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Popular Article

Role of Silicon in inducing fungal disease resistance in Rice

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Abstract

Rice is being consumed by many countries as a staple food, but simultaneously it encounters serious threats from various insect pests and diseases, which leads to its reduced production globally. Nevertheless, rice exhibits exceptional silicon accumulation, conferring resistance to various pathogens and alleviating both biotic and abiotic stresses. Silicon (Si), is the second most abundant element present in earth's crust after oxygen, comprising about 28% of the total composition and accounting for up to 70% of soil mass. Si enhances plant mechanical and physiological traits, aiding in the mitigation of abiotic stresses like metal toxicity, drought, and salt stress. The most important mechanism of Silicon that induces disease resistance in rice and other crop plants comprises of physical Mechanism (formation of double-layered cuticle, enhanced cell wall rigidity), biochemical mechanism (activation of defense-related enzymes, and the production of antimicrobial compounds) and Molecular mechanism (regulation of transcriptomics, proteomics, and the regulation of systemic signaling). Numerous studies conducted, highlight the importance of silicon in improving plant resistance against innumerable fungal, bacterial, and viral diseases. This article focuses on the significant role of Si in rice disease management through the induction of host resistance. Furthermore, this article calls for attention to explore the role of Si as an innovative strategy for more robust and resilient crop production to sustain the ever-growing population worldwide.

Keywords: Silicon, Fungal diseases, Resistance, Mechanism, Management, rice

Introduction

Rice is a primary staple food in many countries and is renowned for its role as a principal provider of both energy and protein. However, rice faces significant threats from pests and pathogens, resulting in substantial annual losses. Fortunately, rice possesses the remarkable capacity to accumulate silicon, enhancing its resistance to diverse pathogens and mitigating abiotic and biotic stresses. Silicon, a key plant nutrient, is a tetravalent metalloid with efficient binding properties. Interestingly, silicon rank second in term of abundance in the earth's crust after oxygen, making up around 28% of the total composition and accounting for up to 70% of soil mass. Typical soil silicon concentrations range from 14 to 20 mg. Si uptake takes place as two aqueous silicate species, *viz.*, monosilicic acid (H_4SiO_4) and some disilicic acid through roots (Epstein, 2009). These compounds move through two silicon transporters *viz.*, Lsi1 and Lsi2 which are influx and efflux transporter, respectively. Once inside the plant, Si is primarily deposited in the cell wall. However, Si absorption faces little competition, mainly from germanium due to their similar transporter affinity (Rains *et al*., 2006). Si content varies between plant species, subspecies, and growth stages. Its concentration in the shoot can range from 0.1% to 10% on a dry-weight basis. The translocation of Si also varies from roots to shoots among different species of plants. Monocots accumulate around 5-7% Si in their shoots, while dicots typically contain only about 0.5%. After deposition, silicon benefits various plant species, especially grasses like rice and sugarcane. It's also environmentally friendly and complements existing disease management methods. This article explores the pivotal role of silicon in enhancing host resistance and its potential in plant disease management, with a particular focus on its application in rice disease management.

Benefits of Silicon

Plant pathogens pose a major threat to crop production rendering huge losses every year. Although the use of chemicals to combat such pathogens is inevitable, conventional methods come with a price as it has been observed that they negatively affect the environment as well as the farmer’s economy. Hence, the pursuit of alternatives should always be a constant consideration. The result of such dedicated efforts is the discovery of the role of silicon in Plant health. Si enhances plant mechanical and physiological traits, aiding in the mitigation of abiotic stresses like metal toxicity, drought, and salt stress. Moreover, it aids plants in mitigating biotic constraints like pathogens (fungi, bacteria, viruses, etc.), and pest attacks (Fig. 1).

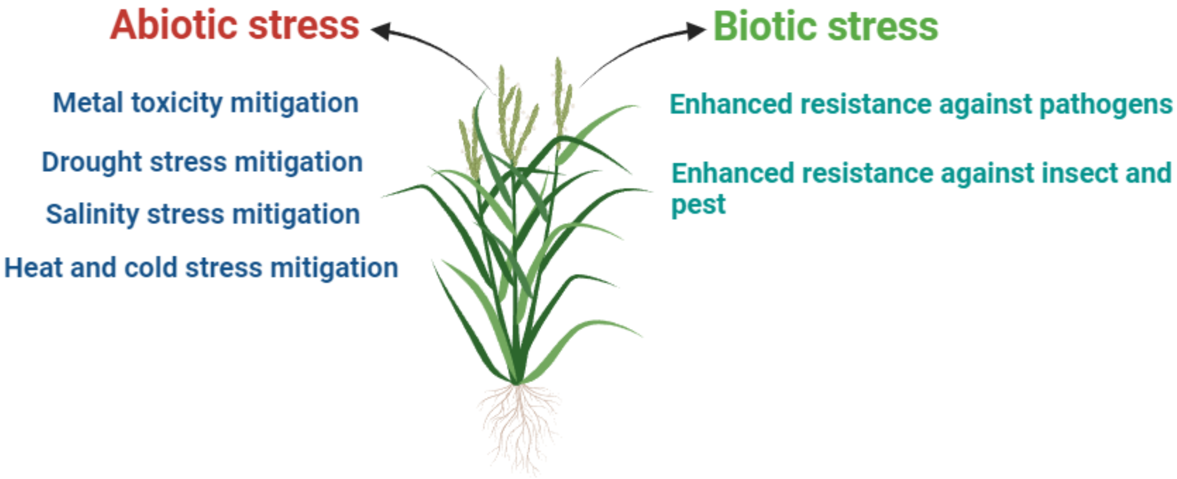

Figure 1 Benefits of silicon in plant

Role of silicon against plant pathogens

Si holds significant potential in reducing disease severity and intensity caused by various pathogens, including fungi, oomycetes, bacteria, viruses, and nematodes. Through studies of numerous host-pathogen interactions, it became evident that silicon positively affected critical components of the pathogen, *viz.*, the colony size, incubation period, inoculum production per infection site, latent period, lesion number, and expansion, resulting in decreased final disease severity (Fortunato *et al.*, 2014). The influence of silicon on various aspects of pathogens provides an explanation for the enhanced resilience of previously susceptible plant varieties.

Table 1 Successful example of silicon-mediated control of phytopathogens

Crop: pathogen	**Remarks**	**References**
Rice- *Pyricularia Oryzae*	Reduce the number of infection pegs	Abed-Ashtiani *et al.*, 2012
Rice-*Monographella albescens, R.solani*	Epidermal cell silicification delays fungal penetration, colonization, and sporulation	Rodrigues *et al.*, 2015
Oat-*Blumeria graminis* f. sp. *avenae*	Silicification of epidermal cell walls reduces penetration	Carver *et al.*, 1998
Wheat- *B. sorokiniana, P. oryzae*	Phenolics and flavonoids	Cruz *et al.*, 2015
French bean & cowpea- *Uromyces vignae*	Accumulation of Si resulted in increased hydroxyproline-rich glycoproteins phenolics in leaves that reduced haustoria numbers.	Perumalla *et al.*, 1991
Banana-*F.oxysporum* f. sp. *Cubense*	Elevated levels of lignin, flavonoids, dopamine, and phenolics were observed in sclerenchyma cells, metaxylem, and phloem vessels of roots.	Fortunato *et al.*, 2014

Silicone-induced resistance in rice

Currently, there is widespread recognition of rice's exceptional ability to accumulate silicon, with its Si accumulation surpassing 10% of the shoot dry weight. This exceeds the Si uptake compared to vital macronutrients such as N, P, and K by several folds (Ma and Takahashi, 2001). This miraculous gift endowed on the rice plant potentiates it to develop resistance against a number of important diseases such as rice blast (*Magnaporthe oryzae)*, stem rot (*Magnaporthe salvinii*), sheath blight (*Rhizoctonia solani*), brown spot (*Cochliobolus miyabeanus*), leaf scald (*Microdochium oryzae)*, bacterial leaf blight (*Xanthomonas oryzae* pv. *oryzae)*, and nematodes (*Meloidogyne incognita*).

Mechanisms of Silicon-mediated resistance

Silicon induces resistance in rice, or any plant, through three fundamental mechanisms. Firstly, the Physical mechanism involves the formation of a double-layered cuticle, enhanced cell wall rigidity, and the development of papillae. Secondly, the biochemical mechanism encompasses the activation of defense-related enzymes and antimicrobial compound production. Thirdly, the Molecular mechanism includes the regulation of transcriptomics, proteomics, and the regulation of systemic signaling.

Physical mechanism

Based on our fundamental knowledge, for a successful infection, a pathogen must breach the plant's physical barriers *viz.,* cell walls, cuticles, and wax to enter the plant system. Si strengthens such barriers and hence prevents the entry of pathogens (Fig. 2). Hence, the positive impacts of silicon on plants can be attributed to the enhanced mechanical strength and the reinforcement of their protective outer layer. Plant mechanical strength is reinforced by factors such as silicified epidermal cell density, thick cuticle layers, Si-cellulose membrane thickening, papillae formation, and organic compound complexes in cell walls. This makes the plant resistant to enzymatic degradation by fungal pathogens which is achieved through silicon's remarkable capacity to cross-link with hemicellulose, enhancing mechanical strength and regenerative capabilities (He *et al.*,2015). In addition, silicon also enhances the elasticity of the cell wall by associating with pectin and polyphenol constituents of the primary cell wall. A good example of conferred resistance through physical mechanism is of rice plant against *Pyricularia oryzae* which failed to penetrate its hyphae inside the host system, and this is mainly due to epidermal cell wall fortification (Kim *et al.,* 2002). Silicon accumulation and polymerization beneath the cuticle, inside the bulliform cells, and within the cell wall may also account for the diminished severity of rice blast. A similar result was obtained in wheat against *Bipolaris sarokiana* (Domiciano *et al.*, 2013). Furthermore, Si treatment significantly stimulates the formation of papillae, as seen in the case of barley epidermal cells post-infection of *Blumeria graminis* f.sp. *hordei.*

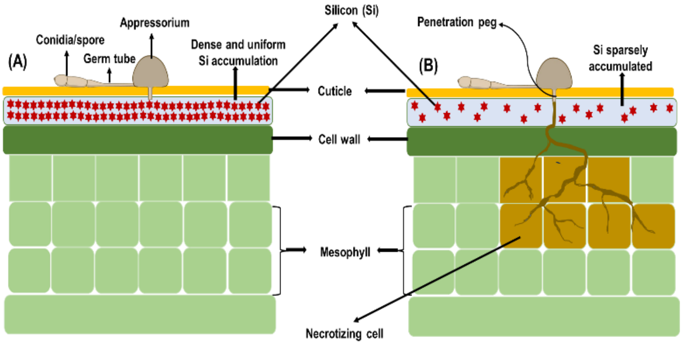

Figure 2 Silicon deposition confers resistance to plant against the pathogen (A), whereas less uniform and low silicon content leads to disease (B)

Biochemical Defence Mechanism

A supply of Silicon increases the activity of defense-related enzymes, such as polyphenol oxidase (PPO), glucanase, superoxide dismutase, chitinases, *β*-1,3-glucanase**,** ascorbate peroxidase, peroxidase (POD), glutathione synthase, catalase, phenylalanine ammonia-lyase (PAL), and lipoxygenase (LOX). These enzymes are further implicated in the production of antimicrobial compounds such as pathogenesis-related (PR), phenolic, phytoalexins, etc. PAL aids in phenolic and lignin-acid compound synthesis, seen in banana and coffee plants for resistance. PPO is responsible for oxidizing phenolics and making lignin for plant defense (Quarta *et al*., 2013). POD plays a role in reinforcing cell walls, participating in the end stages of lignin production, and facilitating the cross-linking of cell wall proteins. Chitinase, categorized as a pathogenesis-related (PR) protein, is responsible for the enzymatic breakdown of the cell walls of pathogenic fungi. The heightened activities of defense-related enzymes induced by silicon treatment may also influence the regulation of gene expression associated with enzyme production. For example, the upregulation of genes encoding lipoxygenase (LOXa) and phenylalanine ammonia-lyase (PALa and PALb) in perennial ryegrass suppressed gray leaf spot (Rahman *et al*., 2015). Also, systemic signals, such as SA, JA, and ethylene, key for triggering resistance have been found to be activated by Si treatment. (Van *et al*., 2013). Some examples where enzyme production triggered by Si application led to disease resistance are listed in Table 2.

Table 2 Silicon-induced activation of defense-related enzymes

Diseases	**Pathogen defense-related enzymes**	**Reference**
Blast (*Magnaporthe oryzae*)	Peroxidase, ascorbate peroxidase, superoxide dismutase, catalase, lipoxygenase, glucanase, polyphenol oxidase, phenylalanine ammonia-lyase, and glutathione reductase.	Domiciano *et al*., 2015
Brown Spot (*Bipolaris oryzae*)	Peroxidase and Chitinase	Dallagnol *et al*., 2011
Sheath blight (*Rhizoctonia solani*)	Peroxidase, chitinase, Phenylalanine ammonia-lyase, and polyphenol oxidase	Schurt *et al*., 2014

Molecular mechanism

Si plays a crucial role in plant-pathogen interactions by activating host plant genes through physiological and biochemical reactions, signal transduction, and inducing disease responses to prevent plant diseases. Si may influence both primary and post-elicitation intracellular signaling, regulating defense gene expression. The molecular mechanism can be further divided into two *viz.*, transcriptomic regulation and proteomic regulation in response.

Transcriptomic regulation in response to silicon

The transcriptomic regulation in rice in response to Si-induced resistance involves a complex interplay of genetic responses, with numerous genes being upregulated or downregulated to support enhanced plant defense mechanisms. For instance, certain genes related to defense-related compound synthesis, such as phenolic compounds, lignin, and antimicrobial proteins, may be upregulated. At the same time, the expression of genes associated with the reactive oxygen species (ROS) production and other reactive molecules involved in pathogen defense may also be influenced. Moreover, the transcriptomic response may involve changes in the expression of genes linked to the regulation of hormonal pathways. In particular, genes encoding for the salicylic acid (SA), jasmonic acid (JA), and ethylene pathways, which are crucial in plant defense responses, may show altered expression patterns in response to silicon treatment. These changes in hormonal regulation can contribute to the defense mechanism activation and the overall resistance of the plant to pathogens (Brunings *et al*., 2009).

Proteomics regulation in response to silicon

Silicon-induced proteomic changes can encompass various aspects, including the upregulation or downregulation of specific proteins related to defense mechanisms. For example, proteins involved in the synthesis of antimicrobial compounds, enzymes responsible for the breakdown of pathogenic cell walls, and those associated with ROS generation may experience altered expression. Additionally, silicon treatment may affect the protein abundance involved in signal transduction pathways. Proteins linked to hormonal pathways, such as salicylic acid (SA), jasmonic acid (JA), and ethylene, may show changes in expression patterns. These alterations can contribute to the activation of defense-related proteins and pathways. Furthermore, Si-induced proteomic changes can provide insights into the plant's metabolic responses. Alterations in the abundance of proteins involved in various metabolic pathways, such as energy production and secondary metabolite synthesis, can influence the plant's overall resistance. In 2014, Min Liu and colleagues conducted a study showing that applying 2.0 mM silicon reduced rice blast diseases by 35% in terms of blast incidence and 55.3% in disease index. They used a proteomic approach to understand how silicon enhances rice resistance to *Magnaporthe oryzae*. Their research revealed an increase in both soluble and total protein content in the leaves of rice. Using two-dimensional gel electrophoresis (2-DE), they identified 143 protein spots, of which 73 were significantly altered, with their abundance exceeding 1.5 times. Through liquid chromatography-mass spectrometry, they identified 61 of these proteins (Liu *et al.*, 2014).

Conclusion

Silicon plays a versatile role in enhancing plant defense mechanisms against both biotic and abiotic stress. It enhances disease resistance against fungi, bacteria, and other pests, while also aiding plants in coping with abiotic stresses like metal toxicity, salinity, and drought. The decrease in symptom expression is due to silicon's positive influence on multiple aspects of host resistance. The disease severity reduction achieved with Si amendments can rival the effectiveness of fungicides. Moreover, susceptible plant cultivars fortified with silicon may attain a level of resistance comparable to cultivars with race-specific resistance. Si primarily induces resistance by acting as a physical barrier, through processes like polymerization and silicification beneath the cuticle and within the epidermal cell wall. Additionally, silicon triggers biochemical resistance, activating defense-related enzymes, antimicrobial compounds, and hormones. Recent findings show that silicon supplementation in many plant species enhances the phenylpropanoid and terpenoid pathways, leading to increased transcription of defense-related genes and heightened activity of defense enzymes. At the molecular level, Si can control gene expression related to defense responses at both transcriptomic and proteomic levels. It greatly enhances antioxidant metabolism, aiding in the removal of reactive oxygen species, and it promotes more efficient photosynthesis. Future research may further elucidate more detail into the molecular mechanisms involved, paving the way for innovative strategies to optimize silicon utilization for even more robust and resilient crop production.

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