



STRENGTHENING SOIL-PLANT RELATIONSHIPS WITH SILICON FOR SUSTAINABLE CROP PRODUCTION

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Abstract

Silicon (Si), though not considered an essential nutrient, plays a crucial role in crop growth and development. Present in soils at varying concentrations, Si is taken up by plant roots and primarily deposited in cell walls, where it enhances structural strength and provides protection against both biotic and abiotic stresses. Silicate minerals serve as the main source of Si, gradually releasing bioavailable forms through weathering. Factors such as soil pH, temperature, and microbial activity influence Si availability by affecting its solubility and release from mineral reserves. In plants, Si dynamics involve uptake, transport, and deposition mediated by specialized root transporters, enabling efficient translocation to aerial tissues. Silicon improves plant performance by enhancing photosynthetic efficiency, nutrient absorption, and water use efficiency. This review emphasizes the benefits of Si fertilization in mitigating the effects of biotic and abiotic stresses while promoting overall soil-crop health. Additionally, Si application helps plants tolerate heavy metal toxicity by reducing their harmful effects. The review also discusses morphological and physicochemical plant responses to Si supplementation and highlights emerging research directions that support food security and contribute to achieving the United Nations' Sustainable Development Goals.

INTRODUCTION

Climate change is one of the major concerns globally that has amplified negative impacts on crop growth and yield due to irregular rain patterns, heat waves, and others (Hussain *et al.*, 2022) which ultimately impact the soil biogeochemical cycling. To sustain the yield and health of crops under environmental stress, it has become necessary to develop mechanisms/approaches that enable plants to withstand biotic and abiotic stresses. While plants have developed certain mechanisms to survive under stress conditions, there lies a gap in doing such research that could mitigate environmental stresses by increasing crop production. So, application of silicon (Si) can be a wonderful approach for plants to tolerate environmental stress (biotic and abiotic) due to its various roles in

different plant developmental stages (Bhat *et al.*, 2019). Silicon plays vital roles in plants growth, yield, quality, by increasing efficiency of photosynthesis, facilitation in nitrogen fixation, and mitigation of adverse abiotic factors such as extreme temperatures, ultraviolet radiation, metal toxicity, nutrient deficiencies, drought, and salinity (Olle, 2020; Pretty & Bharucha, 2014; Zargar *et al.*, 2019). For achieving sustainable agriculture Si can be used as a micronutrient for enhancing crop production and improving soil health. Silicon being a versatile element in the earth's crust and is absorbed by plants in the form of soluble silicic acid. The chemistry of Si is complex due to its abundance in nature as it ranks as second-most abundant element following oxygen in the earth's crust. Particularly



quartz, silica gel, biogenic SiO₂, and silicates (found in diatoms and phytoliths), are among many types of silica that are frequently abundant in soil profile (Liang *et al.*, 2007; Rasoolizadeh *et al.*, 2018; Sommer *et al.*, 2006). In the soil systems, it exists in extractable forms of Si, encompassing water soluble, active, and amorphous states while plants may use Si directly in its water-soluble form which is efficiently translocated to various tissues where it is stored because of its monomeric or mono silicon (HSiO₄) nature (Puppe, 2020).

Nonetheless, various geoenvironmental factors exert a substantial influence on Si bioavailability within the soil matrix and subsequent uptake by the plants. Environmental factors might include excessive rainfall which can lead to silica leaching that lowers soil pH, harming soil silica bio- stock and reducing the bioavailability of Si to plants (Jörg Schaller *et al.*, 2021). The presence of Si content in soil solution can be substantially influenced by inadequate soil management practices and excessive harvesting rates, ultimately induce physiological stress in plants (I. Khan *et al.*, 2021; Puppe, 2020; Jörg Schaller *et al.*, 2021).

However, understanding the benefits of Si for soil health and the environment is crucial for developing effective strategies to promote sustainable agriculture and to mitigate the impacts of climate change (Ahanger *et al.*, 2020; Laing *et al.*, 2006; Mehrabanjoubani *et al.*, 2015; Pati *et al.*, 2016; Pozza *et al.*, 2015; Pretty & Bharucha, 2014; Raza *et al.*, 2023; Verma *et al.*, 2022; Zargar *et al.*, 2019). In terrestrial ecosystems, processes of vertical and horizontal translocation as well as temporary and permanent fixing are carried out on Si produced by silicate weathering. Mineral pools and bio- source pools can be found in natural ecosystem pools. Each pool of Si contains a little amount of reactivity and water solubility because of variations in composition of minerals and reactive contact surfaces (Alhousari & Greger, 2018). The relative contributions of the various Si basins and the characteristics of the water flow that determine how silicon moves from terrestrial to aquatic systems. Dissolved-Si in the soil solution may either precipitate as abiotic available-Si on mineral surfaces or may be redeposited as secondary silicate minerals (allophane or imogolite)(Sommer *et al.*, 2006).

Furthermore, Si application in mitigating biotic and abiotic stress like alleviating heavy metal stress under different environmental conditions as explained by many researchers (Haddad *et al.*, 2018; Hu *et al.*, 2020; Hussain *et al.*, 2019) (Table 1). In a recent study by Hussain *et al.* (2023) mitigation of arsenic (As) was done using foliar application of Si, selenium and phosphorus under paddy conditions in rice genotypes thus Si performed significantly better compared to other treatments. Luyckx *et al.* (2017) explained the role of Si in plants growth and its advances nanoparticles while Ma and Yamaji (2008) unveiled the transporters of Si in plants, particularly in rice plants. Further, Si role in plants has also been explored but this encircles around the concepts and myths not the facts (Epstein, 2001). To address the research gaps and unveil the role of Si a comprehensive review is thus needed to understand Si behavior and its pivotal role in fighting food security. In this review, the sources of Si and its chemistry are explained. Also, the role of Si to increase plants defense mechanism has been elucidated. Silicon application and its potential against emerging pollutants particularly heavy metals has also been discussed in detail.

1. Environmental sources and fate of silicon: Biogeochemical cycling of silicon under reduced conditions

Geochemistry of Si is complex due to its existence in various forms including silica gel, silicates, biogenic SiO₂, and quartz (e.g. diatoms, phytoliths) (Khan *et al.*, 2022; Liang *et al.*, 2007). Primary minerals, secondary crystalline minerals (mostly clay minerals), and secondary amorphous phases can be used to categorize the Si mineral pool in nature (Struyf *et al.*, 2009). The first category can be thought of as a foundation, whereas the other two are products of the ecosystem's process of weathering (de Tombeur *et al.*, 2021). The interaction of dissolved and solid Si deposits in the soil is significantly influenced by aluminum (Al) hydroxide, iron (Fe) hydro(oxide)s, and carbonates. These secondary minerals have Si chemically bonded onto their surfaces (Pokrovski *et al.*, 2003). However, redox mechanisms are thought to affect Si kinetics in the presence of Fe oxides. Recently, a study by de Tombeur *et al.* (2021) reported that revitalizing soil following a period of



waterlogging causes silicate minerals to emit more dissolved-Si (Figure 1). Plants can only take Si in its water-soluble form; the other forms, reactive and amorphous, do not exist in soil. In soil, Si is often found as silicic acid, which ranges in concentration

from 0.1 to 0.6 mM (J Schaller et al., 2021). Hence, plants exclusively uptake silicic acid (uncharged molecules) below pH 9 (Souri n

Table 1: Role as well as the mechanisms used by Si in combating different biotic and abiotic stresses in crop plants.

Crop	Stress	Mechanisms	References
<i>Vigna mungo</i>	Powdery mildew	Elevated levels of defense-related protein expression	(Parthasarathy & Jaiganesh, 2016)
<i>I-Solanum lycopersicum</i>	Anthracnose	Enhanced cuticle thickness and fruit firmness.	(Somapala et al., 2016)
<i>II-Capsicum annum</i>			(Jayawardana et al., 2014)
<i>Oryza sativa</i>	Leaf blast	Elevated levels of chitinase, β -1,3 glucanase, peroxidase, and phenylalanine ammonia-lyase activities.	(Souza et al., 2015)
<i>Oryza sativa</i>	Sugarcane borer	Diminished feeding damage while enhancing exposure to adverse environmental conditions and natural predators.	(Sidhu et al., 2013)
<i>Saccharum officinarum</i> L.	<i>Diatraea saccharalis</i>	Stimulate cuticle thickening and the deposition of crystals on the leaf stomata.	(ViLELA et al., 2014)
<i>Triticum aestivum</i> L.	Cu	Copper forms complexes with organic acids, leading to a reduction in the translocation of copper to the shoots.	(Keller et al., 2015)
<i>Hordeum vulgare</i> L.	Cr	Enhanced the height of barley plants, increased the number of tillers, root length, and leaf size.	(Ali et al., 2013)
<i>Gossypium herbaceum</i>	Pb	Elevated the levels of antioxidant enzyme activity and prevented oxidative damage to plant tissue membranes.	(Bharwana et al., 2013)
<i>Brassica napus</i>	Cd	Facilitated the substantial growth of suberin lamellae in the endodermis near the root tips.	(Vatehová et al., 2012)
<i>Oryza sativa</i>	As	The inclusion of surfactants in the silicon solution led to a decrease in the accumulation of inorganic arsenic in edible rice tissues. This reduction was achieved by significantly inhibiting the relative expression of <i>Lsi1</i> and <i>Lsi2</i> in the root, as well as <i>Lsi6</i> in the blade and sheath, thereby limiting the amount of inorganic arsenic present.	(Zhang et al., 2020)
<i>Cucumis sativus</i>	Salts	Silicon may function as a triggering agent that preconditions and induces stress tolerance.	(Y. Zhu et al., 2019)
<i>Zea mays</i> L.	Na salts	Sodium (Na) was transported to the root apoplast through the up regulation of <i>ZmSOS1</i> and <i>ZmSOS2</i> in the root cortex. Additionally, silicon (Si) increased the expression levels of these genes in the stele, facilitating the active loading of Na^+ into the xylem and consequently raising leaf Na^+ concentrations. The elevated Na^+ concentration in the xylem sap of Si-treated plants was also achieved by the downregulation of <i>ZmHKT1</i> .	(Bosnic et al., 2018)



<i>Pistacia vera</i> Drought	Improved photochemical efficiency, enhanced (Habibi & Hajiboland, 2013) photosynthetic gas exchange, and heightened activation of antioxidant defense capacity.
<i>Oryza sativa</i> Salinity	Decreased sodium accumulation, reduced electrolytic (Kim <i>et al.</i> , 2014) leakage, and lowered lipid peroxidation, while also influencing phytohormonal responses.

Set *et al.*, 2021). Several researchers have reported Si as a promising element for enhancing The availability, solubility and biogeochemical cycling of Si plays a pivotal role in defining its phyto and bioavailability (Imtiaz *et al.*, 2016; Soury *et al.*, 2021). Diverse forms of Si were found in soil, with the majority displaying low solubility like monosilicic acid ($\text{Si}(\text{OH})_4$), another type of water soluble Si, can transform into different forms in response to pH variations in the soil. For instance, at pH values > 9 and 11, respectively, $\text{Si}(\text{OH})_4$ changes into H_3SiO^- and $\text{H}_2\text{SiO}^{2-}$ (Coskun *et al.*, 2019; Exley *et al.*, 2019; I. Khan *et al.*, 2021). Monosilicic acid can be altered into exchangeable silicates, colloidal silicates, and polymeric silicates which are different Si species in soil solutions (Etesami & Jeong, 2018). At high pH level, soil typically exhibits reduced Si concentrations due to adsorption of H_3SiO_4^- on clay particles thus reducing Si phytoavailable (Y.-X. Zhu *et al.*, 2019). The bioavailability and solubility of Si in soil systems are profoundly influenced by numerous soil variables, including soil texture, pH, temperature and organic matter (Imtiaz *et al.*, 2016). In subtropical areas, biochemical weathering and leaching is common because the soils are exposed to hot climates and marginal precipitation makes soil salinized and desiccated, making comparatively small Si contents available to plants (Struyf *et al.*, 2009). The accumulation of Si in plant biomass yields several beneficial outcomes, encompassing improved plant growth, enhanced nutrient uptake, insect control, and endurance to various stresses. According to some reports, Si fertilizers emit silicic acid, that bind various minerals and cause nutrient mobilization. Silicon dioxide (SiO_2) and H_2O make up the majority of plant silica and phytoliths, with different levels of organic matter and

crop development (Bhardwaj *et al.*, 2022; I. Khan *et al.*, 2021; Zhang *et al.*, 2020).

elemental components like calcium (Ca), phosphorus (P), and manganese (Mn) (Reithmaier *et al.*, 2017; J Schaller *et al.*, 2021)

Geochemistry of Si is very complex under varying pH, redox and temperature regimes. For example, Si inputs raise soil pH by reducing electrical conductivity and organic matter content. A strong hydrolysis of exchangeable cations with high proportion of sodium hydroxide (NaOH) in soil are caused by the basicity of the mineral Si (L. Wang *et al.*, 2020). This property of Si facilitates its surface to transport a significant quantity of exchangeable cations while minimizing exchangeable H^+ , results in increased pH of solution in soil (Kumari & Mohan, 2021).

Further biogeochemical processes, for instance the mobility of several important nutrients and contaminants, can be negatively impacted by rapid climate change. Exogenous Si is thought to change the soil pH and redox values that encourage the growth of microbial communities thus constitutes a basic role in maintain the soil nutrients cycling (Khan *et al.*, 2022). Silica-soil input enriches soil bacterial community formation, pH, augments soil enzyme activity, mineral contents, bioavailability, and the mobility of contaminants within both soil and plants. Treatments can directly affect these elements because soil redox status is associated with soil organic matter, pH, and microbial community (Mohammadi *et al.*, 2011). However, more research is still warranted to explore the impact of soil chemical attributes towards Si phytoavailable and its role in enhancing the soil productivity on pilot and lab scale.

Paddy conditions has the maximum unstable redox windows phases with reduced (-250 mV) to slightly oxidic (+150 mV) window that favors the metastable



phase of silicon which can be either becomes available to plants or stay bind to soil fractions (Hussain *et al.*, 2021). Following the application of Si, there is a reduction in the organic matter content of paddy soil. This suggests that Si promoted the decomposition and utilization of organic matter in paddy soil. Mineral-Si, like diatomaceous earth, consists of pores (nanopores) that are strong adsorbent. Adsorption capacity is strongly linked to the hydroxyl (-OH) group of silica, which have ability to dissociate into Si-O^- and H^+ ions, resulting in negative stimulation of surface (Puppe, 2020). On Si surface, ion exchange and electrostatic interactions provide the basis for the real adsorption mechanism. Further absorption and sequestration of heavy metals within soil are intricately linked to soil pH and other soil attributes influenced by the presence of Si (Ali *et al.*, 2019; Rizwan *et al.*, 2019; Yang *et al.*, 2020). Significantly under reduced (paddy) conditions, where losses can be severe, retention of Si is crucial to prevent leaching and runoff losses caused by increased soil pH. Anaerobic conditions during floods cause iron oxyhydroxide surfaces to reduce and dissolve, releasing silicates along with other thus leads to the formation of stable As-Si complexes that reduce the arsenic mobility in rice crop with minimum translocation and bioaccumulation factors.

cations and anions that had been previously adsorbed on these surfaces (Thimo Klotzbücher *et al.*, 2015). However, because H^+ ions are withdrawn from the solution during the reduction reaction, reducing circumstances can also cause soil pH to increase to about 7.0. This encourages the dissolved Si's re-adsorption and, hence, its retention from leaching and runoff losses. Silicon's solubility under submerged conditions naturally rises as the environment becomes anaerobic, but eventually it falls (Kumari & Mohan, 2021).

Through the formation of Si complexes, Si has the capability to alter the states of heavy metals, thereby reducing the bioavailability of Cd in soil. In addition, there are a lot of Si-OH groups on the mineral-Si surface. Due to the ion exchange capacity, Si-containing groups mix with Cd and firmly fix it in the soil. As a result, Fe-O that is present on the surface of ferrihydrite and other geological rocks combines with Si and Cd to form complexes (Fe-O-Cd and Fe-O-Si), which reduces the bioavailability of Cd (Ma *et al.*, 2021). In a recent study by Hussain *et al.* (2023) arsenic mobility is reduced by application of the foliar Si at two different levels

2. Silicon dynamics in the rhizosphere with influence on microbiota

By controlling the cycles of carbon (C), phosphorus (P), and nitrogen (N) and influencing soil organic matter contents, bacteria are also essential for preserving normal soil function.

FATE AND DISTRIBUTION OF SILICON IN TERRESTRIAL ENVIRONMENT

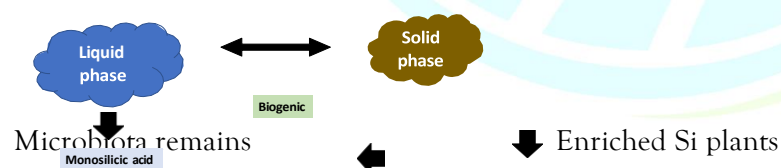


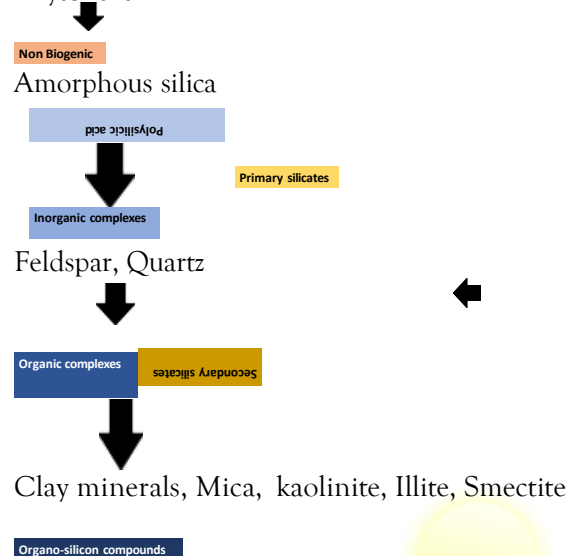
Figure 1: Different fractions of silicon in soils

solubilizing bacteria (SSB) can transform insoluble silicates into soluble silicon, lowering the Si content of the soil. Soil quality and plant health are maintained by the rhizosphere, which is essential (Barea *et al.*, 2005), in this instance, it was discovered that treatment with Si-nanoparticles and regular Si increased soil microbial biomass as well as plant uptake of Si. Silicon also does have a significant impact on the soil microbiota and nutrient levels, hence their application has been shown to encourage plant development (Theng & Yuan, 2008).



Silicon effectively restores microbial communities, minimizes heavy metal pollution in healthy soil micro-ecological zones, and ultimately promotes plant growth (Cheng *et al.*, 2019; Khan *et al.*, 2021; Zhao *et al.*, 2020). Furthermore, the bioavailability of Si in soil is largely

Phytoliths



Amorphous species

Crystalline species

dependent on the Si biostock and Si cycling in terrestrial ecosystems. Through a process called bio-silication, which mostly happens in prokaryotes and eukaryotes, a variety of species use Si to create

According to a recent study, the density of the microbial community discovered in soil grown with tomato (*Solanum lycopersicum* L.) increases with the increased application of Si (Bueno *et al.*, 2022; Lu *et al.*, 2018). However, Si application can reduce the loss of bacterial communities by boosting the colonization of species in soil, improving the diversity and stability of the natural rhizospheric environment. Furthermore, Si is significantly associated with microbes, especially *Actinomycetes*, *Cyanobacteria*, *Sphingomonadaceae*, *Nitrospiraceae*, *Flavobacteriaceae*, *Anaerolineaceae*, *Gemmatimonadaceae*, *Bacillus*, and *Betaproteobacteria* which are also responsible for driving other soil functions and physiological attributes. The size of soil-based Si biobanks is frequently several orders of magnitude more than the annual absorption rate of vegetation (Awan *et al.*, 2021). For instance, Guntzer *et al.* (2012b) demonstrated that the annual Si uptake by temperate forests, natural grasslands, and arable

siliceous structures. Bioderived amorphous silica (bASi) is hydrated amorphous silica that was created using monomeric silicic acid. The bASi stocks, particularly plant-derived stocks that are significant for soil-plant relations, determine the bioavailability in soil.

crops ranged from 5-36, 12-127, and 20-500 kg Si ha⁻¹ year⁻¹, respectively. In contrast, the equivalent amounts of biogenic Si in surface soil have Si contents of 450-17,400, 3,300-67,000, and 800-12,757 kg ha⁻¹, respectively. As a result, plants get their Si from the gradual decomposition of the entire biogenic Si residue pool in the soil, whereas in natural systems, waste replenishes this pool with newly generated botanical Si.

The rhizobacterial communities aid in the growth of plants and can thus modulate the biological and chemical composition of the soil. Additionally present in soil, silica

Anthropogenic activities that result in extensive land usage are the major hazard to the bASi pool and Si cycle. Greater soil erosion results in reduced plant-accessible Si in agricultural soils and greater losses of biologically active silicon (bASi) within soil-plant systems (Haynes, 2017; Schaller *et al.*, 2020; Schaller & Puppe, 2021; Jörg Schaller *et al.*, 2021). The main reasons for lowering bASi deposits include variations in the climate, global population



expansion, and resource depletion. Depending on the type of crop, crop harvesting causes a loss of soil alkali stores of between 100 and 500 kg of Si per hectare per year (Tubana *et al.*, 2016).

Phytoliths and plants derived silica are present in various plant components like in the leaves, stems, roots and other plant parts. The solubility and bioavailability of silicon in soil are influenced by the presence of phytoliths, which exhibit a higher concentration of Si. These phytoliths create a sizable pool of reactive bASi in the soil, which makes it easier for plants to use Si. The Si contents range (1–10% Si per dry weight) exhibit variability among different plant species (Frick *et al.*, 2020; Hodson & Guppy, 2022; Schaller *et al.*, 2021).

3. Impact of silicon on plants growth and production

Silicon applications can increase the plants biochemical and morphological attributes depending on their accumulation potential, functions and tolerance. As plants can be categorized into three groups based on their Si accumulation levels, Si-accumulating, moderate Si-accumulating and non-accumulating. Silicon accumulators hold > 1% Si per dry mass, moderate Si accumulators ranges between 0.5 and 1% and in non-accumulators retain less than 0.5% (Souri *et al.*, 2021). Depending on the plant's ability and species type, plants can accumulate Si in range of 1 to 100 g kg⁻¹ on average. There are many members of the *Poaceae* family that accumulate Si, but advance research is needed to examine the accumulation potential within this plant family (Coskun *et al.*, 2019; J Schaller *et al.*, 2021). Silicon considerably enhances the physiological attributes and productivity of crop plants despite not being on the list of essential elements even under stressful circumstances, Si advantageous and protective functions are more apparent (Luyckx *et al.*, 2019; Zhang *et al.*, 2020). Silicon application has been demonstrated to exert a substantial impact on absorption, accumulation, and transportation of nutrients in addition to other essential elements required for plant growth in both stress-free and stressful conditions in several plant tissues (Hoffmann *et al.*, 2020; I. Khan *et al.*, 2021).

The bioavailability of Si is influenced by the content present in soil minerals, organic matter, precipitation, and soil fractions. The accumulation of Si content within plants may vary significantly, ranging from 0.1% to 10% within different plant species. Monocot plants like grasses and sedges have the highest amounts as compared to dicots (López-Pérez *et al.*, 2018; Savvas & Ntatsi, 2015). Furthermore, activating antioxidant to lessen oxidative damage, repairing damaged cell membranes, enhancing the photosynthetic system, maximizing absorption and accumulating essential nutrients are among the few of based reclamation mechanisms in plants life cycle (Chandra *et al.*, 2020; Fatemi *et al.*, 2020; Khan *et al.*, 2021). While Si also performs variety of biological tasks in plants, including altering morphology, expanding photosynthetic capacity by raising the number, size, and content of chloroplasts, and finally raising dry matter (Saleem *et al.*, 2022; Zeeshan *et al.*, 2020).

The accumulation of Si in plants depends on multiple factors, such as the plant species, Si availability, and the physiological state of the plant. Generally, plant roots take up Si in silicic acid form, which is then transported via xylem to leaves and other plants parts. In leaves, Si is deposited in the cell walls of the cuticle, epidermis, and mesophyll cells (Tubana *et al.*, 2016). For instance, other species, like legumes, tend to collect lower levels of Si in their tissues while some grass species, like rice and wheat, are known to accumulate large quantities of Si in their tissues. In addition, Si distribution in plants might change depending on developmental stage of plant. Water and the pH of the soil are two main environmental elements that affect Si distribution. Due to the production of insoluble silicates, plants growing in soils with low pH levels may have impaired Si uptake. Similarly, under conditions of restricted water supply, plants may preferentially absorb water over Si, which might impair Si uptake (de Tombeur *et al.*, 2021; Schoelynck *et al.*, 2014; Tubana *et al.*, 2016).

In the recent study by Hussain *et al.* (2023) the findings demonstrated that, in comparison to the control, foliar Si treatment considerably decreased ($p > 0.05$) grain arsenic uptake (~ 67%) and enhanced rice growth and chlorophyll content (28–66%) in rice genotypes. As abiotic factors (soil



texture, mineralogy, extent of soil weathering, and pH) are important attributes of soil Si dynamics and its accumulation processes. However, biological procedures associated with the binding of mycorrhizae, silicate-dissolving bacteria, and macrofauna increase Si translocation in soil plant systems, although a root exudation effect is possible, but it is worth further investigation. Furthermore, research work is still warranted to explore the Si impact on the physiological and molecular level.

4. Impact of silicon and its application to control the pest attack

By using Si in agriculture wisely, pesticides that have detrimental effects on crop development and productivity can be used less frequently. The nutritional content of plant tissues is impacted by increased Si availability during plant growth in reed (*Phragmites australis*), which causes variations in decay. Silicon is deposited in plant tissue, where it stiffens the tissue and prevents insects from chewing, penetrating, or digesting it, so acting as a physical or mechanical barrier to insect feeding. Additionally, it controls many metabolic processes, phyto-hormone signaling pathways, and plant defense mechanisms that protect against insect attack (Nazaralian *et al.*, 2017). Utilizing Si to increase plant pest resistance is an environmentally benign tactic. If plants' defenses against insect

(PPO), and peroxidase-trypsin protease inhibitor (POD). The POD plays a role in the generation of reactive oxygen species (ROS), quinones with antibacterial properties, lignification, and suberization, among other processes (Alhousari & Greger, 2018; Liu *et al.*, 2013; Ye *et al.*, 2013). The growth of fungus and the activity of invertebrate decomposers are also impacted by the Si content in the litter, which is important for regulating the rate of straw breakdown (Schaller *et al.*, 2021; Schaller & Struyf, 2013; Schinke *et al.*, 2015).

5. Silicon impact on crop yield through stress mitigation

To meet the global demand for food, agricultural production is expanding, which causes 35% of all vegetal bAsi to accumulate in field crops around the world at harvest time. Vegetative bAsi will

assault enhanced chemically, pest numbers and pest damage can be reduced (Fauteux *et al.*, 2005; Frick *et al.*, 2020; Nazaralian *et al.*, 2017). As plant responses differ based on the pest's feeding technique, Si also relates with phyto-hormone signaling pathways to create a variety of defensive chemicals. Jasmonic acid (JA), salicylic acid (SA), and ethylene represent prevalent plant hormones that perform significant and crucial roles in coordinating different plant defense responses (De Vos *et al.*, 2007; Gupta *et al.*, 2017).

According to studies, insects that feed on cellular material are resistant to JA defensive effects. By controlling the potent interaction between SA and JA, Si improves plant resilience to pests. Techniques for priming plants can also increase their tolerance to pests brought on by Si (Hartley & DeGabriel, 2016; Kessler & Baldwin, 2002; Liu *et al.*, 2017). Plant defense mechanisms can be primed to become stronger and quicker in the event of a future herbivore attack. Secondary metabolites are regarded as the first line of defense against pest attack if they stimulate their formation. As a result of insect threats, Si inputs boosted both the quantity and activity of defense-related enzymes, including phenylalanine ammonia lyase (PAL), polyphenol oxidase

accumulate at a faster rate in the next decades as crop yields rise. Therefore, it is a crucial and urgent time to study anthropogenic silicification in agricultural soils and potential solutions to boost plant development and resilience to biotic (such as fungal infection) and abiotic (such as drought) stress (Carey & Fulweiler, 2016; Puppe & Sommer, 2018; Jörg Schaller *et al.*, 2021). Silicon can reduce the biotic and abiotic stresses by strengthening plant cell walls, promoting root development, and improving water and nutrient absorption. The introduction of Si into the structural matrix of plant cell walls has been observed to develop a defense system against biotic and abiotic stresses. Silicon plays a pivotal role in enhancing plants' ability to mitigate abiotic stresses through mechanisms such as increasing water use efficiency, shrinking excess transpiration rates, and preserving the structural



integrity of cellular membranes. In addition, Si have ability to modulate the expression of stress-responsive genes, enhanced antioxidant enzymes, and to minimize oxidative damage to plant cells, which may contribute to alleviate the negative impacts of stress on crop yield (Ali *et al.*, 2021; Li & Delvaux, 2019; Ma *et al.*, 2021; Jörg Schaller *et al.*, 2021).

Metal elements that are relatively dense and have toxic effects encompassing even low concentrations are called heavy metals. Generally, the atomic density is more than 5 g cm³, which includes cadmium (Cd), lead (Pb), chromium (Cr), arsenic (As), copper (Cu), zinc (Zn), etc. (Awan *et al.*, 2020; Bhat *et al.*, 2019). The uptake of certain heavy metals like Al, Cd, and Zn in cotton, rice, barley, maize, and spinach leaves, is inhibited by Si addition in growth conditions. These include different molecular reactions, chelation, compartmentalization, antioxidant activation, heavy metal co-precipitation of Si, immobilization of heavy metals in soil. So, by the application of Si different antioxidants like proline, organic acids, ascorbic acid, and amino acids, can restrict the oxidative damage to plants (Anwaar *et al.*, 2015; Bhat *et al.*, 2019; Shi *et al.*, 2016).

Direct or indirect association of Si with plant metabolism is still unknown what strengthened plants' defenses against pollutants of variety. Flavonoids, phenolics, and other organic acids are essential detoxifying mechanisms that improve crop tolerance by mediating the chelation of heavy metals by Si. Aluminum toxicity in root tips can be significantly decreased by phenolic substances like catechin and quercetin, which holds strong potential to chelate Al (Kidd *et al.*, 2001). Investigation revealed that the Si addition greatly enhanced the production of citrate and malate in wheat sprouts and decreased the transfer of Cu from roots to its aerial parts. Furthermore, Si initiate P mobility in soil, thereby impacting the accessibility of heavy metals and their competition for uptake by plant roots, ultimately leading to increased nutrient absorption and increased heavy metal accumulation within plants. (Luyckx *et al.*, 2019).

Particularly Si inputs to soil evidence in reduced metal (loids) particularly arsenic (As) uptake and retention in rice plants, achieved through competition for sorption sites within soil minerals and promotes the mobilization of As from these soil

For rice plants, Si is advantageous; it is often absorbed in higher concentrations than basic nutrients like NPK and Ca. (Ma & Takahashi, 2002; Marxen *et al.*, 2016). As Si application enhances plants' tolerance to biotic challenges like fungi and pests also abiotic stresses like intense wind, rain, and salinity (Guntzer *et al.*, 2012a). Monosilicic acid, which involves both active and passive transport, represents the predominant form through which Si is assimilated by rice plants from soil solutions. Notably, approximately 86% of the Si absorbed by the rice plant is subsequently deposited in rice straw. Deposition of crop residues is a significant element influencing the equilibrium of Si in paddy fields (T Klotzbücher *et al.*, 2015; Thimo Klotzbücher *et al.*, 2015; Ma *et al.*, 2007). The solubility of phytoliths, which remains a poorly defined mechanism, exerts a significant impact of rice straw input on Si availability within the soil. This shows that phytoliths slowly cycle through the soil and are stable over longer periods of time. carbon (C) in phytoliths can be found in high concentrations. Hence, a mechanism for long-term C sequestration in soils has been explored in the phytolith cycle. Contrarily, several recent investigations have demonstrated that one of the foremost contributors of Si in soil solution is fresh phytoliths. Clay minerals, natural mafic silicates, or feldspar have 100–10,000 times lower solubilities as compared to phytoliths derived from various plants such as larch, elm, fern, horsetail, etc. (Frayse *et al.*, 2009; Parr & Sullivan, 2011; Piperno, 2014).

On Si release during straw decomposition, there is limited data. However, Si fertilizers can be utilized as an alternate or supplementary option for recycling straw in places with poor Si availability. The incorporation of Si sources has a positive impact on the growth and grain yield of rice. For instance, changing Si availability can influence biomass synthesis, plant nutrient intake, and nutrient mineralization during litter decomposition, all of which have an impact on C and nutrient cycle (Caubet *et al.*, 2020; Chivenge *et al.*, 2020; Watanabe *et al.*, 2013).

particles (Hussain *et al.*, 2021). Silicon supplementation during arsenic stress can upregulate the vascular sequestration of As in rice plants and reduce metabolic damage to plant tissues. Various mechanisms have been associated



with the use of silicon in soil or as a foliar fertilizer to reduce the bioaccumulation and transfer of As to rice seedlings and grains in the roots (Ahmad *et al.*, 2013). These pathways may include: (i) antagonism between Si and As at root uptake sites, since As(III) partitions the Si transport pathway in rice root cells; (ii) Si can promote the formation of surface plaques in rice roots due to the formation of iron oxide-silicate complexes on the root surface, thereby reducing the uptake of arsenic by roots and increasing tolerance; (iii) Si also contributes to the upregulation of genes thought to be involved in rice uptake and transport and expression (Begum *et al.*, 2016).

Foliar application of Si alleviates the As accumulation in rice husk and grain at the tiller or incorporation stage. This mechanism during the tillering stage increases Si levels in both shoots and roots leading significantly downregulating the silicon transporters (*Lsi1* and *Lsi2* in roots and *Lsi6* in leaves and pods). This reduction in Si uptake and transport ultimately results in the limitation of inorganic As accumulation in rice grains. This is very useful technique to reduce the formation of inorganic arsenic in rice grains in As- contaminated rice soil (Zhang *et al.*, 2020). Although it does not affect As levels in rice seedlings also been noticed that root application of Si demonstrated greater efficacy in alleviating nutrient toxicity than foliar application (Liu *et al.*, 2014; Syu *et al.*, 2016).

6. Silicon supplementation for plant nutrition and phytohormones

Through all phases of its life cycle, a plant's growth and development are enormously modulated by the kind, availability, exposure time, and source of its nutrients (Vander Linden & Delvaux, 2019). Under biotic and abiotic stress, exogenous addition of Si can activate plant defense and phyto-hormone signaling pathways. To mitigate the adverse effects of reactive oxygen species and other potentially hazardous ions, it may control the manufacture of phyto-hormones, enhance photosynthetic capabilities, and boost the activity of antioxidant enzymes. Under stressful circumstances, Si supplementation profoundly enhanced physiological and biochemical characteristics, defense systems, hormone regulation, and initiated

the adjustment of gene expression patterns associated with stress response (Khan *et al.*, 2022).

The favorable benefits, however, depend on the type of plant, its developmental stage, the amount of Si present, and adaptations to the surrounding environment. Under nutrient deprivation conditions, Si alters the manifestation of nutrient transporters in root cells, resulting in the translocation of significant quantities of nutrients from the root system to the aerial parts, where nutrients are accumulated and useful for maintaining internal homeostasis (de Oliveira *et al.*, 2019; Hosseini *et al.*, 2019; J. Wang *et al.*, 2020). Likewise, in case of nutrient toxicity, Si interacts with nutrients within the root cell wall. During germination, Si sequesters nutrients excess in the vacuole and produces chelators that sustain redox homeostasis and eventually reduce secondary stress (I. Khan *et al.*, 2021; Khan *et al.*, 2022).

In order to significantly improve plant growth, Si activates endogenous signaling molecules within cells and stimulates their production (Kaya *et al.*, 2020; Tripathi *et al.*, 2021). During plant growth, Si facilitates many signaling pathways and interacts with substances such as phyto- hormones, carbohydrates, amino acids, and H₂O₂ (Debona *et al.*, 2017; Gururani *et al.*, 2015; Khan *et al.*, 2019). Nitrogen serves as fundamental constituent of proteins, amino acids, chlorophyll, metabolites, coenzymes and plant hormones, and is essential for plants to sustain their normal growth. N deficiency in plants or soil directly affects plant productivity (Hosseini *et al.*, 2019). Under limited N supply, the application of Si led to reduction in N absorption in hydroponic rice by upregulating the expression of N-related genes and suppressing the expression of *OsAMT1;1* and *OsGS1;1* genes. Si pretreatment increased biomass, chlorophyll content and nitrate transporter expression pattern in rapeseed plants. Under normal conditions, these plants uptake large amounts of nitrate from the soil, however they show a significant decrease in N use efficiency due to their inability to transport N to leaf (Haddad *et al.*, 2018).

Phosphorus constitutes a primary component of nucleic acids (DNA and RNA). Silicon enhances P uptake of wheat plants (*Triticum aestivum* L.) in acidic soils by upregulating the expression of P



transporter TaPHT1.1 and TaPHT1.2 and promoting the root exudates associated in this mechanism (Kostic *et al.*, 2017; J Schaller *et al.*, 2021). Si blocks plant roots by stopping the flow of hazardous chemicals, including too much salt in the soil. Significant metabolic processes affected by potassium (K) stress including protein synthesis, regulation of stomatal movement, photosynthesis, osmoregulation, and maintenance of membrane potential (Gierth & Mäser, 2007). The Exogenous application of sodium silicate (Na_2SiO_3) reduces oxidative stress by enhancing the activity of antioxidant enzymes in soybean plants subjected to NaCl induced hydroponic conditions. Meanwhile, under conditions of K deficiency, Si enhanced K uptake by roots and shoots in soybean plants (Miao *et al.*, 2010). During such conditions, the long-distance transport and loading of sucrose in the phloem serve as a vital mechanism for energy storage in plants (Jung *et al.*, 2015).

In the current era, plants responses to micronutrients have proven to be crucial for increased growth and survival owing to changing environmental conditions (Ali *et al.*, 2020; Feng *et al.*, 2021). In conditions of iron deficiency, incorporation of Si in barley and cucumber cultivars observed enhanced Fe absorption and subsequent redistribution of metals such as Cu and Zn. Si soil conditioners in nutrient-deficient environments, can overcome micronutrient deficiencies and potentially improve crop growth and productivity (Bityutskii *et al.*, 2018; Nikolic *et al.*, 2019). Furthermore, boron (B) plays a pivotal role in the growth and development processes of plants. In the case of cotton (*Gossypium herbaceum*), it has been demonstrated that the foliar applications of Si results in enhanced photosynthetic efficiency and mitigation of excessive uptake and transport of B, thereby alleviating both B deficiency and toxicity (Pereira de Souza Junior *et al.*, 2019). Si application promotes nutritional and physiological improvements in energy cane with high fiber content in Mn deficiency by, enhancing the production of dry matter in roots, improved antioxidant enzyme activity and accelerated photosynthetic activity (de Oliveira *et al.*, 2019).

7. Silicon role in mitigating abiotic stress conditions

8. By modulating the defense system, Si increases plant tolerance against pathogen stress, salinity, drought, high temperature and heavy metals. Silicon enables the absorption of metal ions, essential nutrients, during complex preparation, provides mechanical resistance to plant cell walls, and increases resistance to adverse environmental conditions.

Salt stress has a significant impact on overall global agriculture yield (Awan *et al.*, 2022). The ionic toxicity, osmotic stress, and other secondary stressors are primarily linked to salt stress (Mir *et al.*, 2022; Thakral *et al.*, 2021). There is a prospective role of Si in reducing salinity stress and damage caused by salinity stress in agricultural products. Si application enhances K distribution in all roots and significantly reduce Na^+ and Cl^- levels in barley crop roots. Likewise, Si also decrease the Na^+ concentration in the roots and leaves of chickpea (*Cicer aritenum* L.) by accumulative K^+/Na^+ ratio (Garg & Bhandari, 2016). Consequently, it is conceivable that Si binds to additional necessary nutrients and offers fewer active sites for Na^+/Cl^- salts, causing decreased uptake of salts. An important environmental risk that can significantly affect crop development and agricultural soil is drought. This happens when water transpiration exceeds the pace at which plant roots can absorb water, which might be brought on by inadequate or bad rainfall (Awan *et al.*, 2021; Kapoor *et al.*, 2020). To ensure their survival, plants must undergo their morphological, physiological, biochemical, and defense mechanisms in response to mitigate drought stress. Drought stress can cause a variety of cell functions, including cell division, growth, and cellular differentiation. It also causes more cell membrane damage, ROS and RNS formation, the breakdown of chlorophyll pigment, decreased photosynthesis, metabolite production, and eventually crop yield reduction (Feghhenabi *et al.*, 2022; I. Khan *et al.*, 2021; Sharma *et al.*, 2020). Si mitigate the harmful effects of drought experienced by plants. Due to improvements in root volume, root length, and plant height, surface area, tiller number, and panicle growth, Si fertilization under drought conditions boosts plant biomass and grain



output in a variety of crops (Ma *et al.*, 2021; Malik *et al.*, 2021). Furthermore, Si has ability to enhance plant's ability to withstand drought by improving antioxidant enzymes activities and reducing oxidative damage (Shi *et al.*, 2016; Thorne *et al.*, 2021).

The greenhouse effect, which is a direct result of global warming and generates heat, has diverse effects on the biological environment. As a means of morphological alteration and heat tolerance, plants modify themselves to face heat stress by making changes in their leaves sequence and increasing the number of trichomes and xylem cells in it (Bickford, 2016; Tozzi *et al.*, 2013). Silicon has a greater capacity to enhance plant heat tolerance compared to its effects on salt and drought stress. At high temperatures, silicon deposition on the cuticle prevents water loss and offers mechanical resistance. Additionally, under stressful circumstances, Si has stimulatory effect on the antioxidant defense system to mitigate the excess production of ROS and other free radicals (Khan *et al.*, 2020; Muneer *et al.*, 2017). Previous studies claimed that rice, tomato, strawberry, cucumber, and barley, (*Fragaria ananassa*) above heat stress grew better with Si supplementation (Hu *et al.*, 2020; Hussain *et al.*, 2019; Khan *et al.*, 2020). Under heat stress Si application results in preventing water loss, mechanical damage and transcriptional modification (Saha *et al.*, 2021).

Salinity exerts significant influence on plant productivity and the value of the resultant product due to the unavailability of several essential nutrients, loss of photosynthetic process. The photosynthetic properties of plants are greatly affected by salinity. It alters leaf water potential homeostasis and segregation of ions in cells and throughout the plant. In sugarcane crop, biochemical observations of cellular metabolism improve understanding of mechanisms of adaptation of saline soils to osmotic and ionic stress (Cavalcante Granja *et al.*, 2018; Verma *et al.*, 2020). Excess Na^+ uptake causes toxicity and osmotic stress, which eventually results in decreased plant growth and development. By controlling Na^+ transport in plants, silicon can lessen these harmful consequences. According to studies, an increase in the expression of specific genes were observed under

Si environment that involved in the exclusion and transit of Na^+ from roots to shoots, lowering the amount of Na^+ that builds up in roots and constraining its transport to shoots. Additionally, Si helps in preserving the integrity of cell membranes under salt stress conditions, avoiding excessive Na^+ uptake and basic ion leaks (Liang *et al.*, 2015; Liu *et al.*, 2019; Shen *et al.*, 2022; Zhang & Shi, 2013).

Salinity is the foremost abiotic factor exerting a significant influence on agricultural productivity. At least 20% of the crops in the globe have suffered harm because of salts. The pace at which plants absorb water will drastically decrease in high salinity environments. This has an impact on the amounts of intracellular and intercellular water and prevents cell growth, resulting in decreased stomatal activity. Increased NaCl input from prolonged salinity exposure causes severe ionic and oxidative damage (Ferchichi *et al.*, 2018; Hussain *et al.*, 2018). Under salt stress environment, ionic and osmotic imbalances the plant normal growth and development. Salt buildups decrease the levels of essential photosynthetic pigments like chlorophyll and carotenoids, which prevents in formation of ribulose 1,5-bisphosphate and weakens the photosynthetic machinery. Consequently, the level of scavenging is suppressed by the generation of more ROS. In addition, excessive ROS harm vital cell macromolecules such as proteins, nucleic acids, and lipids which compromise membrane integrity, and are associated with other critical metabolic processes. Older leaves experience premature senescence, necrosis, and chlorosis because of NaCl interference with photosynthesis, enzyme activity, and protein synthesis. Plants need better ion exclusion, redox homeostasis, osmotic tolerance, and effective photosynthetic process to deal with salinity stress (Ahmad *et al.*, 2019; Gong *et al.*, 2018; Morton *et al.*, 2019). Under saline-alkali conditions, plants absorb higher concentrations of Cl^- which accumulate in leaves, responsible for chlorosis, necrosis, ultimately slowing down plant growth. However, investigations have shown that reduction in Cl^- uptake by plants is influenced by Si and it reduce the activity of Cl^- channels in the plasma membrane of root cells of respective plants. Si also facilitates the Cl^- removal from the leaves,



avoiding accumulation and reducing its toxic effects. By reducing Cl^- uptake, it improves plant growth against salt tolerance by promoting root growth, increasing water uptake, and regulating ion homeostasis. Development of the root system by Si promotes water and nutrients use efficiency in plants. This is accompanied by reducing transpiration and increasing strength, thereby eliminating them from drought stress. Accumulation of beneficial ions such as K^+ and Ca^{2+} and reducing the uptake of toxic ions such as Na^+ and Cl^- helps in maintaining ion homeostasis and improving tolerance against salt stress (Kafi & Rahimi, 2011; Shi *et al.*, 2013; Tavakkoli *et al.*, 2010).

Plant growth and development are negatively impacted by salinity, whereas silicon supplementation has a higher tolerance against salinity stress. Silicon has crucial roles, including reducing Na^+/Cl^- uptake by roots, boosting photosynthetic activity, maintaining homeostatic redox, and effectively managing vital elements. According to numerous research, Si controls redox homeostasis pathways. To resolve redox imbalance, the addition of Si can control antioxidant enzymes activities such as superoxide dismutase (SOD), glutathione peroxidase (GPX), catalase (CAT), and ascorbate peroxidase (APX). Additionally, under stressful conditions, Si inputs enhanced the concentration of non-enzymatic antioxidants having low molecular weight including proline and glutathione (Liu *et al.*, 2019; Manivannan *et al.*, 2015; Soundararajan *et al.*, 2018; Soundararajan *et al.*, 2015).

9. Silicon fertilization and its impact on soil-crop systems

Inorganic Si fertilizers are used in crops to achieve profitable yields. Although Si is a naturally

- Silicon exists in the form of monosilicate in an alkaline pH, and its morphological variation changes the physicochemical properties of the soil. Therefore, selecting plant cultivars according to Si accumulation could prove the best possible strategy to achieve high nutritional value and improved yield in different geographical areas.
- Plants adjust several metabolic pathways to mitigate the effects of stress on growth and

occurring element, it is not readily available to plants. Inorganic Si fertilizers provide plants with Si in a soluble form, which is easily absorbed and utilized by plants. Plants immunity against abiotic stress factors such as drought, heat and salinity are accomplished by Si inputs. In addition to resistance against pests and diseases, Si can make plants able to create defensive systems for future fungal/bacterial or other pathogen attacks as already been explained. It has been noticed that there has been increased root and shoot biomass, enhanced photosynthesis and increased nutrient uptake by the application of Si. Studies have shown that fertilization with inorganic Si can increase yield and improve crop quality, including increased fruit weight, improved fruit color and extended useful life. Common sources of inorganic Si fertilizers include sodium silicate, calcium silicate and potassium silicate. However, it has been noted that not all crops can benefit from Si fertilizers, there are many other factors such as soil type, crop species and environmental conditions that limit plant growth in certain crops (Huang *et al.*, 2019; Li *et al.*, 2009; Meharg & Meharg, 2015; Tayade *et al.*, 2022; L. Wang *et al.*, 2020).

10. Silicon and plant future prospective

Silicon acts as mediator when plants face nutrient deficiency and toxicity, difficulties of interactions with various endogenous hormones that are involved in better growth. There is a close relationship between soil characteristics and plant nutritional status.

- Therefore, the use of Si can alter soil properties and strengthen microbial associations to fix carbon and supply other essential nutrients like nitrogen as a result of microbial biomass accumulation.

development and to adapt to new energetic demands imposed by different climatic and environmental scenarios. Silicon helps the plants to regulate specific and unique hormonal responses when subjected to stress combinations has an important role in plant acclimation. The ability of plants to regulate specific and unique hormonal responses when subjected to stress combinations has an important role in plant acclimation.



Therefore, the interaction of Si with endogenous plant hormones can influence plant metabolic functions.

- Silicon has been widely reported to enhance plant tolerance to various abiotic and biotic stresses, such as drought, salt, freezing, nutrient imbalance, radiation damage, metal toxicity, pests, and pathogens.
- However, more work is still warranted to explore the Si interaction with the soil microbes and its speciation in the rhizosperic zone.
- Further studies are needed to explore the impact of foliar dressing and direct application **impact on soil and crops.**
- Molecular level studies also needed to be conducted to explore the mechanisms of the Si for its role in fighting against several biotic and abiotic stresses.
- Genetic level work also needed to be explored to explore the genes responsible for the mitigation of the heavy metal(lion)s in rhizosphere and inside the plants.

Understanding the factors that influence the effectiveness of Si in plant growth and stress tolerance is essential for developing effective strategies to promote plant growth and mitigate the impacts of environmental stress on plant productivity.

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Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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