



Silicon-microbe symbiosis: redefining plant stress adaptation

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Article Info

Keywords:

Heavy metals, silicon, plant-microbe, stress mitigation, abiotic

Date:

Received: 18 March 2024

Accepted: 22 April 2024

Published: 30 June 2024

Volume: 02 (01), 2024



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Abstract

Increased environmental stresses are among the most limiting factors for agricultural productivity across the world. Reliable and environmentally friendly techniques are needed to sustainably meet growing global food demands. Plant-microbe interactions can alleviate stress, with the application of plant growth-promoting rhizobacteria (PGPRs) that is now widely in use. It has been known that PGPRs enhance plant growth and tolerance to heavy metals by different action mechanisms. Application of silicon (Si) can also stimulate plant growth and heavy metal stress tolerance in plants. Here, we compare the mechanisms, as far as they are known, through which Si and PGPRs can alleviate heavy metal stress in plants. Both alleviate a similar suite of abiotic and biotic stresses, with a few interesting exceptions, though mechanisms differ. The review paper suggests that the combined use of Si and PGPRs can be a powerful and sustainable strategy to enhance plant growth in sub-optimal conditions, and hence, experiments assessing the combined use of Si and PGPRs on plants suffering abiotic and biotic stress can be fruitful in the future.

1. Introduction

Agriculture is the mainstay of growing economies, supplying food and consequently improving the overall quality of life. Different areas of agriculture are confronted with a wide range of challenges, such as climate change, soil pollution from dangerous environmental pollutants like pesticides, heavy metals, and fertilizers, and significantly increased food demand due to a growing world population (Kumar and Sharma, 2022; Liu *et al.*, 2023a; Liu *et al.*,

2023b; Tsoraeva *et al.*, 2020). Increased industrial activities have led to the uncontrolled release of metals into the environment, resulting in a global increase in metal pollution. Heavy metal accumulation has been reported in the atmosphere, the marine environment, and the soil while impacting drinking water sources and raising the hazardous concentration of metal pollutants in foods (Siddiquee *et al.*, 2015). Most of these metal pollutants are easily stored in plants, through which they enter the food chain, and are

passed to humans, causing catastrophic illnesses and diseases (Nedjimi, 2021).

These toxic pollutants are mainly heavy metals and metalloids such as arsenic (As), lead (Pb), cadmium (Cd), chromium (Cr), mercury (Hg), copper (Cu), and antimony (Sb) (Feng *et al.*, 2021). The uptake of these contaminants by plants leads to serious threats to human health living in the contaminated areas, primarily via the food chain (Feng *et al.*, 2021). The occurrence of heavy metals in the soil adversely affects the growth, photosynthesis, biomass, and productivity of various crops and restricts the uptake and translocation of essential nutrients to plants (Adrees *et al.*, 2015; Awan *et al.*, 2020). Hence, there is an urgency to find methods to alleviate the impacts of environmental stresses on agricultural systems to sustainably feed the world's growing population, while decreasing environmental damage (Figure 1).

Manipulating soil microorganisms is one sustainable agricultural practice that can improve crop productivity and

soil health by facilitating interactions of plant roots and beneficial soil microorganisms (Lugtenberg *et al.*, 2002). Some of the beneficial soil bacteria, PGPRs (plant growth-promoting rhizobacteria), can colonize plant roots (rhizosphere) and considerably increase plant growth and yield (Kloepper *et al.*, 1989) (Figure 2). These bacteria can help plants maintain productivity under stressful conditions (Etesami and Beattie, 2017). Since PGPRs are effective in understanding stress tolerance, adaptation, and response mechanisms, they can be used as excellent models to be engineered into crop plants to cope with the climate change-induced stresses (Grover *et al.*, 2011).

2. Silicon

Application of silicon (Si) fertilizer in agriculture is another potentially sustainable option for the alleviation of biotic and abiotic stresses in various plants (Etesami and Jeong, 2018). Silicon (Si) makes up around 70 % of the mass of soil and is one of the most prevalent elements in the Earth's

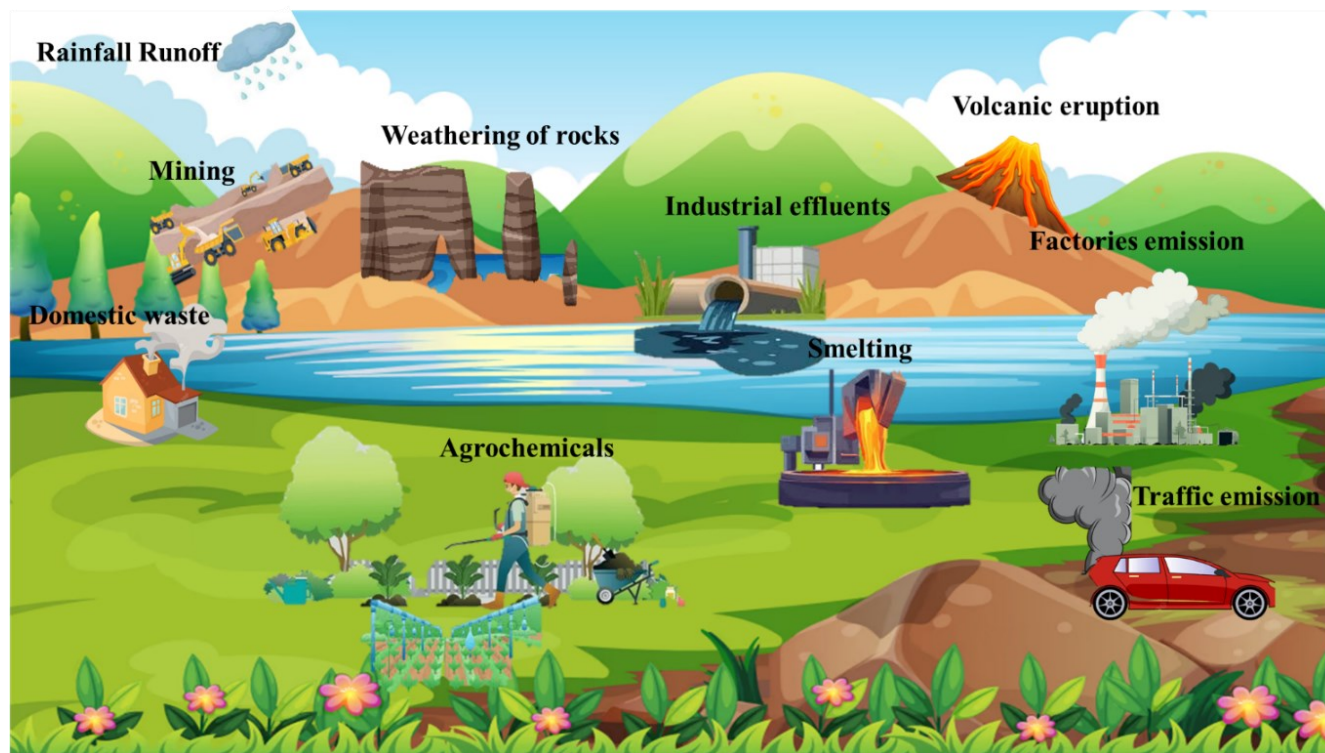


Figure 1. Natural and anthropogenic pathways of potentially toxic elements (PTEs) into the agroecosystem. Volcanic eruptions, rock weathering, and rainfall runoff represent natural sources of PTEs entering agricultural soils. Anthropogenic sources include agrochemicals, wastewater irrigation, traffic emissions, domestic wastes, and industrial activities such as mining, smelting, and factory emissions. These combined routes contribute to the accumulation of heavy metals in the soil–plant system, posing environmental and food safety risks.

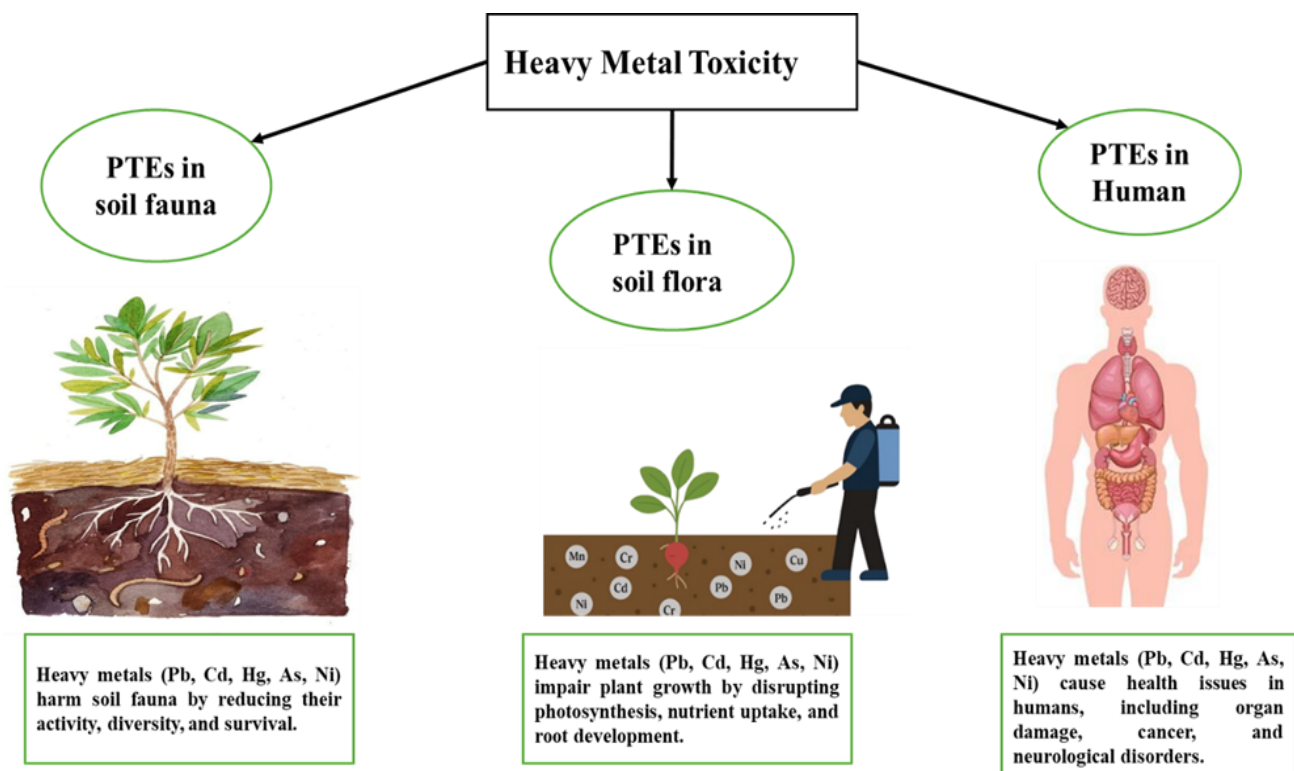


Figure 2. Ecotoxicological impacts of PTEs on soil fauna, flora, and humans within the agroecosystem

Accumulation of heavy metals such as As, Cu, Pb, Zn, Cd, and Hg disrupt soil microbial diversity and biogeochemical cycling, leading to nutrient deficiencies and physiological stress in plants. These disruptions impair germination, pollination, and overall crop productivity, thereby threatening food security. In humans, exposure through ingestion, dermal contact, or inhalation causes severe health issues, including cancers and organ-related diseases.

crust (Siddiqui *et al.*, 2020). Si constitutes a major portion of soil as silicate or aluminum silicate, but despite its abundance, most cannot be absorbed directly by plants (Zhu and Gong, 2014) (Figure 3). It occurs as silicic acid, $\text{Si}(\text{OH})_4$, at concentrations between 0.1 mM and 2.0 mM ($\text{pH} < 9$) and is readily absorbed into the root system. Si concentration in plant aboveground parts ranges from 0.1 to 10.0% dry weight (Epstein, 1994).

3. PGPRs and Si-mediated alleviation of metal heavy toxicity in plants

Si and PGPR have been shown to alleviate the deleterious effects of heavy metals in plants grown on contaminated soils (Adrees *et al.*, 2015; Etesami, 2018). Some of the known mechanisms by which Si and PGPRs alleviate heavy metal stress in plants are shown in the Figure. 3. In this section, the recent progress in understanding the mechanisms of PGPRs and Si-mediated heavy metal tolerance in plants is summarized.

3.1. Decrease in heavy metal toxicity (detoxification)

It was found that PGPRs could reduce heavy metal toxicity by multiple mechanisms. For example, metal-resistant siderophore-producing PGPRs can alleviate metal toxicity by supplying nutrients for plants and binding metals other than iron (chelation reaction), which may be the reason why PGPRs can survive in the mine tailing soil contaminated by multiple metals (Etesami, 2018). The ability to produce the enzyme ACC deaminase is one of the most widely accepted mechanisms of PGPRs under heavy metal stress. This enzyme can lower growth-inhibitory levels of stress ethylene produced in plants exposed to metal stress and subsequently help alleviate the heavy metals' toxicity and confer tolerance to plants (Sessitsch *et al.*, 2013). By producing low molecular weight organic acids (e.g., citric, oxalic, gluconic, succinic, etc.), heavy metal-tolerant PGPRs form complexes with heavy metals (chelation), which result in metal ion detoxification. It is known that these organic

acids have a higher affinity to form complexes with heavy metals than with essential nutrient elements. In addition, organic acids (e.g., citrate and oxalate) can reduce heavy metal toxicity (e.g., Cd) to plants by modulating the antioxidant enzyme response of plants (Etesami, 2018).

By solubilizing mineral phosphate complexes (e.g., calcium phosphate, iron(III) phosphate, and aluminium phosphate) (Gyaneshwar *et al.*, 2002) and subsequently enhancing the P availability to plants, phosphate solubilizing-PGPRs reduce the uptake and translocation of heavy metals via (i) the processes involved in binding heavy metals to cell

wall fraction, (ii) forming heavy metals-phosphate complexes (e.g., formation of pyromorphite and formation of insoluble Cd phosphate precipitates); and (iii) sorption of metals to exopolysaccharide polymers (Etesami, 2018). The biosurfactants produced by PGPRs can also alleviate metal toxicity by preferentially binding toxic metals with stronger affinity than the normal soil metal cations (Pacwa-Płociniczak *et al.*, 2011). By inducing physiological changes and promoting the absorption of essential nutrients as a result of proliferating plant roots, phytohormones (e.g., auxins, gibberellins, and cytokinins) produced by PGPRs can

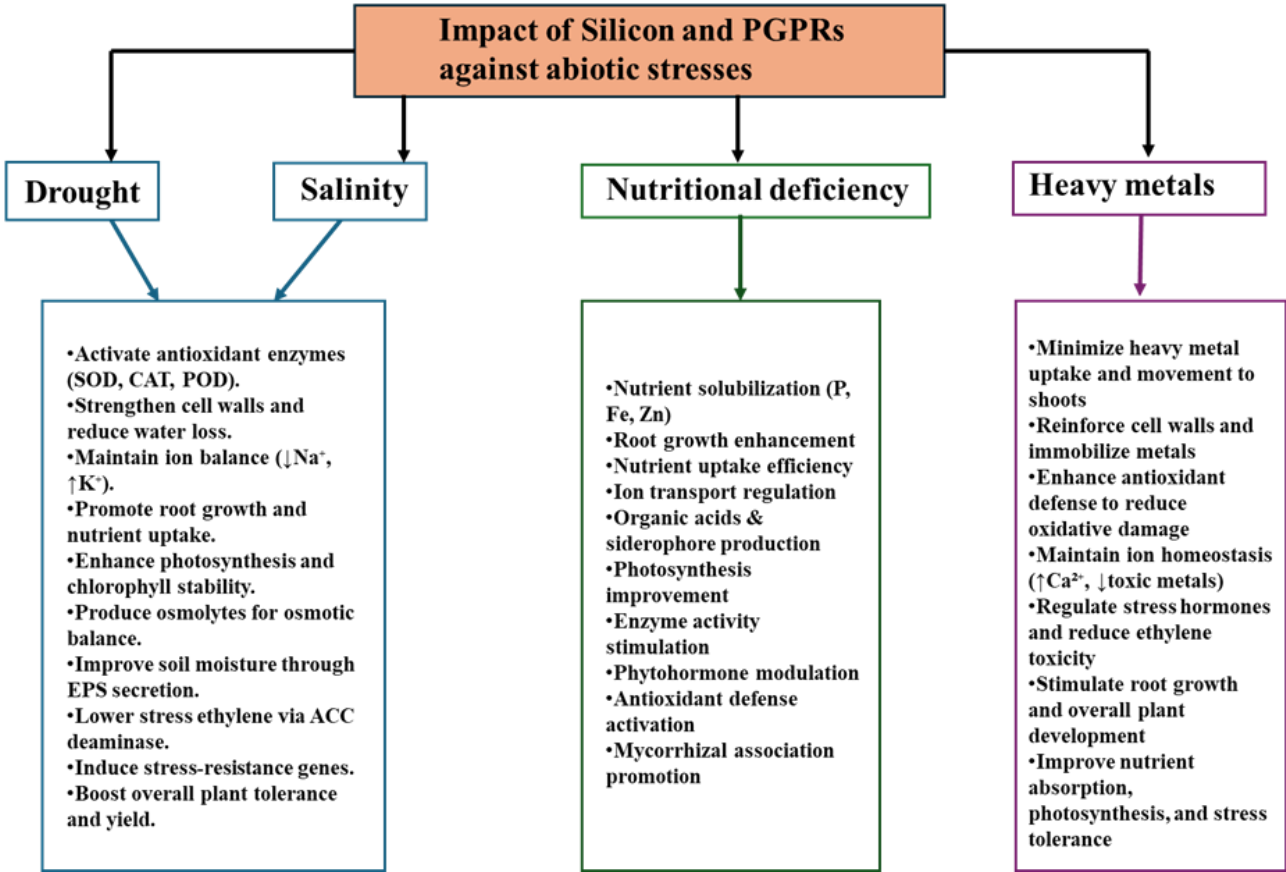


Figure 3. Comparison of the mechanisms through which silicon (Si) fertilizers and plant growth-promoting rhizobacteria (PGPRs) mitigate various abiotic and biotic stresses in plants.

Si and PGPRs enhance plant resilience through multiple physiological and biochemical pathways, including root system development, osmolyte accumulation, ion homeostasis, regulation of phytohormones, and induction of antioxidative and stress-resistance genes. These mechanisms collectively alleviate salinity, drought, heavy metal toxicity, nutrient imbalance, and plant diseases. (Compant et al. (2005); Liang et al. (2007); Dimkpa et al. (2009); Rajkumar et al. (2012); Miransari (2013); Egamberdieva and Lugtenberg (2014); Hernandez-Apaolaza (2014); Zhu and Gong (2014); Adrees et al. (2015); Exley (2015); Pozza et al. (2015); Rizwan et al. (2015); Kaushal and Wani (2016b); Qin et al. (2016); Luyckx et al. (2017); Etesami et al. (2017); Etesami (2018); Etesami and Jeong (2018)).

alleviate metal-induced stress in plants and facilitate adaptation and tolerance to metals, subsequently enhancing plant growth. For example, auxins (e.g., IAA) are implicated in alleviation of Cd toxicity in plants by reducing Cd sorption and translocation or stimulating antioxidant enzymes (Chmielowska-Bąk *et al.*, 2014).

The exopolysaccharides (i.e., polysaccharides, mucopolysaccharides, humic substances, and proteins) produced by PGPRs can strongly bind to toxic trace elements and entrap precipitated metal sulfides and oxides, leading to the formation of organic metal complexes and subsequently alleviating heavy metal toxicity (Etesami, 2018). Similar to PGPRs, Si can also decrease heavy metal toxicity and subsequently mitigate heavy metal stress in heavy metal-stressed plants (Etesami and Jeong, 2018). In previous studies, it was reported that Si reduced the toxic effects of metals in plants by stimulating the production of root exudates (e.g., increase in the concentration of chelates such as flavonoid-phenolics or organic acids such as citrate, malate, and aconitate) (Adrees *et al.*, 2015; Imtiaz *et al.*, 2016). Numerous studies found the co-precipitation of Si with metals in the leaves and roots of varied plant forms (Etesami and Jeong, 2018). It was found that the coprecipitation of Si with heavy metals reduced the cell wall porosity of inner root tissues and free heavy metals (Shi *et al.*, 2005). Si can reduce metal toxicity in plants by increasing the content and accumulation of macronutrients (e.g., Ca, Mg, P, and K) and micronutrients (e.g., Zn, Fe, and Mn) in plants (Etesami and Jeong, 2018). In addition, Si can reduce the metal toxicity as a result of the dilution effect by enhancing the xylem sap and growth and biomass of heavy metal-stressed plants (with larger biomass but similar uptake) (Adrees *et al.*, 2015; Gu *et al.*, 2012; Liang *et al.*, 2005a).

Some of other mechanisms by which Si could detoxify metal heavy in metal-stressed plants include: (i) influencing metal compartmentation in leaves and roots and sequestering these metals in non-photosynthetically active leaf epidermal cells or on cell walls (metabolically less active cell compartments); (ii) accelerating suberin lamellae, Casparian bands, root vascular tissues development, and lignification; (iii) enhancing the activity of gas exchange characteristics (e.g., net photosynthetic rate, stomatal conductance, transpiration rate, and water use efficiency); (iv) changing some of the plant morphological traits (e.g., increase in length of leaves, in leaf area, in number of leaves per plant, in root

volume and number of root tips and length of primary seminal root, in total root length, and in total root surface area); (v) regulating plant phytohormones (e.g., decrease in abscisic acid levels); (vi) helping the formation of the tertiary endodermal cell walls; and (vii) localizing in root endodermis, which serve as a barrier to block heavy metal entrance into cells (Adrees *et al.*, 2015; Imtiaz *et al.*, 2016). Based on these studies, it can be concluded that Si and PGPRs increase heavy metal resistance in plants by reducing heavy metal toxicity.

3.2. Decreasing metal uptake and blocking metal transfer in plants

It has been well known that heavy metals adversely influence the growth, biomass, and photosynthesis of heavy metal-stressed plants (Adrees *et al.*, 2015). Biotransformation of toxic soluble heavy metals has been reported as a crucial step for reducing the uptake of these metals by plants. PGPRs protect the plants from the phytotoxicity of excessive metals by changing the speciation from bioavailable forms to the non-bioavailable forms in soils (Sessitsch *et al.*, 2013). Heavy metal tolerant-PGPRs can decrease the availability of heavy metals to plants, immobilize the metal and subsequently prevent its entry into the plant root by different action mechanisms (Etesami, 2018) including (i) precipitation of heavy metals with microbially produced anions (e.g., sulfides, phosphates, etc.); (ii) acidification and oxidation-reduction; (iii) complexation by producing numerous organic substances; (iv) biosorption or sequestration of heavy metals by bacterial cells; and (v) bioaccumulation of heavy metals. In addition, siderophore-producing PGPRs also result in reduced uptake of heavy metals (e.g., Cd) by improving iron availability, thus conferring heavy metal tolerance, as well as improving plant growth.

It was found that Si could enhance tolerance to toxic metals in many plant species by reducing the uptake and translocation of metals (Adrees *et al.*, 2015; Etesami and Jeong, 2018; Imtiaz *et al.*, 2016). Si can reduce the metal uptake by many ways including (i) increasing the uptake of calcium ion (Ca^{2+}) and decreasing the uptake of aluminum ion (Al^{3+}) by plants (Hammond *et al.*, 1995); (ii) reducing the apoplasmic transport of heavy metals by decreasing free metal concentration in the apoplasm (Iwasaki *et al.*, 2002; Rogalla and Römheld, 2002); (iii) forming the physical barrier by deposition in the vicinity of the endoderm, which

reduces the cell wall porosity of inner root and subsequently decreases the metal concentration in the xylem (da Cunha and do Nascimento, 2009; Keller *et al.*, 2015); (iv) decreasing the contents of heavy metals in shoots relative to the roots of plant (Naeem *et al.*, 2015; Rizwan *et al.*, 2012; Srivastava *et al.*, 2015); (v) stimulating the production of root exudates and releasing organic acids, which chelate metals and subsequently reduce uptake of heavy metals by roots or translocation of metals to shoots (Kidd *et al.*, 2001); (vi) developing the apoplasmic barriers and maturation of vascular tissues root (Greger *et al.*, 2011; Vaculik *et al.*, 2012); (vii) increasing the adsorption of metals on the cell walls (Ye *et al.*, 2012), (viii) reducing the mobility of heavy metals by accumulation in the root endodermis (Keller *et al.*, 2015); and (ix) reducing the net influx of heavy metals in cells (Liu *et al.*, 2013).

Si immobilizes toxic metals by increasing soil pH and altering metal speciation, thereby reducing their availability and plant uptake by (i) forming the insoluble metal silicates, silicate complexes and Si polyphenol complexes in soil; (ii) decreasing the proportion of exchangeable heavy metals in metals-contaminated soil; (iii) increasing the precipitation-bound proportion and the fraction of organic matter bound metals in soil (Adrees *et al.*, 2015; Imtiaz *et al.*, 2016); and (iv) changing the chemical forms of Al in the solution by forming hydroxy aluminosilicate (HAS) species (Hammond *et al.*, 1995). Based on these studies, it can be concluded that Si and PGPRs reduce the heavy metal toxicity in plants by obstructing metal transfer in plants and decreasing metal uptake by plants (Figure 4).

3.3. Improvement in the uptake of nutrient elements by the plant

Minerals' nutritive substances are the major components in the structural body of plants, providing mechanical, biochemical, and physical strength to them. Toxic heavy metals interfere with the uptake and distribution of essential nutrients in the plant, causing deficiencies and nutrient imbalance (Barceló and Poschenrieder, 1990). For example, Cd^{2+} competes with several mineral nutrients having almost similar chemical properties like Ca^{2+} and Mg^{2+} , Zn^{2+} and Fe^{2+} , therefore, causing a mineral deficiency in the plant (Barceló and Poschenrieder, 1990). It was found that the PGPRs with the ability of production of IAA, organic acids, and siderophore enhanced plant growth and plant resistance to metal stress in metal contaminated soils by inducing

physiological changes in plant, reducing heavy metal toxicity partially to the plants, and improving the uptake of nutrient elements (e.g., P, Mg, Ca, N, S, Fe, Zn, Mn, etc.) (Etesami, 2018).

Si can also reduce metal toxicity in plants via improving (interaction with other elements) the absorption of essential nutrients (e.g., Zn, Fe, Mn, Ca, Mg, P, and K) by the plants under metal stress (Adrees *et al.*, 2015; Etesami and Jeong, 2018). Based on these studies, it can be concluded that Si and PGPRs reduce heavy metal toxicity in plants by improving the uptake of nutrient elements in plants.

3.4. Induced plant synthesis of antioxidative enzymes

Oxidative stress may also occur in plants when they are exposed to heavy metal stress (Adrees *et al.*, 2015). It has been well known that PGPRs induce plant synthesis of antioxidant enzymes in response to abiotic stresses, including heavy metal stress (Etesami, 2018). In many previous studies (Kim *et al.*, 2017), it was found that Si could reduce oxidative stress in the plants fertilized with Si by reducing the production of reactive oxygen species and enhancing the activities of antioxidant enzymes (e.g., superoxide dismutase, peroxidase, catalase, and ascorbate peroxidase). Based on these studies, it can be concluded that Si and PGPRs reduce the heavy metal toxicity in plants by inducing plant synthesis of antioxidative enzymes in plants.

3.5. Activation/Regulation of heavy metal resistance genes

PGPRs can induce heavy metal resistance genes (e.g., genes of PaADC, PaSPDS₁, PaSPDS₂, Lemt₂, and LeNramp₁) and the expression of more general stress response mechanisms such as ethylene and stress proteins under different stresses, including heavy metal toxicity in plants (Dimkpa *et al.*, 2009; Rajkumar *et al.*, 2012; Sessitsch *et al.*, 2013; Vannini *et al.*, 2006). It was also reported that Si application activated the important genes (e.g., OsHMA₃ and OsLsi genes in rice under Cu/Cd stress and genes of Os09g26810, Os08g02630 (PsbY), Os03g57120 (PetH), Os05g48630 (PsaH), Os07g37030 (PetC), and Os04g38410 in rice Zn under stress) associated with heavy metal responses, in heavy metal stressed plant responsible for heavy metal tolerance (Adrees *et al.*, 2015; Bokor *et al.*, 2014; Kim *et al.*, 2014; Ma *et al.*, 2015; Nwugo and Huerta, 2010; Song *et al.*, 2014).

In addition, Si also inactivated some transporter genes, e.g., COPT1 and HMA5 in *Arabidopsis thaliana* under Cu stress and Nramp5 in rice under Cd stress, which were involved in transferring heavy metals in heavy metal-stressed plants (Ma *et al.*, 2015; Ping *et al.*, 2008), genes of PAL (phenylalanine ammonia-lyase) under Cu stress, and genes of ZmLsi₁ and ZmLsi₂ in maize roots under Zn stress (Bokor *et al.*, 2014; Khandekar and Leisner, 2011). Based on these studies, it can be concluded that Si and PGPRs reduce the heavy metal toxicity in plants by inducing heavy metal resistance genes in plants. The above studies clearly show that PGPRs and Si could separately alleviate heavy metal stress in stressed plants through different mechanisms.

and Si to reduce the stress of heavy metals in plants, which is recommended for future studies.

4. Which one is the best in alleviating abiotic and biotic stress? PGPRs or Si or both

The successful use of PGPRs in applications, such as phytoremediation, bioremediation, biofertilization, biocontrol, etc., relies much on the ability to establish the desired PGPRs in the already existing community of soil microorganisms (native microorganisms). It was reported that PGPRs were not able to increase the growth and yield of the plant or the plant's tolerance to biotic or abiotic stresses under field conditions, although they were effective in the

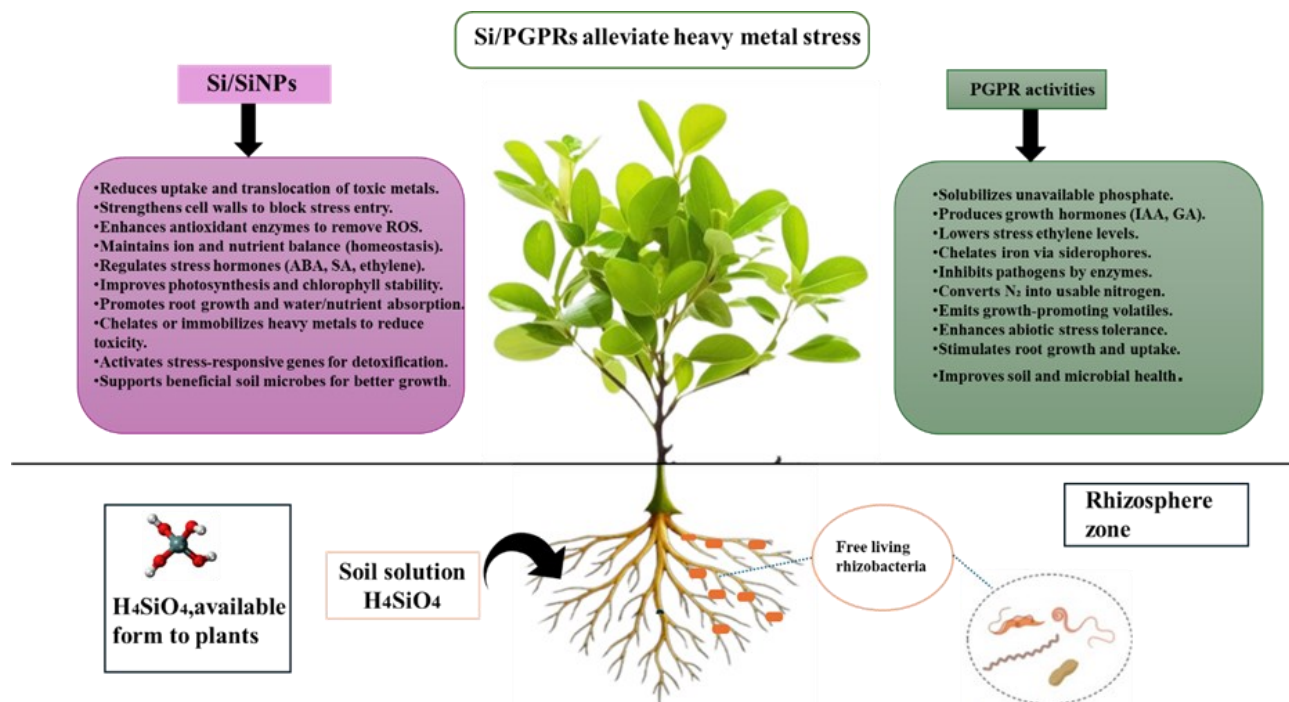


Figure 4. Mechanisms by which silicon (Si) and plant growth-promoting rhizobacteria (PGPRs) alleviate heavy metal stress in plants

Si mitigates heavy metal toxicity by decreasing metal uptake, enhancing plant growth and photosynthetic efficiency, improving nutrient balance, and promoting detoxification processes. PGPRs alleviate heavy metal stress through mechanisms such as siderophore production, ACC deaminase synthesis, organic acid and biosurfactant secretion, phosphate solubilization, and induction of metal resistance genes. Collectively, Si and PGPRs reduce the bioavailability and uptake of heavy metals, thereby enhancing plant tolerance and growth under contaminated conditions.

Accordingly, it can be predicted that if PGPRs and Si are used together, they will be more effective in reducing the stress of heavy metals compared with their use separately. So far, no research has been conducted on the compound use of PGPRs

greenhouse and controlled (in vitro) conditions. There is, for instance, a great deal of evidence that in vitro solubilization of P by phosphate-solubilizing PGPRs was not effective under field conditions (Gyaneshwar *et al.*, 2002). Among the

influential factors impacting colonization with pre-selected PGPRs, variables such as soil type and chemical properties, natural selection, as well as agricultural management practices (e.g., crop rotation or application of pesticides) are of great importance. Therefore, there are many factors that PGPRs can apply to their effect on the plant of interest. For example, to protect the plants from Cd stress, these bacteria must be (i) resistant to Cd, (ii) capable of binding to free Cd²⁺, (iii) actively colonizing rhizoplane, rhizosphere, and/or endorhiza, and (iv) a PGPR with multiple plant growth-promoting traits (Pishchik *et al.*, 2002).

Successful establishment of PGPRs might pursue the first-come-first-served principle. To begin with, in the plant's development, a bacterium can be established, the better the chances that it might out-compete others; however, it has been found that there are bacteria within the embryo or under the seed coat of some plant species. Such bacteria will still have to compete with beneficial bacteria, even when the latter are applied as early as the seed stage. In fact, the prerequisite for a successful establishment of the beneficial bacteria is a continuous supply of carbon and energy sources (Zahir *et al.*, 2003). Hence, in addition to the attraction of neutral and beneficial bacteria, fungi, and other soil microorganisms, mucilage-derived nutrients and root exudates attract deleterious rhizobacteria as well (Walker *et al.*, 2003). Consequently, PGPRs have to be highly competitive to successfully establish in the root zone, and this factor has yet to be improved in the near future.

As mentioned above, Si has been known as the only element that can increase plant resistance to manifold stresses. Although there is a bacterial isolate possessing multiple PGP traits, it is not known whether all the traits of promoting plant growth are expressed concurrently or at different phases of growth of the bacteria. When present excessively, Si does not pose any harm to plants (Epstein, 1994) since Si is noncorrosive and pollution-free. Si fertilizers are, therefore, high-quality fertilizers that can be used for cultivating an ecologically sound agronomy (Zhu and Gong, 2014). From an economic perspective, Si fertilizers are also relatively affordable, assuming 10-20% of the cost of other fertilizers (Yuanqi, 2000). Therefore, to reap the economic and ecological benefits of Si, it is necessary to apply Si-fertilizer in Si-lacking areas. Taken together, it seems that PGPRs and Si can synergistically enhance tolerance to abiotic and biotic stresses in plants. For the first

time, an additive effect and an improved strategy for the amelioration of salinity stress in mung bean upon the combined use of Si and PGPRs were reported (Mahmood *et al.*, 2016, 2017).

5. Conclusions and prospects

Many plant-associated bacteria are well known for their capacity to confer plant growth promotion and increase resistance to stresses. However, when applied in the field, these PGPRs frequently are unsuccessful in conferring their beneficial effects, which is often because of inadequate rhizo- and/or endosphere colonization (Compant *et al.*, 2010). Si can also stimulate plant growth and alleviate various biotic and abiotic stresses in plants. Both have almost the same propensity to alleviate abiotic and biotic stresses in plants. Hence, I suggest that the combined use of Si and PGPRs may have synergistic benefits in alleviating stresses. Currently, only a single study (Mahmood *et al.*, 2016) has explored the potential for the combined application of Si and PGPRs to benefit plant growth. Additional study is necessary to comprehend the mechanisms by which Si and PGPRs alleviate environmental stresses in tandem.

Based on current knowledge, suggest several future avenues of research: (i) additional research is necessary to investigate the influences of Si on plant biochemistry and on the articulation of microbial genes. In addition, it should be determined that whether the combined use of Si and PGPRs might be a general strategy to improve stress tolerance of crop plants under different stressful conditions (e.g., drought, heavy metals, organic pollutants, nutritional imbalance, etc.) (Mahmood *et al.*, 2016); (ii) comparative studies of interactions between Si and PGPRs, now lacking, would shed light on the mechanisms governing biotic and abiotic stresses; (iii) the most important aspect for further studies on Si in plant biology should be focused on making full use of the role of Si along with PGPRs and even fungi in conferring tolerance in plants against abiotic stresses, and thus their roles in environmental remediation; (iv) since most of the PGPRs are heterotrophic and susceptible to environmental stressors and, on the other hand, competition for limited resources by these PGPRs is also crucial, prominent beneficial effects of inoculation with potential PGPRs are to be investigated in poor soils; (v) there is no information on the metabolically active roles of Si and PGPRs in plants under biotic and abiotic stress conditions, particularly on the molecular aspects of plants and PGPRs and Si-mediated nutrient; (vi) mechanisms

of PGPRs and Si-mediated alleviation of abiotic stresses (e.g., drought, salt stress and heavy metals) in plants (monocots and dicots) are poorly comprehend at the molecular and genetic levels; more genetic research is necessitated to determine relationships between these stresses and Si and PGPRs; and (vii) it is needed to study the compound use of Si and silica solubilizing bacteria to alleviate different environmental stresses (abiotic and biotic) and compare their effects on plant.

In general, developing more detailed fundamental knowledge about the interactions between PGPRs and Si would facilitate a better understanding of alleviating abiotic and biotic stresses and perhaps would allow better predictions regarding the plant response. It was foreseen that increasing curiosity to explore the mechanisms of PGPRs and influence stress tolerance among plants is about to come. On the whole, well-crafted, large-scale, and long-term field trials are called for in order to assess the viability of PGPRs and Si application in mitigating biotic and abiotic stresses, along with an investigation into the economic feasibility of different Si bases.

6. Funding

No funding was received for this study.

7. Conflict of Interest

None of the authors declares a conflict of interest.

8. SDG Goals

This review supports *SDG 2 (Zero Hunger)* by highlighting sustainable strategies, silicon and plant growth-promoting rhizobacteria, to enhance crop resilience under environmental stress. It aligns with *SDG 13 (Climate Action)* through its focus on improving plant tolerance to climate-induced stresses, and with *SDG 15 (Life on Land)* by promoting eco-friendly approaches that strengthen soil-plant-microbe interactions for healthier agroecosystems.

References

- Adrees, M., Ali, S., Rizwan, M., Zia-ur-Rehman, M., Ibrahim, M., Abbas, F., Farid, M., Qayyum, M. F., & Irshad, M. K. (2015). Mechanisms of silicon-mediated alleviation of heavy metal toxicity in plants: A review. *Ecotoxicology and Environmental Safety*, 119, 186-197.
- Awan, S. A., Ilyas, N., Khan, I., Raza, M. A., Rehman, A. U., Rizwan, M., Rastogi, A., Tariq, R., & Brestic, M. (2020). *Bacillus siamensis* reduces cadmium accumulation and improves growth and antioxidant defense system in two wheat (*Triticum aestivum* L.) varieties. *Plants*, 9(7), 878.
- Barceló, J., & Poschenrieder, C. (1990). Plant water relations as affected by heavy metal stress: A review. *Journal of Plant Nutrition*, 13(1), 1-37.
- Bokor, B., Vaculík, M., Slováková, L., Masarovič, D., & Lux, A. (2014). Silicon does not always mitigate zinc toxicity in maize. *Acta Physiologiae Plantarum*, 36(3), 733-743.
- Chmielowska-Bąk, J., Gzyl, J., Rucińska-Sobkowiak, R., Arasimowicz-Jelonek, M., & Deckert, J. (2014). The new insights into cadmium sensing. *Frontiers in Plant Science*, 5, 245.
- Compant, S., Clément, C., & Sessitsch, A. (2010). Plant growth-promoting bacteria in the rhizo- and endosphere of plants: Their role, colonization, mechanisms involved and prospects for utilization. *Soil Biology and Biochemistry*, 42(5), 669-678.
- Compant, S., Duffy, B., Nowak, J., Clément, C., & Barka, E. A. (2005). Use of plant growth-promoting bacteria for biocontrol of plant diseases: Principles, mechanisms of action, and future prospects. *Applied and Environmental Microbiology*, 71(9), 4951-4959.
- da Cunha, K. P. V., & do Nascimento, C. W. A. (2009). Silicon effects on metal tolerance and structural changes in maize (*Zea mays* L.) grown on a cadmium- and zinc-enriched soil. *Water, Air, and Soil Pollution*, 197(1), 323-330.
- Dimkpa, C., Weinand, T., & Asch, F. (2009). Plant-rhizobacteria interactions alleviate abiotic stress conditions. *Plant, Cell & Environment*, 32(12), 1682-1694.
- DimkpaKumar, A., & Sharma, P. (2022). Impact of climate variation on agricultural productivity and food security in rural India. *SSRN*. <https://doi.org/10.2139/ssrn.4144089>
- Egamberdieva, D., & Lugtenberg, B. (2013). Use of plant growth-promoting rhizobacteria to alleviate salinity

- stress in plants. In *Use of microbes for the alleviation of soil stresses* (Vol. 1, pp. 73-96). Springer.
- Epstein, E. (1994). The anomaly of silicon in plant biology. *Proceedings of the National Academy of Sciences*, 91(1), 11-17.
- Etesami, H. (2018). Bacterial-mediated alleviation of heavy metal stress and decreased accumulation of metals in plant tissues: Mechanisms and future prospects. *Ecotoxicology and Environmental Safety*, 147, 175-191.
- Etesami, H., & Beattie, G. A. (2017). Plant-microbe interactions in adaptation of agricultural crops to abiotic stress conditions. In *Probiotics and plant health* (pp. 163-200). Springer.
- Etesami, H., & Jeong, B. R. (2018). Silicon (Si): Review and future prospects on the action mechanisms in alleviating biotic and abiotic stresses in plants. *Ecotoxicology and Environmental Safety*, 147, 881-896.
- Exley, C. (2015). A possible mechanism of biological silicification in plants. *Frontiers in Plant Science*, 6, 144273.
- Feng, R., Wang, L., Yang, J., Zhao, P., Zhu, Y., Li, Y., Yu, Y., Liu, H., Rensing, C., Wu, Z., & Ni, R. (2021). Underlying mechanisms responsible for restriction of uptake and translocation of heavy metals by selenium via root application in plants. *Journal of Hazardous Materials*, 402, 123570.
- Greger, M., Landberg, T., Lux, A., & Singh, B. R. (2011). Influence of Si on Cd uptake and accumulation in wheat. In *Silicon in Agriculture* (p. 55).
- Grover, M., Ali, S. Z., Sandhya, V., Rasul, A., & Venkateswarlu, B. (2011). Role of microorganisms in adaptation of agriculture crops to abiotic stresses. *World Journal of Microbiology and Biotechnology*, 27(5), 1231-1240.
- Gu, H. H., Zhan, S. S., Wang, S. Z., Tang, Y. T., Chaney, R. L., Fang, X. H., Cai, X. D., & Qiu, R. L. (2012). Silicon-mediated amelioration of zinc toxicity in rice (*Oryza sativa* L.) seedlings. *Plant and Soil*, 350(1), 193-204.
- Gyaneshwar, P., Naresh Kumar, G., Parekh, L. J., & Poole, P. S. (2002). Role of soil microorganisms in improving P nutrition of plants. *Plant and Soil*, 245(1), 83-93.
- Hammond, K. E., Evans, D. E., & Hodson, M. J. (1995). Aluminium/silicon interactions in barley (*Hordeum vulgare* L.) seedlings. *Plant and Soil*, 173(1), 89-95.
- Hernandez-Apaolaza, L. (2014). Can silicon partially alleviate micronutrient deficiency in plants? A review. *Planta*, 240(3), 447-458.
- Imtiaz, M., Rizwan, M. S., Mushtaq, M. A., Ashraf, M., Shahzad, S. M., Yousaf, B., Saeed, D. A., Rizwan, M., Nawaz, M. A., Mehmood, S., & Tu, S. (2016). Silicon occurrence, uptake, transport and mechanisms of heavy metals, minerals and salinity enhanced tolerance in plants. *Journal of Environmental Management*, 183, 521-529.
- Iwasaki, K., Maier, P., Fecht, M., & Horst, W. J. (2002). Leaf apoplastic silicon enhances manganese tolerance of cowpea (*Vigna unguiculata*). *Journal of Plant Physiology*, 159(2), 167-173.
- Kaushal, M., & Wani, S. P. (2016). Rhizobacterial-plant interactions: Strategies ensuring plant growth promotion under drought and salinity stress. *Agriculture, Ecosystems & Environment*, 231, 68-78.
- Keller, C., Rizwan, M., Davidian, J. C., Pokrovsky, O. S., Bovet, N., Chaurand, P., & Meunier, J. D. (2015). Effect of silicon on wheat seedlings grown in hydroponics and exposed to copper. *Planta*, 241(4), 847-860.
- Khandekar, S., & Leisner, S. (2011). Soluble silicon modulates expression of *Arabidopsis thaliana* genes involved in copper stress. *Journal of Plant Physiology*, 168(7), 699-705.
- Kidd, P. S., Llugany, M., Poschenrieder, C. H., Gunse, B., & Barceló, J. (2001). Root exudates in aluminium resistance and silicon-induced amelioration in maize. *Journal of Experimental Botany*, 52(359), 1339-1352.
- Kim, Y. H., Khan, A. L., Waqas, M., & Lee, I. J. (2017). Silicon regulates antioxidant activities of crop plants under oxidative stress. *Frontiers in Plant Science*, 8, 256717.
- Kim, Y. H., Khan, A. L., Waqas, M., Shim, J. K., Kim, D. H., Lee, K. Y., & Lee, I. J. (2014). Silicon application influenced phytohormonal and antioxidant responses under salinity stress in rice. *Journal of Plant Growth Regulation*, 33(2), 137-149.

- Liang, Y., Sun, W., Zhu, Y. G., & Christie, P. (2007). Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants. *Environmental Pollution*, 147(2), 422-428.
- Liang, Y., Wong, J. W. C., & Wei, L. (2005). Silicon-mediated enhancement of cadmium tolerance in maize. *Chemosphere*, 58(4), 475-483.
- Liu, J., Ma, J., He, C., Li, X., Zhang, W., Xu, F., Lin, Y., & Wang, L. (2013). Inhibition of cadmium uptake in rice cells by wall-bound silicon. *New Phytologist*, 200(3), 691-699.
- Liu, W., Wang, K., Hao, H., Yan, Y., Zhang, H., Zhang, H., & Peng, C. (2023). Predicting climate impacts of bioenergy from perennial grasses by 2050. *Resources, Conservation & Recycling*, 190, 106818.
- Liu, W., Zhang, L., Wu, H., Wang, Y., Zhang, Y., Xu, J., Wei, D., Zhang, R., Yu, Y., Wu, D., & Xie, X. (2023). Cost-effective BMPs for non-point source pollution in an agricultural watershed. *Chemosphere*, 333, 138949.
- Lugtenberg, B. J., Chin-A-Woeng, T. F., & Bloemberg, G. V. (2002). Microbe-plant interactions: Principles and mechanisms. *Antonie van Leeuwenhoek*, 81(1), 373-393.
- Luyckx, M., Hausman, J. F., Lutts, S., & Guerriero, G. (2017). Silicon and plants: Current knowledge and technological perspectives. *Frontiers in Plant Science*, 8, 411.
- Ma, Y., Oliveira, R. S., Wu, L., Luo, Y., Rajkumar, M., Rocha, I., & Freitas, H. (2015). Metal-mobilizing PGPR *Bacillus* sp. SC2b in rhizoremediation. *Journal of Toxicology and Environmental Health, Part A*, 78(13-14), 931-944.
- Mahmood, S., Daur, I., Al-Solaimani, S. G., Ahmad, S., Madkour, M. H., Yasir, M., Hirt, H., Ali, S., & Ali, Z. (2016). PGPR and silicon enhance salinity tolerance in mung bean. *Frontiers in Plant Science*, 7, 876.
- Mahmood, S., Daur, I., Hussain, M. B., Nazir, Q., Al-Solaimani, S. G., Ahmad, S., Bakhshwain, A. A., & Elsafor, A. K. (2017). Silicon and PGPR regulate mung bean under saline irrigation. *Clean - Soil, Air, Water*, 45(8), 1600436.
- Miransari, M. (2013). Soil microbes and nutrient availability. *Acta Physiologiae Plantarum*, 35(11), 3075-3084.
- Naeem, A., Saifullah, Ghafoor, A., & Farooq, M. (2015). Suppression of cadmium in wheat grains by silicon. *Journal of the Science of Food and Agriculture*, 95(12), 2467-2472.
- Nwugo, C. C., & Huerta, A. J. (2011). Silicon effects on the leaf proteome of rice under cadmium stress. *Journal of Proteome Research*, 10(2), 518-528.
- Pacwa-Płociniczak, M., Płaza, G. A., Piotrowska-Seget, Z., & Cameotra, S. S. (2011). Biosurfactants: Environmental applications. *International Journal of Molecular Sciences*, 12(1), 633-654.
- Ping, L. I., Wang, X., Zhou, D., & He, Y. (2008). Amendments affecting rice growth and metal uptake. *Journal of Environmental Sciences*, 20(4), 449-455.
- Pishchik, V. N., Vorobyev, N. I., Chernyaeva, I. I., Timofeeva, S. V., Kozhemyakov, A. P., Alexeev, Y. V., & Lukin, S. M. (2002). PGPR-plant interaction under cadmium stress. *Plant and Soil*, 243(2), 173-186.
- Pozza, E. A., Pozza, A. A. A., & Botelho, D. M. D. S. (2015). Silicon in plant disease control. *Revista Ceres*, 62(3), 323-331.
- Qin, Y., Druzhinina, I. S., Pan, X., & Yuan, Z. (2016). Microbiome-based solutions for saline agriculture. *Biotechnology Advances*, 34(7), 1245-1259.
- Rajkumar, M., Sandhya, S., Prasad, M. N. V., & Freitas, H. (2012). Plant-associated microbes in phytoremediation. *Biotechnology Advances*, 30(6), 1562-1574.
- Rizwan, M., Ali, S., Ibrahim, M., Farid, M., Adrees, M., Bharwana, S. A., Zia-ur-Rehman, M., Qayyum, M. F., & Abbas, F. (2015). Silicon in drought and salt stress alleviation. *Environmental Science and Pollution Research*, 22(20), 15416-15431.
- Rizwan, M., Meunier, J. D., Miche, H., & Keller, C. (2012). Silicon reduces cadmium toxicity in durum wheat. *Journal of Hazardous Materials*, 209, 326-334.
- Rogalla, H., & Römhild, V. (2002). Leaf apoplast in silicon-mediated manganese tolerance of cucumber. *Plant, Cell & Environment*, 25(4), 549-555.

- Sessitsch, A., Kuffner, M., Kidd, P., Vangronsveld, J., Wenzel, W. W., Fallmann, K., & Puschenreiter, M. (2013). Plant-associated bacteria in trace element mobilization. *Soil Biology and Biochemistry*, 60, 182-189.
- Shi, X., Zhang, C., Wang, H., & Zhang, F. (2005). Silicon effects on cadmium distribution in rice. *Plant and Soil*, 272(1), 53-60.
- Siddiquee, S., Rovina, K., Azad, S. A., Naher, L., Suryani, S., & Chaikaew, P. (2015). Heavy metal removal using filamentous fungi biomass. *Journal of Microbial & Biochemical Technology*, 7(6), 384-395.
- Siddiqui, H., Ahmed, K. B. M., Sami, F., & Hayat, S. (2020). Silicon nanoparticles and plants: Current knowledge and future perspectives. In *Sustainable Agriculture Reviews 41* (pp. 129-142).
- Song, A., Li, P., Fan, F., Li, Z., & Liang, Y. (2014). Silicon effects on photosynthesis under zinc stress in rice. *PLoS ONE*, 9(11), e113782.
- Srivastava, R. K., Pandey, P., Rajpoot, R., Rani, A., Gautam, A., & Dubey, R. (2015). Calcium and silicon alleviate cadmium toxicity in rice. *Protoplasma*, 252(4), 959-975.
- Tsoraeva, E., Bekmurzov, A., Kozyrev, S., Khoziev, A., & Kozyrev, A. (2020). Environmental issues of agricultural intensification. In *E3S Web of Conferences* (Vol. 215, p. 02003).
- Vaculík, M., Landberg, T., Greger, M., Luxová, M., Stolaríková, M., & Lux, A. (2012). Silicon modifies root anatomy and cadmium uptake in maize. *Annals of Botany*, 110(2), 433-443.
- Vannini, C., Iriti, M., Bracale, M., Locatelli, F., Faoro, F., Croce, P., Pirona, R., Di Maro, A., Coraggio, I., & Genga, A. (2006). *Osm4* expression increases tolerance to abiotic and biotic stresses. *Physiological and Molecular Plant Pathology*, 69(1-3), 26-42.
- Walker, T. S., Bais, H. P., Grotewold, E., & Vivanco, J. M. (2003). Root exudation and rhizosphere biology. *Plant Physiology*, 132(1), 44-51.
- Ye, J., Yan, C., Liu, J., Lu, H., Liu, T., & Song, Z. (2012). Silicon effects on cadmium compartmentation in *Kandelia obovata*. *Environmental Pollution*, 162, 369-373.
- Yuanqi, F. (2000). Siliceous fertilizer in Chinese agriculture. *Huafei Gongye*, 27(4), 9-11.
- Zahir, Z. A., Arshad, M., & Frankenberger, W. T. (2003). PGPR: Applications and perspectives. *Advances in Agronomy*, 81, 97-168.
- Zhu, Y., & Gong, H. (2014). Beneficial effects of silicon on salt and drought tolerance. *Agronomy for Sustainable Development*, 34(2), 455-472.

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