposited beneath the cuticle, forming a cuticle-silica double layer [115]. Silicon accumulation when deposited beneath the cuticle forming a cuticle-Si double layer prevents pathogen penetration, thereby decreasing disease incidence [3, 116]. According to [9], this double layer delayed penetration of *Pyricularia grisea* in rice leaves. The physical barriers inhibit pathogen penetration and make plant cells less susceptible to enzymatic degradation caused by fungal pathogen [18, 20]. Most Si is cross-linked with hemicellulose in cell walls, which improves mechanical properties and regeneration [117, 118]. In primary cell walls, Si interacts with cell-wall constituents such as pectins and polyphenols, which increase cell-wall elasticity during extension growth [119]. Besides the reinforcement of cell walls by Si, the formation of papillae has also been stimulated by Si during pathogen infection. Silicon accumulation was found to occur in the haustorial neck and collar area of the fungus as well as in papillae, which contributed to preventing pathogen invasion [120, 121] demonstrated that Si, which is deposited in the wax, cuticle, and cell wall, as well as papillae, contributes in part to increased physical resistance against pathogen penetration. Silicon fertilization was reported to have significantly reduced the occurrence of blast in rice plants [122, 123]. The degree of resistance increased in proportion to the amount of silicon accumulated in the plants [124, 125]. From these results it was suggested that resistance to *M. grisea* in plants treated with Si is much more complex than a physical resistance to penetration due to the silicification of the cells or the double layer of Si formed in the cuticle [18]. It has also been found that the trichome bases on the epidermis tend to become silicified changing their morphology against infections [126, 127, 60]. Si deposition in leaf hairs suppressed the fungal penetration as a result of increased density and length [128]. Penetration peg incursion was found to be constrained by rapid Si deposition at the external openings like stomata of the leaves [57]. A fast silicification at intercellular spaces, cuticle layer [38] and along the space between the exocarp and mesocarp made it more difficult for pathogen penetration and dispersion [57]. Altered surface morphology of the host cell walls was observed adjacent to the germinating hyphae [126]. 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 [129]. Although these authors concluded that fortification of epidermal cell walls could be the main cause of the reduction of injuries sustained in the leaves by pathogen attack, they did not assume that this was sufficient evidence to explain the impediment of fungal penetration in the leaves.

In case of bacterial pathogens, the effect of silicon is considered to be a deposition of silicon on cell walls acting as a physical barrier making bacteria penetration difficult [23]. In a study on of *P. syringae* pv. *syringae* and mango plants, silicon gel failed to reduce the bacterial populations on plant tissues, but it reduced disease levels, suggesting a non-

bactericidal mode of action of this compound [130]. These authors proposed that the accumulation of absorbed silicon in the epidermal tissue forms a physical barrier preventing the entry of *P. syringae* pv. *syringae* into mango plants.

In case of virus diseases [94] noticed that the foliar accumulation of silicon may be part of a defense response in tobacco to *Tobacco ringspot virus*. Later [131, 132] found that silicon application to cucumber plants significantly reduced the severity of *Papaya ring spot virus* by mechanically preventing its accumulation in leaves.

Biochemical Mechanisms

Silicon-enhanced biochemical resistance is associated with (a) increasing the activity of enzymes, such as polyphenoloxidase, glucanase, peroxidase, and phenylalanine ammonia-lyase (PAL) (b) inducing antimicrobial compounds production, such as phenolic, flavonoids, phytoalexins and pathogenesis-related (PR) proteins in plants and (c) regulating systemic signals, such as salicylic acid (SA), jasmonic acid (JA), and ethylene [24]. Antimicrobial compounds help higher plants to combat disease, Si has been reported to stimulate the activity of these compounds during plant-pathogen interactions [17, 18, 20]. Generally, lower disease incidence in plants after Si application is associated with the production and accumulation of antimicrobial compounds, such as phenols, flavonoids, phytoalexins, and PR proteins in plants after pathogen penetration [79, 133]. Si application can induce the production the antifungal compounds after the penetration of pathogens and its entry into the epidermal cell [68, 79, 133]. Si supply could increase the total concentration of soluble phenolic compounds in host plants and enhance plant disease resistance through delaying the growth of invading pathogens [69, 134]. Si application not only increased production of phenolic compounds, phytoalexins and lignin it also increased the activity of enzymes such as chitinases and beta-1, 3 glucanases. Several studies showed that lower disease severity in the Si-treated plants was in line with higher activity of protective enzymes (POD, PPO and PAL) in leaves of rice [80], wheat [135] and cucumber [64, 60], these enzymes has important role in regulating the production of accumulation of antifungal compounds such as phenolic metabolism product (lignin), phytoalexins and pathogenesis-related proteins in plants. It was demonstrated that Si treatment resulted in the increase of flavonoid phytoalexin in cucumber plants infected by powdery mildew (*Podosphaera xanthii*) [63]. antimicrobial phenols or lignin-associated polyphenolic compounds increased by Si resulted from the induced activities of PAL and PPO following pathogen invasion [75]. Si enhanced lignin and flavonoid production is attributed to higher PAL activity induced by Si. PAL converts L-phenylalanine into trans-cinnamic acid, which in turn is the precursor of lignin and flavonoids [136, 137]. The higher PAL activity after Si treatment contributed to an accumulation of total soluble phenolic and lignin-thioglycolic acid derivatives in the leaves of banana and coffee plants, and this corresponded with low disease incidence [58, 19]. Polyphenol oxidase (PPO), which mainly exists in cytoplasm in a free form or bound in chloroplasts, mitochondria, and other subcellular organelles, is the main enzyme of phenolic substance oxidation and its activity has been positively correlated with Si application [138]. Several studies have reported the role of Si in increasing activity of enzymes such as chitinase, peroxidases, polyphenoloxidases, b-1,3-glucanase, phenylalanine ammonia-lyase, dismutase, ascorbate peroxidase, glutathione reductase, catalase,

lipoxygenase, and glucanase and PAL, involved in the synthesis of plant secondary antimicrobial substances that is essential for plant disease resistance responses [139]. Furthermore, PPO was found to be involved in the synthesis of lignin and to increase the antibacterial ability of host plants [140]. Si application could also increase peroxidase (POD) and chitinase (CHT) activities, which play important roles in host-pathogen interactions. POD is involved in cell-wall reinforcement and the final steps of lignin biosynthesis, as well as the cross-linking of cell-wall proteins [141], while CHT is one of the PR proteins that contribute to hydrolyze the cell walls of many phytopathogenic fungi [142, 143]. Si also enhanced JA-inducible responses to herbivory in rice [144]. Si enhanced lignin and flavonoid production is attributed to higher PAL activity induced by Si. Another study reported that Si-induced resistance to blast (*M. grisea*) in rice was related to the production of phytoalexin(s), which were mainly momilactones A and B. Si can increase the production lignin-carbohydrate complexes in the cell wall of rice epidermal cells [145]. The application of Si to rose increased the concentration of antimicrobial flavonoids and phenolic compounds in response to inoculation with *Podosphaera pannosa* (causal agent of downy mildew of rose), simultaneously, there was the expression of genes that encode key enzymes in the pathway of phenylpropanoids (phenylalanine ammonia lyase, cinnamyl alcohol dehydrogenase and chalcone synthase) [13]. Studies on cucumber leaves treated with Si showed that the resistance to infection may be involved in the expression of the gene encoding proline-rich protein (PRP1) [146]. In cells of the root of cucumber plants, Si presented a rapid and extensive increase in electron density caused by the presence of phenolic compounds and antifungal activity against the pathogen *Pythium ultimum* which attacks the root [147] as well as an increase in the activity of chitinase, peroxidases and polyphenoloxidase in the tissues of cucumber plants. In addition, extracts of plant tissues treated with Si in the presence of *P. ultimum* showed a marked increase in the concentration of antifungal phenolics [60, 72] reported an increased activity of chitinase and β -1,3-glucanase in pea seeds inoculated with potassium silicate in plants that had been previously inoculated with *Mycosphaerella pinodes*. Other research in wheat [34] and rice [79] has indicated that this element is capable of increasing the production of glycosylated phenols and antimicrobial products such as diterpenoid phytoalexins [148].

In case of bacterial pathogens soluble silicon in plant tissue may be associated with an increase in resistance to diseases [68, 140]. One of the reason for resistance is the increased activity of enzymes and chemicals. Studies demonstrating the suppressive effect of silicon on bacterial pathogens make it evident that the role of biochemical response was more important than physical defense [140, 149] found that the decreased soluble sugar content in rice leaves applied with silicon increased field resistance to bacterial blight (*X. oryzae* pv. *oryza*). Enhanced β -1,3-glucanase, exochitinase and endochitinase activities in rice plants supplied with silicon decreased the intensity of *X. oryzae* pv. *Oryza* [150, 140] found that the total concentrations of soluble phenolics and lignin, and activities of polyphenoloxidase and phenylalanine ammonia-lyase in rice leaves were higher in the plants treated with silicon in case of bacterial blight. Moreover symptoms in rice plants treated with silicon, increased phenylalanine ammonia-lyase *Pal* transcription, and inhibited catalase *CatA*

expression in the earlier and later stages of bacterial inoculation respectively. In the pathosystem of *R. solanacearum* and tomato plants [151], observed that silicon induced changes in the pectic polysaccharide structure in the cell walls of tomato plants after infection with *R. solanacearum* [152]. Observed that the enhanced concentrations of total protein, catalase, ascorbate peroxidase, and chitinase decreased the severity of *R. solanacearum* on sweet pepper plants treated with calcium silicate. Increased chitinase activity and tissue lignification, and probably peroxidase activity with the highest concentration of the total soluble phenolics and lignin thioglycolic acid derivatives in silicon treated wheat plants decreased the severity of leaf streak [58]. In the pathosystem of *X. citri* subsp. *malvacearum* and cotton plants [153], found that decreased levels of angular leaf spot in plants treated with silicon were due to enhanced accumulation of soluble proteins, superoxide dismutase, ascorbate peroxidase, guaiacol-peroxidase, phenylalanine ammonia-lyase and β -1,3-glucanase, and reduced levels of H₂O₂. Higher levels of polyphenol oxidase and ascorbate peroxidase in melon plants supplied with silicon decreased the severity of bacterial blotch by *citruilli* [68]. Hence biochemical changes induced by silicon plays an important role in developing resistance against pathogens.

Some studies have described the joint action of physical barrier and biochemical changes [80]. Discussed that the reduction in severity of rice diseases such as rice blast, by Si, is a complex process which is not limited to the formation of passive mechanical barriers, deposition and polymerization of Si below the cuticle, or the induction of biochemical reactions (production of phenolic compounds), but results from the combined action of these two mechanisms. Sorghum leaves inoculated with *Colletotrichum sublineolum* and supplemented with Si showed high Si deposition on infection sites and fewer and smaller acervuli compared with the non-treated leaves, in addition, there was a higher concentration peroxidases and polyphenol, and anthocyanin in Si-treated leaves [42, 39] Found a rapid accumulation of silica deposit on the leaves of cucumber as well as deposit of phenolic compounds in a large number of cells of plants of cucumber amended with Si and inoculated with *S. fuliginea*. Biochemical analysis of the extracts of the leaves of the plant inoculated with the pathogen indicated the presence of flavonoids and phenolic acids which were specifically and strongly induced in a pattern typical of phytoalexins [63]. These findings support the theory that the resistance provided by Si to pathogen attack cannot be attributed solely to the presence of Si in the cell walls of the epidermal cells [146]. Have reported that during the induction of systemic acquired resistance (SAR) in cucumber, the expression of a gene encoding a novel proline-rich protein was enhanced. This protein has C-terminal repetitive sequences containing an unusually high amount of lysine and arginine. The synthetic peptide derived from the repetitive sequences was able to polymerize orthosilicic acid to insoluble silica, which is known to be involved in cell wall reinforcement, at the site of the attempted penetration of fungi into epidermal cells. This study provided a mechanical and biochemical basis of Si-enhanced resistance to diseases. It is believed that the induction of resistance to plants by silicon is as a result of phenolics and phytoalexins accumulation and is related to the activity of P-R genes [12, 154] investigated the ultrastructural changes of the rice-*M. grisea* interaction upon silicon application, which provided the first cytological evidence that

silicon-mediated resistant to *M. grisea* was related with the deposition of the osmophilic material that occluded the epidermal cells. These amorphous materials contain phenolic compounds which play a crucial role in rice defence response against infection by *M. grisea* [79], further hypothesized that the alteration of the development of *M. grisea* in leaf tissue of rice plant amended with silicon was not only because of development of a physical barrier but also due to enhanced production of phytoalexins. It is also possible that in certain areas of heavy silicon deposition, delayed fungal ingress and colonization provide the rice plant enough time for synthesizing the antifungal compounds in response to infection by *M. grisea* to accumulate considerable levels and to express their fungi toxicity within the zone of the infection site.

By Activating Plant Defence Reaction

Activating plant defence reaction and production of biochemicals are inter-related [8]. Suggested a model to explain how Si would play a role in induced resistance. According to their model, Si bioactivity was compared to that of known activators/secondary messengers of systemic acquired resistance (SAR) whereby it would act as a modulator influencing the timing and extent of plant defense responses. Like secondary messengers, the effects of Si on secondary metabolism are significant only after elicitation. Both Si and known activators are characterized by a saturable effect. A difference between known SAR activators and Si is the loss of activity when Si feeding is interrupted, because polymerization of Si leads to its inactivation as an inducer of resistance. Thus Si acts as a signal in inducing defense responses. Silicic acid may modulate the activity of post-elicitation intracellular signaling systems [155]. Has distinguished three classes of active defense mechanisms. The primary response occurs in cells infected by the pathogen, the secondary response is induced by elicitors and limited to cells adjacent to the initial infection site, and the systemic acquired response is transmitted hormonally to all tissues of the plant. Silicon is perhaps acting in the primary response, and the integration of enhanced signal transduction at the single cell level that should result in increased levels of induced systemic resistance. Post-elicitation intracellular signaling leads to the expression of defense genes directing hypersensitive response, structural modifications of cell walls, and synthesis of stress hormones, antimicrobial compounds and PR proteins. In a given cell, if Si modulates the signaling events leading to the synthesis of antimicrobial compounds, it should also modulate the generation of systemic signals given that both processes depend on primary elicitation. Accordingly, silicic acid, without being itself a secondary messenger, could play a positive role in both local and systemic resistance [17]. The target of plant signaling upon pathogen elicitation is the cell nucleus, which receives information for de novo protein and antimicrobial compounds synthesis [17]. Gene expression control through the phosphorylation of transcription factors and their inhibitors is a major plant stress response. Signals leading to the expression of plant defense responses are transmitted to the nucleus through the activation of specific kinases/phosphatases cascades. This can be generalized to both endogenous [156, 157, 158] and exogenous [159] signaling events. Responses to biotic stresses are largely dependent on mitogen activated protein (MAP) kinases [160, 161, 162, 163]. Protein kinases transmit information to the nucleus by the phosphorylation of hydroxyl group on amino acid residues.

Silicon is known to bind to hydroxyl groups and may thus affect protein activity or conformation. The mode of action of Si in signal transduction may also derive from interactions with phosphorus. As early as 1906 [164], reported interactions between Si and phosphorus in barley. It is now considered that the internal improvement of P utilization and the broadening of P fertilization range is provided by Si fertilization [165] and is derived from interactions with cationic metals such as Mn and Fe [166]. Silicon-fed plants will naturally translocate silicic acid throughout the tissues. Upon pathogen attack, the infected tissue will synthesize, among other defense reactions, antimicrobial compounds together with systemic stress signals such as salicylic acid, jasmonic acid and ethylene [44]. Reported that once absorbed by the plant, Si operates as a mediator of defense reactions and can control the activity of cell signaling systems. Si is a bioactive element in different biological systems, this element has been shown to increase the expression of the natural defense mechanisms of plants and the accumulation of phytoalexins in monocots and dicots [24]. The results reported for Si indicate that it may be acting locally through the induction of defense reactions and may also be contributing to systemic resistance through an increase in the production of stress hormones [25]. However, the exact mechanism by which Si operates signaling in plants is still unclear. The evidence has shown that Si could act as an enhancer of the defense responses of plants or as an activator of protein-mediated cell signaling, implying that Si may interact with many key components of stress signaling systems in plants and direct induced resistance against fungal pathogens. Silicon could negate many transcriptional changes induced by pathogen infection, for example, Arabidopsis infected with the fungus *Erysiphe cichoracearum* resulted in alteration of the expression of a set of nearly 4000 genes, whereas the number or expression level of up-regulated genes, which are defense-related, were not changed compared to Si-treated plants, while the magnitude of the down-regulated genes, which are involved in primary metabolism, were attenuated when treated with Si [17]. In wheat plants infected with *Blumeria graminis* f. sp. tritici, about 900 genes responding to pathogen infection were altered in control leaves, while few genes were changed by the pathogen in Si-supplied plants, suggesting that Si almost eliminated the stress imposed by the pathogen invasion [101]. Similar findings were obtained by [82], the impact of *Magnaporthe oryzae* inoculation on the transcriptome of rice was diminished by Si application. Therefore, rather than inducing resistance by transcriptional reprogramming of defense-related genes, Si seems to eliminate the impact of pathogen infection on the transcriptome of host plants, probably through preventing the exploitation of pathogen virulence factors [84]. Defense-related enzyme activities induced by Si may regulate gene expression related to enzyme synthesis, for example the expression of genes encoding phenylalanine ammonia-lyase (PALa and PALb) and lipoxygenase (LOXa) were significantly up-regulated in Si-treated perennial ryegrass plants, associated with suppression of gray leaf spot [75]. Si could elevate the activities of defense-related enzymes (e.g., peroxidase and polyphenol oxidase) via enhancing or priming JA-inducible responses to herbivory in rice [144]. Several studies have suggested that Si may regulate plant stress responses by modulating phytohormone homeostasis and signaling pathways [167, 96, 168]. Si was also found to regulate wound-induced JA biosynthesis [169]. In Si-treated Arabidopsis plants infected with powdery mildew

pathogen (*Erysiphe cichoracearum*), the biosynthesis of SA, JA, and ET in leaves were stimulated, leading to increased resistance [45]. Similarly, tomato infected with *Ralstonia solanacearum* showed that Si triggers activation of the JA and ET signaling pathways [170, 167, 96]. The stimulating effects of Si on the JA and ET signaling pathways in rice challenged with *Magnaporthe oryzae* demonstrate that the Si-mediated signaling pathway is critical for enhancing rice resistance to blast disease [171, 172, 82]. Silicon is involved in the metabolic processes of plant-pathogen interaction, activating defense genes of host plants via a series of physiological and biochemical reactions and signal transductions, as well as inducing the resistance response in plants to prevent plant diseases [17, 22]. Transcriptomic and proteomic studies have been conducted to illustrate the defense responses of Si in various pathosystems [173, 96, 174]. Si could induce tomato resistance to *Ralstonia solanacearum* via upregulating the expression of genes involved in defense and stress responses, such as WRKY1 transcription factor, disease resistance response protein, ferritin, late embryogenesis abundant protein, and trehalose phosphatase [96]. Similar result have been found in tomato stems of rhizobacteria and silicon treated-tomato genotypes upon inoculation with *R. solanacearum* compared to the non-treated, pathogen inoculated control, in which most of the up-regulated genes are involved in signal transduction, defense, protein synthesis and metabolism, while a large proportion of down regulated genes were involved in photosynthesis, lipid metabolism [175]. Hence it is clear from the above studies that Si activates the defense mechanisms of plants, but the exact nature of the interaction between this element and the biochemical pathways that direct resistance still remains unclear.

Conclusion

Although many treatments are reported to induce resistance against plant pathogens, there are very few strategies that induce broad-spectrum disease resistance. Silicon is one of the only exceptions, rendering plants more resistant towards a wide range of abiotic and biotic stresses. Undoubtedly, silicon can contribute a great deal in reducing the intensity of diseases of crop plants. Silicon is absorbed and translocated and can be found at the infection sites forming both physical and biochemical resistance barriers and also inducing defence. Silicon, in the form of silicic acid, would act locally by inducing defense reactions in elicited cells and would also contribute to systemic resistance by enhancing the production of stress hormones. From the gathered evidence, Si could act as a physical and biochemical barrier and also act as a potentiator of plant defense responses. Thus knowing its effects, it can be included in disease management plans, not as the only method able to solve all pest problems, but as an important component of the integrated pest management.

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