REVIEW

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J. Mycopathol. Res. 60(4) : *515-521, 2022;*
ISSN 0971-3719

J. Mycopathol. Res. **60(4)** : 515-521, 2022; (ISSN 0971-3719)

doi:10.57023/JMycR.60.4.2022.515

REVIEW

Silicon fertilizers inciting plant defence against pathogenic fungi

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Received : 17.08.2022 Accepted : 10.10.2022 Published : 26.12.2022

Silicon (Si) is the second most abundant element on earth's crust after oxygen. It is present abundantly in the soil and is taken up by plant root in the form of silicic acid. It is most prevalent in plants of Gramineae and Cyperaceae families. A number of translocators such as LSi1, LSi2, and LSi6 are involved in Si uptake by root and its translocation in shoot. Si generally helps the plants to combat against a number of biotic and abiotic stresses. It plays an effective role in plant defence by enhancing resistance against diseases and pests. In this review an extensive study has been carried out to evaluate the role of Si in plant defence against pathogenic fungi. Si can induce resistance against pathogenic fungi through formation of physical barriers that can inhibit the fungal penetration. Si can also trigger biochemical defence by activating systemic signals like SA, JA or ET inside the plant cells. This post elicitation intercellular signalling system causes expression of defence related genes leading to hypersensitive response, structural modifications of cell wall, synthesis of antimicrobial substances like phytoalexins, defence related enzymes, phenolics and PR proteins. Application of Silicon fertilizers as soil treatment or foliar spray are found to be effective in controlling a number of plant diseases caused by fungi in the field and thus they can be used as an alternative to chemical synthetic fungicides. This study indicates the positive role of Si in plant defence response and also emphasizes on the eco-friendly approach of using silicon in plant disease management.

Key words : Disease management, fungal pathogen, plant defence, silicon fertilizer

INTRODUCTION

Silicon being the second most abundant element on the earth's crust after oxygen (Ma and Yamaji, 2006) comprises up to 70% of soil mass. It rarely occurs as a pure element but is found mainly as its oxides , silica and silicate. Although silicon is abundantly present in soil, but onlyin the form of monosilicic acid [$Si(OH)_4$] is taken up by the plants roots (Ma and Yamaji, 2006).

Several studies have shown the beneficial effects of Si in plants, especially in Gramineous plants such as rice, sugarcane and also in some plants of Cyperaceae (Liang *et al.* 2005).

Si improves the mechanical as well as physiological properties of plants and helps in overcoming several biotic and abiotic stresses (Richmond and Sussman, 2003; Ma, 2004; Fauteux *et al*. 2005; Ma and Yamaji, 2006; Tripathi *et al*.2020). Several studies revealed that Si is effective in enhancing the resistance to diseases and pests. In this review the role of Si in plant defence and application of Si fertilizer in the field against plant pathogenic fungi has been discussed. The physical and biochemical mechanisms involved in disease resistance have also been elucidated.

HOW DO PLANTS UPTAKE, TRANSLOCATE AND ACCUMULATE SILICON ?

Si uptake

In soil Si is available for plants in the form of uncharged monomeric monosilicic acidin neutral pH (Sommer *et al*. 2006). Recently it has been noticed that alkaline pH may lead to decrease in

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plant available Si, given an increase in adsorption of Si on mineral rich surfaces (Haynes and Zhao, 2018). The study of Si mobility in soil-plant systems is very essential for optimizing its benefits towards plant protection.Plants take up monosilicic acid and transport it from the roots to the shoots and when the concentration is over a critical level (approximately 100 ppm at biological pH) it gets polymerized as opalinephytoliths(Jones and Handreck, 1967)which constitutes the bulk of a plant's Si content. Plant species differ with respect to their size and shape of the phytoliths that they accumulate.Si uptake in vascular plants is quite complicated due to the selectivity of transporters and accumulation in specific tissues.Low Silicon 1 or Lsi1 was the first influx Si transporter identified from Rice (Ma *et al*. 2006) .The Lsi1 gene is expressed constitutively in the root. The site of Si uptake in plants is near the mature region of the roots and not in the root tips (Yamaji and Ma 2007).Lsi1 is found in the main and lateral roots but not in the root hairs (Ma *et al*. 2001). The Lsi1 transporter protein is found in both exodermis and endodermis where the Casparian strips are present. Following the Lsi1 identification in rice, Si influx transporters are identified in maize (ZmLsi1) and barley (HvLsi1) (Chiba *et al*. 2009; Mitani *et al*. 2009).

Lsi2 is the efflux transporter gene of Si that was cloned using a novel rice mutant (Ma *et al*. 2007). In contrast to the Si influx transporter Lsi1, Lsi2 is an efflux transporter of Si that is capable of transporting Si out from the cells and similar to that of Lsi1, Lsi2 is also localized at the exodermis and the endodermis cells of the roots. Both Lsi1 and Lsi2 are essential for the transcellular transport of Si to the stele (Vaculik *et al*. 2020). In rice, Si is transported by Lsi1 into the endodermis cells and by Lsi2 the Si is released into the stele. Lsi1 thus facilitates the passive transport of Si from the external environment to the plant cell and Lsi2 mediates the loading of Si into the xylem of stele for root to shoot translocation.

Si Translocation

Si , after being transported to the stele by Lsi1 and Lsi2 , is translocated to the shoot through xylem. A transporter Lsi6 has been observed that is involved in exporting silicic acid from the xylem to the shoot for translocation.Lsi6 is expressed in theadaxial side of xylem parenchyma of leaf sheath, leaf blades and root tips unlike Lsi1 and Lsi2 (Yamaji *et al*.2008).

Si Accumulation

Si deposition in the shoots varies from 0.1% to 10% in dry weight (Ma and Takahashi, 2002). In an experiment it is observed that plants of Gramineae and Cyperaceae show a high accumulation of Si, whereas plants that belong to Cucurbitales, Urticales, and Commelinaceae show intermediate Si accumulation and most other plants species show low accumulation of Si. This difference in Si accumulation in plants depend on the ability of the roots to take up Si from soil .In the shoot due to water loss by transpiration, Si gets transformed into amorphous Si by polymerization. The amorphous Si is accumulated in the cell walls of leaves and stem (Ma and Yamaji, 2006). Si can also be deposited in cells of roots, tubers and inflorescence of certain plant species (Lux *et al*. 2011; Chandler-Ezell *et al.* 2006).

MECHANISMS OF SI MEDIATED RESISTANCE IN PLANTS AGAINST FUNGAL PATHOGENS

Several studies revealed that Si is effective in enhancing resistance to diseases against plant pathogens and pests. This review highlights an extensive role of Si in plant defence against phyto-pathogenic fungi and the physical and biochemical mechanisms involved in disease resistance have been elucidated.

Physical mechanism

Silicon acts as a physical barrier against plant fungal infections in the form of cell wall rigidity and reinforcement, papillae formation and callose deposition.Si provides mechanical strength to a plant by enhancing its resistance through silicification of the epidermal cells, double cuticular layer formation, deposition of silica under the cuticle, papilla formation, and deposition of complex organic compounds in epidermal cell walls. These physical barriers inhibit fungal penetration and make plant cells less susceptible to enzymatic degradation caused by fungal infection (Fauteux *et al*.2005; Datnoff *et al.* 2007).

Si also stimulates papillae formation during pathogen infection. Si accumulation occurred in the haustorial neck and collar area of fungus as well as in the papillae which prevents the invasion of the pathogen. Shetty *et al*. (2012) observed that Si supply increased the number of papillae in the leaf cells of rose when infected by *Podosphaera pannosa*. The formation of papillae after application of Si increased the resistance of rice against blast disease (Cai *et al*. 2008). During the infection of barley by *Blumeria graminis f. sp. hordei*, application of Si enhanced the deposition of callose and phenolics causing the formation of effective papillae and thus inhibiting the fungal growth by trapping the penetration peg inside the papillae (Chowdhury *et al*. 2014).

Biochemical defence mechanism

Si activates plant defence by enhancing various biochemical mechanisms. This includes induction of defence related enzyme activities such as polyphenoloxidase (PPO), glucanase, peroxidise (POX), and phenylalanine ammonia-lyase (PAL), increasing the production of antimicrobial compounds such as phenolics, flavonoids, phytoalexins and pathogenesis related (PR) proteins, induction of ROS production and antioxidative metabolism and upregulating several defense signalling pathways mediated by salicylic acid (SA), jasmonic acid (JA) and ethylene signalling (ET) (Fauteux *et al*., 2005; Datnoff *et al*., 2007; Fortunato *et al.,* 2012; Van Bockhaven *et al.,* 2013).

Signal Transduction Cascade Triggered by Si

Plants fed with Si, naturally translocate silicic acid throughout all tissues. Upon pathogen attack, these infected tissues synthesize antimicrobial compounds and other defense reactions along with systemic stress signals such as salicylic acid (SA), jasmonic acid (JA) and ethlylene (ET). Silicic acid is said to modulate the post-elicitation intercellular signalling system activities. Silicic acid being a secondary messenger itself, plays a positive role in both systemic and local resistance. The post-elicitation intracellular signalling causes the expression of defense genes leading to hypersensitive responses, structural modifications of the cell wall, synthesis of stress hormones, synthesis of antimicrobial compounds such as phytoalexins and PR proteins.The signalling pathways mediated by SA, JA and ET play an important role in Si induced defense responses in plants. In powdery mildew infection of *Arabidopsis*, Si increased the expressions of EDS1, EDS5,PAD4and SID2 genes which can regulate SA biosynthesis (Shah, 2003). Li *et al*. (2004) observed that Si induced higher expressions of the EDS1 and PAD4 genes along with NPR1 and three pathogenesis related defense genes PR1, PR2 and PR5 in *Arabidopsis*. The regulatory protein NPR1 triggered the activation of PR gene expression in response to SA and NPR1 itself got positively regulated by some SA inducible WRKY proteins whose activity was enhanced by Si application. A certain correlation observed in the increase of the level of endogenous SA and subsequent defence expressions by Si treatment (Durrant and Dong, 2004; Kurabachew *et al.*2013).

There are also earlier reports that Si induces expression of several defense responses in plants by JA signalling pathway (Johnson *et al.* 2021). JA also promotes leaf silicificationand maturation of phytolith bearing silica cells by increasing the Si accumulation (Fauteux *et al.,* 2006; Ye *et al.,* 2013). Dreher and Callis (2007) observed that application of Si in plants after pathogen attack, activated the defense signalling pathway by up regulation of ubiquitin protein ligase which is involved indegradation of the JA negative regulator JAZ1 domain.In the ET and JA signalling pathway associated marker genes, JERF3, TSRF1 and ACCO are important in view of disease resistance. The transcription factor JERF3 activates the defence response of ET and JA signalling pathways, while ACCO helps in ethylene biosynthesis and TSRF1 involves in activation of ET-responsive transcription factor (Pirrello *et al.* 2012). In tomato plants it was observed that the application of Si upregulated the expression of JERF3, TSRF1 and ACCO genes supporting the fact that Si induced resistance is mediated via ET and JA signalling pathways (Ghareeb *et al.*2011).

Defence responses induced by Si against fungal pathogens

A common defence mechanism initiated by Si against biotic stress is production of ROS and enhanced antioxidant metabolism (Vanbockhaven *et al*. 2013). Generation of ROS and simultaneous increase in oxidative machinery help to reduce oxidative damage to the plants . ROS play an important role in triggering different defence signaling pathways mediated by JA and SA (Torres, 2010). In addition to inducing a number of plant

Table 1 : Some Examples of Si induced resistance in plants against fungal pathogens

Host	Diseases	Pathogen	Biochemical Defence response	Reference
Bean	Anthracnose	*Colletotrichum lindemuthianum*	SOD, APOX, GR	Polanco *et al.*2014
Cucumber	Crown and root rot	*Pythium spp.*	Chitinases, POX, PPO	
Melon	Pink rot	*Trichothecium roseum*	POX	Bi *et al*. 2006
	Powdery mildew	*Podosphaera xanthii*	Chitinases, SOD, β-1,3 Glucanase	Dallagnol *et al.*2015
Chinese Cantaloupe	Pink rot	*Trichothecium roseum*	POX, PAL	Guo *et al.*2007
Pea	Leaf spot	*Mycosphaerella pinodes*	Chitinase, β-1,3-glucanase	Dann and Muir, 2002
Perennial Ryegrass	Gray leaf spot	*Magnaporthe oryzae*	POX, PPO	Rahman *et al.*2015
Rice	Blast	*Magnaportha oryzae*	Glucanase, POX, PPO, PAL	Domiciano *et al.* 2015
	Brown spot	Bip*olaris oryzae*	Chitinase, POX	Dallagnol *et al.*2011
	Sheath blight	*Rhizoctonia solani*	PO, PPO, PAL , chitinases	Schurt *et al.*2014
Soybean	Target spot	*Corynespora cassiicola*	Chitinases, β-1-3-glucanases, PAL, oxidases	Fortunato *et al.* 2015
Wheat	Blast	*Pyricularia oryzae*	Chitinases, POX	Filha *et al.*2011

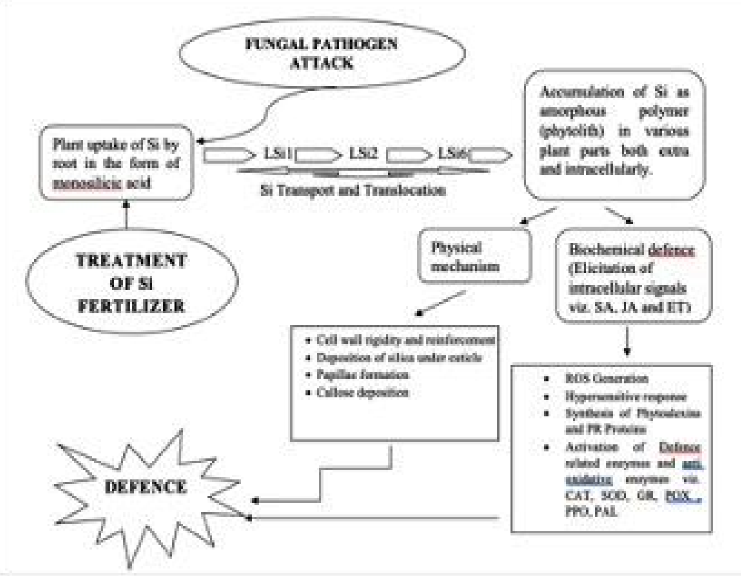

Fig.1.: Mechanism of Induction of resistance against fungal pathogens by application of Si fertilizer.

gene expression, resulting in the accumulation of defence related compounds, ROS may also stimulate antioxidative enzymes such as Catalase (CAT), superoxide dismutase (SOD), peroxidises (POX), Glutathione reductase (GR) and Ascorbate peroxidase (APOX) in response to Si treatment in plants (Thoma *et al*. 2003). Gulzar *et al*. (2021) reported that Silicon treatment can confer resistance against early blight in tomato by modulating the expression of defense-related genes and antioxidant enzymes.There are earlier reports thatwhen subjected to biotic stress,Si induced the activity of defence related enzymes namely, chitinases , POX , PPO, β-1,3-glucanase, PAL and lipoxygenases (LOX) (Table 1).Si has been found to be associated with expression of genes involved in defence related enzyme synthesis (Rahaman *et al.* 2015) .

APPLICATION OF SILICON FERTILIZER FOR INDUCTION OF DISEASE RESISTANCE

Silicon constitutes about 28% of the total earth crust (Singer and Munns, 1987, Epstein, 1991). Si in the soil reacts with oxygen to produce silicates and alumina silicates that form the chief component of rocks. Monosilicic acid is released from the rock by the process of weathering and absorbed by plant root in soluble form (Verma *et al*. 2021). However due to extensive weathering and repeated cropping, the amount of Si has been found to be decreasing in available forms to plants grown in the soil of tropical and subtropical region (Rodrigues *et al*. 2005). Besides, low solubility of silicon compounds (as SiO_2, up to 70% of the soil mass) in the soil as monosilicates does not dissolve below pH 9, is another reason of unavailability of Si for plant uptake (Rizwan *et al*. 2012). So Silicon fertilization is a better alternative to increase the level of soil silicon content. Two main sources of available silicon in the form of solid and liquid have been used as fertilizers. Calcium silicate ($CaSiO_3$) fertilizer is the solid source which is incorporated into the soil. Potassium silicate (K_2SiO_3) or sodium silicate (Na_2SiO_3) are the liquid forms which can be applied as a soil drench or as a foliar spray (Datnoff and Heckman, 2014).The most common Ca silicate Si fertilizers are Wollastonite and slag.Wollastonite is a natural calcium silicate which is considered as most efficient Si fertilizer for soil application as higher fraction of soluble Si is released in the soil whereas calcium silicate slags are by-products of melallurgical smelting process which contain different percentages of Si (Dallagnol *et al*, 2020). It has been reported that silicate fertilizer can not only improve growth, nutrition and plant yield, but it also has a potential role to mitigate biotic stresses against pests and pathogens. There are number of reports of management of fungal plant pathogens by using silicon fertilizers in Si accumulator plants. It has been observed that uptake and accumulation of Si could activate defence mechanisms of hosts through a series of physiological and biochemical reactions and signal transduction pathways (Fig.1). Application of Si fertilizer to rice can control a number of rice diseases such as rice blast, sheath blight (Rodrigues *et al*. 2003), brown spot (Ning*et al.* 2014). Similarly in wheat, Si fertilization can initiate defence response against a number of fungal diseases of wheat viz. powdery mildew, spot blotch , tan spot , leaf blotch, Fusarium head blight (Dallagnol *et.al*. 2020). Soil application was found to be more effective than foliar spray. Besides rice and wheat, silicon fertilizers can also enhance disease resistance in other crops such as *Arabidopsis* against powdery mildew (Ghanmi *et al*. 2004), pearl millet against downy mildew (Deepak *et al*. 2008), bean against angular leaf spot (Rodrigues *et al*. 2010), strawberry against powdery mildew (Liu *et al*. 2020), melon against powdery mildew (Dallangol *et al*. 2015) , soybean against Asian rust (Arsenault-Labrecque *et al*. 2012) and rose against powdery mildew (Shetty *et al.* 2012) . Recently silica nanoparticles have been used as more bioavailable and safer agro chemical to induce systemic acquired resistance in plants (El-Shetehy *et al*. 2021).

CONCLUSION

Si can induce resistance against fungal pathogens through physical barrier formation and activation of biochemical signal transduction pathway inside the plants. Plants treated with Si, can translocate silicic acid and trigger systemic signals like SA, JA or ET inside the plant cells that can finally induce defence responses.Silicon fertilizers are found to be moreeffectively appliedby soil treatment or foliar spray for fungal plant disease management and thus it can reduce the use of chemical fungicides in the agricultural field. Potential use of eco-friendly and cost effective silicon fertilizers to control fungal plant pathogens can open up a new avenue in the field of integrated plant disease management worldwide

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