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Review

# Mechanisms of silicon-mediated alleviation of heavy metal toxicity in plants: A review

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ABSTRACT

In present era, heavy metal pollution is rapidly increasing which present many environmental problems. These heavy metals are mainly accumulated in soil and are transferred to food chain through plants grown on these soils. Silicon (Si) is the second most abundant element in the soil. It has been widely reported that Si can stimulate plant growth and alleviate various biotic and abiotic stresses, including heavy metal stress. Research to date has explored a number of mechanisms through which Si can alleviate heavy metal toxicity in plants at both plant and soil levels. Here we reviewed the mechanisms through which Si can alleviate heavy metal toxicity in plants. The key mechanisms evoked include reducing active heavy metal ions in growth media, reduced metal uptake and root-to-shoot translocation, chelation and stimulation of antioxidant systems in plants, complexation and co-precipitation of toxic metals with Si in different plant parts, compartmentation and structural alterations in plants and regulation of the expression of metal transport genes. However, these mechanisms might be associated with plant species, genotypes, metal elements, growth conditions, duration of the stress imposed and so on. Further research orientation is also discussed.



**Contents**



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## 1. Introduction

Soil contamination is indeed considered one of the main threats to agricultural soil as identified in the European Union soil communication (CEC, 2002). This contamination originates from natural sources by means of mineral dissociation, weathering of parent material and atmospheric deposition as well as anthropogenic sources related to mining, industrial emissions, disposal or leakage of industrial wastes, application of sewage sludge to agricultural soils, fertilizer and pesticide use (Nagajyoti et al., 2010). Heavy metals like cadmium (Cd), lead (Pb), chromium (Cr), copper (Cu), manganese (Mn) and zinc (Zn) contribute the major share of soil contamination. Due to the potential toxicity and high persistence of heavy metals, soils polluted with such elements create an environmental problem that threats the plant, animal and human health (do Nascimento and Xing, 2006; Adrees et al., 2015).

Among heavy metals, some metals such as Cd, Pb and Cr have no known biological role while others such as Cu, Zn and Mn are required in small amount for normal plant growth and developments but are extremely toxic to plants and animals slightly larger than the required concentrations (Kabata-Pendias and Pendias, 2001). It has been widely reported that accumulation of heavy metals in plants may cause many biochemical, structural and physiological changes (Nagajyoti et al., 2010; Afshan et al., 2015). Heavy metals negatively affected plant growth, biomass and photosynthesis (Wuana and Okieimen, 2011; Adrees et al., 2015; Ali et al., 2015a, 2015b). In an excess, heavy metals also affect the accumulation and translocation of essential elements by plants (Wagner, 1993; Wuana and Okieimen, 2011; Zia-ur-Rehman et al., 2015). Consequently, there is growing concern related to heavy metal pollution issues worldwide in order to reduce toxic metal bioavailability and plant uptake for increasing plant growth and yield and ultimately safe food production.

Silicon is a very important part of the earth's crust and it consists about 28% of the earth's crust (Sommer et al., 2006). However, Si is only 0.03% of the biosphere (Fauteux et al., 2005). In fact, Si is accumulated in many plants up to 10% by weight (Hodson et al., 2005) that is greater than some macronutrients (Epstein, 1994). Silicon has been shown to alleviate the deleterious effects of heavy metals in plants grown on contaminated soils (Chen et al., 2000). Experiments have demonstrated that certain crops benefit significantly from Si application (Takahashi et al., 1990). Various beneficial effects of Si have been identified in plants (Epstein, 1994, 1999). Various studies describe the ameliorative effect of Si application on plants under heavy metals or dangerous toxic elements, like Al, Cd, Pb, Cr or Cu (da Cunha and do Nascimento, 2009; Ali et al., 2013; Li et al., 2013; Shen et al., 2014; Keller et al., 2015). Thus, use of Si to enhance plant growth and alleviate heavy metals toxicity is predicted to become an emerging trend in the agriculture in near future. This review article summarizes the recent progress in understanding the mechanisms of Si-mediated heavy metal tolerance in plants.

## 2. Silicon in soil

Silicon is the second most abundant element in the soil ranging from 50 to 400 gSi $kg^{-1}$ of soil (Kovda, 1973). Silicon compounds in the soil are usually present as $SiO_2$ and in various alumino-silicate forms. Silicon dioxide comprises about 50–70% of the soil mass (Ma and Yamaji, 2006). External sources of Si include calcium and magnesium silicates, silicate slag, dolomite, rock phosphate and diatomite (Savant et al., 1997; Guntzer et al., 2012; Rizwan et al., 2012). Silicon compounds exist both in the liquid and in solid phase in the soil. In the solid phase, Si compounds can be divided into amorphous, poorly crystalline and crystalline forms. Amorphous silica (ASi) is comprised of both ASi from plants including phytoliths and other inorganic forms of ASi (Sauer et al., 2006) and it is considered to be the first pool of available Si for plants (Alexandre et al., 1997). The amount of biogenic silica (phytoliths) in soils ranges from 0.03 to 0.06 wt% (Desplanques et al., 2006). Grassland soils contain phytoliths up to only 1–3% of total Si pool (Blecker et al., 2006). The phytoliths are mainly composed of about 92 wt% silica and 6 wt% water with small amounts of carbon and traces of Al and Fe (Meunier et al., 1999). In liquid phase, Si is present as mono- and poly-silicic acids, complexed with organic and inorganic compounds (Cornelis et al., 2011). In natural soil solution, Si is mainly present in the form of uncharged orthosilicic acid, $H_4SiO_4$ ranging from 0.1 to 0.6 mM (Epstein, 1994; Sommer et al., 2006) and it is thought to be the only form which is taken up by plants (Epstein, 1994, 1999; Ding et al., 2005).

## 3. Silicon uptake and accumulation in plants

All plants grown in soil contain some Si in their tissues varying from 0.1% to 10% by weight of plants (Epstein, 1994, 1999; Ma and Yamaji, 2008). Silicon uptake by plants varies greatly between species and cultivars, i.e., gramineous vs leguminous plants, and plants are classified as high-, intermediate-, and non-Si-accumulators (Takahashi et al., 1990; Ma et al., 2001). However, Si concentration in plant tissues depends upon the characteristics of Si uptake and transport, variability between species and genotypes within a species (Epstein, 1994; Ma and Yamaji, 2008). Plant roots take up Si in the form of un-dissociated $H_4SiO_4$ (Casey et al., 2003; Ding et al. 2008) and Si uptake mechanisms differ between plant species (Ma and Yamaji, 2006). The mechanisms of Si absorption by roots are still controversial. However, there are three possible mechanisms of Si uptake by higher plants namely passive, active and rejective (Ma et al., 2004; Mitani and Ma, 2005). Passive uptake of Si takes place along the transpiration stream and it is shown that most dicotyledonous plants absorb Si passively (Ma et al., 2001). Active Si uptake is dominant in many plant species such as rice, maize, sugarcane and wheat (Casey et al., 2003; Rains et al., 2006). Transporters responsible for Si uptake by roots have been identified in different plant species such as rice, barley, maize, wheat and cucumber (Ma et al., 2007, 2011; Chiba et al., 2009; Mitani et al., 2009).

Once absorbed by roots, Si moves to the shoots by transpirational water flow via the xylem (Ma et al., 2006). In many plants, more than 90% of Si taken up by the roots is translocated to the shoots (Ma and Takahashi, 2002). In the xylem sap, Si is mostly present in the form of monosilicic acid and some as disilicic acid (Casey et al., 2003; Mitani and Ma, 2005). Recently, Si transporters responsible for xylem unloading in leaves (*Lsi6*) and inter-vascular transport have been identified (Yamaji et al., 2008, 2012). After translocation to shoots, Si is ultimately deposited as amorphous