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Unlocking the role of silicon against biotic stress in plants

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The requirement for agricultural crops continues to enhance with the continuous growth of the human population globally. Plant pathogenic diseases outbreaks are enhancing and threatening food security and safety for the vulnerable in different regions worldwide. Silicon (Si) is considered a non-essential element for plant growth. It regulates the biological functions, plant development and productivity, and balance the defense mechanism in response to fungal, bacterial and pest attacks. The optimum crop yield can be achieved by applying Si in agricultural systems through different methods to replace or minimize the use of synthetic fertilizers. This approach can be effective on crop production during limited resources, extreme climates, pests and diseases, and environmental pollution. Silicon can be applied as foliar spray, priming of seeds, soil water irrigation, soil amendment and soilless medium (hydroponic) to enhance plant performance and stress tolerance capacity during stress conditions. This article summarized the effective roles of Si and the ability to perform in agroecosystems for better crop production, food security and safety for sustainable agriculture in the future.

KEYWORDS

pathogenic diseases, disease tolerance efficiency and management, crop productivity, plant nutrition, silicon

Introduction

Silicon (Si) has a brittle crystalline structure with enormous application in biological sciences. Si finds a second position in the abundance of the earth's crust (Verma et al., 2023a, b). Due to its affinity towards oxygen (Verma et al., 2019), Si forms two oxides, silica (SiO₂) and silicon monoxide (SiO), as the SiO bond is unusually strong. The average Si

content in normal soil is very high, i.e., 28% (weight basis). Soil carries silicon dioxide, silicate minerals, and aluminosilicates are not available to plants through their uptake process. The uptake and accumulation of Si depends on the variety of crop plants, soil properties, sources and concentration of Si *in planta*. Si content can vary from 0.1 to 10% (dry weight basis) near the detection limit (Coskun et al., 2019; Verma et al., 2020a, b; 2023a). Monosilicic acid is soluble in water and adsorbed by plant roots (Matichenkov and Calvert, 2002; Verma et al., 2020c; Paton, 2023).

Interestingly, the concentration of plant-accessible Si exceeds the phosphorus in the soil solution. Different factors, including pH, water status, temperature, and accompanying ions, influence Si availability in the rhizospheric soil (Bityutskii et al., 2019; Verma et al., 2020d, e). Specific soil types, such as extensively weathered acidic soil and calcareous paddy soil, may experience Si deficiency. Si can be detected in nearly all land-dwelling plant species but in different concentrations range. Some plant species have optimum Si accumulation capacity, while most have relatively low levels (Verma et al., 2020f; Hernandez-Apaolaza, 2022).

Plant diseases negatively impact plants' growth, development and food grain quality. It is a severe problem for sustainable agriculture and food security. Unsuitable agricultural approaches are degrading the atmospheric environmental variables and facing population pressure due to less crop productivity as required (Verma et al., 2021a, b). Si was reported to enhance the defense system against biotic stresses occurring in the form of plant pathogens, such as fungi, insects, weeds, bacteria and viruses or animals, i.e., vertebrates and arthropod herbivores. The deposition of Si upregulated the abrasiveness of plant tissues and thus reduced palatability and digestibility for herbivores (Massey and Hartley, 2009; Luyckx et al., 2017). The physical strength of the leaf resulting from the accumulation of Si can afford mechanical protection and control the frequency and severity of the infection (Zhang et al., 2013; Ning et al., 2014; Song et al., 2021). The postulation of potential physical obstruction formation is based on the type of Si deposition in foliage, especially in the cell wall. Si in the plant cell wall and apoplast protects pathogen penetration (Luyckx et al., 2017; Gulzar et al., 2021). Recent demonstrations have shown that the biochemical mechanisms of Si compared to physical mechanisms play a significant role in enhancing plant tolerance efficiency during pathogenic diseases (Song et al., 2016, 2021).

The current global scenario presents humanity with an alarming level of hunger, primarily driven by rapid population pressure. Unfortunately, the limited availability of inadequate resources is incapable to fulfilling the demand of food (Verma et al., 2021c, d). The era of climate change is a significant obstacle to achieving sustainable agricultural productivity (Verma et al., 2024). However, biotic stress adds to the challenges faced by plant production systems worldwide, and a transition towards environmentally friendly approaches is necessary (Kumari et al., 2022; 2023; Verma et al., 2022a, b, c). Si offers a natural defense system against various insects and pathogens by strengthening plant tissues, inducing the production of defense compounds, and activating systemic defense

responses. Si significantly reduce the reliance on synthetic pesticides, i.e., nematicides (Santos et al., 2022).

This review thoroughly discussed how Si mitigates biotic stress in plants. It provides technical and theoretical knowledge, and action of defense mechanisms on Si-based strategies to enhance plant resilience and productivity in adverse climatic conditions. It aims to understand how plants acquire and allocate Si in plant parts during biotic stress.

Impact of biotic stress on plant development

Pathogenic diseases have significant implications for plant growth, development and crop protection. Fungal pathogens invade plant tissues, causing diseases, such as rust and powdery mildew, which cause wilting and reduce crop productivity and quality. Similarly, bacterial and viral pathogens release toxins that induce symptoms like wilting and rotting, disrupting plant cell processes, impeding nutrient absorption, and stunting plant growth (Muthu et al., 2022). Insects and pests damage plant tissues and downregulate plant growth and photosynthetic CO₂ assimilation rate. These biotic stresses compromise photosynthesis, nutrient absorption, and plant defense mechanisms, making plants more vulnerable to secondary infections. Different plant species possess some specific action mechanisms for the uptake and accumulation of Si in other plant parts during stress conditions.

Role of Si on insects, pests, and weeds infection

In natural ecosystems, plant communities coexist with plant-feeding insects. However, agricultural productivity is directly damaged in agricultural systems by attacks from pathogens, pests, and weeds (Al-Gaashani et al., 2023). The impact of pest attacks on plants is observed by their effect on yield, which refers to the amount of economically viable product per unit area. Insect pests pose a significant threat to crops for human and animal consumption, directly damaging plants. In agri-systems, direct losses caused by pathogens and weeds account for a significant portion of the reduction in global crop production (Sharma et al., 2017; El-Ramady et al., 2022). Wheat and cotton were particularly susceptible, with potential losses exceeding 80%. Rice is affected by more than 800 insect species, resulting in actual losses of nearly 40% worldwide. In India, yield loss (21-50%) was observed in the rice by insect pests attack (Fahad et al., 2019). In wheat, actual losses of more than 30% worldwide (Jasrotia et al., 2021). Substantial yield loss was also observed in sorghum by pest challenges, such as *Atherigona soccata Rondani* and stem borer (Table 1).

Rapeseed-mustard crops damage from pests, like mustard aphids, leading to yield losses (35-73%) in India (Tyczewska et al., 2018). Leguminous crops, like chickpeas and pigeon peas are affected by various pests, which result in considerable yield

TABLE 1 Potential of Si against biotic stress mitigation strategies.

Crop	Pathogen	Response	Source
Pumpkin (<i>Cucurbita pepo</i> L. Howden)	<i>Podosphaera xanthii</i>	Reduce powdery mildew disease and increase crop productivity, soil nutritional efficiency and uptake and accumulation of silicon	Lepolu Torlon et al., 2016
Bitter gourd (<i>Momordica charantia</i> L.)	<i>Erysiphe</i> sp.	Suppress disease severity and upregulate enzymatic activities, i.e., POD, PPO and pathogenesis-related genes, chitinase and β -1,3-glucanase.	Ratnayake et al., 2016
Chili pepper (<i>Capsicum annuum</i> 'Muria F ₁)	<i>Colletotrichum gloeosporioides</i>	No significant impacts on plant development and fruit/flowering quality. Cell wall-bound phenolic compounds and thickness of cuticle were increased by the application of Si.	Jayawardana et al., 2015
Melon (<i>Cucumis melo</i> L.)	<i>Acidovorax citrulli</i>	Improved plant nutritional status, and minimize the bacterial fruit blotch disease	Conceiaco et al., 2014; Ferreira et al., 2015
Tomato (<i>Solanum lycopersicum</i>)	<i>Ralstonia solanacearum</i> , <i>Tuta absoluta</i> and <i>Colletotrichum dematium</i>	Control disease index, and enhanced Si accumulation in roots, soil bacterial content and actinomycetes and downregulate fungi/soil bacterial ratio (ca. 54%). Changes the soil microorganisms and enzymatic activities. Upregulate gene expressions in salicylic acid pathway but downregulate jasmonic acid and ethylene expression genes. Suppress disease resistance capacity. Controls leaf miner due to toxic effect of <i>Tuta absoluta</i> during larval stage.	Wang et al., 2013; dos Santos et al., 2015; Chen et al., 2015; Somapala et al., 2015
Cucumber (<i>Cucumis sativus</i> L.)	<i>Meloidogyne incognita</i>	Significantly minimize root-knot nematode activity	Dugui-Es et al., 2010
Soybean (<i>Glycine max</i> L.)		Downregulate the silver leaf white fly population	Ferreira and Moraes, 2011
Arabidopsis (<i>Arabidopsis thaliana</i> L.)	<i>Erysiphe cichoracearum</i>	Suppress disease and balance mechanical resistance capacity	Ghanmi et al., 2004
Banana (<i>Musa</i> spp. cv. Maca)	<i>Fusarium oxysporum</i> f. sp. <i>cubense</i>	Si level enhanced in the roots and reduced disease symptoms upto 27%. Lignin deposited in the roots cortex. Resist phenylpropanoid pathway during disease infection with Si application.	Fortunato et al., 2014
Banana (<i>Musa acuminata</i> L.)	<i>Cylindrocladium spathiphylli</i> and <i>Pseudocercospora fijiensis</i>	Reduced root necrosis disease and enhanced plant growth after Si-application during disease infection. The disease severity index (DSI) reduced during 21 and 35-days of pathogen inoculation.	Vermeire et al., 2011; Gbongue et al., 2019
Barley (<i>Hordeum vulgare</i> L.)	<i>Blumeria graminis</i> f. sp. <i>Hordei</i> race A6	Enhanced pathogen inoculation resistance efficiency.	Wiese et al., 2005
Bell Pepper, Sakata Hybrid Xpp 6115 (<i>Capsicum annuum</i> L.)	<i>Phytophthora capsici</i>	Enhanced Si concentration uptake in roots but not in stems during Si application on disease infected plants. Disease and relative lesion extension were downregulated and plant drymass enhanced. Si reduced the disease severity and upgrade plant growth and development.	French-Monar et al., 2010

(Continued)

TABLE 1 Continued

Crop	Pathogen	Response	Source
Carrot (<i>Daucus carota</i> L.)	<i>Pectobacterium carotovorum</i> pv. <i>carotovorum</i>	Enhanced plant development, photosynthetic pigments, dry weight during pathogenic inoculated plants with Si application.	Siddiqui et al., 2020
Coffee (<i>Coffea Arabica</i> L.)	<i>Hemileia vastatrix</i>	The more Si deposition on the plant leaves Disease severity reduced the application of Si on inoculation plants.	Carre-Missio et al., 2014
Melon (<i>Cucumis melo</i> L.)	<i>Podospaera xanthii</i>	The disease curve was minimize (65% and 73%), infection efficiency, expansion rate of colony, colony area, conidial production during foliar and root irrigation of Si application.	Dallagnol et al., 2012
Cotton (<i>Gossypium hirsutum</i> iL.)	<i>Fusarium oxysporum</i> f.sp. <i>vasinfectum</i>	Significant phenolic compounds were present in root during Si application followed by pathogenic inoculation. The lignin content in roots found higher than inoculated plants without Si. Si may affect cellular defense systems in cotton roots.	Whan et al., 2016
Asian Ginseng (<i>Panax ginseng</i> L.)	<i>Ilyonectria morspanacis</i>	Minimize disease severity, no direct effects against the pathogen. Decreased expression of <i>PgSWEET</i> leading to regulated sugar efflux into apoplast and increased resistance efficiency against applied pathogen.	Abbai et al., 2019
Oat (<i>Avena sativa</i> L.)	<i>Rhizoctonia solani</i> Kuhn	Physio-biochemical responses decreased during fungal inoculation with Si application. Si assists to protect the harmful effects caused by fungal inoculation. Disease index reduced when the fungus was applied with Si application.	Ahmad et al., 2023
Finger millet (<i>Eleusine coracana</i> Gaertn.)	<i>Sesamia inferens</i> Walker.	Si application induces the interactive action defense mechanism by upregulating the transcript level of silicon transporter genes (<i>EcLsi1</i> , <i>EcLsi2</i> and <i>EcLsi6</i>) and defense hormone regulating genes (<i>EcSAM</i> , <i>EcPAL</i> and <i>EcLOX</i>) during 72 hr of post infestation in stem and roots	Jadhao et al., 2020

losses. Forage leguminous plants such as berseem, alfalfa, and Persian clover encounter challenges from the pod borer, *H. armigera*, leading to substantial losses in seed yield. Cotton plants require the optimum amounts of insecticides compared to other crop plants. Insecticides account for a significant portion of the total expenditure in cotton production (15-42%). Cotton accounts for nearly 23% of the worldwide insecticide use (Shahrajabian et al., 2020). Various insect pests, including whiteflies, bollworms, aphids, and various sucking pests, cause yield losses (up to 82%). Bollworms have triggered yield losses before 20 years (Lashari et al., 2022).

Pest insects pose a significant damage to global food production. Much more research is available to support the idea that Si application on plants can boost resistance to insects, pests, and diseases, leading to increased crop yield (Song et al., 2021). Si deposits in monocots can act as a “mechanical barrier against

insects,” and their active role in biological resistance is now acknowledged. Si is a promoter in triggering biological resistance by generating compounds like tannic and phenolic chemicals (Tayade et al., 2022). Application of Si exhibits resistance to stalk borer damage. It was demonstrated that applying Si to maize plants reduces larval survival of the borer. Increasing the silica content and lowered larva survival efficiency (Rajput et al., 2021). An association of notable significance was discovered between the resistance of maize to the subsequent generation of *Ostrinia nubilalis* Hübnera and the Si concentration present within the sheath and collar tissues. Si in the epidermis of plant leaves can dislodge young borer larvae, hindering their establishment in the stem. It is well known that Si increases plant tissue toughness, interfering with insect larval boring and feeding. High Si content in rice plants damages the mandibles of rice stem borer larvae (Juma et al., 2015; Cabrera-Ponce et al., 2019). The physical arrangement of Si along the sheath of leaves could cause

varietal resistance to the insects. When plants attack, signaling cascades are triggered, regulating target genes by entering proteins into the nucleus. The soluble Si protects cucumbers against fungal diseases (Song et al., 2021; El-Ramady et al., 2022).

By developing physical barrier, Si deposition under leaf cuticles enhances plants' resistance to insect pests. It makes the tissue rigid and abrasive, reducing palatability and digestibility for herbivores (Nikpay et al., 2023). Differences in epidermal Si deposition among cultivars contribute to variations in resistance. Leaf abrasiveness and digestibility are influenced by spine and phytolith morphology. Si upregulates the gene expression associated with defense systems and promotes the accumulation of defensive compounds. It improves pest resistance in wheat and cucumber, and upregulates the activities of defensive enzymes. In response to pathogen infection, Si-mediated defense includes forming papilla, developing callose, and accumulating phenolic compounds. Si hinders fungal ET production, preventing suppression of the innate immune system and enhancing resistance against brown

spot disease in rice plants (Akhtar et al., 2018) (Table 2). The cell wall of fungi consists of the carbohydrates chitin and β -1,3-glucan, Si-induced chitinases, and β -1,3-glucanases enzymes can hydrolyze these compounds to oligosaccharides and, as a result, the plant's defense responses are elicited (Cruz et al., 2013). Si-enhanced tolerance to fungal diseases, there is limited information is available on the Si and bacterial disease interaction in plants (Song et al., 2016).

Silicon nanoparticles (SiNPs) have shown efficacy as pesticides with the interactive application of commercial pesticides. SiNPs are assimilated into the cuticular lipids, resulting in the physical mortality of insects (Mittal et al., 2020). Applied SiNPs with garlic essential oil has successfully managed agricultural insect pests. SiNPs can act as nano-pesticides or nanocarriers, enhancing the effectiveness of commercial pesticides. SiNPs can lead to insect mortality through desiccation and damage to the digestive system. The effects of SiNPs on pests have primarily been studied in laboratory conditions, focusing on specific pests and applied

TABLE 2 Plant pathogens and insects reported to be suppressed by Si application.

Type of pathogen and insect	Host	Pathogen	Source
Fungal	Arabidopsis (<i>Arabidopsis thaliana</i> L.)	<i>Erysiphe cichoracearum</i>	Fauteux et al., 2006; Vivancos et al., 2015
	Banana (<i>Musa</i> spp. Cv. Maca)	<i>Mycosphaerella fijiensis</i> , <i>Fusarium oxysporum</i> f. spp. <i>Cubense</i> and <i>Cylindrocladium spathiphylli</i>	Kablan et al., 2012; Fortunato et al., 2015
	Barley (<i>Hordeum vulgare</i> L.)	<i>Blumeria graminis</i>	Wiese et al., 2005
	Bean (<i>Phaseolus vulgaris</i> L.)	<i>Pseudocercospora griseola</i>	Rodrigues et al., 2010
	Pepper (<i>Capsicum annuum</i> L.)	<i>Phytophthora capsici</i>	French-Monar et al., 2010
	Bentgrass (<i>Agrostis stolonifera</i> L.)	<i>Sclerotinia homoeocarpa</i>	Zhang et al., 2006
	Bitter melon (<i>Momordica charantia</i> L.)	<i>Erysiphe</i> spp.	Ratnayake et al., 2016
	Capsicum (<i>Capsicum annuum</i> L.)	<i>Colletotrichum gloeosporioides</i>	Jayawardana et al., 2016
	Wheat (<i>Triticum aestivum</i> L.)	<i>Pyrenophora tritici-repentis</i>	Dorneles et al., 2017; Pazdiora et al., 2018
	Soybean (<i>Glycine max</i> L.)	<i>P. sojae</i>	Guerin et al., 2014; Rasoolizadeh et al., 2018
Virus	Mango (<i>Mangifera indica</i> L.)	<i>P. syringae</i> pv. <i>syringae</i>	Gutierrez-Barranquero et al., 2012
	Tobacco (<i>Nicotiana tabacum</i> L.)	<i>Tobacco ringspot virus</i>	Zellner et al., 2011
Bacterial	Banana (<i>Musa</i> spp.)	<i>Xanthomonas campestris</i>	Mburu et al., 2016
	Cotton (<i>Gossypium</i> spp.)	<i>X. citri</i> subsp. <i>Malvacearum</i>	Oliveira et al., 2012
	Melon (<i>Cucumis melo</i> L.)	<i>Acidovorax citrulli</i>	Conceição et al., 2014
	Rice (<i>Oryza sativa</i> L.)	<i>X. oryzae</i> pv. <i>oryza</i>	Song et al., 2016
	Sweet pepper (<i>Capsicum annuum</i> L.)	<i>Ralstonia solanacearum</i>	Alves et al., 2015
	Tomato (<i>Solanum lycopersicum</i> L.)	<i>Pseudomonas syringae</i> and <i>Ralstonia solanacearum</i>	Andrade et al., 2013; Chen et al., 2014; Ghareeb et al., 2011; Jiang et al., 2019
	Wheat (<i>Triticum aestivum</i> L.)	<i>X. translucens</i>	Silva et al., 2010a
Nematode	Coffee (<i>Coffea arabica</i> L.)	<i>Meloidogyne exigua</i>	Silva et al., 2010b
	Rice (<i>Oryza sativa</i> L.)	<i>M. graminicola</i>	Zhan et al., 2018

(Continued)

TABLE 2 Continued

Type of pathogen and insect	Host	Pathogen	Source
Chewing	Sugarcane (<i>Saccharum officinarum</i> L.)	<i>Diatraea saccharalis</i> , <i>Eldana saccharina</i> and <i>E. saccharina</i>	Meyer and Keeping, 2001; Keeping and Meyer, 2002, 2006
	Alfalfa (<i>Medicago truncatula</i> L.)	<i>Beet armyworm</i>	Korth et al., 2006
	Rice (<i>Oryza sativa</i> L.)	<i>Chilo suppressalis</i> (Walker) (Lepidoptera: Crambidae)	Hou and Han, 2010
	Maize (<i>Zea mays</i> L.)	<i>Busseola fusca</i>	Juma et al., 2015
	Rice (<i>Oryza sativa</i> L. Susceptible)	<i>C. medinalis</i> Guenee	Han et al., 2015
	Cabbage (<i>Brassica oleracea</i> L.)	<i>Plutella xylostella</i>	Shoaib et al., 2018
	Rice (<i>Oryza sativa</i> L.)	<i>Scirpophaga incertulas</i> and <i>S. incertulas</i> (Walker)	Jeer et al., 2017; Han et al., 2018
	Soybean (<i>Glycine max</i> L.)	<i>Helicoverpa armigera</i>	Alves et al., 2018
Sucking	Wheat (<i>Triticum aestivum</i> L.)	<i>S. graminum</i> Rond.	Basagli et al., 2003; Goussain et al., 2005
	Maize (<i>Zea mays</i> L.)	<i>Rhopalosiphum maidis</i>	Moraes et al., 2005
	Cucumber (<i>Cucumis sativus</i> L.)	(<i>Gennadius</i> spp.) (Hemiptera: Aleyrodidae)	Correa et al., 2005
	Eggplant (<i>Solanum melongena</i> L.)	Thysanoptera: Thripidae	De Almeida et al., 2008
	Tomato (<i>Solanum lycopersicum</i> L.)	Whitefly (Homoptera: Aleyrodidae)	Inbar and Gerling, 2008
	Zinnia (<i>Zinnia elegans</i> Jacq.)	<i>Myzus persicae</i> Sulzer	Ranger et al., 2009
	Bean (<i>Phaseolus vulgaris</i> L.)	<i>Tetranychus urticae</i> Koh	Gatarayiha et al., 2010
	Rice (<i>Oryza sativa</i> L.)	<i>Cnaphalocrocis medinalis</i> Guenee	Ye et al., 2013
	Wheat (<i>Triticum aestivum</i> L.)	<i>Sitobion avenae</i> (F.) (Hemiptera: Aphididae)	Dias et al., 2014
	Maize (<i>Zea mays</i> L.)	<i>R. maidis</i>	Boer et al., 2019
	Rice (<i>Oryza sativa</i> L.)	<i>C. medinalis</i>	Liu et al., 2017
	Lime (<i>Citrus latifolia</i> L.)	<i>Diaphorina citri</i>	Ramirez-Godoy et al., 2018
	Phloem Feeding	Grass species	<i>Sitobion avenae</i> .
Rice (<i>Oryza sativa</i> L.)		<i>N. lugens</i>	Yang et al., 2018

concentration. Weeds exert a harmful influence on the crop yield loss. A nano-herbicide formulation has been developed to combat weeds. It enhances the accumulation of Si in plant tissues. Nanoparticles assist for better customization, facilitating improved penetration through the plant's protective cuticle and targeted release of active ingredients. The loss in herbivore populations is notably noted in Si-accumulating and non-accumulating plants (Mathur and Srivastava, 2022; Sarraf et al., 2022; Verma et al., 2023a).

Biochemical and molecular mechanisms of Si on plants to biotic stress

Si effectively mitigates biotic stresses in plants, serving as a key player in their adaptation and survival under unfavorable

plant growth conditions. Si exerts its protective effects through various biochemical mechanisms, enabling plants to combat stresses effectively (Khan et al., 2024). It enhances the biochemical activities, i.e., peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD). The generation of reactive oxygen species (ROS) and antioxidant metabolism have been linked with bacterial and fungal infection, and in response to damage from chewing and sucking insects (Debona et al., 2014; Yang et al., 2017; Frew et al., 2018). ROS played significant roles in different signaling pathways with plant hormones (Glazebrook, 2005; Torres, 2010). However, ROS can activate plant defense genes and the associated accumulation of defense metabolites, such as phytoalexins and allelochemicals (Thoma et al., 2003).

Si plays a significant role during the uptake and translocation of nutritional elements. It enhances the absorption of essential nutrients from the rhizospheric soil, i.e., nitrogen, phosphorus,

potassium, and calcium. It affects the action of nutrient transporters and balances the nutritional efficiency. It influences hormonal signaling pathways in plants, contributing to their ability to respond to stress. It involves the synthesis, transport, and signaling of phytohormones. Si induces the production of ABA, stress hormone implied in regulating stomatal closure and stress responses (Mukarram et al., 2022; Chen et al., 2024). Si also activates JA signaling pathways for plant defense mechanisms in response to biotic stresses (Figure 1).

Biochemical and molecular functions are also induced or reinforced by Si, allowing the plant to enhance stress tolerance efficiency and include defensive compounds, i.e., phenolics, phytoalexins and momilactons, but also activate the enzymatic defensive system, like polyphenol oxidase (PPO), lipoxygenase (LPO) and phenylalanine ammonia-lyase (PAL) (Remus-Borel et al., 2005; Rahman et al., 2015; Verma et al., 2021d). Applied Si can upregulate transcript levels corresponding to defensive-related genes during stressed conditions. Si also attracts predators or parasitoids to plants in response to herbivore attacks. However, soluble Si enhances herbivore-induced plant volatiles to upregulate or maintain predator attraction by pest-infected plants. The insect's life cycle phenology is also downregulated in Si-applied plants, making it more prone to predation (Cai et al., 2008; Reynolds et al., 2016).

Si can control the stress-responsive gene expression, activating pathways that enhance plant tolerance efficiency. It upregulates stress-responsive transcription factors (SRTFs), heat shock proteins (HSPs), and pathogenesis-related proteins (Song et al., 2021; Mir et al., 2022). The modulation of gene expression, Si plays a

significant role in triggering stress signaling pathways, facilitating the establishment of stress tolerance in plants (Figure 1). It promotes the accumulation of osmoprotectants, which are organic compounds that help to maintain cellular osmotic balance and protect against osmotic stress (Shomali et al., 2022, 2024). Subsequent solutes, such as sugars, proline, betaine, and glycine, accumulate in higher concentrations in Si-treated plants. These osmolytes act as osmoprotectants, maintaining cell turgor and stabilizing macromolecules, ultimately contributing to stress resilience (Song et al., 2021).

The application of transcriptomic strategies, i.e., microarrays alongside more targeted assays such as real-time quantitative PCR (qPCR) are critical in developing an understanding of how Si impacts the expression of plant genes. The pathogenic infection enhanced defense genes and reduced primary metabolism genes, but following the use of Si reduced genes were not as severely impacted, while they found limited information to suggest an impact of Si without pathogen stress (Fauteux et al., 2006). The application of Si nearly eradicated the effects of pathogen stress on the plant transcriptome. Some transcriptomic research work has been reported, limited research has assessed the impact of Si on enhanced plant resistance efficiency to insect herbivores. However, further studies on the interactions of Si with the transcriptome of a variety of crop plants varying in their Si uptake and accumulation ability, like accumulators, non-accumulators under different forms of insect herbivory, such as chewers, suckers should provide valuable insight into how Si changes plant gene expression in response to insect stressors (Chain et al., 2009; Bockhaven et al., 2015) (Figure 1).

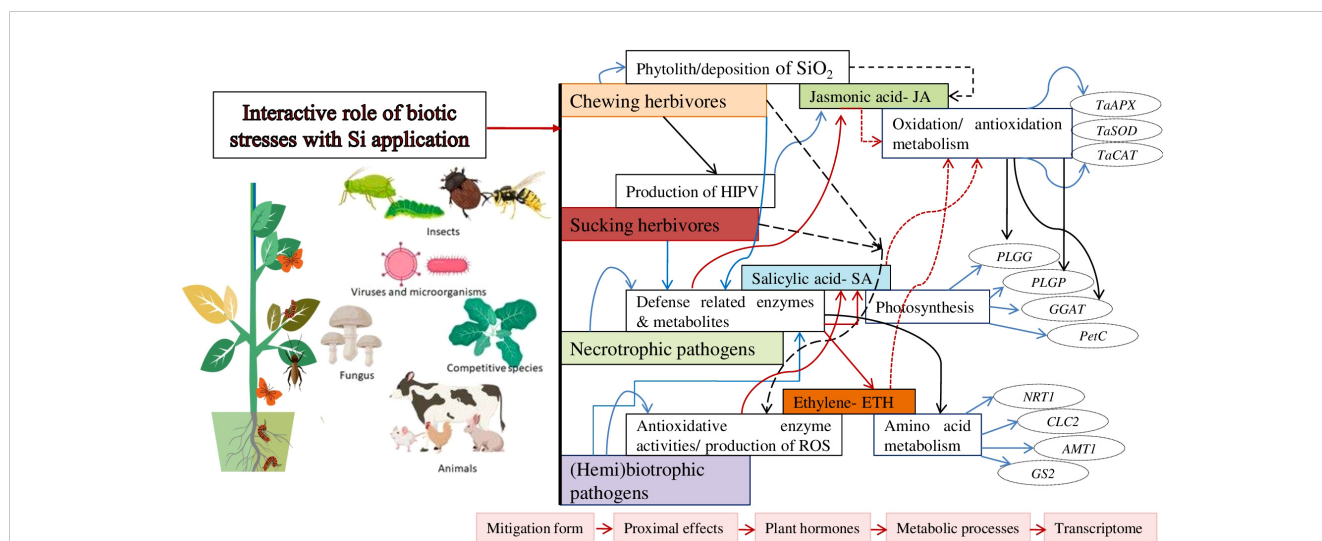


FIGURE 1
The outline of the major mitigation effects of Si on biotic stresses and some of the progressively more fundamental proximate and underlying phenomena associated with the mitigation of stress. The stress responsive genes associated with metabolic processes with variation in the response of transcription factors in response to Si. The essential Si transporter genes for the uptake of Si in plants are as *Lsi1*, *Lsi2*, *Lsi6* (Frew et al., 2018). Arrows shows linkages for which there is significant support and potential interactions.

Mitigation of pathogenic bacteria, fungi, and viral diseases by Si application

Applying Si formulation opens a new window in plant-pathogen interaction and management strategies. Si enhances resistance against diverse fungal pathogens in different plant-pathogen interactions. It effectively reduces plant diseases, such as black point in barley (*Alternaria* spp (Al-Sadi, 2021), leaf and glume blotch in wheat (*Septoria nodorum*), root rot in cucumber (*Pythium ultimum* and *Pythium aphanidermatum*) (Sun et al., 2022), damping off and stem rots in maize (*Pythium aphanidermatum*) (Haq et al., 2021), ascochyta blight in pea (*Mycosphaerella pinodes*), cercospora leaf spot in coffee (*Cercospora coffeicola*), blue mold decay and brown rot decay in cherry (*Penicillium expansum* and *Monilinia fructicola*), root rot in melon (*Pythium aphanidermatum*) (Sakr, 2018), wilt in potato (*Fusarium sulphureum*), black sigatoka in banana (*Mycosphaerella fijiensis*), and gray mold in strawberry (*Botrytis cinerea*). Foliar application of Si significantly reduces *Fusarium* crown and root rot in tomato plants. Si also reduces the intensity of hemibiotrophic fungal pathogens in different pathosystems, such as black spot in rose (*Diplocarpon rosae*), phytophthora blight in bell pepper (*Phytophthora capsici*), anthracnose in sorghum (*Colletotrichum sublineolum*), anthracnose in bean, and blast in wheat (*Pyricularia oryzae*). Si application reduces powdery mildew disease in wheat, cucumber, muskmelon, grape, arabidopsis, pearl millet, sugarcane, bean, strawberry, soybean, coffee, and rose, as well as powdery mildew in melon caused by *Podosphaera xanthii* (Farhat et al., 2018).

Si application upregulates plants' efficiency for epiphytic and endophytic bacterial pathogens in mango plants where bacterial apical necrosis was reduced (Etesami et al., 2020; Verma et al., 2023b). Si treatments have also controlled bacterial wilt on tomato (Jiang et al., 2019), bacterial spot on *Passiflora edulis*, bacterial streak on wheat, angular leaf spot on cotton, bacterial wilt on sweet pepper, and bacterial blight on rice. Applied calcium silicate in soil (1.41 g Si kg⁻¹) defense against *Acidovorax citrulli* in melon plants (Bakhat et al., 2018). Different research groups' demonstrations have confirmed the suppressive effects of Si application on viral pathogens. For instance, Si treatments have effectively reduced the incidence of *Cucumber mosaic virus* and *Papaya ring spot virus* on cucumbers. Applied Si in tobacco plants (0.1 mM) showed no systemic symptoms caused by the *Tobacco ring spot virus* than control plants, and higher Si rates slowed reduce the development of virus systemic symptoms. Si-mediated biotic stress tolerance by promoting various functions as shown in Figure 1 and summarized in Tables 1, 2.

Conclusion and future prospects

Si can influence the ecophysiology and cellular metabolism of plants. It stimulates antioxidant mechanisms and photosynthetic apparatus, maintain nutritional balance, regulates nutrients' uptake

and accumulation, promotes the production of secondary metabolites, ROS, and toxic metal chelation, changes plant cell walls, and regulates stress resistance proteins. However, the most significant effect of Si is the reduction in the intensities and frequencies of different plant diseases caused by biotrophic, hemibiotrophic, and necrotrophic plant pathogens causing seed-borne, soilborne, and foliar diseases in a variety of crops of great economic importance. The plant responses during pathogen infection and pest attack at the physio-biochemical and molecular levels are remarkably similar when Si is taken up by the plant roots and translocated to shoots, indicating an active role played by this element in one or more plant defense signaling pathways. The regulatory functions of Si during stressed conditions discussed how Si tolerates stress efficiency. While Si is associated with various plant proteins, it is unclear which other transcription factors and signaling proteins interact with Si to enhance plant stress. It will be very interesting to discover the functional role of signaling pathways and interactions with phytohormones at the cellular level to understand better how plants react during biotic stress with Si application. However, upcoming research demonstrations should focus on deciphering the role of Si in crop plants at field trials rather than laboratory conditions. The CRISPR/Cas system should be explored to Si-encoding proteins to enhance the stress resistance capacity in response to pathogenic diseases in major crop plants.

Author contributions

KV: Writing – original draft, Software, Resources, Methodology, Investigation, Formal analysis, Data curation. X-PS: Writing – review & editing, Visualization, Validation, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. QL: Writing – review & editing, Supervision, Software, Resources, Data curation. H-RH: Writing – review & editing, Software, Resources, Methodology, Formal analysis, Data curation. RB: Writing – review & editing, Software, Resources, Methodology, Formal analysis, Data curation. LX: Writing – review & editing, Software, Resources, Formal analysis, Data curation. G-LC: Writing – review & editing, Validation, Supervision, Resources. Y-RL: Writing – review & editing, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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