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REVIEW

Insights into the molecular mechanisms of uptake, phytohormone interactions and stress alleviation by silicon: a beneficial but non-essential nutrient for plants

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Abstract

Silicon is one of the most abundant elements found in nature and also abundant in the earth's crust. Although it is not considered one of the essential elements, it has several fruitful effects on plant evolution, expansion and amelioration of biotic and abiotic stress factors. In present time of climate change, silicon supplementation can be an environment friendly and inexpensive way towards improved crop yield. Major food crops of world including rice, barley and sugarcane are accumulators of silicon. Silicon accumulation which varies among the species is dependent on abundance and expression of Si transporters. The accumulation of silicon not only acts as a mechanical barrier for pathogen and pest infestation into the plant tissue but also modulates phytohormone balance and maintains redox homeostasis to counteract stress. The present review discusses in detail the mechanism of silicon uptake, interaction with different phytohormones and transport on molecular level. Also, it provides comprehensive vision of the molecular mechanism regarding stress tolerance induced by silicon application.

Keywords Crop improvement · Phytohormone balance · Plant stress silicon · Silicon transporters

Abbreviations

Si	Silicon
$CaSiO_{3\_}$	Calcium silicate
$MgSiO_3$	Magnesium silicate
K_2SiO_3	Potassium silicate
Al	Aluminium
Fe	Iron
SiO2	Silica
H_4SiO_4	Monosilicic acid
$SiO_2.nH_2O$	Hard silica gel
Lsi1, Lsi2	Silicon transporters
NIP	Nod26-like major intrinsic protein
PPO	Polyphenol oxidase
POD	Peroxidase
CHT	Chitinase
ET	Ethylene
JA	Jasmonic acid
SA	Salicylic acid
PRR	Pattern recognition receptor
MAMPs or PAMPs	Pathogen-Associated Molecular Patterns
PTI	PAMP triggered immunity
ETI	Effector Triggered Immunity
NRA	Nitrate reductase activity
O_2	Superoxide
OH	Hydroxyl
HO_2	Per hydroxy
RO	Alkoxy
H_2O_2	hydrogen peroxide
CAT	Catalase
SOD	Superoxide dismutase
POD	Peroxidase
APX	Ascorbate peroxidase

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Introduction

Silicon is numbered as second utmost prevalent element on the earth's crust following oxygen and a crucial micronutrient for various plants (Raza et al. 2023). It is mostly obtained in combination with oxygen as silica (SiO_2), or with other elements to form silicates like $CaSiO_3$, $MgSiO_3$ and K_2SiO_3. Silicate minerals are also renowned as one of the biggest rock forming minerals present on earth. The content of silicon (Si) in soil, depends on the type of the parent rock that ranges from 1 to 45% (Sommer et al. 2006). Silicon is easily available to plants in the form of monosilicic acid in soil. Silicon has an important role as a beneficial macronutrient that is widespread in monocot and dicot plants. In many plant species, particularly monocots the uptake of Si from soil even surpasses the uptake of essential nutrients (Epstein 1994), still Si is not considered an essential element due to the lack of conclusive indication on direct involvement of Si in plant metabolism. Also, most of the plants complete their life cycle even in the absence of Si, which is one of the criteria to classify an element as essential (Arnon and Stout 1939). Si stimulates defense-related enzymes, encourages the formation of antimicrobial compounds, controls signalling pathways, and induces the expression of defense-related genes to activate defence mechanism, hormone regulation and gene expression patterns (Shanmugaiah et al. 2023).

Several investigations have been made on effect of Si on plant growth and development. Despite this, several studies show that silicon has a positive impact on plant development, agricultural productivity, and the reduction of biotic and abiotic stressors. The current review highlights recent advances in silicon absorption and transport mechanisms, as well as their significance in biotic and abiotic stress tolerance.

Uptake and transport of silicon

Silicon can be found in soil in liquid or solid or adsorbed phase fractions. Poorly crystalline and microcrystalline, crystalline, and amorphous forms of silicon make the solid Si phase. Primary and secondary silicates, as well as other silica materials, include the biggest fraction of crystalline form. Amorphous phase of silicon is either derived from silicon complexes with Al, Fe, heavy metals and soil organic matter or as biogenic form that is originating from plant residues and microorganisms (Matichencov and Bocharnikova 2001; Sauer et al. 2006). Monosilicic acid (H_4SiO_4) and polysilicic acids make both the liquid and adsorption phase fractions of Si. Weathering of silicate minerals as well as biogenic silica contribute to Si in soil solution and adsorbed phase (Fraysse et al. 2006). The type of silicon taken by plant roots is monosilicic acid (H_4SiO_4). The pH of soil and amount of clay, minerals, organic matter, and Fe/Al oxides/hydroxides in the soil solution determine the concentration of H_4SiO_4 in the soil solution (Tubana and Hackman 2015).

At pH greater than 9, monosilicic acid is converted into ionic silicates (Imtiaz et al. 2016). Plants have been classed as Si accumulators (10–15% of shoot dry weight) or intermediates (1–3% of shoot dry weight) including dry land grasses, and excluders or non-accumulators (< 1% of shoot dry weight) based on their silicon accumulation (Jones and Handreck 1967). However, it is also found that many non-accumulators, such as tomatoes, accumulate more Si in their roots than in their shoots (Huang et al. 2011). The H_4SiO_4 is absorbed by the root cells and is translocated via xylem to the leaf epidermal cells. Through transpiration, the accumulated leaf H4SiO4 is further condensed and polymerized into hard silica gel (SiO2.nH2O). Phytolith is a hard, immobile type of silica that is accumulated in shoots and cannot be translocated to fresh emerging leaves (Jones and Handreck 1967; Raven 1983).

In higher plants, three types of uptake of Si in relation to water uptake was proposed by Takahashi et al. (1990) that is, passive (uptake of Si is analogous to the uptake of water), active (uptake of Si is faster compared to that of water) and rejective (Si uptake is even slower than water). However, these modes of Si uptake are based upon the measurement of relative Si content and transpiration rates and here transpiration rate was assumed to be 500 and Si content of the soil to be 35 mM (Kathryn et al. 2003; Ma et al. 2001).

Active Si uptake involves specific silicon transporters. Several silicon transporters have been discovered in plants of various species (Mitani and Ma 2005). In plants, there are two types of Si transporters: channel-type (Lsi1) and efflux transporters (Lsi2). Lsi1 transfers silicon into plant cells from the surrounding environment whereas, efflux transporters are involved in the movement of Si from plant cells to the xylem (Fig. 1). Using a rice mutant (Lsi1, low silicon 1) that was deficient in Si uptake, the first Si transporter (OsLsi1) in higher plants was found and cloned (Ma et al. 2006, 2007). Lsi1 is a member of the Nod26-like major intrinsic protein (NIP) aquaporin-like protein subfamily. In the projected amino acid sequence of 298 residues, there are six transmembrane domains and two NPA motifs that are highly conserved in the aquaporin water channel family. Rice's efflux transporter (Lsi2) was also discovered and cloned using a rice mutant that was deficient in Si uptake. Lsi2 is a hypothetical anion transporter that is not related to Lsi1. Lsi1 takes up the Si form distal side of exodermis and its deprotonated form is passed by Lsi2 in aerenchyma at the proximal side of cell. Unloading of silicon from xylem and its distribution to different aerial parts is accomplished by Si

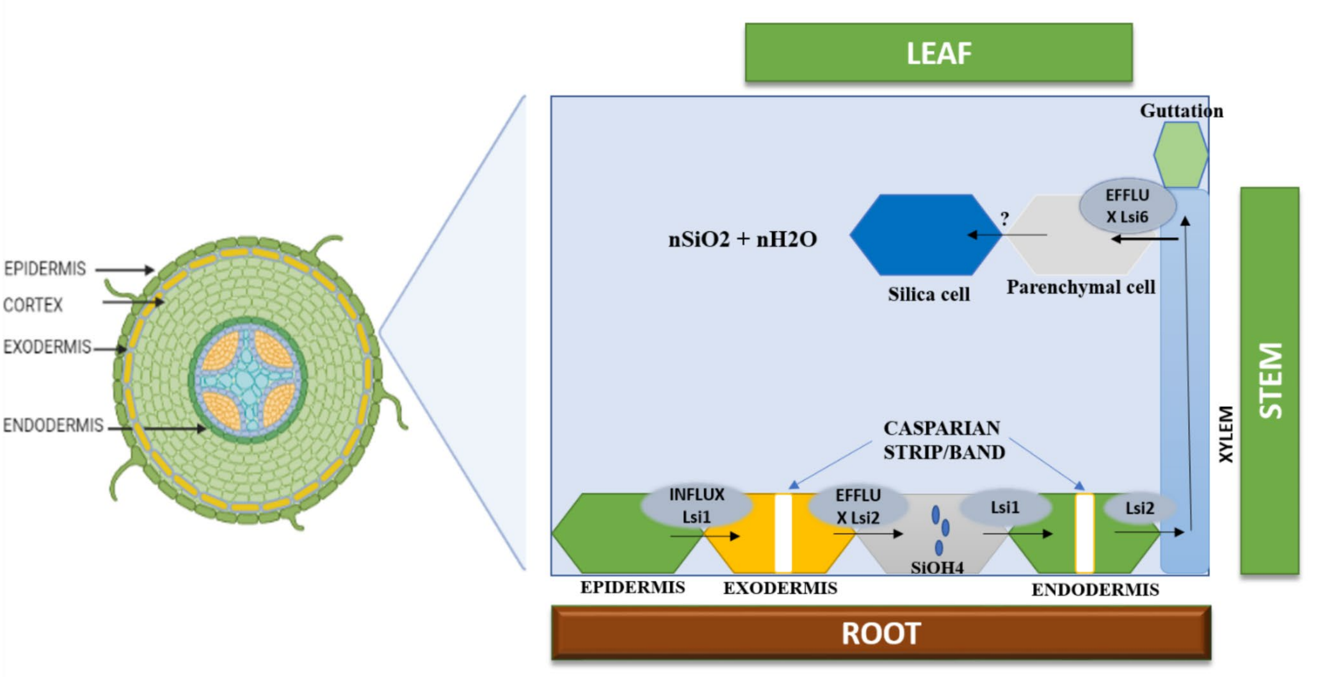

Fig. 1 Possible mechanism of silicon transport and deposition in plant cells

transporter Lsi6 (Yamaji et al. 2008). Lsi6 is located mostly in xylem transfer cells and the enlarged vascular bundles' outer margins. When the Lsi6 gene is knocked out, the panicles accumulate less Si, whereas the flag leaf accumulates more Si (Ma 2010). Lsi6 appears to be a carrier betrothed in silicon transfer from major vascular bundles of roots to diffuse vascular bundles linked to the panicles (Yamaji and Ma 2009). Along with Lsi2 and Lsi6, another Si transporter, Lsi3 also distributes Si in plant tissues.

Si deposition in the tissues was affected in Lsi2, Lsi3 and Lsi6 knockout rice mutants, but there was no influence on Si uptake from the environment, which is predominantly controlled by Lsi1. Si transporters found in other crops such as maize and barley perform comparable activities to those found in rice, but their localization and expression patterns differ (Mitani et al. 2009). The functional analysis of tomato Si-influx and Si-efflux transporter-encoding genes, SiLsi1 and SiLsi2, revealed that low Si accumulation in tomato leaves was caused by non-functioning state of SiLsi2 (Sun et al. 2020). The overexpression of a cucumber Lsi 2 gene in tomato led in the accumulation of Si in the shoots of tomato (Sun et al. 2020).

Silicon in biotic stress tolerance

Living organisms, for instance fungal, bacterial, and viral pathogens, mycoplasma, oomycetes, nematodes, insects, birds, weeds and parasitic plants cause biotic stress that is the major concern worldwide for agricultural production. Application of Si to plants help in alleviating various biotic stresses including disease incidence and pest attack. Plants having high Si content in shoots or roots resist pest attack than those devoid of Si. The main consequence, however, is that it aids in the prevention of soil-borne or foliar disease in major crops that are attacked by various biotrophic, hemibiotrophic, or necrotrophic pathogens (Cai et al. 2008). It also reduced the development, reproductive period, longevity, and fecundity of insect pests by prolonging incubation and latent periods, lowering conidial production, and reducing numerous characteristics of fungal, bacterial, and viral lesions (expansion rate, size, and number) (Wiese et al. 2005). Disease development and insect preference rates dropped considerably as a result, and susceptible cultivar's resistance was enhanced nearly equal to the cultivars with full or partial resistance in several circumstances. Silicon enhanced resistance helps in avoiding the penetration of pathogen with the help of structural reinforcement (Epstein 2001) or biochemical modification. To successfully infect the host plant, the virus must cross physical barriers such as wax, cuticles, and cell walls. The mechanical strength of the plants is aided by density of silica in long and short epidermal cells, the thick layer of silica under the cuticle (the double cuticular layer), strengthened Si-cellulose membrane, papilla development, and complexes created with organic compounds in epidermal cell walls. Physical barriers serve to limit pathogen penetration and make plant cells less susceptible to enzymatic damage caused by fungal pathogens.

Plant defence against disease and insect pest attack can also be induced by (1) increased activity of enzymes that are responsible for activating defense mechanism in leaves that is phenylalanine ammonia-lyase, polyphenol oxidase, peroxidase and glucanase (Liang et al. 2015), (2) increased production of anti-disease and anti-insect compounds and defensive chemicals in plants, such as phenolic metabolism product (lignin), flavonoids, phytoalexins and pathogenesis-related proteins (Sakr 2018). Antimicrobial compounds help to prevent the disease occurring in plants. The main enzyme for oxidation of phenolic substance that is polyphenol oxidase (PPO) is present in free form in the cytoplasm or are bound in chloroplast, mitochondria as well as other subcellular organelles (Quarta et al. 2013). It has been linked to be involved in lignin synthesis there by increasing antibacterial resistance of host plants (Song et al. 2016). Si is utilised to induce the accumulation of antimicrobial compounds like phenols, flavonoids, and phytoalexins after pathogen infection (Rodrigues et al. 2004; Remus et al. 2005). Peroxidase (POD) and chitinase (CHT), the enzymes involved in host-pathogen interactions, are boosted by silicon. POD is linked to cell-wall reinforcement and cell-wall protein cross-linking (Brisson et al. 1994).

ET, JA and SA also play a vital role in providing immunity to plants to regulate defense response by plants (Clarke et al. 2000). Silicon exhibits a defense mechanism called systemic acquired resistance that triggers when pathogen attacks the plant. Silicon triggers the local defence by activating SA signalling, plant organs after receiving the signals, stimulate SAR for further defence. The uptake of silica in root and leaves lowers the accumulation of ROS and also lipid peroxidation in the membrane. Deposition of silica in the leaf tissue, on the other hand, improves protection of plant against various diseases (Mathur and Roy 2020).

Insect pest tolerance

Silicon increases plant tolerance to insect manifestation mainly by deposition of Si in leaves as phytoliths which results in weakening of insect mouth parts and poor digestion. Its effect on the decrease of pathogens and insect pest attack is also attributed to the chemical protection by enzyme synthesis. The reduced digestibility of feeding on silicon enriched tissue reduces digestibility of food and reduces insect growth. In fact, plant resistance to herbivory is largely due to silicon accumulation, which causes changes in plant nutritional quality and lowers herbivore performance (Frew et al. 2019).

Stress related hormones such as jasmonic acid also acts as a master regulator in resistance against arthropod herbivores and pathogen (Erb et al. 2012). Jasmonic acid regulates defense mechanism for tissue chewing herbivore while salicylic acid and jasmonic acid pathway together activates the defense mechanism against fluid feeding herbivores (Zust and Aggarwal 2016). Different forms of silica were used against several insects (Table 1) such as in case of cucumber for protection from white fly *Bemisia tabaci*, calcium silicate was used which reduced the oviposition and mortality of nymph (Correa et al. 2005), in sweet cherry, sodium metasilicate was used where spore germination and germ tube extension of *Penicillium expansum* and *Monilinia fructicola* were suppressed (Qin and Tian 2005). In sugarcane insect population of spittlebug was affected by applying Si in plant defense. There was an increase in nymphal mortality as well as decreased longevity of males and females was observed (Korndorfer et al. 2011). Ebrahimi et al. (2012) noticed the effect of sodium silicate where it inhibited the mycelial growth in apple whereas calcium silicate was used to protect sugarcane plants from stalk borer (Keeping et al. 2013). Significance of silicon in rice plants was detected against rice leaf folder both at lower and higher rates.

Table 1 Role of Si in mitigation of insect pest resistance in different crop species

Plant	Form	Stress	Effect	Reference
Cucumber	Calcium silicate	White fly *Bemisia tabaci*	Reduced oviposition and mortality of nymph	Correa et al. 2005
Sweet cherry	Sodium metasilicate	*Penicillium expansum* and *Monilinia fructicola*	Germination of spores and elongation of germ tubes inhibited	Qian and Tian 2005
Sugarcane	Silicon	Spittlebug	high mortality of nymph while males and females longevity decreased	Korndorfer et al. 2011
Apple	Sodium silicate	*Penicillium expansum*	Inhibition of mycelial growth	Ebrahimi et al. 2012
Sugarcane	Calcium silicate	Stalk borer	Enhanced mechanical barrier and biochemical properties	Keeping et al. 2013
Rice	Calcium silicate	Rice leaf folder	Survival and pupation rates of larvae decreased	Han et al. 2015
Rice	Fly ash	*Leptocorisa acuta*	Feeding activity of the insect inhibited	Peera and Khanam 2020
Maize	Silicon oxide	Fall armyworm	Decreased larval and pupal biomass in fall armyworms	Haq et al. 2021
Onion and garlic	Potassium silicate and sodium meta silicate	*Stromatinia cepivora*	Enhanced systemic defense enzymes and expression of genes into proteins stimulated	Elshahawy et al. 2021

Silicon modification at higher rate lowered third-instar weight gain and pupal weight. The larval development was prolonged at both low and high levels of Si content, and the larval survival rate and pupation rate was also suppressed. As a result, resistance to rice leaf folder was developed in the susceptible rice variety (Han et al. 2015). Similarly, fly ash was used in rice plants to avoid the adverse effects by ear head bug and increase in yield was also observed (Peera and Khanam 2020). In maize, foliar application and soil drenching techniques were used to treat silicon dioxide (SiO_2) and potassium silicate (K_2SiO_3) in plants. The findings revealed that foliar treatments of SiO_2 and K_2SiO_3 increased mortality percentage and developmental period in autumn armyworms but decreased larval and pupal biomass (P 0.05). Likewise, both Si sources significantly (P 0.05) reduced lipase activity of larvae and adult fecundity, but the adults had a longer life expectancy (Haq et al. 2021).

Silicon is also involved in induction of plant defense responses in phytophagous insects. It also induces biochemical responses such as increased antioxidant enzyme activity and synthesis of secondary metabolites which reduce insect infestation. Silicon amendment to rice plant enhanced silicification of leaf sheaths. Thus, affecting the working of brown spot hopper. Compared to non-amended plants, silicon amended plants infested with brown plant hopper had higher catalase and superoxide dismutase (SOD) activity. Also, higher activation of polyphenol oxidase, β1, 3- glucanase and phenylalanine was observed (Yang et al. 2017). Potassium silicate and sodium meta-silicate offered protection against Stromatinia cepivora in onion and garlic by activating defense-related genes (Elshahawy et al. 2021).

Disease resistance

The interaction between disease resistance and plant pathogens is a complex process mediated by pathogen and plant derived chemicals. Silicon application also triggers immune response against various pathogens. The first interaction between a plant and a pathogen occurs at the apoplast, when membrane-localized receptors called Pattern Recognition Receptor (PRR) recognise microbe- or pathogen-associated molecular patterns (MAMPs or PAMPs), triggering the first line of defence known as PAMP triggered immunity (PTI) (Bigeard et al. 2014). Further, in response to PTI, pathogen secrete various effectors recognised by R genes and induces second line of defence called ETI (Effector Triggered Immunity). Mechanical barrier posed by Si deposition in the apoplast prevents secretion of effectors by pathogen. It also prevents the pathogen from suppressing the immune response by preventing the effectors from reaching these target locations (Vivancos et al. 2015). Physical barrier was formed by applying slag-based Si fertilizer in rice where immobile Si deposited in cell wall and papillae sites of host plant protects them from brown spot disease (Ning et al. 2014). Si- deficient plants showed a poor defence response than Si- treated plants, according to a transcriptomic analysis of the effect of Si on *Phytophthora sojae*-infected soybean plants. On Si-treated plants, *P. sojae* had substantially lower diversity and intensity of effector transcripts. These findings back up the theory that Si disrupts the signalling mechanism between a plant and a pathogen, resulting in an incompatible connection (Rasoolizadeh et al. 2018). Another well studied aspect of transcriptome analysis in tomato against *Ralstonia solanacearum* revealed that Si primes the defense capacity of plants by enhancing expression of jasmonic acid/ethylene genes. They overexpressed the genes JERF3, TSRF1and ACCO, the oxidative stress markers (FD-I and POD) and the basal defense marker (AGP-1 g) thereby alleviating stress imposed by the pathogen (Ghareeb et al. 2011). Furthermore, Si treatment may improve tomato resistance to *R. solanacearum* infection in three ways: by activating PTI-related responses; by influencing multiple hormone (e.g., SA, JA, ET, and auxin) signalling pathways; and by alleviating adverse effects (e.g., senescence, water deficiency, and oxidative stress) caused by infection (Jiang and Zhang 2021). Silicon is proposed to improve disease resistance through increasing the generation of secondary metabolites and antioxidant/defense related enzymes, as well as scavenging ROS. Effect of silicon against bacterial wilt in sweet pepper was recorded where Si directly affected colonization of the pathogen, increased Ca^{+2} absorption, and signalled to produce plant defence enzymes (Alves et al. 2015). Potassium silicate was used in case of bitter gourd to enhance the activity of all the defense related enzymes and pathogenesis-related proteins providing protection against powdery mildew (Ratnayake et al. 2016). Silicon also effects metabolism of defence hormones like ethylene, jasmonic acid and salicylic acid. In rice, silicon induces brown spot resistance by interfering with the action of fungal ethylene (Bockhaven et al. 2015). Applications of silicon has shown to reduce disease incidence in various plant species (Table 2). In Chinese cantaloupe, sodium silicate inhibited growth of pathogen that was responsible for postharvest rotting (Guo et al. 2007). Potassium silicate was used in case of soybean against soybean rust and reduced intensity of soybean rust was detected after applying potassium silicate in the field (Rodrigues et al. 2009).

Table 2 Effect of silicon in mitigating stress from various bacterial and fungal pathogens in different crops

Plant	Form	Stress	Effect	Reference
Chinese cantaloupe	Sodium silicate	Postharvest rot	Radial growth of the pathogen was inhibited	Guo et al. 2007
Soybean	Potassium silicate	Soybean rust	Reduced intensity of soybean rust	Rodrigues et al. 2009
Rice	Slag-based silicon fertilizer	Brown spot (*Bipolaris oryzae)*	Physical barrier against penetration of fungus	Ning et al. 2014
Oil palm	Silicon oxide	Basal stem rot	Host cell walls detered the penetration of pathogen	Najihah et al. 2015
Sweet pepper	Calcium silicate	Bacterial wilt	Production of plant defence enzymes	Alves et al. 2015
Bitter gourd	Potassium silicate	Powdery mildew	Activities of enzymes peroxidase, polyphenol oxidase and PR proteins chitinase and β-1,3-glucanase enhanced	Ratnayake et al. 2016

Role of silicon in abiotic stress tolerance

Being sessile organism plants are continuously being challenged by adverse environmental conditions such as heat, cold, drought, frost, heavy metal toxicity. These conditions negatively affect plant growth as well as reduce the crop yield. During environmental stress, ROS gets accumulated and its production is an obvious result of abiotic stresses and it is gaining importance not only due to its widespread production and subsequent damage to plants, but also for its diverse roles in signalling cascades, that affect other biomolecules, hormones involved in growth, development, and stress tolerance regulation. Superoxide (O_2), hydroxyl (OH), per hydroxy (HO_2), and alkoxy (RO) group are examples of free radicals, while hydrogen peroxide (H_2O_2) and singlet oxygen are examples of non-radicals that are covered by ROS. Their production and reactivity are well understood. When ROS levels exceed a cell's antioxidative capabilities, oxidative stress occurs, which can cause the cell to malfunction and eventually the cells die. Most biomolecules in the cell react easily with singlet oxygen, superoxide, hydroxyl and hydrogen peroxide, causing their breakdown and death, contributing to cellular stress. ROS are generated in plant cells as a result of environmental changes and developmental transitions such as seed germination. Plant cells are equipped with antioxidative machinery (Fig. 2), which includes both enzymatic and non-enzymatic components, to combat oxidative stress and excess ROS (Yadav and Sharma 2016). As a result, maintaining a favourable balance between ROS generation and antioxidant defence becomes necessary so that it preserves photosynthetic machinery, membrane integrity and nucleic acid and protein degradation (Hasanuzzaman et al. 2020). ROS must be effectively controlled and eliminated in order for organisms to survive. A powerful antioxidant defence system is responsible for that and includes antioxidant enzymes such as SOD, CAT, POD, APX and GR as well as low molecular weight antioxidants that is ascorbic acid, GSH or lipid like tocopherol, carotenoids, quinines and also some polyphenols. Metalloenzyme SOD helps in mediating the disproportionation of O_2^{-} into H_2O_2 and O_2 and is present in all aerobic organism and subcellular components that are vulnerable to oxidative stress (Kim et al. 2017). Other antioxidant enzyme catalase removes H_2O_2 generated in peroxisome and controls peroxisomal H_2O_2 synthesis whereas peroxidase is specific for GSH and uses H_2O_2 to oxidise the other substrate. MDHAR is also found in chloroplast and cytosol that regenerates the reduced ascorbate and was typically found in drought stressed conditions in rice seedlings (Yadav and Sharma 2016). Silicon has shown to reduced ROS accumulation by increasing the activity of these enzymes (Mostafa et al. 2021) thus providing tolerance to various abiotic stresses (Table 3).

In salt stressed tomato plants, application of sodium silicate along with NaCl enhanced the activity of SOD and CAT enzyme (Al-aghabary et al. 2005). A decrease in H_2O_2 level and MDA concentration showed that silicon reduces oxidative stress caused by salinity. Wheat growth under salt stress was improved using calcium silicate which lowered the sodium absorption and increased potassium uptake (Ali et al. 2009; Liang 1999) noted that Si has a protective effect against salt stress by allowing for the selective absorption and transport of potassium and sodium. Both sodium and potassium silicate were used to check sugarcane's resilience to drought stress. Regardless of the water conditions, it was discovered that Si leads to lower C concentrations by causing the stomatal closer for longer periods of time throughout the day. Additionally, the type of Si also had an impact on the concentrations of nitrogen and phosphorus (Teixeira et al. 2020). In sorghum under drought stress, silica enhanced the leaf area index, chlorophyll content, leaf dry weight, specific leaf weight, shoot dry weight, total dry weight, and root dry weight of the plant (Ahmed et al. 2011). At low temperatures the impact of Sodium silicate was tested in barley where it was observed that biochemical properties of leaf apoplasm was modified, which further mitigated the cold stress (Joudmand and Hajiboland 2019). Similarly, in maize, silica showed cold-protective effects with enhanced

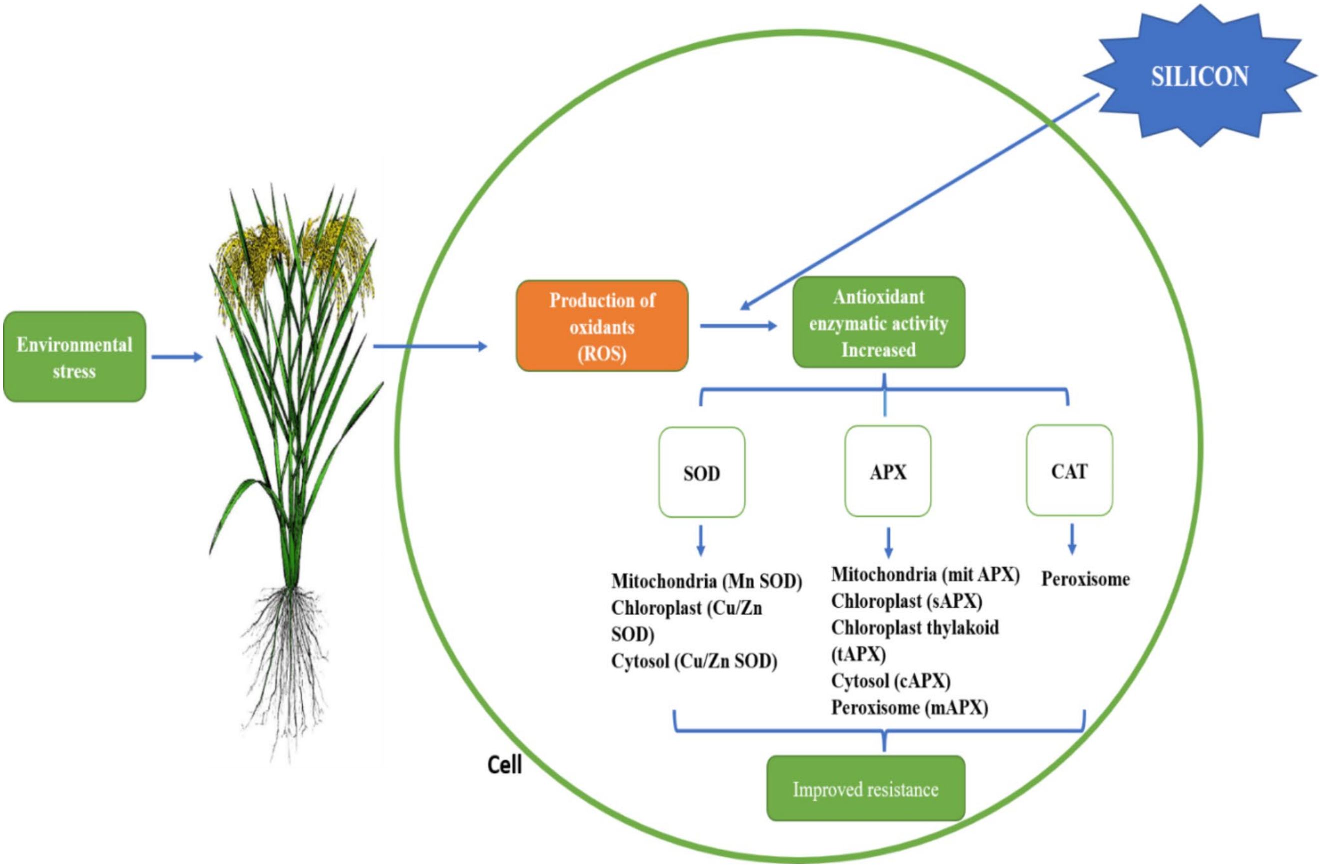

Fig. 2 Schematic representation of the interaction of silicon against different environmental stresses

Table 3 Role of silicon in alleviating different abiotic stresses in various crops

Plant	Form	Stress	Impact	Reference
Barley	Potassium silicate	Salt stress	Potassium and sodium absorbed and transported selectively	Liang et al. 2003; Liang 1999
Wheat	Calcium silicate	Salt	Reduced Na + and increased K + uptake	Ali et al. 2009
Sorghum	Silicon	Drought	Specific leaf weight (SLW), leaf dry weight (LDW), increased leaf area index (LAI), chlorophyll content (SPAD), root dry weight (RDW), shoot dry weight (SDW), total dry weight (TDW) (TDW)	Ahmed et al. 2011
Tomato	Sodium silicate	Salt	H2O2 level and MDA concentration fell as Superoxide dismutase, CAT, and APx activity increased	Al-aghabary et al. 2005
Rapeseed	Silicon dioxide	Cadmium	Modulated AsA-GSH Pathway and Glyoxalase System	Hasanuzzaman et al. 2017
Maize	Silicon	Chilling	Increased superoxide dismutase activity in the shoots and roots, as well as a reduction in Zn and Mn losses from germinating seeds	Moradtalab et al. 2018
Sorghum	Calcium silicate	Drought	Dry forage yield and water use efficiency enhanced	Niyazi et al. 2018
Barley	Sodium silicate	Cold	Modified activity of apoplasmic enzymes and concentration of metabolites	Joudmand and Hajiboland 2019
Oil palm	Sodium silicate	Drought	Seedlings tolerant to drought	Amanah et al. 2019
Sweet pepper	Foliar application	Salt stress	Enhanced antioxidant activity of enzyme	Abdelaal and Hafez 2020
Sugarcane	Sodium and potassium silicate	Water deficit	Modified C: N: P stoichiometry and increased C use efficiency	Teixeira et al. 2020

superoxide dismutase (SOD) activity in shoot and roots as well as an increase in concentrations of proline, phenolics, and antioxidants and reduced levels of H_2O_2 in the tissues (Moradtalab et al. 2018).

In sorghum, foliar spray of calcium silicate increased the forage dry yield and water use efficiency (Niyazi et al. 2018), while in leaves of oil palm seedlings, enhanced proline concentration, nitrate reductase activity (NRA), stomatal closure and chlorophyll content was observed. Amanah et al. (2019) also tried Na_2SiO_3 in oil palm against drought stress and observed that the oil palm seedlings showed tolerance against drought. Foliar application of silicon in sweet pepper helped to defend salt stress by enhancing the activity of antioxidant enzymes (Abdelaal et al. 2020). In sugarcane, silicon (Si) supplementation mitigated the damage caused due to water deficiency by improving the C:N:P balance, increasing C, N, and P use efficiencies and the biomass conversion, and finally enhancing the yield (Teixeira et al. 2020, 2022). Si treatment increased rice submergence tolerance and decreased yield loss by reducing the unfavourable impacts of reactive oxygen species and quiescence strategy. Through, the synergistic regulation of endogenous hormones ethylene (ET), gibberellic acid (GA), and jasmonic acid (JA), Si dramatically suppressed elongation and internode length in wild type rice under submergence (Pan et al. 2022). However, the addition of Si had no effect on the expression of the SUB1A gene, which is responsible for submergence tolerance features of rice (Xu et al. 2006; Pan et al. 2022).

Silicon contributes in the alleviation of heavy metal stress caused by cadmium, copper, aluminium, and other metals (Table 4). Si application alters soil physical qualities such as pH, electrical conductivity, and organic matter, as well as soil microorganisms, causing nutrient release that competes with heavy metals for uptake and translocation to plant roots to be expedited. Furthermore, Si significantly reduced heavy metal uptake through chelation or arresting heavy metals in the soil. Heavy metal bioavailability is reduced which as a result limits their transmission from root to shoot. Also, Si reduces adverse effects of heavy metal toxicity in the cells by stimulating the antioxidant enzyme activity, complex formation with metal ions and compartmentalization of metal -silicon complex and exerting change in the cell wall, thus controlling the transport of heavy metals (Tubana and Heckman 2015). Application of Si in cadmium stressed rapeseed, reduced MDA content and H_2O_2. There was an increase in AsA and GSH pools as well as activities of glyoxalase system (Gly I and Gly II) enzymes and CAT, leading to an improved antioxidant defense (Hasanuzzaman et al. 2017). Rice showed the positive effect of Si against cadmium stress by reducing the accumulation of heavy metals in rice roots (Kim et al. 2014). The combined stress of Cd and Pb in quinoa led to 11-fold increase in H_2O_2 generation and a 13-fold increase in TBARS synthesis, as well as a decrease in membrane stability (59%). Exogenous injection of K and Si in combination reduced oxidative stress caused by metals by eight times. SOD, CAT, APX, and POD activities increased 9-fold, 7-fold, and 11-fold, respectively (Algharby et al. 2022).

Interaction of silicon with other phytohormones for growth, development and stress alleviation

Silicon (Si) plays a crucial role to enhance the nutritional state of crop plants for the promotion of development and productivity. Under biotic and abiotic stresses, the exogenous application of Si activates plant defense and phytohormone signalling mechanisms (Khan et al. 2022) (Fig. 3). Plant biological processes are frequently influenced by phytohormones that also control cellular signalling in response to salt, drought, extremely high temperatures and nutrient shortage stress (Salvi et al. 2021). In order to better understand the mechanism, regulation and interaction of silicon with various phytohormones, the findings from diverse investigations have been discussed.

In rice plants, it was observed that under arsenate stress, the expression of auxin biosynthesis genes (*OsYUCCA1* and *OsTAA1*) dropped along with the decrease in root biomass. However, the presence of Si significantly boosted the expression of *OsYUCCA1* and *OsTAA1*, which ultimately leads to an increase in the number of roots and biomass. It was suggested that Si-driven root development under arsenate stress in rice plants is mediated by auxin biosynthesis genes (Tripathi et al. 2021). The addition of IAA to the AgNPs + Si

Table 4 Effect of silicon for alleviating various metal stress in different crop species

Plant	Form	Stress	Effect	Reference
Rice	Silicon	Aluminium (Al)	Alleviation in aluminium accumulation	Singh et al. 2011
Rice	Silicon	Cadmium (Cd) and copper (Cu)	Ameliorated root function	Kim et al. 2014
Maize	Sodium silicate	Cadmium (Cd)	Enhanced thylakoid formation and photosynthetic rate	Vaculik et al. 2015
Tobacco	Potassium silicate	Copper (Cu)	Elevated ET and PA biosynthetic genes	Flora et al. 2019
Quinoa	Sodium silicate	Cadmium (Cd) and Lead (Pb)	Improved antioxidant capacity	Alharby et al. 2022

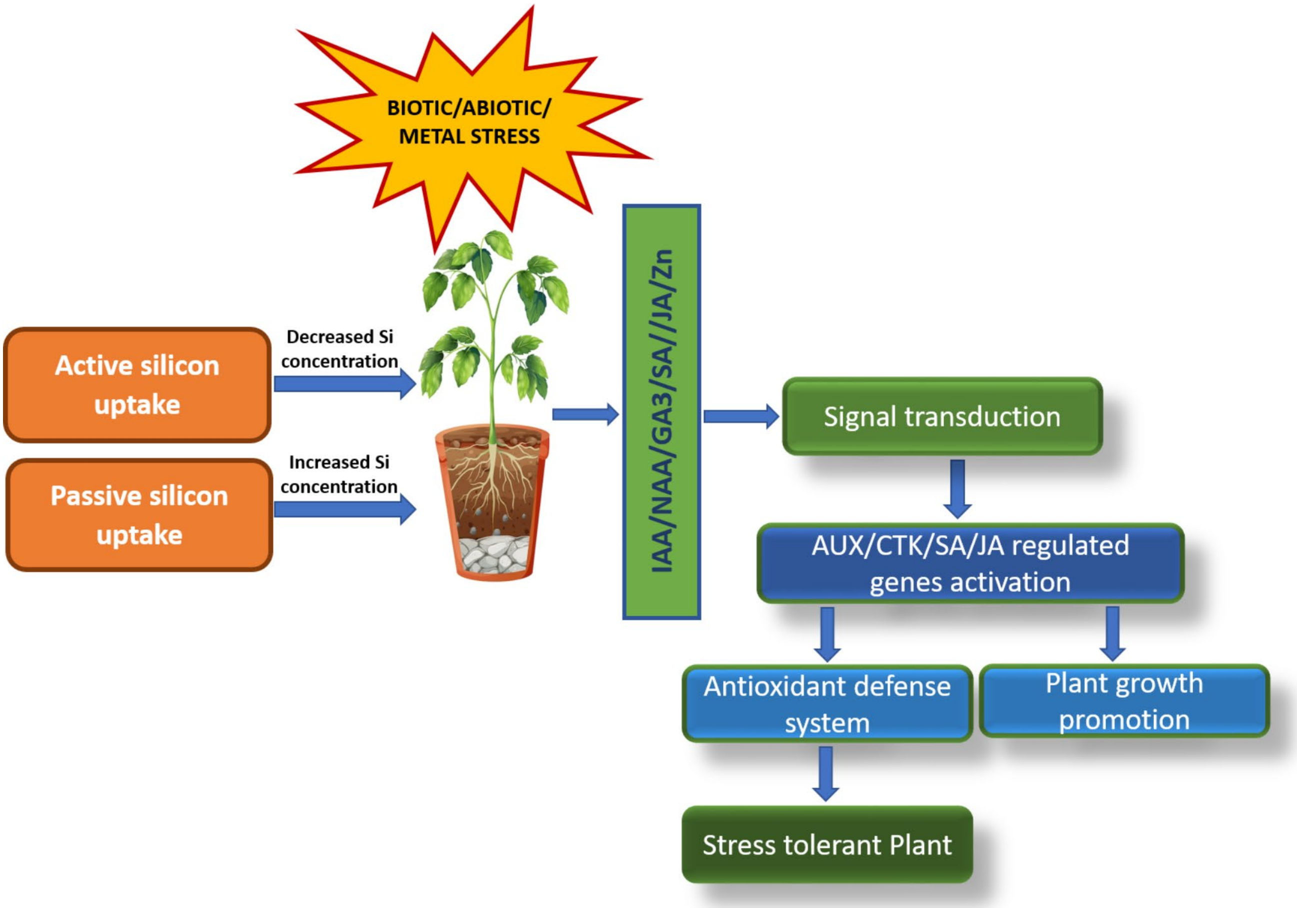

Fig. 3 Pictorial representation for interactions of silicon with different phytohormones for growth promotion and stress resilience

mixture was also effective in reducing the harmful effects of the silver nanoparticles in *Brassica juncea*. Increased length of shoots and roots as well as reduced nitric oxide levels under AgNPs stress was observed in *Brassica juncea* (Vishwakarma et al. 2019). In maize, phytohormones (auxin IAA, gibberellins GA and abscisic acid ABA) and antioxidant enzyme activity (superoxide dismutase SOD, ascorbic peroxidase APX, and catalase CAT) were used to determine if plants were resistant to drought stress. Stressed plants without silicon treatment showed enhanced SOD and CAT activity along with a decrease in IAA. Plants grown on non-tillage soils applied with silicon treatment showed increase in IAA concentration with decreased SOD and CAT activity (Merhij et al. 2019).

Silicon supplementation along with NAA indicated that silica might have contributed in polar transport of auxin as an elicitor of ABA biosynthesis leading to initiation of lateral root growth of cowpea (Hu et al. 2020). However, exogenous GA_3 and potassium silicate proved to be extremely successful in reducing salt-induced damages in okra cultivars. Along with that, fresh weight and dry weight of roots and shoots, plant height, root and shoot length were also increased (Ayub et al. 2018). In date palm, exogenous application of Si and GA_3 activated the genes associated with the heat shock factor. Moreover, the combined treatment of Si and GA_3 dramatically reduced the transcript accumulation of genes involved in ABA signalling (*PYL4*, *PYL8*, and *PYR1*). These results imply that the combined application of Si and GA_3 promotes plant growth and metabolic regulation and confers stress resilience (Khan et al. 2020). Cytokinin is also a major plant growth hormone which is responsible for cell division and shoot proliferation in plants. Si treatment enhanced zeatin concentration in the root and shoot tissues of maize which finally lead to protect plants from cold-stress (Moradtalab et al. 2018).

Si also encourages the production of phenylalanine ammonia-lyase, which is a precursor to SA biosynthesis (Souri et al. 2020). Silicon in combination with SA promotes arsenic toxicity tolerance in wheat by inducing plant morphological characters, minimise electrolyte leakage and decreased ROS lipid peroxidation (Maghsoudi et al. 2020, Arif et al. 2021). The physiological effects of methyl jasmonate (MeJA) (0.5 mM) and silicon nanoparticles (2 mM) on some salinity-related genes (*DREB*, *cAPX*, *Mn-SOD*, and *GST*) in strawberry cv. Paros was noticed under saline (50 mM NaCl) and non-saline conditions. The use of MeJA and Si nanoparticles boosted the transcription of the *DREB*, *cAPX*, *MnSOD*, and *GST* genes which ultimately leads to enhance salinity tolerance in strawberry cultivars. The strawberry plants responded better to salt stress by improving enzymatic and non-enzymatic antioxidants' physiological defence systems and by upregulating the transcription of salinity-related genes in response to MeJA and Si application (Moradi et al. 2022).

Si increased the levels of endogenous hormones in *G. uralensis* seedlings. Si had an increasing impact on IAA and GA_3 concentrations after 10 days of application. Whereas, at a concentration of 2 mM, Si had also a greater impact on ABA biosynthesis after 20 days. Hence, Si can control endogenous hormone concentrations and thereby enhance the growth of *G. uralensis* seedlings under salt stress conditions. This study showed that Si had a concentration and time-dependent positive effect and might also reduce the negative effects of salt stress by controlling the levels of endogenous hormones (IAA, GA_3, and ABA) (Lang et al. 2019).

Future perspectives and conclusion

Silicon is a major component of soil and has a proven role in plant growth, development, and biotic and abiotic stresses resilience. It is commonly known that silicon has positive impacts on agriculture production and productivity. Si has been shown to positively modulate the physiological characteristics of agricultural plants, aiding in the fight against abiotic stress situations. Si's ability to upregulate phytohormones and the signalling cascades that they use to survive abiotic stressors is essential to its function. Surprisingly, Si is said to increase the resilience to abiotic stress conditions by overexpressing the genes that control the production of phytohormones. Through signal transduction pathways, Si-induced phytohormones mediate stress tolerance, which is predominantly controlled by these mechanisms. The molecular mechanisms underpinning Si absorption, transport, and accumulation in various crops are still poorly understood. It needs to be understand whether manipulation of Si transporters and further accumulation of Si in non-accumulators can improve stress tolerance.

An in-depth understanding of Si's crucial function in overcoming stress tolerance is still lacking, largely because the molecular mechanism is very little understood. Furthermore, considerable scientific research into how Si and phytohormones work together to improve plants' ability to tolerate drought is still in its early stages. To confirm the significance of Si as the key component in fertilisers for fortification and sustainable agricultural development, it is also necessary to uncover other genes related to physiological functions. Detailed investigation of the cross-talk between Si and phytohormones can be improved by cutting-edge omics technologies including transcriptomic, proteomic, and metabolomic research in order to elucidate new signalling molecules responsible for alleviating the stress tolerance in plants. Additionally, Si's function in controlling signal transduction pathways under a variety of abiotic stress conditions requires specific attention. Silicon has a strong impact on crop quality, strength, and yield and therefore silicon supplementation holds a great potential as a plant protectant and growth stimulant for sustainable resilient agriculture.

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Declarations

Conflict of Interest The authors declare that they have no known competing interest.

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