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Review

Silicon occurrence, uptake, transport and mechanisms of heavy metals, minerals and salinity enhanced tolerance in plants with future prospects: A review

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A B S T R A C T

Recently, heavy metals pollution due to industrialization and urbanization, use of untreated wastewater and unreasonable use of pesticides and fertilizers is increasing rapidly, resulting in major threat to the environment and contaminate soils. Silicon (Si) is the second most abundant element in the earth crust after oxygen. Although it's higher accumulation in plants, yet Si has not been listed as essential nutrient however, considered as beneficial element for growth of plants particularly in stressed environment. Research to date has demonstrated that silicon helps the plants to alleviate the various biotic and abiotic stresses. This review article presents a comprehensive update about Si and heavy metals, minerals and salinity stresses, and contained the progress about Si so far done worldwide in the light of previous studies to evaluate the ecological importance of Si. Moreover, this review will also be helpful to understand the Si uptake ability and its benefits on plants grown under stressed environment. Further research needs for Si-mediated mitigation of heavy metals and mineral nutrients stresses are also discussed.

Contents

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1. Introduction

Environmental pollution is considered major threat to arable lands, water reserves and ultimate to food chain (CEC, 2002). This contamination is originated from various sources including combusting, industries, mining, weathering as well as human activities (Nagajyoti et al., 2010). Among the toxic substances arsenic (As), lead (Pb), cadmium (Cd), chromium (Cr), zinc (Zn), manganese (Mn), copper (Cu), nickel (Ni) and sodium (Na) are the major concern for plants, soil, environment and human health. Because these pollutants are persistent and highly toxic in nature, soil contaminated with such kind of metals pose environmental problems that affects the plants, animals and ultimately human health (do Nascimento and Xing, 2006; Adrees et al., 2015). It has been reported that plants growing in polluted environment exhibit altered metabolism (Liang et al., 2007), growth reduction (Imtiaz et al., 2015, 2016), lower biomass production (Zhang et al., 2014) and oxidative damage and accumulation of pollutant (Gangrong et al., 2010). In this respect, there is a growing need to manage toxic elements to protect the agricultural land.

Silicon (Si) ranked 2nd among all the discovered elements and constitutes about 28% of the Earth's crust and 0.03% of biosphere (Sommer et al., 2006). Plants accumulated Si up to 10% by weight (Hodson et al., 2005), and this amount is greater than some micronutrients (Epstein, 1994). Previous studies have confirmed that Si remediate the toxic effects of toxic substances moreover, various beneficial effects of Si has been identified in various plant species (Takahashi et al., 1990). Hence, use of Si for better crop production and to alleviate the toxic effects of toxic substances is predicted to become an emerging approach in agriculture in future. This review article contains recent progress made against the major toxic element in plants.

2. Defensive and beneficial role of silicon

Previous studies reported silicon (Si) as beneficial element for various plant species such as wheat, rice, maize and bamboo however, still not listed as essential element for plants (Collin et al., 2014; Feng et al., 2010; Ma and Takahashi, 2002; Epstein, 1994). Application of Si offers resistent lodging in plant species by providing mechanical support. This mechanical support might be due to attachment of Si with cell walls which enhanced the rigidity in plant cell walls (Raven, 1983). Addition of Si also helps the plants against excessive water lost via transpiration by deposition in epidermal tissues (Emadian and Newton, 1989). Silicon remediates the plants from various stresses such as heavy metals, diseases, radiation and drought (Ma and Yamaji, 2006; Côté-Beaulieu et al., 2009; Epstein, 2009). The beneficial role of Si under stressed conditions can be pointed out because Si may play role at numerous levels in plants and also in soils. Below, Figs. 1 and 2 exhibits some major examples of advantages of Si for plants and soils as indicated in recent studies under stressed environment.

3. Silicon in soil

Mostly, the solid phase of Si in soil comprises of quartz, together with crystalline forms of silicates (plagioclase, orthoclase and feldspars), secondary clay minerals (kaolonite, vermiculite and smectite) and amorphous silica (Savant et al., 1999). These forms of Si are only sparingly soluble and usually bio-geochemically inert (Savant et al., 1997). The liquid phase of Si in soil is more complex but agronomically important. It includes Si in soil solution mainly as monosilicic acid (H_4SiO_4) and may range from 3 to 17 mg of Si per liter at a pH below 9 (Knight and Kinrade, 2001). At a higher (pH > 9), silicic acid dissociates into silicate ions $(OH)_3 SiO^{-1}$. The solubility of silicic acid in water is 2 mM at 25 °C. When dissolved Si in soil solution exceeds 2 mM, polymerization of Si usually occurs and a mixtures of monomers and polymers of Si $(OH)_4$ and Si organic compounds may be found in soil solution at a given time (Tan, 1994).

3.1. Soil silicon bioavailability

Silicon is found in soils as silica minerals like primary and secondary silicates. Sand and silt fractions exhibit mainly primary silicate whereas clay fraction contained secondary silicates, this happened due to pedogenic processes. Moreover, soils also concentrated amorphous forms and inorganic and biogenic silica, including phytoliths (Cornelis et al., 2011). These are the major Si forms through which Si is released into soil solution and then reaches to rivers and oceans via weathering (chemical and physical) and anthropogenic activities (Guntzer et al., 2012).

Monosilicic acid is a weakly acid that represents the major soluble form of Si in soil solution. Actually, monosilicic acid is an uncharged monomer molecule ($H_4SiO_4^0$) from pH 2 to 9, while at pH > 9 it found as ionized form ($H_3SiO^{4-}/H_2SiO_4^{2-}$) (Knight and Kinrade, 2001). Therefore, most soils with pH less than 9 contained Si as undissociated silicic acid over concentrations range from 0.1 to 0.6 mM (Epstein, 1999).

Generally, due to dissolution of Si-compounds and sorption reactions between soluble silica and soil components, the Si concentration in soil solution can be varied (Wickramasinghe and

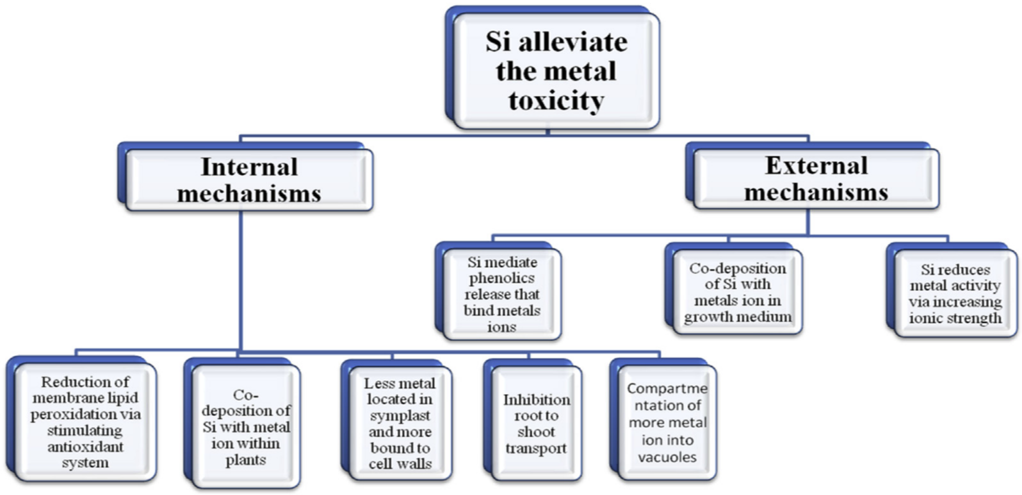

Fig. 1. Mechanisms for Si-mediated metals toxicity alleviation (Liang et al., 2005).

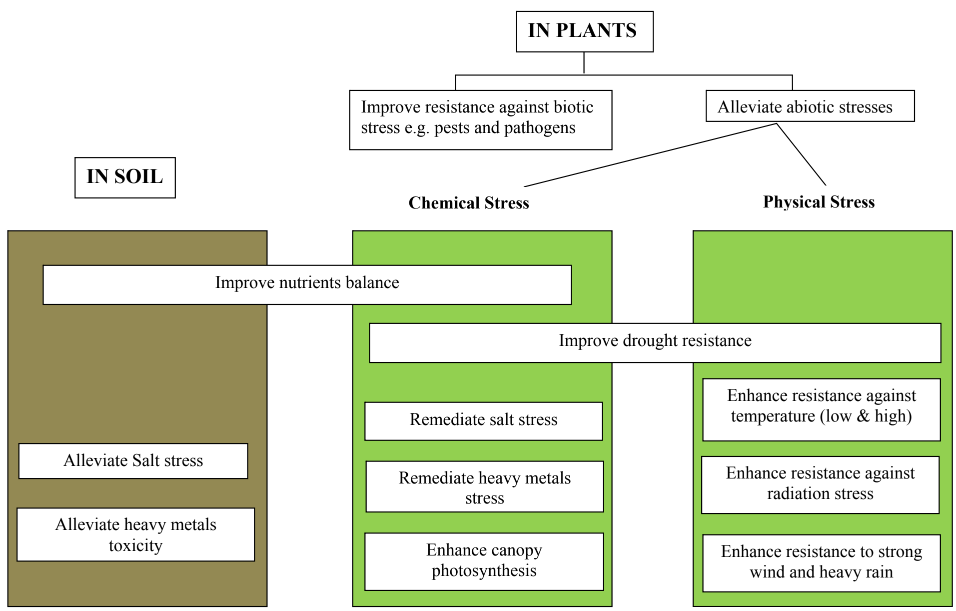

Fig. 2. Beneficial effects of silicon (Si) on plants growth and soil health under various environmental stresses.

Rowell, 2006). The ligand exchange sites on oxides and hydroxides of Fe and Al can also compete with Si and other anions on mineral surfaces for sorption. The major factors involved in limited uptake of soluble Si can be weathering, leaching, typically acid soils and soils with low base saturation. Usually, plants can uptake plenty of soluble Si from less weathered soils, geologically younger mineral soil as compared to typically acid soils, weathered soil, leached soils and soils contained lower bases (Cornelis et al., 2011).

4. Silicon in plants

Plants absorb silicon (Si) exclusively as monosilicic acid (H_4SiO_4) by diffusion and also by the influence of transpiration induced root absorption known as mass flow. The concentration of Si in the xylem of some plant species is usually many times higher than that of the soil solution indicating that the uptake of Si might be metabolically driven (Ma et al., 2001). Plants differ greatly in their ability to accumulate Si depending upon the mechanisms involved in Si uptake (Casey et al., 2003; Liang et al., 2007). Jones and Handreck (1967) classified the plants into accumulators (10–15% dry weight) including wet land grasses, intermediate 1–3% dry weight including dry land grasses and excluders or non-accumulators (<1% dry weight) including dicots. Three modes of Si uptake (active, passive and rejective) have been proposed for the corresponding Si accumulators, intermediate and excluder plants, respectively (Takahashi et al., 1990; Ma et al., 2001, 2006). Following uptake by the roots, Si is translocated to the shoot via xylem. The amount of monosilicic acid in plant tissues varied depending upon plant species from 6 to 38% and polysilicic acid from 10 to 70% of the total Si content in plants. Silicon contained in phytoliths, cell walls and epidermal tissues (apparently in the form of biogenic silica strongly bound to organic matter) is from 15 to 79% (Matichenkov et al., 1997). Silicon is deposited as a 2.5 μm layer in the space immediately beneath the thin (1.0 μm) cuticle layer forming a cuticle-Si double layer (Sangster and Hodson, 1992).

4.1. Forms of silicon absorbed by plants

Previous studies have confirmed that only monosilicic acid (H_4SiO_4) can be absorbed by plants roots. Monosilicic acid is also known as orthosilicic acid and silicic acid is taken up by the plants through active process (Mitani et al., 2005). Moreover, the roots and shoots of plants differ greatly for their Si concentration and this variation is due to mechanisms of Si uptake and transportation by plants (Hodson et al., 2005). In plants, Si-cellulose structure contained 90% of absorbed and transformed Si as amorphous silica (Yoshida, 1965). Silicon solubility in soil medium is the major difficulty for plants because plants only can absorb Si as monolsilicic acid.

4.2. Silicon uptake mechanisms and transport in plants

Silicon (Si) concentration in plants vary greatly, this variation in Si amount in tissues of plants is mainly due to different Si uptake and transports system in plant species (Jarvis, 1987; Epstein, 1994). Previous studies have confirmed that rice plants had specific system for Si uptake and transportation (Tamai and Ma, 2003). Ma et al. (2006) have reported a gene that is responsible for xylem loading of Si in rice plants and is localized on plasma membrane of the distal side of exodermis and endodermis. Mitani and Ma (2005) reported that Si concentration was reduced in the xylem sap than in the external solution, indicating that xylem loading of Si was regulated by passive diffusion in cucumber plants. However, Liang and his co-workers have confirmed that *Cucumis sativus* L. uptake and transport Si via active process (Liang et al., 2005). Recent studies have also confirmed that active and passive are the key mechanisms to uptake and transport of Si in Si-accumulators, intermediate and excluders plant species (Liang et al., 2006). After the roots uptake, silicic acid is transported from cortical to stele, and moved in xylem and finally translocated into shoots via transpiration stream. In shoots, Si is concentrated due to transpiration and then converted into amorphous silica ($SiO_2{-}nH_2O$) via Si polymerization (Ma and Yamaji, 2006). Consequently, this amorphous silica is concentrated in cell wall, and also can be deposited in roots cells in plants (Ma and Yamaji, 2006; Chandler-Ezell et al., 2006).

5. Silicon-mediated alleviation of heavy metal stresses

Metal toxicity has great impact and relevance not only to plants but also affects the ecosystem in which the plant forms an integral component. Plants growing in metal polluted environment exhibited reduced growth and high metal accumulation (Liang et al., 2007). One of the evident impacts of metal toxicity is their binding to protein sulphydryl groups, disordering the uptake of other essential elements and thus disturbing physiological and molecular homeostasis (Christopher, 2000). The relationship between Si and metal tolerance in plants has been extensively studied. However, it is worth mentioning that Si amelioration of metal phytotoxicity is not only due to Si action inside the plant but also relies on the decreased bioavailability of metals in Si-treated soils (Liang et al., 2005).

6. Silicon and heavy metals

Agricultural land, all over the world is contaminated with a variety of heavy metals such as As, Pb, Cd, Cr and Hg moreover, polluted soils can be categorized as slightly, moderately and severely/highly contaminated. Heavy metals like arsenic (As), lead (Pb), cadmium (Cd) and chromium (Cr) contribute the major share of soil contamination and considered very toxic even at low concentrations (Nagajyoti et al., 2010). It is widely reported that heavy metals badly affect the normal physiological and biochemical processes as well as structural growth of plants through interference with activities of various enzymes as well as through direct interactions with macromolecule like protein and pigments, etc. (Nagajyoti et al., 2010; Afshan et al., 2015).

6.1. Silicon and arsenic stress

Environmental pollution with arsenic (As) is a serious problem due to its deleterious effects on soil health, plants growth and development and ultimately to human health. Arsenic pollution is widespread due to human activities, weathering and industrialization (Zhao et al., 2010). Silicon-mediated alleviation of As toxicity is a better approach to decontaminate the As-contaminated sites.

A study conducted by Lílian et al. (2016) reported that Si efficiently remediated the toxic effects of As in rice plants. The findings also indicated that Si supplementation markedly reversed the negative effects of As on photosynthesis and carbohydrate amounts when rice plants challenged with As. They also agreed that Si nutrition significantly limited the As uptake and translocation in rice plants through expression of genes. Chuan et al. (2015) also indicated that addition of Si significantly enhanced the straw biomass while, there was non-significant effects on root biomass. The results also suggested that Si nutrition was a central player to restrict the As accumulation of in shoots and roots in six genotypes of rice. Marmiroli et al. (2014) also reported that application of Si markedly increased the seeds germination and accumulation and distribution of As in shoots and roots of tomato was also inhibited by addition of Si however, the accumulation of As was cultivars dependant. Additionally, the results showed that deleterious effects caused by As on seedling shoots lengths was not mitigated by Si. Moreover, Si-nutrition efficiently limited the accumulation of As in tomato fruits of some cultivars while, in fruits of some cultivars was failed to limit the As accumulation. Preeti et al. (2013) also reported that Si enhanced the As-tolerance in rice cultivars. Silicon made remediation more prominently in Triguna as compared to IET-4786 cultivar. Silicon application significantly remediated the oxidative stress induced by As in Triguna by limiting the As uptake and improving antioxidant and thiolic systems than IET-4786.

6.2. Silicon and lead stress

Among the listed heavy metals, lead (Pb) is one of the most toxic pollutants of the environment and air, water reserves and agricultural land contaminated with Pb is an ecological concern due to its lethal effects on plants and human health. Additionally, the uptake and toxic effects of Pb depends on plant species, soil type and soil properties (Reddy et al., 2005).

Liu et al. (2015) conducted a trial to investigate the effects of nano-silicon and common silicon on uptake and translocation of lead (Pb) and reported that silicon (Si) markedly reduced the uptake and translocation of Pb in rice cultivars. The results showed that addition of nano-silicon and common silicon increased the biomass yields of rice plants from 3.3% to 11.8% and 1.8%–5.2% under soil treated with 500 and 1000 mg kg^{-1} as compared to control plants (without Si). Moreover, grains accumulated the lowest amount of Pb when treated with Si-salts. The application of nano-Si and common-Si significantly reduced the Pb translocation factor from roots to shoots and shoots to grains. Generally, nano-Si efficiently remediated the toxic effects of Pb on rice growth. Bharwana et al. (2013) also carried out an experiment to investigate the alleviative effects of Si on Pb toxicity in cotton and indicated that addition of Si significantly reduced the Pb uptake, electrolyte leakage and hydrogen peroxide (H_2O_2) and malondialdehyde (MDA) contents in cotton plants when treated with Si plus Pb.

While, the antioxidant enzymes activities in roots and leaves of cotton plants were increased in the presence of Si. The findings also confirmed that biomass yield, growth, chlorophyll contents and photosynthetic parameters were markedly increased by Si application under Pb stress.

6.3. Silicon and cadmium stress

Cadmium (Cd) is highly toxic and one of the most important environmental pollutants in developed countries. It is required in very minute quantity, otherwise it causes toxicity and it accumulates in the plant body during life time and can induce problems for plant health.

Shi et al. (2005) investigated that added Si significantly overcomes the reduction in growth due to Cd. This amelioration was correlated with the reduction in Cd uptake and transport from root to shoot. Silicon increased Cd accumulation in the roots and decreased its distribution in the shoot up to 30%. Energy dispersive X-ray analysis showed that Cd was mainly deposited in the vicinity of the endodermis and epidermis of root but there was a heavy deposition of silica in the vicinity of endodermis. This deposition of silica in endodermis might be a possible mechanism by which Si physically block the apoplastic bypass flow across the root and restrained the apoplastic transport of Cd. Marek et al. (2009) also reported Si in the presence of Cd improved all growth parameters compared with the only Cd treated plants. Si increased the cell wall extensibility both in Si and Cd + Si treatments when compared with the control. Gangrong et al. (2010) evaluated that Cd exposure alone depressed plant growth and caused oxidative stress for peanut (*Arachis hypogaea* L.) cultivars. Silicon supply significantly alleviated the toxicity and reduced the shoot Cd accumulation, an alteration of Cd sub cellular distribution in leaves, and a stimulation of antioxidative enzymes. The mechanisms of Si amelioration of Cd stress were cultivar and tissue dependant. Chika and Alfredo (2011) showed that Si-induced Cd tolerance is mediated by the enhancement of instantaneous water-use-efficiency, carboxylation efficiency of ribulose-1, 5-bisphosphate carboxylase oxygenase (RuBisCO), and light-use-efficiency in leaves of rice plants. This study identified 60 protein spots that were differentially regulated due to Cd and/or Si treatments. Among them, 50 were significantly regulated by Si, including proteins associated with photosynthesis, redox homeostasis, regulation/protein synthesis, and pathogen response and chaperone activity. Interestingly, they observed a Si-induced up-regulation of a class III peroxidase and a thaumatin-like protein irrespective of Cd treatment, in addition to a Cd-induced up-regulation of protein disulfide isomerase, a HSP70 homologue, a NADH-ubiquinone oxidoreductase, and a putative phosphogluconate dehydrogenase, especially in the presence of Si.

6.4. Silicon and chromium stress

Recently, environmental pollution with chromium (Cr) through industrialization and human activities has become a serious problem. The global emission of Cr exceeds than other heavy metals like Cd, Hg and Pb (Kabata-Pendias and Mukherjee, 2007). Chromium exists in various forms however, the most toxic form to living organisms is Cr(VI) because it can easily pass through membranes and enter into cytoplasm and affect the metabolic processes (Shanker et al., 2004; Singh et al., 2013). Chromium induced deleterious effects on plants growth and reduced seed germination, induces oxidative damage affects nutrients uptake, interact with photosynthesis processes, affects water balance and N-metabolism (Ali et al., 2011; Gangwar and Singh, 2011; Singh et al., 2013). Therefore, alleviation of Cr is needed to increase the crops productivity and as well as reduced the Cr entry in food to minimize the health risks.

Durgesh et al. (2015) conducted a study to evaluate the effects of Si on Cr toxicity and indicated that Si-nutrition significantly alleviated the toxic effect of Cr in wheat plants. The results of laser induced breakdown spectroscopy (LIBS) showed reduction in Cr accumulation in wheat seedlings following Si-nutrition. The results obtained by LIBS and inductively coupled plasma atomic emission spectroscopy (ICAP-AES) indicated that Si-nutrition improved the nutrients (K, Ca, Mg and Na) uptake in wheat seedling which affected by Cr stress. The increase in nutrients uptake in wheat was supported by the results of similar distribution pattern of nutrients measured by LIBS, ICAP-AES and atomic absorption spectrophotometer (AAS). Shafaqat et al. (2013) also concluded that addition of Si noticeably remediated the toxicity of Cr via enhancing the plant growth, net photosynthetic rate (Pn), cellular CO_2 concentration (Ci), stomatal conductance (Gs) and transpiration rate (Tr) and chlorophyll fluorescence efficiency. Additionally, Si-nutrition efficiently alleviated the ultra-structural changes induced by Cr toxicity both in roots and shoots such as changes in leaves and roots structures, swelling of chloroplast, damage in thylakoid membranes, increase in plastoglobuli amount, structural disorders of starch granules in leaves, damage in vacuolar size and shape, accumulation of Cr in cell walls and disruption of nucleus.

7. Silicon and microelement nutrients

Essential nutrients play important roles in cellular function and metabolic processes to promote the growth of plants. The essential elements are divided into two categories on the base their essentiality: 1) macro elements required in higher amount like nitrogen, phosphorus and potassium etc. 2) micro elements required in lower amount like zinc, manganese, copper and nickel etc. Plants also vary for micronutrients requirement (Robert and Ralf, 2009). Though, micronutrients are essential for plants growth while, at elevated concentration induced toxic effects and alter the metabolic activities in plants (Adriano, 2001).

7.1. Silicon and zinc stress

Zinc (Zn) is listed as essential micronutrients. However, its higher concentration leads to Zn toxicity for plant's life and ultimately death of plants. Cengiz et al. (2009) investigated that plants growing with high Zn alone had lower chlorophyll contents and produced less biomass. However, added Si decreased the Zn-toxicity by protecting the membrane permeability under high Zn. Neumann and Zurnieden (2000) concluded that large amounts of Zn were measured in the vacuoles, the main storage compartment for this metal in *Cardaminopsis halleri* when grown in contaminated soil. Zinc was co-localized with Si in these structures in the form of Zn-silicate. The formation of Zn-silicate is a part of the heavy metal tolerance mechanism. Karina et al. (2008) also reported that adding Si to Zn contaminated soil effectively diminished the metal stress and resulted in the biomass increase in comparison to metal-contaminated soil not treated with Si. Silicon altered the Zn distribution in soil fractions, decreasing the most bioavailable pools and increasing the allocation of metals into more stable fractions such as organic matter and crystalline iron oxides. Kaya et al. (2009) studied that compared with the plants treated with high Zn alone, added Si significantly increased plant growth and chlorophyll content and reduced the membrane permeability. As expected, addition of high Zn increased leaf and root Zn, but reduced leaf phosphorus (P) and iron (Fe). Added Si reduced Zn concentration and increased Fe in leaves of maize. They concluded that improvement in the growth parameters and mineral nutrition status in maize plants grown at high Zn induced by Si and improved the growth of maize plants.

7.2. Silicon and manganese stress

Manganese (Mn) is also an essential micronutrient and required in very low quantity for plants. Its high quantity causes detrimental effects on plants health. Rogalla and Romheld (2002) investigated that effect of Si on Mn-toxicity in cucumber *(Cucumis sativus)* grown in nutrient solution with low to elevated Mn concentration. The results indicated that plants not treated with Si showed higher Mn concentration in the intercellular washing fluid (IWF) compared with plants treated with Si. In Si-treated plants less Mn was located in the symplast (less than 10%) and more was bound to the cell wall (more than 90%) compared with non-Si treated plants (about 50% in each compartment). Manganese present in Si-treated plants is therefore less available and for this reason less toxic than in plants not treated with Si. The Si-mediated tolerance of Mn in cucumber is a consequence of stronger binding of Mn to cell walls and a lowering of Mn concentration within the symplast. Kozo et al. (2002) also conducted study to evaluate the Si treatment period; Si concentrations in the bulk leaf tissue were increased in cowpea (*Vigna unguiculata* (L.). However, the Si concentrations in the apoplastic washing fluids (AWF) of the plants pretreated without Si were lower than those of plants supplied with Si and Mn concurrently. The severity of Mn toxicity symptoms were reduced with increasing Si concentrations in AWF. A possible role of apoplastic soluble Si was indicated for detoxification of Mn toxicity. Jelena et al. (2007) demonstrated that high external Mn supply induced both growth inhibition of the whole plant and the appearance of Mn toxicity symptoms in the leaves. However, application of Si alleviated Mn toxicity, although the total Mn concentration in the leaves did not differ significantly between + Si and −Si plants moreover, symptoms of Mn toxicity were not observed in Si treated plants. The concentrations of phenolic compounds, particularly in the leaf extracts at high external Mn concentrations, differed from those of plants grown without Si. The increased tissue concentrations of phenols (e.g., coniferyl alcohol, coumaric and ferulic acids) were in agreement with enhanced enzymes activities, i.e., peroxidases (PODs) and polyphenol oxidases (PPO) in the tissues of −Si plants. The activities of both enzymes were kept at a lower level in the tissue extracts of +Si plants grown at high external Mn concentrations. These results suggested that Si nutrition modulates the metabolism and utilization of phenolic compounds mainly at the leaf level, most probably as a consequence of the formation of Si-polyphenol complexes.

7.3. Silicon and copper stress

Copper (Cu) is also included in the list of essential micronutrients however, its excessive quantity causes toxicity to plants. Sushant and Scott (2011) conducted an experiment to study the effect of Si on Cu toxicity in *Arabidopsis thaliana*, and the expression of genes involved in responses to Cu toxicity was examined by quantitative reverse transcription-polymerase chain reaction. Expression levels of three metallothionein (MT) genes were increased under Cu stress conditions whereas Cu-stressed plants treated with Si either maintained high levels or contained even higher levels of MT-RNA. Plants treated with elevated Cu showed increased phenylalanine-ammonialyase (PAL) activity that was reduced when the plants were also provided with extra Si. They also suggested that Si permitted plants to respond to Cu toxicity more effectively and that these changes occurred at the gene expression level. Li et al. (2008) reported that Si alleviated the toxicity of Cu. Based on plant symptoms and a reduction of phenylalanine-ammonialyase (PAL), a stress-induced enzymes activity in the shoot, Si was found to alleviate Cu stress. Copper transporter-I and heat metal ATPase subunit 5 (HMA5) were induced by high levels of Cu, but were significantly decreased when Si levels were also elevated. They indicated that addition of Si could improve of the resistance of *Arabidopsis thaliana* to Cu stress. Sabina et al. (2011) studied the influence of Si on responses to Cu excess in plants of *Erica andevalensis*. Plantlets grown with high Cu showed differences in growth and shoot water content depending on Si supply. The addition of Si in high Cu nutrient solutions significantly improved plant growth and reduced water loss preventing plant death related to Cu excess. Si supply reduced significantly leaf Cu concentration and increased Cu concentration in roots. Phytoliths isolated from leaves were also analyzed by scanning electron microscopy coupled with energy-dispersive X-ray spectroscopy. Such phytoliths consisted in silica deposits associated with Cu and other elements (K, Ca, and P). Improvement by Si of Cu tolerance in *Erica andevalensis* was clearly related to the inhibition of Cu upward transport.

7.4. Silicon and nickel stress

Nickel (Ni) has just recently won the status as an essential trace element for plants. However, it is essential for some higher plants (Brown et al., 1987; Eskew et al., 1984) at low levels but the other scientist reported that Ni can be toxic to plants at high levels (Bingham et al., 1986; Foy et al., 1978). Crop plants grown on soils with higher Ni concentration; exhibit a reduction of growth and yield, because the plants are in general very sensitive to Ni (Davis and Beckett, 1978; Frank et al., 1982). Rubio et al. (1994) reported that rice plants accumulate high quantity of Ni when grown for 10 days in a medium containing these heavy metals. Accompanying Ni uptake, a decrease in shoot and root length was observed. Metal treatments also induced a decrease in K, Ca and Mg contents in the plants, particularly in the shoots, indicating that Ni interfered not only with nutrient uptake but also with nutrient distribution into the different plant parts. Ashraf et al. (2013) conducted a pot experiment irrigated with municipal wastewater containing excess amount of Ni to investigate the effects on tomato plants. The results indicated that tomato plants accumulated more nickel when irrigated with wastewater and major portion of accumulated Ni was transported to aerial parts of plants when treated without silicon (Si). The dry matter of tomato plants was also decreased when plants were irrigated only with wastewater. However, results confirmed that Si supplementation precipitated the Ni in soil and reduced its uptake. Moreover, Si supplementation ameliorated Ni-induced toxicity and retained more Ni in roots, reducing its translocation to the aerial parts and, consequently, improved biomass accumulation. Idrees et al. (2013) also confirmed that Ni stress decreased the growth parameters and enhanced the antioxidant enzymes together with an increase in electrolyte leakage and proline contents in periwinkle (*Catharanthus roseus* L.). The plants, undergoing Ni-stress also exhibited a significant decrease in total alkaloid contents. However, foliar application of silicon (Si) considerably alleviated the Ni toxicity and decreased the harmful effects of Ni on growth attributes (plant height, leaf area and fresh and dry biomass) by regulate the restoration of growth processes. Moreover, added Si enhanced the total alkaloid contents and content of anticancer alkaloids vincristine and vinblastine in *Catharanthus roseus* treated with higher dose of Ni. Foliar application of Si significantly enhanced the chlorophyll and carotenoid contents and also improved the level of proline and antioxidant enzymes in plants grown with or without Ni-stress.

8. Silicon and salinity

Soil salinity is a major abiotic stress worldwide especially in arid and semi-arid regions (Rizwan et al., 2015). In total, salt affected land in the world is about 20% (62 million hectares) of the total cultivated land is affected by salinity and sodicity with annual increase 1–2% (Munns and Tester, 2008). Recently, comprehensive studies about salt stress and plants growth indicated that salinity markedly limits growth of plants, interact with physiological and biochemical processes and also affect the uptake and transportation of essential nutrients and induces oxidative damage in plants (Abbasi et al., 2014). Xu et al. (2015) conducted a study to evaluate the effects of silicon (Si) on growth, quality and ionic homeostasis in aloe plants exposed to salt stress. The results indicated that silicon-nutrition significantly alleviated the toxic effects induced by NaCl in aloe plants. Si-nutrition also enhanced the potassium uptake and reduced the sodium uptake and also increased the K/Na ratio. Silicon-nutrition promoted the selectivity of aloe roots to uptake and distribution of K and Na. Silicon-nutrition improved the stabilizing effects on proton pump activity in roots tips under salt stress in aloe plants. Moreover, addition of Si maintained the ionic equilibrium in aloe plants and ionic homeostasis in photosynthetic cells of leaves in aloe under salt stress. Li et al. (2015) also studied the effects of Si on salt stress in tomato seedlings. They also reported that the Si-nutrition significantly alleviated the tomato growth, photosynthetic pigments, photosynthetic performance, soluble protein contents and morphological traits of roots subjected to salt stress. Under salt stress, stomatal conductance and leaf transpiration rate were also improved. Application of Si significantly reduced the uptake of Na and Cl by roots and limited their translocation from roots to shoots and leaves. Addition of Si improved the antioxidant defense system, water contents in leaves and roots hydraulic conductivity of tomato plants under salt stress. Abdollah et al. (2010) also reported that Si remediated the toxic effects and increased the fresh and dry weights of canola under salt stress. Silicon-nutrition also improved the scavenging capacity of canola plants against reactive oxygen species under salt stress. Addition of Si reduced the Na uptake and improved the membrane integrity of roots cells which was confirmed by reduction in lipid peroxidation and lignifications.

9. Conclusions and future perspectives

Soil contamination with heavy metals is the major concern and environmental problem affecting agricultural productivity worldwide. It is well known that silicon (Si) mitigates the various biotic and abiotic stresses including heavy metals stress in plants. Moreover, Si plays imperative role in plants to improve the stress resistance against heavy metals via stimulation antioxidant enzymes, chelation, precipitation and complexation of metals with Si, compartmentation and structural changes in plants and regulation of metals transporter genes. However, Si-mediated alleviation mechanisms might be correlated with plants species, growth environment, heavy metals, mineral nutrient, time of the stress imposed and so on. Therefore, it is worth mentioning here that alleviation of heavy metals by Si should be made with caution. This review article illustrates briefly about Si-mediated mitigation of heavy metals, minerals and salinity stresses in plants and improvement of crops productivity under stress environment. However, further research needs to be made to know the mechanisms involved.

Based on the previous studies, it can be concluded that silicon (Si) is an important element for plants growth, and plays critical role as mechanical and physical barrier in plants especially under stress conditions. According to the newly established definition of essentiality of nutrients for plants growth proposed by Epstein and Bloom (2005), it may be expected that Si will also be acquired the status of essential nutrient for higher plants. The key important role of Si does not consist in the status of essential element, but rather in its main unique function in its most striking and alleviating of deleterious effects of abiotic and biotic stresses in plants. Further research needs to evaluate the exact role of Si in plant biology, and should be focused to illustrate the evidence that Si is part of metabolic system of plants, and its alleviating role against abiotic stresses in plants. Further studies is also needed for uptake and xylem loading of Si in plants which will be more helpful to study deeply about role of Si in stress physiology and biochemistry of plants. Recent studies made rapid progress to clone and characterization of gene encoding Si-transporter in rice (Ma et al., 2006; Ma et al., 2004). Research to date, yet not give in-depth information about characterizing of Si uptake and transport in roots systems in plants even in Si-accumulator plants.

Previous studies have confirmed that Si can alleviate the various abiotic stresses including heavy metals and mineral elements in plants, however; the mechanisms are still not fully demonstrated. The survival mechanisms of plants under metals stress rely on tolerance and avoidance (Colzi et al., 2011) however, detoxification processes of metals and mineral nutrients in plants by silicon are not fully know in terms of tolerance or avoidance. It is well known that Si can increase the antioxidant enzymes and non-enzymes activities to mitigate the oxidative stress in plants induced by heavy metals (Song et al., 2011). Migocka and Klobus (2007) indicated that heavy metals were pumped from cytosol by proton-coupled transport system in cucumber roots and few transporters play important role in heavy metals tolerance, like *AtATM3* (Kim et al., 2006), *AtPDR8* (Kim et al., 2007), *AtPDR12* (Lee et al., 2005) and *ZntA* (Lee et al., 2003), although there is no information about effect of Si on these transporters performance. Research to date reports that effect of Si in alleviating and compartmentation of heavy metals to the cell wall/or vacuole extensively has been studied while, the possible effects of Si on transportation system of heavy metals in plasma membrane and/or tonoplast yet not checked. Therefore, the molecular mechanisms of Si-mediated mitigation of heavy metals and mineral elements stresses should be further studied in the future, especially to determine the possible contribution of Si in regulating of heavy metals transporters.

Previous studies indicated that most experiments related to Si were done in hydroponic culture and with single heavy metal. These experiments can be resulted overestimation of metal uptake and translocation. Further study needs to find the effects of Si remediation in naturally contaminated soil and these soils may have mixed contamination. Previous studies also indicated that mostly short term experiments were conducted to remediate the soil contained heavy metals with Si however, long term effects of Si on heavy metals still needs to be explored. Therefore, future work needs to be focused on long term and large scale trials to evaluate the effects of Si on pollutants uptake and transportation as well as on the soil health.

Competing interests

None of the authors have any competing of interest.

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