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Review Article

Importance of silicon in combating a variety of stresses in plants: A review

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Abstract
The abundance of silicon (Si) in the earth's crust is found as silicon dioxide (SiO_2). But this abundance of Si is not a sign that the plants take up an adequate amount of Si. This review article incorporates research based on Si to understand the importance of Si in plants under various stress conditions and its role in sustainable agricultural production. Si's application is considered a better approach to providing stress tolerance to plants under stress conditions. The review describes the different phases of Si, its absorption, transport in plants, and its various mechanisms of action to tolerate specific stresses. The uptake and transport of Si through various Si transporters have also been reported. This review also discusses the various mechanisms of Si under biotic or abiotic stress in different plants. The application of Si improves soil quality and soil health and enhances the soil microbial population. In addition, the role of Si in the upregulation and down-regulation of proteins under stressful conditions has also been reported. The information can help to better understand the importance and mechanism of Si in plants and its application in agriculture.

Keywords: Abiotic stress, Pathogen stress, Proteomics, Silicon, Transporters

INTRODUCTION

Silicon (Si) is defined as the utmost important element in earth's crust and generally present as silicon dioxide (SiO_2) along with various ranges of Si-binding minerals in three phases, i.e., amorphous, crystalline, and poor-crystalline phases (Sommer *et al*., 2006). In past years, among 15 elements, Si was known to be one required for plants' life (Halligan, 2013). But even at this time, the beneficial role of Si is not recognized for higher plants because of the absence of proof that shows the essentiality of Si in plant processes. Before that, Si is only considered beneficial for the algae (golden or brown), diatoms, and scouring rushes. Due to the non-availability of a proper definition of the essential nutrient, Si is considered a main inorganic component in higher plants (Epstein, 1999). Many researchers have conducted their experiments to explore the role of Si in agriculture, and they also concluded that Si helps plants enhance their overall production (Epstein, 1994; Snyder *et al*., 2007). Because of this reason, Si is also used as a supplement in the form of fertilizers in many countries. Many plant species can store Si in their dry matter. Based on this ability, seven different plant species are reported that can accumulate around 1% Si in their dry matter. According to Bhardwaj & Kapoor (2021), Si is a vital nutrient from agricultural perspective, which increases production yield by supporting plants under various phases of their lifecycle in stressful conditions.
In some cases, like horsetail and rice, the plant grows well without Si presence, but their absence of Si drags plants towards fungal infection (Datnoff and Rodrigues, 2005; Law and Exley, 2011). Ma (2004) believed that

apart from its significance in abiotic stress, Si also helps the plant enhance their tolerance to different biotic stress and protects them from different diseases. Plants usually absorb the Si in the form of silicic acid [$Si(OH)_4$] (Ma and Yamaji, 2006). Deshmukh *et al*. (2015) reported that the conserved NPA domains, which contain exactly 108 amino acids spacing in between, regulate the permeability of silicic acid. Based on the quantities of Si present on the plant parts, they are categorized into three types, i.e., accumulators, intermediate, and excluder plants (Mitani and Ma, 2005). Equisetales, Cyperales, and Poales are the best Si accumulators, among which rice is considered the highest Si-accumulating plant, in which around 10% of dry matter is contributed by Si (Ma *et al*., 2002). Stinging nettle (*Urtica dioica*) is a Si-intermediate plant, while tomato is considered in the excluders group (Trembath-Reichert *et al.*, 2015). The integration of Si as SiO_2 in plant cells and its precipitation into the cell wall forms a physical barrier protecting the plant from different biotic stresses. But the passive mechanism of Si transport in the plant does not clear its role in how it is good for plants for different stresses. According to Guerriero *et al*. (2016), precipitation of Si is generated by the specific components of the cell wall in plants. In stress conditions, Si accumulation is increased with the high level of stress in the plant cell wall and provides stability to the membrane. Si has multiple positive effects on plants under different biotic and abiotic stresses via different mechanisms (Pooja et al., 2021). During cell culturing of the rice plant, Si was found as a hemicellulose confined structure (He *et al*., 2015), and in horsetail, the establishment of SiO_2 occurs with the help of mixed-linkage glucan (MLGs) (Fry *et al*., 2008). The importance of MLGs in Si formation has been proved by the overexpression of a hydrolase enzyme on MLGs, which resulted in lower silicification (Kido *et al.*, 2015). Based on the structural differences, various Si transporters were found in the roots of both monocotyledonous and dicotyledonous plants (Zargar *et al*., 2019). Documentation has been gathered on the advancement of Si study in agriculture to see its worth globally, but in many countries, little work is done for Si in agriculture (Tubana *et al*., 2016).

This review discusses a brief account of the abundance and activity of Si in plants and soil, along with the different methods of uptake and transport and their application in various stress management.

Si in soil environment

Around 28% of the weight is considered for Si in the earth's crust. About 0.52% to 47% Si is present in basalt rock and 23 to 47% Si in orthoquartzite rocks, while some evidence of Si is also found in carbonites and limestones of carbonaceous rocks (McKeague and Cline, 1963; Wedepohl, 1995; Monger and Kelly, 2002). Almost 50-70% of the soil aggregates are formed of silicon dioxide (Ma and Yamaji, 2006). Dissolved Si as mono silicic acid (H_4SiO_4) is produced by the chemical breakdown of rocks rich in Si-comprising components. This breakdown of Si-rich rocks comes up with soil formation through different biogeochemical reactions, which is the main source of silicic acid (Basile-Doelsch *et al*., 2005). Usually, the process of Si discharge to the soil environment is slow and is ruled by accumulation and new development of Si deposit components of rocks. Adsorption of these authigenic partitions of Si is done on the different phases of rock soils. After being adsorbed on a solid phase, uptake and incorporation are performed by plants and other soil microbes (Cornelis *et al*., 2011). This phenomenon of formation and development is interconnected. The major inter-pool transmission of Si occurs among biomass (biogenic silica) and soil environment (H_4SiO_4 in dissolved form) that ranges from 1.7 to 5.6 x10^{12} kg Si per year (Conley, 2002) and in oceans among diatoms (biogenic silica) and dissolved Si (around 6.7 x 10^{12} kg Si per year (Treguer *et al*., 1995; Matichencov and Bocharnikova, 2001). Laruelle *et al*. (2009) reported that the Si quantity converted to biogenic silica form is approximately 2.5 x 10^{12} kg per year (Laruelle *et al*., 2009). Based on their state, Si is divided into three phases in the soil environment such as adsorbed, liquid, and solid-phase fragments. These Si component fragments with their composition are shown in Fig. 1.

Solid-phase is considered the first phase of Si, which is made of crystalline, poor-crystalline, and amorphous Si. Higher fragments of solid-phase Si are present in crystalline forms, mostly as former and later silicates and silica matters. On the other hand, the amorphous form of Si is formed in two ways, i.e., through rocks (pedogenic) or by plant matter and microbes (biogenic). Si is found in complexes with heavy metals and soil material in this form. The amount of Si in the liquid phase is majorly disturbed by the dissolvability of Si in the solid phase. The dissolvability of Si in the amorphous phase is between 1.8 to 2 mM, whereas, in quartz, a crystalline Si ranges from 0.11 to 0.26 mM approximately. Thus, amorphous Si is better soluble than crystalline Si (Drees *et al.,* 1989; Monger and Kelly, 2002). These components of Si in the soil form the soil structure. Mostly, different forms of Si are low in solubility and immovable in the soil to plants. Monosilicic and polysilicic acids are the two forms of Si that have high solubility in soil and belong to Si's liquid and adsorbed phase fragments (Matychenkov and Snyder, 1996b). Monosilicic acid is majorly present in a poorly adsorbed form and is less mobile in the soil environment (Matichenkov *et al*., 1997; Khalid and Silva, 1980). By raising the level of H_4SiO_4 in soil, plant roots can absorb Si in them. With H_4SiO_4, plants also absorb phosphate from the soil solution because of the similar-

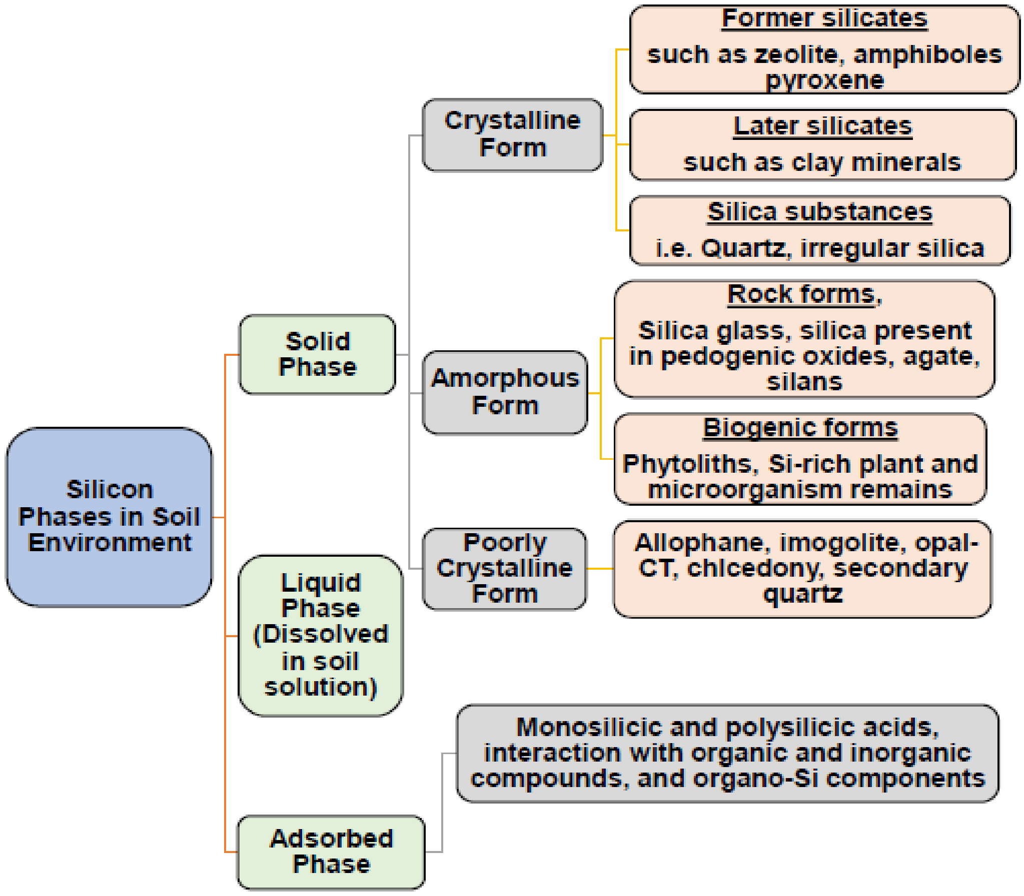

Fig. 1. *Phases of Si in the soil environment, revised from Matichencov and Bocharnikova, (2001); Sauer et al. (2006)*

ity in the chemical structure of phosphate and silicate ions. This process resulted in an increase in the amount of H_4SiO_4 in soil and gave competition to phosphate ions (Matychenkov and Ammosova, 1996a). By interacting with ions and different types of heavy metals and making complexes with them, the insoluble nature of H_4SiO_4 declines to some extent (Lumsdon and Farmer, 1995).

However, polysilicic acids contribute to soil formation with soil compounds and affect their properties (Exley and Birchall, 1993). Plants uptake Si mostly in the plant -available form of soil, i.e., H_4SiO_4, a monomeric unit of silicic acid. These units form a chain of silicic acid that results in polymeric silica through polymerization (Williams and Crerar, 1985). Polysilicic acid is not a plant-available form like H_4SiO_4, but it upgrades the soil quality, maintains the water carrying capacity, and forms the connection between Si and soil (Norton *et al*., 1984). These different forms of Si support the dynamics of Si in soil (Tubana *et al*., 2016). Sometimes, Si bioavailability for plants becomes very low and plants are unable to take up a certain amount of Si from the soil environment due to the leaching of Si through heavy rainfall and some other factors. At that time, plants are more sensitive to stressed conditions and are badly affected in the absence of Si (Schaller *et al*., 2021). Moreover, poor management practices and frequent harvesting in agricultural soils reduce the level of Si in the soil environment, affecting crops with various stresses (Puppe, 2020; Schaller *et al*., 2021).

Agricultural production can be improved by the application of Si in the form of fertilizer. Likewise, it is used for agrochemicals as a dispersal medium (Vasanthi *et al*., 2012). As Si contains the organic compound, it is harmless in agriculture and has a better saturating capacity. It is also considered a spreading agent in the agricultural field due to its ability to spread easily (Vasanthi *et al*., 2012a). Seed priming with Si application also gives good results under different abiotic stressed conditions. The prior effect of Si in seed priming increases the harvest index and yield production under stressed conditions (Sirisuntornlak *et al*., 2021).

Uptake, absorption, and mechanisms of Si

Plants absorb Si in the form of H_4SiO_4, whose concentration ranges from 0.1 to 0.6 mM in the soil solution (Knight and Kinrade, 2001). The absorption of Si in various plant parts differs significantly as it involves different phases of Si transformation at the time of absorption, accumulation and transportation (Kaur and Greger, 2019). Cornelis *et al*. (2011) reported that uptake of Si in plants is occurred by three different mechanisms, i.e., active, passive, and rejective. Most dicot plants take up Si through the passive mechanism along with transpiration bypass flow (Ma *et al*., 2001). Absorption of Si, via an active mechanism, is common in many plants like rice, wheat, maize, and sugarcane (Casey *et al*., 2004; Rains *et al*., 2006). Various transporters of Si have been reported in rice (Ma *et al*., 2006), barley (Chiba *et al*., 2009), and maize plant species (Mitani *et al*., 2009a). Si is taken up by two main types of transporters i.e., influx and efflux transporters, which are mainly located at the plasma membrane of the plant cells. These transporters vary in their position and action in various plants (Kaur & Greger, 2019).

The uptake of Si is mainly by roots, and after that, it is transferred from the root xylem towards the shoot with a transpirational bypass flow mechanism (Ma *et al*., 2006). Around 90% Si is transferred directly to shoots from roots via different mechanisms (Ma and Takahashi, 2002). Si transporters are present in high concentrations in the Si-accumulating plant species. The transportation of Si from the root region to the shoot region is increased via these transporters through the active mechanism. Si transport type is always more than the passive mechanism (Mitani and Ma, 2005). Lsi1, Lsi2, and Lsi6 are Si-transporters present in rice plant and helps in loading of xylem and transporting Si in roots and shoots (Mitani and Ma, 2005; Ma *et al*., 2006, 2007). Si is accumulated as amorphous silica in the shoots after the transfer, majorly at the transpiration area, and after accumulation in the shoots, it became immovable and not reallocated anywhere (Ma and Takahashi, 2002; Hodson and Sangster, 1990). Phytoliths have been seen in some plants and differ individually in many plant species based on their location in particular plant part, structure, and type (Guntzer *et al*., 2012; Li *et al*., 2014). Phytoliths are rigid structures of amorphous silica accumulated in plant parts' intracellular and sometimes extracellular regions, which cannot decompose even after the plants die. Si is deposited in various plant parts like plant cell walls, root endodermis, and shoot epidermis (Lux *et al*., 2003, Keller *et al*., 2015).

Cell walls form a physical barrier to prevent the entry of a pathogen or insect and protect it from suffering from any pathogen-related diseases (Alhousari and Greger, 2018). The formation of phytoliths enhanced cell wall protection by strengthening the wall's layer in plants. Due to the presence of Si in leaves, leaves become rigid and hard, and this nature of silica-containing leaves provides plant resistance, tolerance, protection, and strength from pathogens. Many plants like coffee (*Coffea*) (Carre-Missio *et al*., 2009), peppers (*Capsicum*) (French-Monar *et al*., 2010), and tomatoes (*Solanum lycopersicum*) (Huang *et al*., 2011), accumulate higher concentration of Si in their root region as compared to shoots region.

It is supposed that most of plants absorb Si from the soil environment but those plants which do not accumulate Si in their plant parts are known as non-accumulators. So, most scientists have explained the different categories of plants as high Si-accumulators, intermediate Si-accumulators and low Si-accumulators. Plants that accumulate around 10-100 g kg^{-1} Si in their dry matter are in the category of high Si-accumulators. In this category, plants belong to monocots mostly and from the Poaceae family, like wheat, rice, sugarcane, and barley (Liang et al., 2007; Ma et al., 2001; Ma and Ma Takahashi, 2002). Those plants that accumulate around 5-10 g kg^{-1} Si in their dry matter are intermediate Si-accumulators and also belong to monocot plants. In contrast, the plants considered low accumulators for Si belong to dicots and contain a lesser amount of 5 g kg^{-1} Si in their dry weight. In most cases, Si is absorbed by the roots and it gets accumulated in the leaf epidermis. At the time of transpiration, water is lost through the leaf, and the Si in the leaf becomes polymerized into amorphous silica and forms phytoliths in plants (Yoshida *et al*., 1962; Jones and Handreck, 1965, 1967; Raven, 1983).

Deposition of Si in the form of amorphous silica is immovable in plants and cannot be reallocated anywhere. In the case of metal toxicity, Si makes complexes with different metal ions and slows their transport into the different plant parts, resulting in reduced toxicity (Richmond and Sussman, 2003; Ma *et al*., 2004). Different plants have different abilities to take up Si in their plant parts but it also depends on the soil environment whether the efficient amount of Si is present or not (López-Pérez *et al*., 2018). Si mediates three types of mechanisms i.e., physical, biochemical and mechanical by deposition of Si in plants. These mechanisms aid the plant in different biotic and abiotic stresses and provide plant resistance by modulating the changes in plant physiology (Luyckx *et al.,* 2017). Absorption of Si is mainly through the different water channel proteins like aquaporins. So, this uptake and absorption depend on the flow of water-related to the transpiration process (Exley, 2015; Sakurai et al., 2017).

According to a hypothesis, Si accumulation occurs in cells of leaf and shoots, which provide mechanical supports and form a barrier for resistance to pathogens (Ma, 2004). Due to this mechanical barrier, the pathogen's penetration is inhibited, making the plant's wall more resistant to the destruction by fungi and bacteria. This hypothesis is supported by the positive impact of Si on the inhibition of pathogen infection and diseases. Secondly, in some plants, Si acts as a signal molecule in the plant cells to trigger the formation of phytoalexins with respect to the pathogen's attack (Chérif *et al*., 1994). In the cucumber plant, Si induces the activation of antioxidant enzymes and activates the chitinase activity in the plant after a pathogen attack with *Pythium* species (Ma, 2004). New perceptions are made for Si on providing plant resistance to antagonize the pathogen's entry and infection via host plant resistance mechanisms (Rodrigues *et al*., 2015). In the host plant resistance mechanism, the R gene is present in plants which forms the amino acids, proteins, and biochemical products to activate the defense system in plants which spreads the resistance all over the plants for any plant pathogens attack. The Si in plants regulates the interaction between host and pathogens with different defense responses. Si helps in the ups and downregulation of R genes, providing a defense response in plants like wheat and tomato (Bélanger *et al*., 2003; Chain *et al*., 2009; Ghareeb *et al*., 2011).

Si was supposed to be involved in a defense mechanism regarding fungal infection in plants on behalf of these. Datnoff *et al*. (1992), accepted this theory by showing his experiment outcome in the form of fungitoxic components found in Si treated rice plant infected by fungi pathogen named *Magnaporthe oryzae.* These components are recognized as momilactones, a phytoalexin of rice plants, in response to activation of the defense system via Si application (Rodrigues *et al*., 2003, 2004). Si acts as a stimulus in plants in stress conditions and activates all the stress signaling molecules to make a defensive response, eventually leading to resistance in the plant against the pathogens (Fauteux *et al*., 2005). According to Alhousari and Greger (2018), Si is found in different forms in different plant cells like oval-shaped silica cells in wheat and butterfly-shaped silica cells in rice and maize plants. These shapes were observed by scanning electron microscopy (SEM). The silica structures in plants also differ at different stages of development. The accumulation of Si changes from small simple cells to complex bulliform cells with increasing Si concentration in plants (Dorairaj and Ismail, 2017). Even though the mechanism of Si is not clearly understood until now, its role in enhancing plant stress hormones concerning defense response against any pathogen is currently under debate.

According to microarray studies, it has been proved that the application of Si in plants infected with pathogens contains an increased level of jasmonic acid, ethylene and salicylic acid. These are the plant stress hormone-induced in plants during stress conditions as a defensive response (Rodrigues *et al*., 2015). A molecular study of rice, wheat, and tomato plants, which were grown in soil with Si application, and injected with a specific pathogen, resulted in a variance genetic expression of different types of genes that were involved in the antioxidant defense system of the plants when compared with the control. This study of Si and pathogen infection is supported by Vivancos *et al*. (2015). Indirect evidence shows that there might be other mechanisms of Si involved in plant stress management. Documentation has been done on the beneficial role of Si in plants, and it mainly shows the positive effect of Si fertilizer in enhancing agriculture production under different stress environments (Epstein, 1999; Li *et al.*, 2007). Although Si as a biofertilizer improves the soil quality and fertility by increasing the population of soil microorganisms and their colonization with improving their soil environment. Because of this, Si has a significant role in reducing the loss of soil microorganisms and soil bacteria and improving their population in the soil (Wang *et al*., 2020). Different mechanisms maintain agriculture production, improve their status,

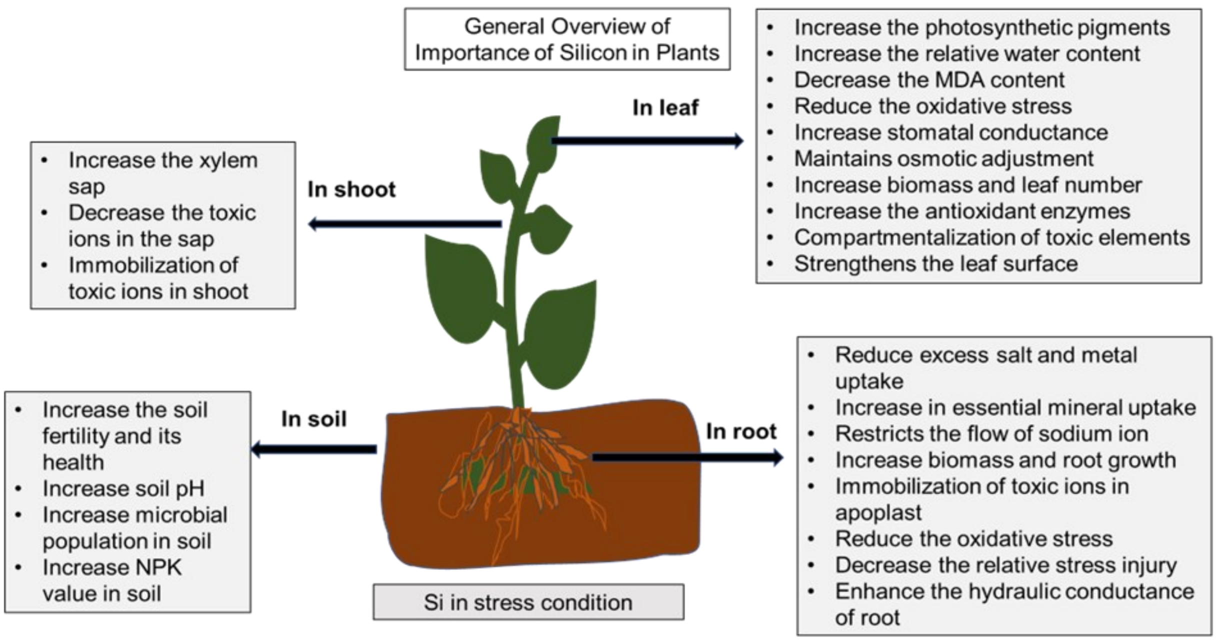

Fig. 2. *Various role of Si in different plant parts and soil under stress conditions*

and provide resistance to various diseases under stress conditions via Si application in plants.

DIFFERENT MECHANISMS OF Si

Si-induced changes in the apoplast

Si plays a key role as SiO_2 (amorphous silica) in forming the plant cell wall via interacting with different components. Si provides stability, resistance, and mechanical assistance to the above-grounded plant parts by increasing the silica deposition, lignin formation, and suberization (Guerriero *et al*., 2016). It is mainly found in monocot plants rather than dicots. The binding of Si with hemicellulose of the cell wall resulted in greater mechanical support, which helped in drought conditions (He *et al*., 2013, 2015). In drought-stressed conditions, Si maintains the structural integrity by binding with the hemicellulose in the cell wall of plants (Ma *et al*., 2015). Hemicellulose in cell wall is a very important part of the plant, which holds the water in large amount during water-deficit conditions and shield the cell wall in maintaining membrane stability (Souri *et al*., 2020). Si-accumulation occurs in amorphous silica form, which acts as a barricade in apoplast of plant cells via polymerizing the chain of silicic acid; this is called biosilicification in plants (Exley, 2015). The mechanical assistance in plants via Si contributes to the major elimination of stress, i.e., biotic or abiotic stresses. The Si-forming barrier greatly reduces penetration and pathogen-associated infection in plants (Fauteux *et al*., 2005). It also helps in alleviating different kinds of heavy metal stresses such as cadmium (Cd) (Ma *et al*., 2015), manganese (Mn) (Rogalla and Römheld, 2002), aluminium (Al) (Wang *et al*., 2004), and sodium (Na) (Saqib *et al*., 2008). The transcription of genes involved in lignification and suberization is regulated by Si application in plants. Lignin and suberin are the main components for forming the Casparian strip. Si application in rice plants helps them in Casparian strip formation in root endodermis and exodermis and increases the process of suberization and lignin formation (Fleck *et al*., 2011, 2015; Suzuki *et al*., 2012). Moreover, in soybean, Si upregulates the expression of lignin formation genes and enhances the mechanical strength of lignin formation in plants in stress situations (Hussain *et al*., 2021).

In rice plants, an increase in the formation of suberin and lignin due to Si may impair the transport of sodium ions through the apoplast in the roots and provide tolerance to salinity (Krishnamurthy *et al*., 2011). Deposition of Si helps restrict sodium ion transport from root to shoot region through “transpirational bypass flow” pathway in rice cultivars (Gong *et al*., 2006). Si is deposited on the apoplast and extracellular matrix via polymerization and adding Si in roots and leaves and builds the cell walls of leaves, xylem vessels, and root epidermal cells of plants (Fawe *et al*., 2001, Kim *et al*., 2002). In a study of the wheat plant, it was found that Si application alleviates cadmium (Cd) toxicity by enhancing the suberization process at the root endodermal cell (Wu *et al*., 2019). It is suggested that Si may also diminish the toxicity of other heavy metals via maintaining lignin and suberin formation in root cells (Xiao *et al*., 2022).

Transpirational bypass flow pathway

Transpirational bypass flow is a mechanism by which sodium ion or other solute is accumulated in the leaf and other parts of the plant, and it mostly takes place through the apoplastic pathway of the plants (Yadav *et al.*, 1996; Krishnamurthy *et al.*, 2009; Faiyue *et al.*, 2012). The transport of mineral ions from root to stem normally includes a number of phases through transmembrane in roots; these membrane permits the mineral ions to pass the filtration blockage of root endodermis and enters the ions into the xylem stream. Many sodium ions (almost around 50%) can pass this filtration blockage through the apoplastic pathway (Maathuis *et al.*, 2014). In this pathway, mineral ions and solutes can enter the xylem directly via gaps created where endodermis does not develop properly (in young stems and roots and where lateral root arises) without even passing the membrane filter (Ranathunge *et al.*, 2005).

The sodium ions which are easily absorbed by roots in high salt stress conditions and pass through apoplast cells via bypassing the separation barricade of the root endodermis, which generally stops the non-restricted flow of sodium ions and other elements in the transpirational flow (Yeo *et al.*, 1999; Gong *et al.*, 2006). This transpirational bypass flow of sodium ions and water is inhibited by applying Si in rice plants under saline conditions (Yeo *et al.*, 1999). In rice plants, Si restricted the movement of sodium ions from root to stem by blocking the transpirational flow pathway and decreasing the concentration of sodium ions in plants. This resulted in greater improvement in plant growth as well as development under salinity stress (Gong *et al.*, 2006). Excessive absorption of sodium and chloride ions in plant roots causes severe damage to plant growth and their physiology (Flowers and Colmer, 2015). Similarly, in a study, it was found that the deposition of Si in plants may reduce the bypass flow of salt ions and metals through apoplastic barrier and supports the plant to endure in stressed conditions (Coskun *et al*., 2019).

The process through which blockage in bypass flow occurs is not much clear, but it might be through the polymerization of Si in endodermis as well as exodermis of root along with the increase in suberin and lignin formation in the apoplast (Lux *et al.*, 1999; Ranathunge *et al.*, 2005; Krishnamurthy *et al.*, 2009; Maathuis *et al.*, 2014; Yeo *et al.*, 1999; Gong *et al.*, 2006). Despite creating a blockage in the bypass flow, Si has a great role in increasing transpiration and stomatal conductance. But this can vary with the species and stress conditions. Like in rice plants, Si enhanced the transpiration rate in salt and drought-stressed conditions (Chen *et al*., 2011). However, it got reduced in control plants of rice by Si application (Ma and Takahashi, 1993; Agarie *et al*., 1998). The importance of Si deposition in the apoplast and blockage of bypass flow has been observed in plants under abiotic and biotic stresses (Coskun *et al*., 2019). Moreover, Si promotes the transport of essential nutrients in plants through root to shoot by regulating the apoplastic pathway. It is suggested that this increase in nutrient uptake may be due to Si binding with the different plant cells component (Greger *et al*., 2018). Better approaches and research are needed to understand the mechanisms underlying these variations among different plant species. The Si-induced mechanisms involved in enhancing the plant's tolerance to biotic stress (Pathogen's stress) are mentioned in Table 1.

Si-transporters

The application of Si provides tolerance and resistance to the different types of stresses in plants. Various Si transporters are comprised of the absorption, translocation via xylem loading, and supply of Si in the plant parts; these transporters are influx and efflux transporter of Si. The influx transporter of Si is a Nod26-like major intrinsic protein (NIP) that belongs to the aquaporin proteins class. In contrast, the efflux transporter belongs to a well-known anion transporter (Ma, 2013). Many studies found that the process of Si uptake by plants depends upon the influx channel type of transport, which is important for the Si uptake and transport from the outer soil environment to inner plant cells. This influx channel is known as Lsi1, a Si influx transporter that was firstly found in rice plants (Ma *et al*., 2006). The Lsi1 influx transporter is found in almost all Si-accumulator plants which include monocot plants like wheat, rice, maize, and barley (Yamaji *et al*., 2008; Chiba *et al*., 2009; Mitani *et al*., 2009b; Montpetit *et al*., 2012) as well as in dicot plants like soybean and pumpkin (Mitani-Ueno *et al*., 2011; Deshmukh *et al*., 2013). Apart from Lsi1 transporter, a different transporter is also found in rice plant, and other species for Si transport, that is known as Lsi2 transporter, an efflux Si transporter that transport Si to the xylem of the plants (Ma *et al*., 2007; Ma and Yamaji, 2015).

The Lsi2 transporter was found significant for the long-distance transportation of Si in plants. However, its role and nature are unclear until now and have been defined only for monocots and horsetail plants (Vivancos *et al*., 2016). Both Lsi1 and Lsi2 transporters are normally present in the cell membrane, and their dispersal in various species is different. They are mostly found in the endodermis and exodermis of the developed area of primary and adjacent roots of rice (Ma *et al.,* 2006), whereas in maize and barley, they are found in the epidermal, hypodermal, and cortical cells of the plants (Chiba *et al*., 2009; Mitani *et al*., 2009a). According to a study on maize plants, it was found that two genes are responsible for Si accumulation in plants i.e.,

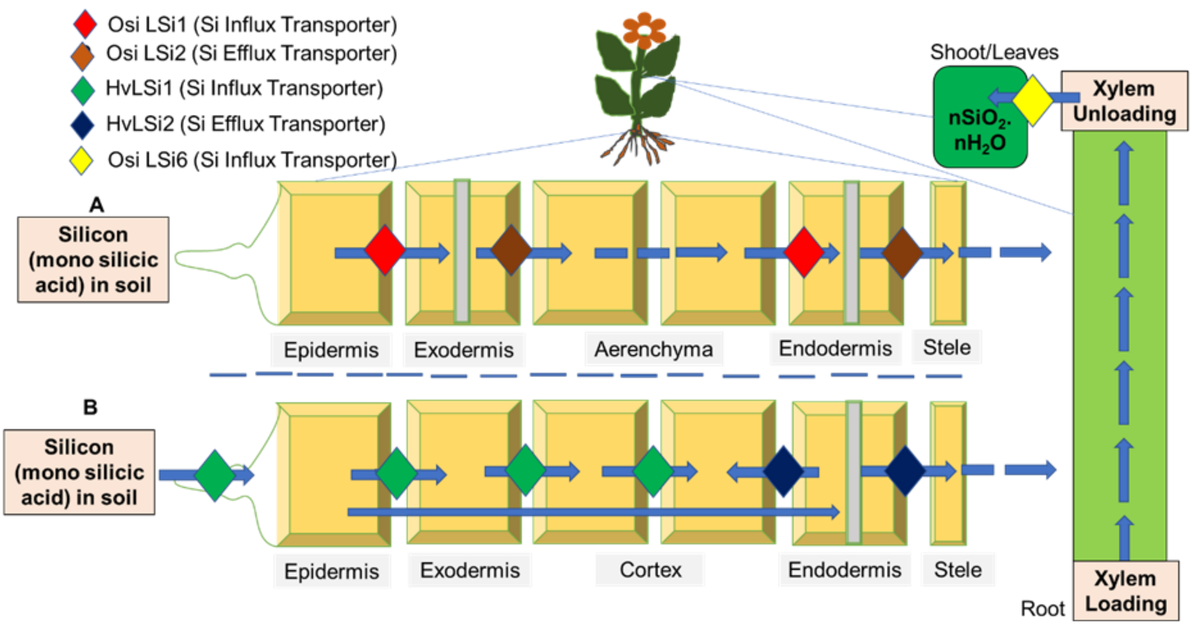

Fig. 3. *Uptake of Si and its transportation from root to shoot through different Si transporter: A simple pathway. This model of Si transport is supported by Chiba et al., 2009; Mitani et al., 2009; Ma and Yamaji, 2006; YAN et al., 2018; Dhiman et al., 2021).*

Table 1 Si-induced mechanisms involved in enhancing the plant's tolerance to biotic stress (Pathogen's stress)

Biotic Stress	Study	Crop	Mechanisms	References
Pathogen's attack	Cytological study	Rice plant	Formation of mechanical barricade	Rodrigues *et*
	Microscopic study		Strengthens the cell wall by forming a physical barrier	Kim *et al*. (2002)
	Cytological study	Rice plant	Papilla Cells Formation	Bélanger *et al*. (2003)
		Wheat plant	Increase the enzymatic activity of chitinase, peroxidase (POD), polyphenol oxidase (PPO), phytoalexins	Zhang *et al*. (2006)
		Cucumber plant		Chérif *et al*. (1994); Fawe *et al*. (1998
Pathogen's Penetration	Biochemical study		Regulate the formation of antifungal compounds like pathogenesis-related proteins and phytoalexins in plants	Chérif *et al*. (1992, 1994); Remus-Borel *et al*. (2005); Rodrigues *et al*. (2003)
			Formation of flavonoid phytoalexins	Fawe *et al.* (1998)
Penetration and pathogen-associated infection	GC-MS, GC-FID study	Rice plant	Formation of Casparian strips in root endodermis and exodermis	Fleck *et al*. (2015); Suzuki *et al.* (2012)
	Microarray study		With deposition of Si, it increased the process of suberization and lignin formation in the cell	Cai *et al*. (2008); Fleck *et al*. (2011)
	UV spectroscopy, Raman microspectroscopy		Si and components of cell wall can make cross-links and organo-silicate complexes in the silica body	Bokor *et al*. (2019); Inanaga and Okasaka, (1995); Soukup *et al*. (2020)
Pathogen's Stress	TEM, SEM Study		Accumulation of Si and formation of biosilicification in plant cells	Guerriero *et al*. (2016)

ZmLsi1 and *ZmLsi6. ZmLsi1* transporter gene helps in loading of Si from roots while *ZmLsi6* is for translocating Si from xylem to leaves (Bokor *et al.*, 2015). Due to lots of research on Si transporters, it is found that Si can be used as a biofertilizer to alleviate the arsenic metal stress from soil. Because Si and arsenic are absorbed by the same transporters in the plants, and addition of Si in the soil decreases the absorption of arsenic and increases the absorption of Si (Vats *et al*., 2021; Kumawat *et al*., 2021).

Influx transporter of Si

Plants uptake Si as mono silicic acid (H_4SiO_4) from the external soil solution. The first Lsi1 (Low Silicon 1) influx transporter was found on the rice plant, a Si-accumulator plant (Ma *et al*., 2006). It is a NIP2 homolog aquaporin and belongs to NIP family of aquaporin proteins, as we discussed earlier, and contains around 298 amino acids. The estimated amino acid chain comprises six transmembrane domains and 2 NPA motifs; these structures are well maintained in aquaporin channels (Ma, 2013). Lsi6, a NIP2 aquaporin, is also a Si transporter found in rice plants that transfers Si from the xylem to the leaves part of the plants (Yamaji *et al.,* 2008). Moreover, NIP2 aquaporins were observed in those plants only in which Si shows a positive effect on the growth and physiology of plants.

The role of the Lsi1 influx transporter is also reported in the *Xenopus* oocyte to uptake silicic acid (Ma *et al*., 2006). This influx transporter is constitutively exhibited in root region, but its mode of action is reduced with the quarter rate with the addition of Si. At the lower tip of the root among 0-10 mm, the mode of action of Lsi1 transporter is highly low than the root's basal area, which is more than 10 mm. The basal area of the root is constantly taken up by the Si from its site (Yamaji and Ma, 2007). In the progressive stage, when Si is much needed for plants, there is a temporary increase in the mode of action of Lsi1 transporter in the plants. The Lsi1 transporter is present on the plasma membrane of endodermis and exodermis of different roots like main root and adjacent roots where the Casparian bands are developed, and these bands stop the transport via apoplastic pathway into the root xylem (Ma *et al*., 2006).

Moreover, the influx transporter shows a polarity in localization on the exodermal and endodermal layers of roots (Ma, 2013). On the other hand, Lsi6 is a transporter similar to Lsi1 and also takes part in transporting Si from the xylem to the plant's leaves. It is mainly found in the leaf blade and leaf surfaces rather than the root membrane (Yamaji *et al*., 2008). The Lsi6 transporter is present on the upper side of the leaf surface and blade of xylem cells; its damage does not disturb the transport of Si by the roots, but Si accumulation does not take place between the leaf blades and surfaces. The process of guttation excretes Si through another method in rice plants (Ma, 2013). Lsi6 transporter mostly shows its activity at node one beneath the panicles and is generally found at the leaf xylem cells in front of xylem vessels where Si transport occurs. These transfer cells of Si are present in the external region of vascular bundle cells and distinguished by the enlarged area due to the development of the cell wall. At maturity, this transporter is needed for the intervascular transport of Si in the node (Yamaji and Ma, 2009). Non-functional Lsi6 reduces the Si deposition in panicles but enhances its deposition in leaves. This transporter is needed for the Si transport, which is taken up by roots and transfers the Si from the enlarged vascular bundle cells to the diffuse bundle cells, which are linked to the panicles of the plant (Ma, 2013). In addition, Lsi6 transporters help transport Si from the xylem-to-xylem parenchyma and stop the excess accumulation of Si in the xylem. The deposition of Si is preserved in plant cells despite the disintegration of the plants (Imtiaz *et al*., 2016; Khan *et al*., 2019; Al Murad *et al*., 2020).

Efflux transporter of Si

Lsi2 transporter was also found in the rice plant for the first time, which is also called an active efflux transporter of Si in plants. It contains around 472 amino acid sequences and has 11 transmembrane domains. It deals with efflux transport of Si rather than influx transport (Ma *et al*., 2007). It is almost similar to the Lsi1 transporter in the mode of action and distribution. However, the Lsi2 is found on the origin of the surface of the endodermal and exodermal cells. The proton-energy gradient conducts Si transport via Lsi2 transporter (Ma *et al*., 2007). Similar mechanism of transporter was also found in maize and barley plants (Mitani *et al*., 2009a). Lsi2 transporter helps load Si in xylem and transport Si from root to shoot in plants. Along with this, it also aids in the formation of biosilicification in plants (Coskun *et al*., 2021). Therefore, the presence of Lsi2 is essential for Si uptake and deposition by actively releasing out Si toward the xylem. In a study of cucumber plants, it was observed that Si deposition is enhanced in the plant parts by the action of Lsi2 Si-transporter (Sun *et al*., 2020). Likewise, Mitani-Ueno and Ma, (2021) also reported that Lsi2 transporter is very important in the accumulation of Si in plants, as it pumps out Si from root to xylem.

ROLE OF SI IN DIFFERENT TYPES OF STRESSES

Si in pathogenic stress

Pathogens result in a serious problem in the plants by causing various diseases with which plant development generally halts. Around 10% of agricultural production is destroyed by pathogen-induced diseases every year worldwide. The loss of agriculture production includes the loss of yield or quality of the crop (Strange and Scott, 2005). To overcome the loss of yield production due to pathogens, many campaigns or research was carried out in the past, including the development of resistant varieties, high-yielding varieties, the use of pesticides and various farming techniques, etc. The production of resistant varieties is not long-lasting as the pathogens evolve with the plants through their complex genetic diversity.

Application of pesticides on a large scale causes severe problems in plants and animals and environmental health. After the long use of these pesticides make the pathogens resistant to them. Thus, there is a great requisite to study and produce environment-friendly techniques against plant pathogens (Cai, 2013). The exogenous application of Si in plants changes the colony structure and incubation time of pathogens and inhibits the development of pathogens at infection sites in plants. The formation of lesions by the fungi in plant cells is reduced by the application of Si. Accumulation of Si in plants not only provides mechanical strength to plants but also prevents the entry of pathogens into them (Debona *et al*., 2017).

Supplementation of Si partially alleviates the negative effect of these plant pathogens on plant growth and development. A number of reports showed the positive impacts of Si on plant resistance against various pathogen diseases like powdery mildew in wheat, cucumber, and barely; blast in rice; red rot in sugarcane; rust in cowpea, etc. But the protective role of Si in these pathogen diseases is not as clear, and it is a topic of debate.

Si-induced pathogen resistance in plants

It states that with the application of Si, the plant induces resistance against the pathogen infection and improves the overall status of the plant. Si deposition occurs in the leaf, shoot, and roots with the absorption of Si in a high amount. This deposition of Si induces a mechanical barrier on the cell wall of the plants and reduces the risk of pathogen penetration and infection. Application of Si creates not only the physical barrier but also the biochemical barrier in response to the pathogen infection. This defense response of Si in plants protects it from pathogens and provides resistance against them (Cai, 2013). In wheat plants, high deposition of Si content in the leaf's bulliform cells helps the plant form a mechanical barrier and increase resistance (Meunier *et* *al*., 2017). Song *et al*. (2021) stated that plants with high Si content in root or shoot are less susceptible to any biotic stress (pathogens or insects) and have high-stress tolerance to the particular stress.

Once Si is taken up by roots and then transferred towards the shoot through the xylem, it can be accumulated as amorphous silica (the polymerized form of Si) all over the plant. It is highly accumulated in the plant's cell walls, where it cooperates with polyphenols and pectins, the cell wall component, increases the inflexibility of the cell wall and provides its resistance to defend the plants from different biotic stresses (Epstein, 1994). Many plant species respond differently in their ability to uptake Si by roots, and so their mechanism of transport of Si into the plants is also different (Ma and Yamaji, 2008).

Moreover, Si has a greater positive role in mitigating the different biotic and abiotic stresses. These include diseases caused by pathogens or pests, fungi and bacteria (biotic stress), drought, salinity, metal toxicity, etc. (abiotic stress). It has been considered in various plant species (Fauteux *et al*., 2005; Ma and Yamaji, 2006; Liang *et al*., 2007). Zhou *et al*. (2018) observed that Si as sodium silicate helps inhibit the development of fungi disease named Fusarium wilt in cucumber plants by enhancing the antioxidant enzyme activity in plants. Likewise, supplementation of Si enhances the tolerance of *Castanea sativa* plants against *Cryphonectria parasitica,* by increasing the activity of defense enzymes like catalase and superoxide dismutase and reducing the H_2O_2 content in plant leaves (Carneiro-Carvalho *et al*., 2019). A thorough consideration of the mechanisms of Si on the biotic stress can be a better option to increase the tolerance of plants against the pathogen attack for the active application of Si.

Mechanisms of Si-induced pathogen resistance

Many studies have been performed to discover the probable mechanisms related to the positive role of Si against pathogen infection and diseases (Fauteux *et al*., 2005; Cai *et al*., 2009). Firstly, Si forms a mechanical barrier in the cell wall by deposition, and this deposition of Si prevents the entry of pathogens through this barrier. Second, the Si can act as a signal molecule to generate the different biochemical defense mechanisms in plants against the pathogen attack and confer resistance throughout the plant. Various genetic studies reported that Si could trigger the action of defense-related genes that confer resistance and defense system to the plant. Si provides stress tolerance and pathogen resistance to plants by increasing the formation of reactive oxygen species (ROS), which stimulates defense-related genes and activates antioxidant enzymes involved in the defense mechanism. The production of ROS in plants also promotes the formation of phytoalexins and phenolic compounds which helps in pathogen resistance (Song *et al*., 2021). According to Kapilan *et al.* (2018), ROS production altered the structure of aquaporins proteins in the plant cells and acts as a signal molecule to activate and deactivate the aquaporin proteins.

Mechanical barrier

As we discussed earlier, Si was forming a barrier with their deposition into the cell wall of the leaves and preventing the entry of the pathogen. A cytological study found that a rice plant caused blast diseases with a pathogen named *Magnaporthe oryzae,* and this disease was suppressed by inhibiting the development of the pathogen by Si-induced resistance and Si deposition in leaf cells (Rodrigues *et al.*, 2003). With the help of microscopy and X-ray studies, it has been found that in susceptible and partially resistant varieties, Si strengthens the cell wall and decreases the severe effects of blast diseases (Kim *et al*., 2002). Zargar *et al*. (2019) reported that Si forms a dual cuticle deposit on the cell wall and helps in providing stress tolerance and mechanical strength. Si reacts with the cell wall components in the plant and forms complexes with them, modulating the gene expression related to stress tolerance.

Many researchers report that the deposition of Si can prevent the pathogen attack and infection by forming a physical barrier. In the cucumber plant, the supplementation of Si in the root medium can induce resistance throughout the plant against the pathogen infection, but the foliar application of Si can prevent only the infection of *Podosphaera xanthii* via a physical barrier (Liang *et al*., 2005). Pathogens enter the plant cells by penetrating the wall layer and causing diseases. Research on rice plants shows that Si supplementation forms a dense layer of Si on the plant cell wall and fills the site of pathogen penetration. Due to this, pathogens entries are inhibited in rice plants, and mechanical strength is increased (Wang *et al*., 2022).

Papilla cells formation

In the case of rice and wheat, papilla was formed in response to the increase in resistance against the powdery mildew diseases (Bélanger *et al*., 2003; Zhang *et al*., 2006). According to a study, a rice plant that was treated with Si and infected with *Rhizoctonia solani* and *M. oryzae,* was found to have more silica and papilla cells upon stomata's guard cell, where the pathogen would have started to develop (Zhang *et al*., 2006; Cai *et al*., 2008). Moreover, the presence of papilla cells in Si-treated plants can enhance the resistance in wheat plants against the pathogen of *B. graminis f. sp. Tritici* (Bélanger *et al*., 2003). Consequently, based on these results, it was concluded that the process of silicification with Si accumulation was related to the Si-induced pathogen resistance.

Si-induced biochemical resistance

A different mechanism was introduced for Si-induced biochemical resistance in plants through which Si may act as a signal to generate the various defense system against pathogens. These defense responses are similar to Si's systemic acquired resistance (SAR) induced (Fawe *et al*., 2001). Si has been found to be involved in the stimulation of various defense enzyme related to biotic stress in which peroxidase and chitinase are the most common that helps in lignin formation and cell wall reinforcement (Gulzar *et al*., 2021). Application of Si in cucumber plant leads to an increase in the enzymatic activity of chitinase, peroxidase (POD), polyphenol oxidase (PPO), and phytoalexins in response to the *Pythium*'s infection (Chérif *et al*., 1994; Fawe *et al*., 1998). Reduction in the disease's brutality and prevention of the blast attack was related to the supplementation of Si in the plants by enhancing the enzymatic activities such as peroxidase, and phenylalanine ammonia-lyase (PAL), etc. (Zhang *et al*., 2006; Cai *et al*., 2008). These antioxidant enzymes played a great role in regulating the formation of antifungal compounds.

Many reports revealed that the application of Si leads to the formation of major antifungal chemicals like pathogenesis-related proteins and phytoalexins in plants after pathogen penetration (Chérif *et al*., 1992, 1994; Remus-Borel *et al*., 2005; Rodrigues *et al*., 2003). Bizuneh (2020) reported the accumulation of phytoalexins around the infected areas and inhibited the development of pathogens or insects. Phytoalexins are very important biochemical compounds that play a great role in defense mechanisms against pathogen attacks. Formation of flavonoid phytoalexins in cucumber plant in response to powdery mildews diseases caused by *Podosphaera xanthii,* when Si was supplemented to the plant (Fawe *et al*., 1998). Si, as a signal molecule, triggers the formation of defensive genes and pathogen-related genes in the plants, which further modulates the inner environment of plants and helps in making stress-tolerant against stress conditions (Wang *et al*., 2022).

Si in salinity stress

Salt stress is the major abiotic stress that directly affects crop production and yield (Zhu *et al*., 2019). Many studies showed that Si has the capacity to decline the salt ions uptake and their transport in plant parts under salinity in different plant species like soybean, wheat, rice, and barley (Liang *et al*., 2005b; Tuna *et al*., 2008; Lee *et al*., 2010; Gong *et al*., 2006; Shi *et al*., 2013). Stomatal conductance and transpiration process was increased with the reduction in sodium ions absorption by the Si application in rice (Gong *et al*., 2006). The formation of Casparian strips in the endodermis and exodermis of cells as a barrier for the transport of ions declines the transport of sodium ions in the plants. And Si was found responsible for the formation of this barri-

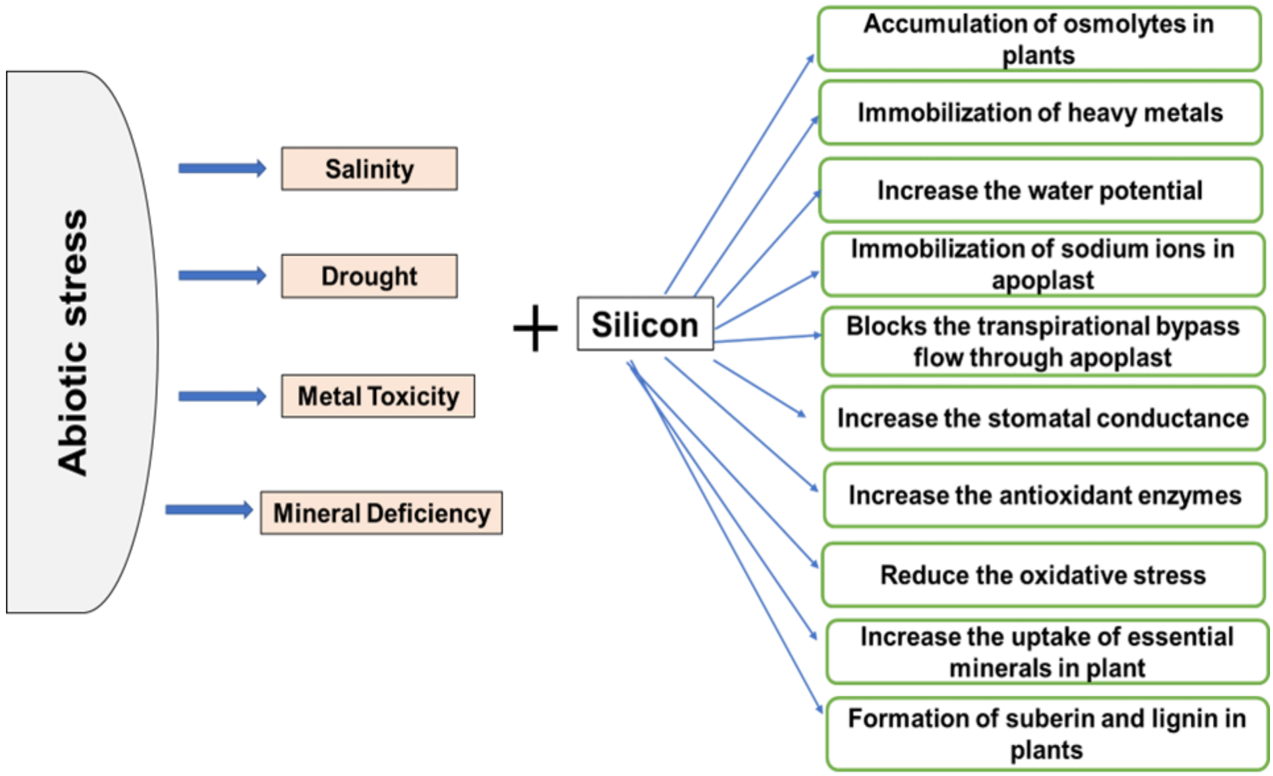

Fig. 4. *Involvement of Si in different mechanism to alleviate various abiotic stress*

er. This mechanism is most common in the Si-accumulating plant species. In the case of the Si-excluder tomato plant, in which Si application balanced the concentration of Na^+ and Cl^- rather than reducing the negative impact of salt stress (Romero-Aranda *et al*., 2006). In a study of wheat plants at booting stage, it is found that Si supplementation under salt stress increases the activity of antioxidant enzymes like superoxide dismutase (SOD) and catalase (CAT). The researcher suggested that this increase in activity of the antioxidant enzyme is due to a decrease in H_2O_2 content in plant cells which further suppresses the oxidative stress generated by reactive oxygen species on the cell membrane and enhances the growth of plants under salt stress (AM *et al*., 2018). Si reduces the negative impacts of salt stress by reducing the osmotic stress in plants via aquaporin proteins, which helps maintain the plant's water status (Liu *et al*., 2015). Hence, an almost equal positive effect has been reported in Si-accumulators and Si-excluders plants. The hydraulic conductance of root was re-established after Si treatment in barley plants under salt stress conditions, as Si controlled the mode of action of plasma membrane intrinsic protein (PIP) aquaporin proteins. So that the plants can regulate the water status and their photosynthetic rate. Sometimes, Si mitigates the osmotic stress of salinity even before the symptoms appear in plants (Liu *et al*., 2014; 2015).

Moreover, salt stress decreases the hydraulic conductance of roots by inactivating the activity of aquaporins through hydrogen peroxidase (Boursiac *et al*., 2008). However, Si could increase hydraulic conductance by reducing the action of hydrogen peroxide, which suppresses the activity of PIP aquaporins in plants (Liu *et al*., 2015). Enhancement in the growth of suberized structures in the endodermal and exodermal cells of the root with Si supplementation in plants (Fleck *et al*., 2015). The formation of lignin and suberin in the endodermis and exodermis resulted in a decrease in sodium ions transport from apoplast and its accumulation in the shoot (Krishnamurthy *et al*., 2011). It leads to reactivating the action of PIPs aquaporins to regulate the water movement via the symplast pathway. In a study conducted on cucumber plants under salinity stress, it was found that Si enhanced the mode of action of PIP aquaporins of root and reduced the osmotic potential by increasing the carbohydrate content in the roots, which helps in the absorption of water from the outer environment. Si application helps the plant in an osmotic adjustment under stress conditions (Zhu *et al*., 2015). The application of Si provides salt tolerance to plants by modulating the expression of transcriptional genes associated with salt stress, ionic transport, water-channel proteins, and plant-hormone-related genes. Very little work has been done on transcriptomic studies under salt stress with the effect of Si (Dhiman *et al*., 2021).

Ion transport

Maintaining ionic pools in the plant cells is very important to regulate the plant processes. Maintaining the flow of ions into the cells is essential to reduce the level of toxic ions and collect the required ions in high quantities. H^+-ATPases act as a primary active transport which helps the plant cell to maintain higher content of K^+ and lower content of Na^+ in the cytosol. Along with primary transport, secondary transport is performed by other transporter and channels (Zhu, 2003). However, in salt stress conditions, it is difficult to maintain the level of these ions in plants. High accumulation of Na^+ into the plant cells becomes toxic to the enzymatic activity of plants. This results in the loss of metabolic processes in plants and may retard plant growth. Therefore, to prevent growth and inhibition of plant processes, excess Na^+ has to be taken out of the cell or dissociated into the vacuole (Hasegawa *et al*., 2000). There were two similar mechanisms shown by a report in which the first, a decline in the inflow of Na^+ from the outer environment into the cytosol, and the second dealt with the outflow of Na^+ from the cytosol into the vacuole, both of which resulted in a decline in the cytosolic Na^+ pool, leading to tolerance in plants for salt stress (Munns and Tester, 2008).

Moreover, it is essential to maintain the intracellular K^+ pools in plants under salinity conditions to regulate the activity of plant cells (Kronzucker *et al*., 2013). Si application mitigates the salt stress by balancing the ionic ratio of Na^+ and K^+ in the plants (Zhu and Gong, 2014; Rizwan *et al*., 2015). Hurtado *et al*. (2020) also stated that the addition of Si increased absorption of K^+ and Ca^{2+} and reduced the uptake of Na^+ in sunflower and sorghum plants under salt stress. Si enhances the H^+-ATPase activity and helps in formation of physical barrier in the plant cells which further results in an improvement in ion homeostasis under salt stress. Si maintains the balance of K^+/Na^+ and protects the plant from the over-transport of Na^+ through roots (Dhiman *et al*., 2021).

Si in drought stress

Like salt stress, drought stress is also an important environmental stress factor that alters the morphological, physiological, metabolic, and genetic processes of plants. It occurs due to various reasons like minimum rainfall, salt stress, water-deficit conditions, high fluctuations in temperatures, etc. Many results supported the Si application in response to drought stress. The main mechanism underlying the processes includes an increase in uptake and transport of water, accumulation of compatible solutes, increase in osmoprotectant, enhancement in stomatal conductance, and activation of defensive genes involved in stress mitigants, which are all driven by addition of Si in plants under water-deficit conditions (Wang *et al*., 2021). Sonobe *et al*. (2009) showed an experiment on sorghum plants and found that the addition of Si in the root medium enhanced the uptake of water in plant parts, including stomatal conductance. Supplementation of Si in plants increased the root hydraulic conductance under stress conditions (Hattori *et al*., 2008). This increment in the hydraulic conductance occurs in a radial direction in the root. This was mainly due to alteration in the mode of action of aquaporin proteins or changes in the size or number of xylem vessels (Sonobe *et al*., 2009). The role of Si on stomatal conductance and transpiration has been debatable till now (Agarie *et al*., 1998; Gao *et al*., 2006). The addition of Si decreases the transpirational rate, increases water uptake in plants under water deficit conditions, and prevents the plant from wilting (Gao *et al*., 2005). The higher the hydraulic conductance of the root, the higher the rate of transpiration, resulting in higher uptake of water in plants (Sonobe *et al*., 2009). The importance of Si in drought stress is linked with the increase in the water potential in plants, but so far, there is not enough proof to show the defined role of Si in this.

Antioxidant enzymes and plant water status are the two main parameters that maintain drought stress in any particular plant. Moreover, relative water content (RWC) in plant parts (root, leaves, and stem) is also a drought stress indicator parameter that shows the overall water status of the plants (Gui *et al*., 2021; Knipfer *et al*., 2021). An association between drought stress and Si has been reported in different plant-like tomatoes, in which increased resistance to drought stress was observed in response to the high-water potential of the leaf (Romero-Aranda *et al*., 2006). According to a report, Si regulated the membrane integrity together with an increase in hydraulic conductance of root and reduced the oxidative stress by increasing the defense system of the tomato plant (Shi *et al*., 2016). Moreover, Si was also found to positively impact growth under water-deficit conditions in many plant species like tomato, maize, and sorghum (Agarie *et al*., 1998; Hattori *et al*., 2008; Sonobe *et al*., 2009; Shi *et al*., 2016). Although the mechanism of action is not much precise, the involvement of aquaporins and hydraulic conductance has been reported in many studies.

Plant-water relation

Stomatal conductance and transpiration are the two significant factors that affect the plant water status (Farooq *et al*., 2009). The positive role of Si in the plant has been linked with the transpiration rate. The water potential of the leaf is greatly reduced when the plants are placed under drought stress (Siddique *et al*., 2000; Farooq *et al*., 2009). The leaf water status and stomatal conductance are both the processes that are linked to each other and connected to the water potential of plant leaves (Arif *et al*., 2021). In a study, it was observed that Si's supplies enhanced the water status of the plant under drought stress by reducing water transpiration (Haghighi and Saharkhiz, 2022). With Si supplementation, maintenance of transpiration rate in the plant leaves is achieved by improving the hydraulic conductance of root through up-regulation of aquaporin genes and fixing the potassium ions in the xylem water (Chen *et al.,* 2018). It was found that stressed plants with Si application retain the water capacity to a higher level when compared with the stressed plant without Si application, confirming that Si can enhance the water capacity of the plant under drought conditions (Gong and Chen, 2012). A case study showed that to maintain the water level in the plant, Si reduces the transpiration rate of plant leaf and water transport in xylem vessels, leading to more water efficiency. They hypothesized that Si accumulates in the root cell wall, which might affect the dampening character of xylem vessels that ultimately affect the passage of water and solute transport (Gao *et al*., 2006). Even though this hypothesis is yet to be established experimentally, they proposed that Si can maintain the water status in plants. The addition of Si in the rooting medium increases the water uptake by roots in drought stress conditions by gathering soluble solutes or amino acids in the cell (Sonobe *et al*., 2010). This research finding was supported by Ming *et al*. (2012) in rice plants. Proline is an essential compatible solute that helps in the osmotic adjustment of cells during stress conditions (Nayyar and Walia, 2003).

Apart from enhancing the hydraulic conductance of root and changes in the mode of action of aquaporins protein for water transport, Si helps in the enhancement of essential compatibles solutes like proline, sorbitol, betaine, soluble sugar, etc. in the plant cells, which maintain the osmotic adjustment in the cell under stress condition (Pei *et al*., 2010; Sonobe *et al*., 2010; Ming *et al*., 2012; Liu *et al*., 2014). Water absorption from the soil can be improved by the Si application by activating osmotic adjustment and increasing water-channel activity under stressful conditions in plants (Chen *et al.,* 2018). According to Chen *et al*. (2016), Si supplementation improves the water relation in sorghum plants by improving the potassium concentration in plants. Under drought stress, the root volume and weight were found to be increased by Si application by reducing the loss of water from plant parts via the transpiration process. Deposition of silica in the plant leaves helps decline the cuticle-transpiration process and pore diameter of the leaf's stomata (Gaur *et al*., 2020, Malik *et al*., 2021).

Si in heavy metal stress

Different types of heavy metals, such as cadmium (Cd), lead (Pb), chromium (Cr), copper (Cu), and manganese

(Mn) share a large proportion of soil pollution. This results in a major environmental hazard that affects the plants, animals, and human health in the environment by creating heavy metal toxicity and contamination of soil (Nascimento and Xing, 2006; Adrees *et al.,* 2015). Plant absorbs these heavy metals from the soil with the roots and ultimately, these heavy metals enter the food chain and affect all the processes. Many studies showed that Si could mitigate the various types of biotic and abiotic stresses, together with metal toxicity. Different mechanisms have been discovered by which Si can mitigate the negative effects of metal toxicity in plants as well as in the soil environment (Adrees *et al*., 2015). Xiao *et al*. (2022) reported the interaction between Si and aluminium (Al) and showed that Si suppresses the expression of Al in roots and increases the expression of resistance genes for Al toxicity. Addition of Si down-regulated the genes related to Al uptake from soil to plants.

In the case of Si-accumulator plants, the role of Si is not clearly defined in plant tolerance, but it is believed that it is involved in the structural and biochemical responses of plants which aid the plant in reducing the stress level (Epstein, 2001). Si is reported to decrease the apoplastic Mn content of the cell. It also helps in modifying the cation-binding ability of the cell wall, which alleviates the Mn stress in cowpea (Shivaraj *et al*., 2017a, b). Zargar *et* al. (2019) stated that Si interferes with the transport of Cd from the shoot to the root region in peanuts. Si also improves the expression of genes that are responsible for metallothionein's production, which can chelate toxic metals (Jiang *et al*., 2019). A report showed that Si confers plant tolerance against the aluminium (Al) heavy metal by co-accumulation of Al with Si in the plant cells of some monocot plants (Sangster *et al*., 2001). Si has been found effective in improving the plant response to the negative effect of heavy metal stress (Chen *et al*., 2000). It was found that Si can decline the absorption of Cd by plant roots and transport Cd from shoots to grains (Naeem *et al*., 2015; Hussain *et al*., 2015). Similar results were also observed in wheat plants under Cu toxicity (Nowakowski and Nowakowska, 1997; Keller *et al*., 2015). Supplementation of Si also declines the accumulation of Al in different parts of rice plants and peanut plants (Singh *et al*., 2011, Shen *et al*., 2014). In addition, the monosilicic acid forms complexes with Cd, Pb, and Zn by reacting with them in the soil and decreasing the solubility of these metals. Due to alteration in the dissolution equilibrium of these metals, soil pH is improved. The Si present in soil may improve soil quality and fertility under stress conditions (Luyckx *et al*., 2017; Wang *et al*., 2020). The contaminated soil due to metal toxicity can be used as fertile soil by improving the physicochemical properties of soil with the application of Si (Zhao *et al*., 2022). So, it can be predicted that the application of Si in the agricultural sector to reduce heavy metal stress will soon emerge as an approach in the future.

Si-induced metal detoxification in plants

Detoxification of metals in plants is necessary to reduce metal stress, and this detoxification occurs by the supplementation of Si. Therefore, it is essential to understand detoxification mechanisms via the application of Si in plants. The mechanisms of detoxification of metals

Table 2. Si-mediated mechanisms in alleviating heavy metals stress (Tubana and Heckman, 2015).

Sr. No.	Heavy Metal	Plant	Mechanisms	References
1.	Arsenic	Rice (*Oryza sativa* L.)	Si restricts the entry of arsenic metal by competing with it in the root-soil environment	Seyfferth and Fendorf, (2012)
2.	Aluminium	Barley (*Hordeum vulgare* L.)	Deposition of Si at the root epidermis prevents the uptake of aluminium metal	Hammond *et al*. (1995)
3.	Lead	Cotton (*Gossypium* L.)	Reduction of oxidative stress by enhanced production of antioxidant enzymes	Bharwana *et al*. (2013)
4.	Manganese	Cowpea (*Vigna unguiculata*)	Si interacts with phenolic compounds and prevents the oxidation of manganese by maintaining the reduced state of apoplast	Iwasaki *et al*. (2002b)
5.	Cadmium	Rice (*Oryza sativa* L.)	Accumulation of Si into the cell wall prevents the uptake of cadmium metal through formation of a covalent bond with cadmium and make difficult the diffusion of cadmium through the cell wall	Nwugol and Huerta, (2008)
6.	Zinc	Corn (*Zea mays*)	Accumulation of Si in the root endodermis, structural changes on the epidermal cell, mesophyll cell, xylem cell	Cunha and Nascimento, (2009)

are different at different levels, such as in plants. It involves enhancing the antioxidant system, reducing oxidative stress, physical changes in plants, metal precipitation with Si, compartmentalization of metals, alteration in expression of genes and chelating process in plants, and soil detoxification involves the fixation of metal in soil. Adrees *et al*. (2015) also observed the Si-induced metal detoxification in different plant species. Fatemi *et al.* (2020) reported that Si as a signal molecule activates all the antioxidant enzymes, which are helpful in defense mechanisms by declining the oxidative stress on plant cells. In contrast, Si plays a great role in repairing damaged plasma membranes which is due to oxidative stress and protects the plants from a membrane stress injury. Different plants have different mechanisms of metal detoxification through the application of Si (Tripathi *et al*., 2021). Si-mediated mechanisms in alleviating heavy metals stress (Tubana and Heckman, 2015) are shown in Table 2.

Si in proteomics

Proteomics is a new strategy to study the proteomes, i.e., the expression of all the proteins in an organism at a specific interval and time (Wilkins *et al*., 1996). With the help of this strategy, scientists have found the role of Si in the upregulation and down-regulation of proteins under stressed conditions (Dhiman *et al*., 2021). It is very necessary to examine the alteration in the expression of genes or proteins as various transcripts can pass off post-transcriptional and post-translational modifications. Zhao *et al*. (2013) reported that around 900 salt-responsive proteins are already found in the root proteomes of fourteen different crop species under saline stress. These salt-responsive proteins are helpful in various pathways such as carbohydrate and energy metabolism; regulation in different antioxidant enzymes like peroxidase (POD), superoxide dismutase (SOD), catalase (CAT); transportation; signal transduction; cell wall formation; formation and destruction of DNA, RNA, and nucleic acid; translation and transcription, etc. (Zhao *et al*., 2013; Passamani *et al*., 2017). In the case of the tomato plant, Si enhanced salt-responsive genes were found in the root proteome, which was associated with the secondary metabolites, antioxidant enzymes, Si-transporters, and transcription regulators under salt stress (Muneer and Jeong, 2015). Si upregulates around 72 protein spots which were downregulated by salt-stressed conditions in a more number due to decline in gene expression intricate in different pathways in the capsicum plant (Ali *et al*., 2016). In *Rosa hybrida*, 40 protein spots were found under salt stress with Si application, which was related to different processes like photosynthesis, antioxidant enzymes, gene regulation, etc. These were calibrated with the application of Si and resulted in improved tolerance (Soundararajan *et al*., 2017). According to transcriptomic research, it is found that the plants with high salt stress concentration and the presence of Si are much similar in gene expression as compared to non-stressed plants (control). However, those plant with high salinity and absence of Si was found to be badly affected by altered gene expressions (Zhu *et al*., 2019).

Conclusion and future perspectives

The application of Si is an eco-friendly and environmentally safe practice for sustainable agriculture production. Most of the fertilizers that are used in agriculture are helpful in increasing production but harm the soil and soil microbial population. To resolve this issue, Si is a good substitute. Supplementation of Si in the stress condition defends the plant from the external stress and improves its status to a great level. Si, as an ameliorate, interferes with different soil components and improves soil health. It provides stress resistance to the plant under stress conditions. The research work has been done at the biochemical and molecular level for many years, but it is not much known at the field level. The conditions of the fields are far more different than laboratory experiments as, in the field, several environmental factors immensely affect plant production. Therefore, it is time to focus on the different environmental factors that adversely affect crop production. The use of natural soil mitigants such as Si should be promoted to alleviate various stress conditions and improve yield production under these stress conditions. Using Si as a fertilizer may not only decline the stress level of soil but also appear environmentally safe. It will also improve soil fertility and health and promote the microbial population in the soil. It may improve the NPK level (Nitrogen, Phosphorous, and Potassium) in the soil and enrich its quality under stress conditions. So, there is a great requisite to address the role of Si, its interaction with different soil components, its availability to plants, and its defense mechanism in plants. More research is needed on Si for its application in field management and its use as a fertilizer to improve the plant status in stress conditions.

Conflict of interest

The authors declare that they have no conflict of interest.

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