



REVIEW ARTICLE

Silicon-mediated regulation of plant stress responses: Transport mechanisms, molecular crosstalk and agricultural prospects

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Abstract

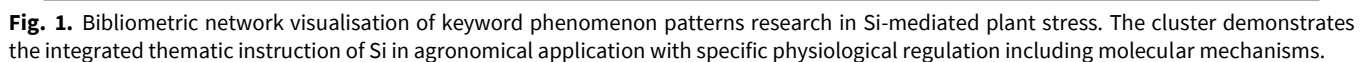
Plants face diverse environmental stresses throughout their life cycle that establishes a perennial evolutionary pressure for plants. This creates a challenge for plant health and survival, raising major concerns about global health and food security. Plant stress plays a vital role in understudying plant physiology and its impact on the yield of agricultural fields, which will elucidate key aspects of plant morphological, physiological and metabolic changes. This study explores the multifaceted role of silicon (Si) in mitigating plant stress and its application for improving agricultural yield. It moves beyond the current paradigm of passive mechanical support by exploring the Si transport cascade through the influx-efflux transporter and its crosstalk with plant defence hormones. Furthermore, this paper highlights different techno-economic assessments (TEA) of Si-based biofertiliser including life cycle assessment (LCA) and reinforce its commercial viability of Si-mediated involvement in sustainable strategies in agriculture. Unlike previous reviews, this work uniquely integrates Si transporter biology, hormonal crosstalk and TEA/LCA perspectives, while explicitly identifying key knowledge gaps including transporter diversity across non-model crops, long-term nano-Si field safety and species-specific variability and their practical implications for sustainable agriculture. This underscores the significance Si-based stress management as a sustainable and eco-friendly strategy for climate-resilient agriculture, offering significant potential to enhance global food security. Future research should focus on developing Si-efficient crop varieties and integrating Si management with precision agriculture technologies to maximise stress tolerance and agricultural productivity.

Keywords: climate-resilient agriculture; nanoparticles; Si transporters; stress signalling; sustainable agriculture

Introduction

As sessile organisms, plants endure a wide range of unfavourable conditions and still manage to thrive in extremely harsh environments such as drought, high salinity, varying temperatures, heavy metal accumulation and biological agents like pathogen and pests, which can significantly affect their growth potential (1). The cumulative impact of these factors can disrupt the plant's overall physiological process, thereby reducing plant growth potential, development, hampering agricultural yield and, in severe cases, leading to plant death. Abiotic stress is a major challenge in traditional agriculture, which leads to significant losses in crop productivity and arable land quality. With the global population continuing to rise, the impacts of climate change are becoming increasingly complex, for managing abiotic stress. Addressing these challenges is crucial for advancing sustainable agricultural practices and ensuring resilient food security. Extreme climatic events, including heavy precipitation, abrupt temperature fluctuations, drought and elevated UV radiation, impose significant abiotic stress on plants, often leading to severe adverse effects on their growth and productivity. As a result, large areas of land are affected by drought, leading to a global decrease in crop productivity.

Additionally, abiotic stress, such as salinity, shows significant effects on crop productivity. Most plants are highly salt-sensitive, depending on salt concentration, which causes a reduction in yield rate (2). Furthermore, rampant use of chemical pesticides and excessive mining operations increase the level of cadmium (Cd), arsenic (As), copper (Cu) and lead (Pb) in soil, which induces heavy metal toxicity; as a result, it has negative effects on plant metabolic process, physiological process such as photosynthesis, respiration, transpiration, soil fertility, microbial interaction and overall agricultural productivity. In addition to abiotic stress, biotic stress also significantly impacts natural habitats and reduces plant productivity, creating an obstacle to food security (3). Collectively, biotic stressors that consist of viruses, fungi, pathogens, disease-causing bacteria and nematodes create a web network to hazard that hampers plant natural vegetation as well as crop production (4). The bibliometric analysis of global research trends on silicon (Si)-mediated plant stress responses is illustrated in Fig. 1, highlighting the growing scientific interest and major thematic clusters in this field over the past two decades. The natural habitat of the plant, its physiological, morphological, genetic and environmental living conditions, is completely influenced by the biotic stressors. Diseases and pests exacerbate the levels of toxicity and deficiency, which



Modern agriculture increasingly relies on agrochemicals to control diseases and pests, which contaminate the natural ecological habitat and have a detrimental impact on the human health and ecosystem. Prolonged and indiscriminate application of chemical fertilisers and pesticides may also reduce the effectiveness of pest and disease management strategies, such as fungicides and bactericides, over time (5). To cope with these biotic challenges, plants have evolved a range of defense mechanisms that enable them to resist and adapt to such biological stressors for survival. Among these, Si is a trace element that plays a vital role in enhancing stress tolerance against various biological elements and stimulating gene expression in response to stress conditions (6). Despite not being considered an important element, Si plays a crucial role in plant structural strengthening, cell membrane restoration, stabilising biochemical regulation, maintaining hormones, regulating antioxidant and hormonal signalling and significantly enhancing the physiological performance under a stressful environment. Silicon is a sustainable, eco-friendly strategy for climate-resilient agriculture. Silicon has become a useful trace element that can greatly improve the ability of plants to withstand stress, including both biotic and abiotic (7). Silicon reinforces the cell wall; silica cuticles make leaves more rigid and straight. It also

influences the cell wall during root elongation, which helps roots to penetrate more deeply into dense soil. Apart from the molecular mechanism, Si also acts as a physical defense mechanism that creates a barrier against herbivores and disease pathogens. Silicon contributes to the formation of silica aggregates in plant tissues, which act as a physical barrier against pathogen invasion and deter grazing by herbivores (8). Numerous methods enable Si to have a broad spectrum of effects on abiotic stress and the molecular mechanisms involved during the stress period. Silicon provides multiple benefits to improve osmolytes, stress proteins and photosynthetic rate, also helps plants conserve water during drought and salinity conditions (6). Importantly, Si makes plants more tolerant without interfering with any vital metabolic processes and it is far safer for the environment than conventional agrochemicals (6). Due to its various advantages, the use is encouraged in both physiological research and agricultural practice. Despite the high recognition of Si's involvement in plant defence mechanisms and diverse stress reduction, its incorporation with traditional plant breeding practices is still constrained. The primary gap begins to create an incomplete understanding of the core molecular events, the varying accumulation of Si among different plant species and the diverse responses under various conditions. Therefore, this review provides a comprehensive overview of Si-mediated stress tolerance in plants by integrating current knowledge on Si uptake and transport mechanisms, molecular and biochemical signalling pathways and their roles in mitigating both abiotic and biotic stresses. Particular

emphasis is placed on the crosstalk between Si-mediated physiological responses, hormone signalling and stress-responsive gene regulation. In addition, this review highlights emerging perspectives on Si-based agronomic strategies and nano-formulations that may contribute to sustainable crop production under changing environmental conditions.

Silicon uptake and transport in plants

Based on macronutrient classification, Si is generally regarded as a non-essential element for most plant life cycles. However, Si is considered a quasi-element that also increases many plants' production, growth and the ability to endure stress. Silicon is abundantly present in soils and occupies around 28.8 % of earth's crust (9). Over the decades, traces of elemental Si have been found, increasing gradually in the soil. In soil, Si fractions occur in various dissolved forms, including polysilicic acid, monosilicic acid and complexes of silicic acid with incorporated inorganic solutes, which are predominantly found in the soil solution's aqueous phase (10). Additionally, the binding of silicic acid species with organic compounds has been proposed. These dissolved forms of Si complexes were absorbed by plants by different mechanisms. Silicic acid is the most significant accessible form for many plants' uptake. The concentration of Si accumulation is distinct among different plant species. As referred to in this assertion, in monocotyledon plants Si conservation rate is 10 % approximately. It has been established that Si accumulation in *Oryza sativa* is around 1–10 % (11).

Upon being absorbed by plants, silicic acid gets incorporated into plant tissue and produces biogenic amorphous silica (bASi). The bASi accumulation in plants promotes plants to gain the ability to resist and tolerate diverse abiotic elements, including drought, salinity, UV, nutrition deficiency and harmful chemicals, along with biotic elements that involve pest infestation and herbivores (12). These resilience characteristics emerge via numerous mechanisms, including enhanced structural integrity, augmented physical barriers and stimulation of the defence-related metabolic pathway cascade. The changing dynamics of Si reservoir in environments and the various factors governing the availability of Si for plant growth and ecological function have drawn many scientific researchers' attention (13). Silicon uptake in plants is a meticulously regulated process featuring dedicated carriers, afterwards relocation via the vascular network and precisely controlled polymerisation initiated by various biomolecules. Plants usually uptake monosilicic $[\text{Si}(\text{OH})_4]$ acid, a form of Si, via root channels (14).

The significant breakthrough in understanding Si absorption in rice was achieved with the discovery of two distinct Si transporter channels, Lsi1 and Lsi2. The uptake phase entails specialised transporter proteins located inside the plasma membrane of the root cell, encompassing efflux transporter (Lsi2) and influx transporters (Lsi1), which are situated in root endodermal and exodermal cells that permit the active and passive movement of Si (15). Lsi1 has been associated with the nodulin 26-like intrinsic proteins (NIPs) family and the subfamily of the aquaporin family. Lsi1 is distinguished by its ability to permit the passage of specifically free charge silica acid into the root cell. Structural investigation reveals that all the aquaporins retain a similar conserved glass hour structure with six alpha-helical transmembrane domains (H1–H6) that are joined by five loops (LA–LE). Among these five loops, LB and LE contain the highly conserved NPA domain motif (16). The recent studies highlighted the control mechanism and the evolutionary changes of Lsi1 alongside other transporters, which have additional

future studies in different plants and boost comprehensive knowledge of evolutionary adaptivity and plant mineral nutrition of the Si transportation mechanism. The primary role of Lsi1, an influx aquaporin type transporter, is strategically located on the distal plasma membrane of the endodermis and exodermis cells of seminal, crown and lateral roots, where it facilitates the specific entry of silicic acid from soil to root cells (17). Adjacent to Lsi1, similarly, Lsi2 acts as an efflux transporter that mediates the Si transfer from the cytosol into the apoplast, which ultimately permits its integration into the xylem. Silicon is conveyed upwardly after absorption to the shoot via the transpiration system. This procedure is facilitated by the transpiration process in which water evaporates from the leaves and it exerts a suction force that raises the water level and disperses substances like Si (18). The Si content increases in the shoots when water is reduced drastically in the shoots during transpiration, especially in the zones of high photosynthetic activity and a higher percentage of transpiration rates. This efficiently managed process ensures the effective allocation of Si in the apical tissue of the plants. The pattern of expression of the Si transporter substantially varies among the plant species and profoundly affects their ability to accumulate Si. In the basal regions of the root exodermis and endodermis, both Lsi1 and Lsi2 in rice plants demonstrate pronounced, strong and segregate expression (15). Their activity peaks around the reproductive stage, which is associated with high plants' needs for Si. It has been identified in different varieties of plants, including tomatoes, rice, maize, soybean, wheat, tobacco, sorghum and pumpkin; all these plants have different capacities to accumulate Si. In the form of silicic acid (H_4SiO_4), through the Lsi1 which is present outside of root exodermis, Si enters the aerenchyma through influx aquaporin channels called NIPIII. After the root takes Si, it is transported to the apoplast until it reaches the endodermis (19). Apoplast along with the Casparian strip, which blocks this path and moves Si to the symplastic pathway as H_4SiO_3 by the endodermis via the Lsi2 and moves into the xylem (20). Depending on different functions, localisation and expression patterns, it can differ from species to species. In the case of tomatoes, Si accumulation in the shoot is very low due to the uptake mechanism's active, passive and rejective modes.

SiLsi1 is responsible for Si uptake in the root through functional influx, but due to a lack of an essential functional efflux transporter for shoot transportation, SiLsi2 is not identified. Once silicic acid enters the xylem, it moves upward in the transpiration process to the shoot and is released from the xylem vessels through Lsi6 (21). Subsequently, Si is deposited as SiO_2 in leaves and other aerial parts of the plant. Lsi6, an influx-type transporter localised in xylem parenchyma cells, is structurally similar to Lsi1 and plays a key role in Si distribution within leaves. To date, Lsi6 has been identified primarily in crops such as maize, rice and barley. The spatial localisation and functional roles of Si transporters (Lsi1, Lsi2 and Lsi6) across root and shoot tissues, along with the pathway of Si movement from soil to aerial parts, are illustrated in Fig. 2. Several hypotheses exist about the Si accumulation in root cell walls and the cross-connection between Si and root cell ingredients, such as lignification for further cell wall strengthening (22).

Moreover, limited insights into how nutritional imbalances (deficiency or excess) affect silicon (Si) uptake hinder our understanding of Si accumulation during root-to-shoot transport and its distribution across plant tissues. This complicates the understanding of the Si transport and regulatory factors that influence Si accumulation and uptake in plants. So far, some

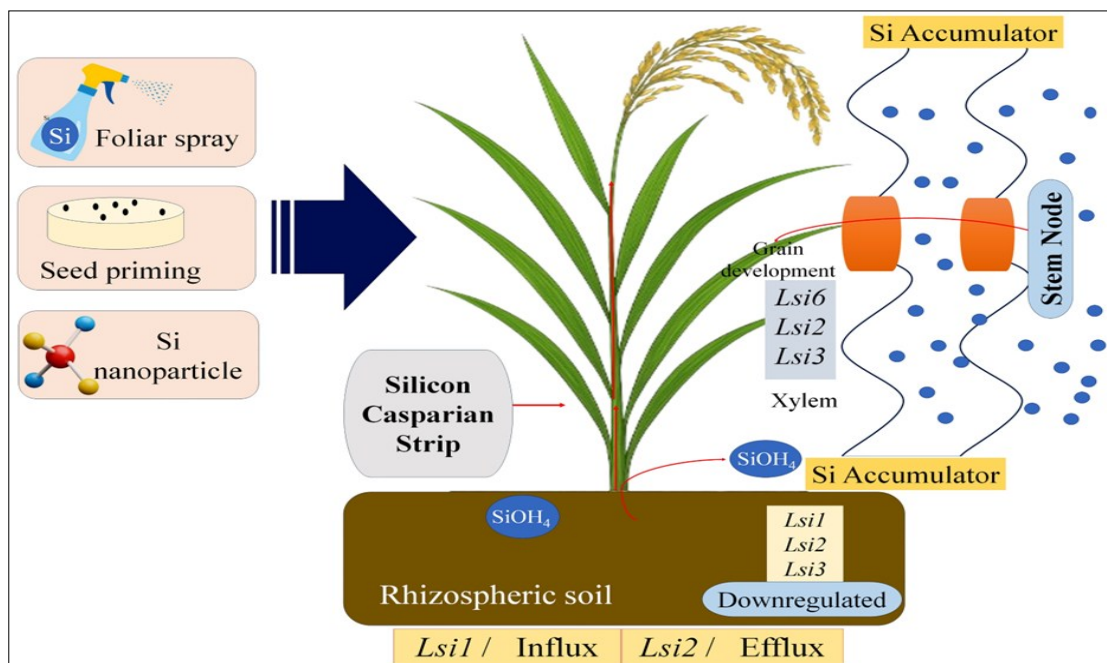


Fig. 2. Silicon transporters in monocot plant via root xylem and shoot. Whole cascade channelled the Si loads through different protein channels. When Si accumulation is high the *Lsi1/Lsi2/Lsi3* proteins are downregulated. Apart from that the Si accumulation in leaves creates an unknown root-to-shoot signal which suppresses the root *Lsi1/Lsi2* transcription.

studies have identified that Si down-regulates influx and efflux in rice, named *OsLsi1* and *OsLsi2*. Silica is found in various locations, including cell walls, partially or fully filled lumen, intercellular spaces, roots and special cells like silica cells. Silicification mainly occurs in fibres, sclerenchyma, storage tissue, epidermis and vascular tissue (23). However, the deposition and accumulation of silicon vary significantly among different plant tissues. Many Si transporters remain unidentified, highlighting existing gaps in our understanding of Si uptake, accumulation and deposition mechanisms. Collectively, these studies highlight that Si uptake and transport are tightly regulated processes involving specialised transporters and coordinated tissue-level deposition. However, the diversity of Si accumulation patterns among plant species indicates that additional transporters and regulatory mechanisms remain to be identified. Understanding these mechanisms will be critical for developing Si-efficient crop varieties and optimising Si-based agronomic interventions.

Role of silicon in abiotic stress tolerance

Sustainable agriculture is now at stake due to unfavourable climate change and environmental stress. Global crop production is hampered by various abiotic stresses like drought, salinity, heat, cold, heavy metal stress and nutrient imbalance. Therefore, the abiotic stress factor has a severe, harmful impact on global food security. Abiotic stresses disrupt key physiological and metabolic processes in plants, ultimately impairing growth, photosynthesis and nutrient homeostasis. Stress conditions often lead to excessive accumulation of reactive oxygen species (ROS), resulting in oxidative damage to cellular components (24). Plants counteract abiotic stress through coordinated physiological, biochemical and molecular defence mechanisms. These responses involve activation of signalling pathways and stress-responsive genes that regulate metabolic adaptation and cellular protection. Silicon was recognised as a nonessential element that improved crop resilience to abiotic stress through the expression study of essential genes that regulate plant growth and development. Prior literature indicates that Si enhances physiological activities, gives protection against oxidative stress

and induces antioxidant defence induction (25). Among these, drought causes critical conditions and changes the physiological and plant growth patterns. Drought conditions lead to nutrient imbalances, water shortage, oxidative stress and ion toxicity, which a decline in plant growth and development parameters. Drought increases osmolyte accumulation, phytohormone level change and activation of stress response gene. A drought-prone environment is highly susceptible to elevated stress levels, which affects crop biochemical change and growth rate (26). The integrated physiological, biochemical and molecular mechanisms through which Si mitigates major abiotic stresses are illustrated schematically in Fig. 3, providing a conceptual overview of Si-mediated stress regulation.

Several strategies have been adapted to combat drought stress and improve water status. Exogenous application of nutrients in soil is an effective strategy for alleviating the adverse effects of drought stress. In this context, Si has been reported to protect against water deficits in wheat and maize. It benefits plants by forming a protective silica-cellulose and silica-cuticle double layer on the leaves and stems surface to improve cell rigidity and strength and show resilience to stress (27). Silicon enhances drought stress tolerance by stimulating physiological processes, including transpiration, photosynthesis, intercellular CO_2 maintenance and stomatal conductance and it protects cell membranes from drought-related damage. Silicon supplementation improves drought stress tolerance, which may cause the activation of secondary metabolites, GA pathway efficiency, the suppression of chlorophyll degradation and enhances photosystem II (PSII) (28). Silicon eliminates ROS by releasing enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and non-enzymatic antioxidants such as ascorbic acid, carotenoids and glutathione, which provide relief against oxidative stress (29).

Nowadays, salinity is among the major constraints and destroys crops in significant amounts. Drought and salinity cause heavy impacts such as water deficiency, nutrient imbalance and ion toxicity, which can hamper the downregulation of proteins involved in cell expansion and protein synthesis (30). Besides the

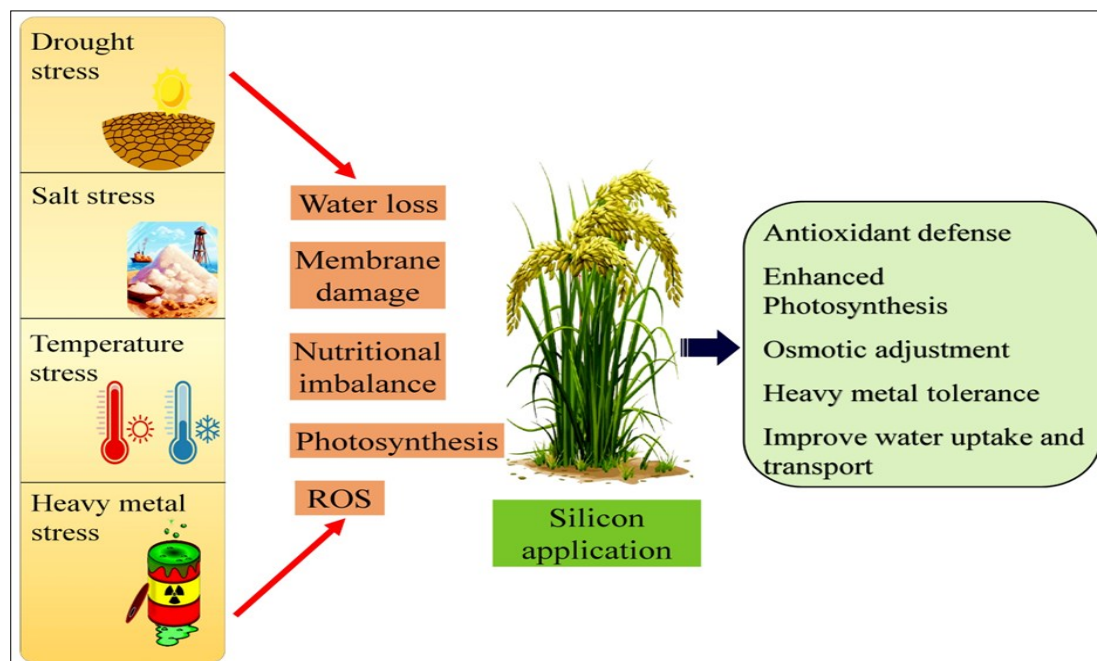


Fig. 3. Abiotic stress like drought, cold, salinity and heavy metals (Cd, Cr, Cu) affects crop productivity and reduces crop yield capacity. In response plants, accumulated reactive oxygen species (ROS) lead to reduced photosynthetic activities, which ultimately affect plant growth and crop production.

osmotic effect, high salt levels severely affect the plant and cause ionic toxicity, interfering with cellular imbalance and nutrient uptake (31). Excess sodium ions (Na^+) compete with potassium (K^+) uptake sites, disrupting nutrient balance and impairing enzyme activity in plant cells. Moreover, in the apoplast, calcium ions (Ca^{2+}) are interfered with by Na^+ ions, which play a crucial role in cell wall integrity and membrane function (32). Under stress conditions in rice plants, Si promotes growth and development due to higher biomass production and increased photosynthesis. In salt stress conditions, Si significantly protects the plant and enhances the crop quality. Silicon intensifies the stomatal conductance, improves chlorophyll content and chloroplast structure and enhances photosystem efficiency. Salt tolerance in plants like tomato, cucumber and rice can be enhanced by modifying antioxidant enzyme activities and improving nutrient balance through Si. It increases the antioxidant enzyme activity such as SOD, CAT, POD and glutathione reductase (GR), maintains the membrane integrity by decreasing lipid peroxidation and permeability (33). Silicon helps to reduce sodium uptake levels, manage nutrient imbalance and increase essential nutrients like phosphorus. Silicon elevates transport and improves photosynthetic efficiency. In some plants, Si facilitates polyamine accumulation, such as spermidine, spermine and putrescine, which involves ion transport regulation and osmotic potential to enhance salt tolerance (34). In response to salinity conditions, glycophyte plants show excluder types of behaviour, which is highlighted by a negative correlation between shoot Na^+ concentration and plant growth. Sodium ion accumulation is reduced in plants by recirculation or low xylem loading of Na^+ from the shoot to the root through the phloem. Na^+ is typically transported into the xylem through the root symplastic pathway, crossing the endodermal barrier at the Casparian stripe (35). The bypass flow due to an undeveloped root allows Na^+ to move directly to the xylem via the cell walls. By adapting salinity, plants increase lignification and endodermal suberisation for toxic ion blockage.

Heavy metal contamination arising from industrial activities and agricultural practices leads to the accumulation of metals, such as Cd, Zn, Ni, Cu and As in soils, negatively affecting plant growth and metabolism. However, few of these metals act as essential micronutrients to the plant, but beyond a threshold amount may interfere with plant growth and development and affect physiology and metabolism. Plants employ detoxification mechanisms such as chelation and sequestration of metal ions into vacuoles to reduce their cytotoxic effects (36, 37). Silicon plays an essential role in reducing heavy metal uptake into plants. Silicon can intensify the chelated ions by enhancing root exudates, limiting heavy metal uptake by roots in plants. It reduces the free metal ion concentration within plant tissue, eventually decreasing translocation to the aerial part. By lignin, Si concentration increases in the cell wall and restricts more metal ions from moving forward from roots to leaves. Furthermore, Si binds with the metal ions and enhances the precipitation process (38). High Si accumulation is associated with increased production of organic acids, such as malic and formic acid, which help regulate aluminium uptake in plants (39). Silicon also enhances plant resilience through its accumulation in root cell walls, stems and leaves, where it forms physical barriers that strengthen tissue integrity. Silicon reduces apoplastic bypass flow in roots, which leads to increased metal ion binding and decreases toxic metal (Cd) translocation to the shoot (40). Further, Si reduces transpiration in cuticles to enhance plant stress resistance. Studies have demonstrated that Si reduces Cd uptake and translocations to the shoot by forming phytoliths at water evaporation sites (41). Root anatomy plays a crucial role in heavy metal toxicity by helping limit metal intake. Abiotic stress, such as heat, limiting nutrition, climate change and different stress conditions, hinder plant growth and development. Silicon shows a positive impact on plant growth and its molecular mechanism. Plants activate heat stress response (HSR) pathways that involve multiple signalling networks to mitigate cellular damage caused by elevated temperatures (42). Heat stress induces morphophysiological, biochemical and transcriptional adjustments in plants. Due to interrupted biochemical

pathways and cellular damage, water potential of the cell is imbalanced and heat stress is triggered. Plants intensify internal stress tolerance strategies to camouflage heat stress and cope with different temperature changes, like heat shock proteins or stress proteins or stress-induced proteins (HSPs), Phyto level changes and various oxidation enzymes to remove ROS (43). Heat stress protein is generally a group of proteins synthesised under high heat stress. Under heat stress, two-thirds of the chloroplast HSP transfers into the thylakoid, which gives an insightful view about HSP adaptation under heat stress. Heat shock proteins transfer is an integral part of the plant and helps to stabilise the membrane. Molecular chaperones, especially HSPs, play a crucial role in folding and restraining the whole formation by denatured proteins, which affects apoptosis or cell death. Previous studies in peanut have demonstrated that the accumulation of small HSPs improves tolerance to high-temperature stress (44). Further, during grain filling and maturation phases in the embryo, abscisic acid level increases along with the HSPs development (45). Taken together, these findings suggest that Si-mediated abiotic stress tolerance is achieved via a combination of structural reinforcement, physiological regulation and molecular signalling pathways. While several protective mechanisms such as ROS detoxification, improved osmotic regulation and stabilisation of photosynthetic processes are shared across different stresses, their relative contribution varies depending on the specific stress condition and plant species.

Role of silicon in biotic stress tolerance

Plant pests and diseases continuously hamper agricultural production globally. Most plants are affected by different pathogens, such as bacteria, viruses, nematodes and fungi (46). Silicon exposure primes plant defence responses by stimulating signalling cascades that activate defence-related hormones such as jasmonic acid (JA), salicylic acid (SA) and ethylene (ET), thereby enhancing the transcription of pathogen-responsive genes and strengthening systemic resistance. Plants absorbed Si by enhancing defence response against pathogenic insect and diseases which are crucial factors for restricting crop production. Silicon acts synergistically with plant defence signalling pathways by modulating hormone-mediated responses, particularly those involving JA, SA and ET, which regulate defence gene expression and systemic resistance. The collective changes in plants make it more capable to resist against biotic stress. During the plant growth and development stage, plants fight against insect pests and diseases with the help of Si deposition and chemical defence by enzymatic secretion. In plants, amorphous silica acts as a mechanical barrier that protects the plants from further damage by insects and diseases (47). Silicon presents a sustainable strategy

in agriculture and horticulture for enhancing crop quality and defence against variable stresses. A comprehensive overview of Si-mediated resistance across various crop species against key fungal, bacterial, viral and nematode pathogens is provided in Table 1. The molecular signalling cascade triggered by Si during plant defence against biotic stresses, including activation of JA, SA and ET pathways is illustrated in Fig. 4.

Furthermore, one of the most significant effects of Si is its ability to reduce the severity of soil-borne, seed-borne and foliar diseases caused by hemibiotrophic, biotrophic and necrotrophic pathogens that limit crop production (63). Recent research has shown that many crops treated with Si show phenylpropanoid and terpenoid pathways, which play a role in faster and more robust defence gene activation and transcription (64). This activation also enhances photosynthesis efficiency and enzymatic activity. Silicon enhances the plant's resistance against fungal pathogens. Silicon forms a polymerised structure, creating a mechanical barrier under the cuticle inside the cell wall. This further helps to stop the fungus from penetrating the cell wall and makes the plant disease-resistant (65). Additionally, Si-mediated priming enhances the accumulation and signalling of defence hormones, which regulate downstream transcriptional networks involved in plant defense (66). Currently, plant disease management largely relies on chemical-based pesticides, which can negatively impact sustainable agriculture and may contribute to the development of pathogen resistance. The growing global population has also raised concerns about the effects of pesticide use on human health. In this context, eco-friendly alternatives such as biological control have gained importance. Biological control involves the use of natural substrates or beneficial microorganisms to suppress pathogens, either directly through antagonistic interactions or indirectly by enhancing plant immunity. This approach can be integrated with plant genetic strategies for disease resistance and the induction of systemic resistance (ISR), offering a sustainable solution for crop protection (67). Following ISR, long-distance signalling molecules transmit defence signals to distal tissues, enabling rapid activation of defence responses upon pathogen attack. Induction of systemic resistance commonly relies on JA and ET pathways dependent but SA-independent (68). However, recent updates show that salicylic and jasmonic-ethylene pathways synchronise with each other by small RNAs to regulate ISR. *Aspergillus tubingensis* is the most used antifungal and antibacterial factor, which can produce glucose oxidase (GOD) and catalyse β -D-glucose oxidation into H_2O_2 and gluconic acid (69). Overall, Si-mediated resistance against biotic stress involves both structural and signalling-based defence strategies. In addition to forming physical barriers through silica deposition, Si primes plant

Table 1. Summary of Si suppressing the different diseases causing pathogen in monocot and dicot plants

Pathogen	Plants name	Disease	Caused by	References
Fungi	Oats	Powdery mildew	<i>Puccinia graminis</i> f. sp. <i>avenae</i>	(48)
	Rice	Rice blast	<i>Magnaporthe oryzae</i>	(49)
	Bitter gourd	Rice leaf scald	<i>Monographella albescentis</i>	(50)
	Cucumber	Powdery mildew	<i>Erysiphe cichoracearum</i>	(51)
		Fusarium wilt	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i>	(52)
	Sorghum	Powdery mildew	<i>Podosphaera xanthii</i>	(53)
		Anthraxnose	<i>Colletotrichum sublineolum</i>	(54)
	Wheat	Root rot	<i>Bipolaris sorokiniana</i>	(55)
		Powdery mildew	<i>Blumeria graminis</i> f. sp. <i>tritici</i>	(56)
	Rose	Powdery mildew	<i>Podosphaera pannosa</i>	(57)
Bacteria	Banana	Panama disease	<i>Fusarium oxysporum</i> f. sp. <i>cubense</i>	(58)
	Rice	Leaf blight	<i>Xanthomonas oryzae</i> pv. <i>oryzae</i>	(59)
	Tomato	Bacterial wilt	<i>Ralstonia solanacearum</i>	(60)
Virus	Rice	Black-streaked dwarf	<i>Sogatella furcifera</i>	(61)
Nematodes	Cucumber	Root-knot	<i>Meloidogyne incognita</i>	(62)

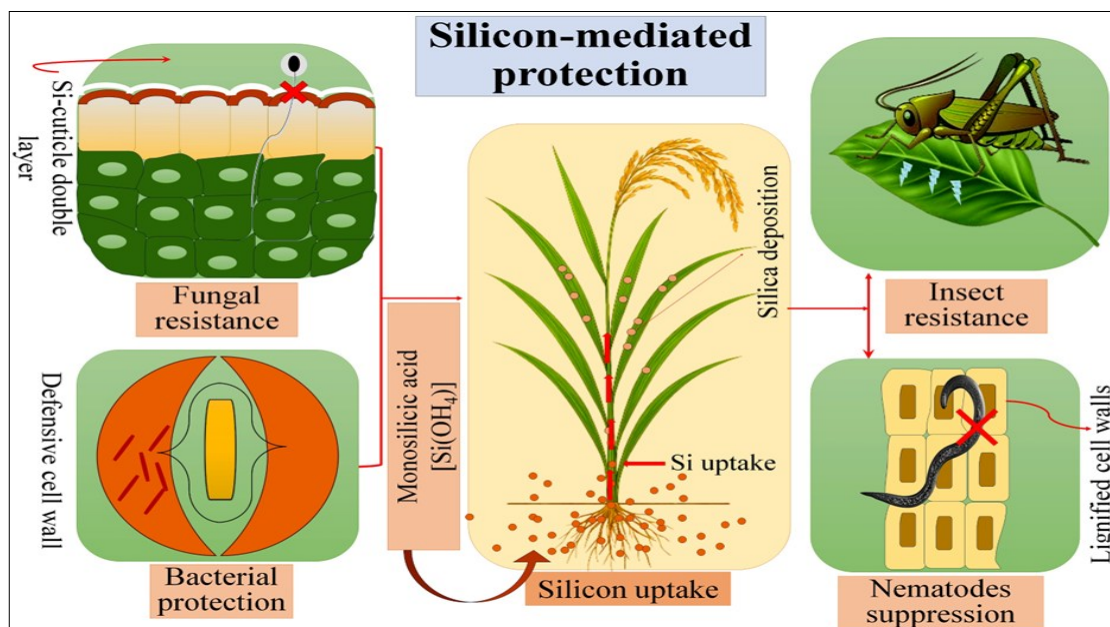


Fig. 4. Plants always face challenges from bacteria, insects, fungi and nematodes. Silicon gives physical protection to plants in the fight against microbial diseases and insect pests. Silicon not only reduces insect damage but also protects plants from stress. Silicon enhances crop quality, disease resistance and control of pest attacks.

immune responses by modulating hormone-dependent defence pathways and enhancing systemic resistance. This dual mode of action highlights the potential of Si as a sustainable strategy for strengthening crop resistance against diverse pathogens.

Molecular and biochemical mechanisms

Silicon is considered a beneficial element that plays a crucial part in enhancing plant growth and decreasing the maturity duration. Despite Si abundance in soil, plants only absorb Si mainly as monosilicic acid $[\text{Si}(\text{OH})_4]$. Silicon promotes plant growth, boosts high crop productivity, increases nitrogen fixation and photosynthetic efficiency and stimulates antioxidant defence factors to fight against various environmental stresses. Collectively, Si accumulates during the plant's synthesis of many phenolics and phytoalexins, which enhance pathogenic resistance in plants (70). In this context, Si provides protection through the soil via different Si transporters. Following absorption, Si is deposited in plant tissues primarily as amorphous silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$), forming silica bodies within cell walls, intercellular spaces and beneath the cuticle, where it contributes to structural reinforcement and enhanced stress tolerance. Silicon enhances stress tolerance capacity against environmental stresses such as salinity, drought and metal toxicity to resist ROS toxicity. Silicon regulates oxidative stress-related gene expression and regulates hormone metabolism. Silicon positively activates SOD, guaiacol peroxidase (GPX) and CAT helps in nutritional level and plant growth development. Under salinity stress, peroxidation, proline, phenol and electrolyte levels increase. Thus, plants typically exhibit enhanced antioxidant enzyme activity, including SOD, CAT and POD, as part of the cellular defence system against oxidative damage. However, Si supplementation increases the antioxidant level under stress conditions and improves development. Phytohormone regulation in plants is necessary for plant physiology, metabolic and biochemical levels, which maintain the equilibrium within the plant (66). Hormone regulation, like cytokinin, controls plant growth, cell differentiation and proliferation (71). Furthermore, cytokinins (CTKs) play a crucial role in internode elongation and bud growth. In addition, hormone like

gibberellin is essential in seed development, leaf and stem elongation and flower development (72). Auxin is produced in the growth area to increase cell differentiation and extension. It also regulates genes involved in the abscisic acid (ABA) signal transduction, which is primarily involved in growth promotion and regulates metabolic pathways (73). The integrated molecular framework illustrating Si-mediated regulation of antioxidant enzyme activity, phytohormone crosstalk, stress-responsive gene expression and downstream effects on plant growth and stress tolerance is presented in Fig. 5.

In addition to these, other phytohormones, like ET, SA, JA and brassinosteroids (BRs), protect plants in stressful environments (74). Under stressful conditions, Si shows an impeccable effect on plant physiology and metabolic cascade. These plant growth hormones with Si protect plants and act as a defence mechanism under various environmental stresses. Several transcriptomic and proteomic studies have identified multiple genes and regulatory proteins that respond to Si supplementation and contribute to improved stress tolerance in plants. For instance, the Si-responsive gene *SbPIP*, which encodes a plasma membrane intrinsic protein (PIP) belonging to the aquaporin family, plays an important role in regulating cellular water transport and maintaining water balance under stress conditions (70). Molecular studies in tomato have shown that Si application can downregulate SA-related defence genes, such as *SIR1b1*, *SIPR-P2*, *SLICS* and *SIPAL*, which are involved in SA biosynthesis and pathogen-responsive signalling pathways, thereby preventing excessive SA accumulation and reducing programmed cell death. Similarly, in rice the Si-mediated upregulation of stress tolerance genes, such as *Os03g57120* and *Os09g26810* and increased the activity of S-adenosyl-L-methionine decarboxylase (SAMDC), a key enzyme in the polyamine biosynthesis pathway, which contributes to cellular protection and osmotic stress tolerance. In drought conditions, Si upregulates the expression of *OsRDCP1*, a dehydration-responsive gene that contributes to improved cellular tolerance against water deficit, to protect from dehydration (75). Apart from that, Si protects plants

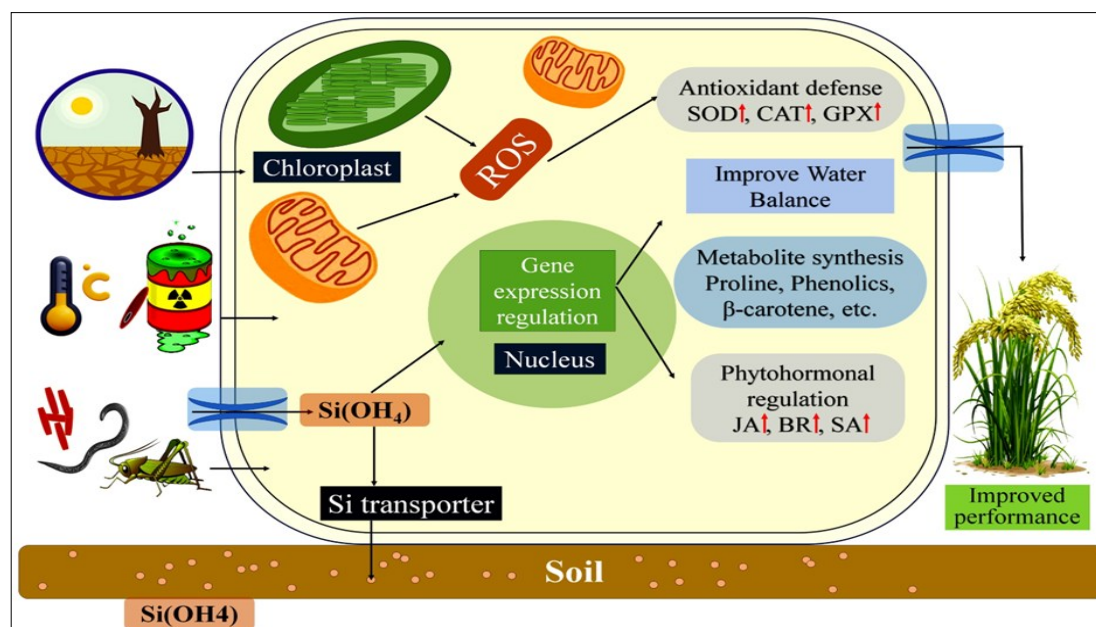


Fig. 5. A schematic illustrating the integrated molecular and biochemical framework of Si-mediated stress tolerance in plants.

from environmental stress by inducing β -carotene synthesis protein-like chaperon protein, carotene desaturase such as ClpC3, ATP synthetase subunit CF1 α , phosphoglycerate kinase protein (cupin family), β -keto acyl reductase, PIP1 and NIP2. Under stress conditions, Si eases sulfur deficiency, osmotic stress tolerance and gene alteration related to glyceraldehyde-3-phosphate dehydrogenase, CYC (cyclophilin), ADP-ribosylation factor (ADP-RF1) and smoothenes the metabolic pathway under stress condition (64).

Overall, Si-mediated stress tolerance in plants is regulated by a well-coordinated regulatory network integrating molecular signalling, biochemical pathways and phytohormonal dynamics. One of the early protective mechanisms involves the modulation of ROS homeostasis in response to stress stimuli. On the other hand, Si application has been reported to activate the enzymatic (SOD, POD and CAT) and non-enzymatic antioxidants to reduce oxidative damage under stress conditions (66). These biochemical responses are closely linked with transcriptional regulation of stress-responsive genes regulating various physiological processes, including osmotic adjustment, ion homeostasis and photosynthetic efficiency. Recent studies have further strengthened the roles of Si in regulating the expression of important transcription factors, such as DREB, NAC and WRKY, which in turn confer stress tolerance (76). Furthermore, Si extensively interact with phytohormone signalling in regulating the stress response in plants. Silicon has been reported to modulate the levels of key phytohormones including auxins, gibberellins, ABA, JA, SA, BR and ET. For instance, Si-mediated regulation of auxin and gibberellin helped in the improved plant growth and development, while the activation of JA-dependent signalling pathways enhanced plant defense responses under both abiotic and biotic stresses (77). Moreover, the coordinated interaction between ROS signalling and phytohormone-mediated pathways acts as a central nexus that controls downstream transcriptional responses and genetic reprogramming in plants (78). The integrated relationships among antioxidant regulation, phytohormone crosstalk and stress-responsive gene expression are schematically summarised in Fig. 5, providing a conceptual overview of the integrated framework for Si-mediated stress tolerance in plants.

Future prospects and research directions

Increasing climatic variability and the reduction of available agricultural land due to expanding human populations have intensified the stress pressures faced by crop plants. Novel and improved Si-based formulations represent an urgent priority for modern stress-resilient agriculture. This problem is often exacerbated in low-income countries, where research funding is limited. Hence an economic rationale exists for use of Si and its application. Silicon has already demonstrated itself to be viable in protecting plants in various stress conditions still certain fissures in the research exist, that necessitates further exploration and validation. Elucidation of precision molecular mechanism, optimisation of Si delivery mechanism and coating it with nanoparticles to increase its bio viability and efficiency. Silicon interaction with staple crops is well studied but beyond those further explorations has to be conducted in dicots and nontraditional crops.

Techno-economic assessment (TEA) must be done to develop an integrated pest management system using Si. Sustainable use and synthesis of silicon nanoparticles (SiNPs) and its detailed environmental risk assessment needs to be sanctioned in order for it to be deployed in the field. Silicon nanoparticles and Si-based nano formulation can enhance the efficiency of fertiliser and is programable for controlled release which decreases its frequency of use hence is economically more viable of its use by farmers. Silicon-based nano-formulations may reduce input costs by improving nutrient use efficiency and enabling controlled release of fertilisers, although their compatibility with organic agricultural systems requires further regulatory evaluation. Various *in silico*-based tools can be deployed for acceleration of role of Si in plant stress management. Open source Techno-economic feasibility (TEF) assessment tools like SuperPro Designer and its life cycle assessment (LCA) tools can help to stimulate its financial feasibility in real world application setting. The relatively low toxicity and environmental compatibility of Si-based nano-formulations highlight their potential as sustainable agricultural inputs. However, their large-scale adoption will require careful regulatory evaluation and environmental risk

assessment. Silicon-based nano-formulations, when integrated with precision agriculture systems including real-time sensor data, remote monitoring and site-specific management hold significant promise for enhancing farm efficiency and optimising resource use.

Future research on nano-fertiliser and Si signalling pathways will provide the fate regarding Si effectiveness depending on plant species, growth and environmental stresses (79). To comprehend the knowledge about how silicon functions, future research should focus on the combined multi-omics approaches of different isomers of Si, applications and dose concentrations of silicon interaction with various plants (80). It becomes important to distinguish whether Si affects the plant directly by improving chloroplast function or indirectly by hormonal changes so that the Si-responsive molecular marker can be identified (81). A research gap exists for long-term field trials and the poorly formulated nano application, which could hamper the plant metabolites, rhizosphere communities and the wider environment. Further, by linking the transport mechanism with precision application, one can develop fertiliser formulation and enhance yield, which may help the crop to withstand the climate change.

Plants can technically finish their growth cycles without extra Si, but when they don't have enough Si, they cannot handle environmental stressors and reach their full potential. This makes it necessary to think of Si as a “conditionally essential” nutrient, especially since the climate is becoming less predictable and biological stress factors are on the rise. Si-based fertilisers and soil amendments are classified according to their chemical makeup and physical form, with calcium silicate products being the most prevalent solid forms for agricultural field applications, typically derived from industrial waste materials such as steel manufacturing slag or naturally occurring wollastonite mineral deposits, offering the double advantage of supplying bioavailable Si while simultaneously neutralising acidic soil conditions, effectively serving as substitutes for conventional lime materials like calcium carbonate, with application quantities generally determined by soil pH levels and lime requirements, ranging from one to six tons per acre. Modern agriculture uses Si not only because it is good for crops, but also because it is a good business and environmental choice. This is shown by thorough cost-benefit analyses that show Si fertilisation is a very profitable business. For example, studies of rice production show that applying calcium silicate slag costs \$48.50 per acre (including application costs) and results in \$152.94 per acre in extra net returns through several benefit streams: \$59.40 per acre in extra gross revenue from higher yields, \$60.45 per acre in cost savings from not needing fungicides, \$8.50 per acre in lower insecticide costs and \$22.30 per acre in better grain quality (82). Si-based fertilisers lower the need for expensive synthetic fertilisers, fungicides and pesticides across a wide range of crop systems. This lowers overall input costs and increases farm profitability. Foliar Si applications are especially known for being cost-effective and easy to use and they provide a good return on investment. This makes Si a smart fertiliser that boosts agricultural efficiency while also lowering economic and environmental pressures (83). Life cycle assessment is a method that looks at the environmental effects of a product from cradle to gate or cradle to grave. It is a strong way to evaluate the sustainability of Si use. Most LCA research has focused on

industrial Si use in photovoltaics and electronics, but these methods can also be used in agriculture (84).

Conclusion

Silicon significantly contributes to crop sustainability and improves crop resilience to abiotic and biotic stresses. Silicon accumulation and absorption capacity vary among plant species and are crucial factors in determining the potential for stress tolerance. Silicon not only protects the plant from stresses but also plays an essential role in regulating enzymatic activity, seed germination, gene expression, plant development and vitalises other physiological responses, which improve the plant's adaptivity under stress conditions. Integrating Si-based nano-fertilisers with precision agriculture provides a commercially viable path to reducing pesticide dependence while significantly improving crop net returns. Silicon modifies the gene expression, which is involved in signalling pathways and biochemical and physiological responses under stress conditions. Silicon application is an intelligent move toward sustainable agriculture. Unlike previous published review articles, this review uniquely synthesises Si transporter biology with TEA/LCA. Under current climate change and environmental challenges, Si plays an impeccable role, which further helps in global food security.

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Authors' contributions

CB and SN conceptualised the study. CB and AN collected and analysed the data and drafted the manuscript. SG and SN critically reviewed the manuscript and supervised the work. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

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