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Silicon Management for Mitigating Abiotic Stress Effects in Plants

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ABSTRACT

Abiotic stress factors including salinity, drought, heat, frost, lodging, shading and ion toxicities may adversely affect the crop productivity and quality. Increasing evidences suggest that adequate regulation of silicon (Si) may enable the plants to survive the stress environment in a wide variety of crops. Si, once absorbed by the xylem veins, is deposited in the cell wall of roots, reducing the apoplastic bypass flow, provides binding sites for salts and, thereby, reduces the uptake and translocation of salts from roots to shoots. Si deposition in the cell wall increases the rigidity of cell wall and reduces the loss of water through transpiration with a resultant decrease in salt uptake. An increase in internal storage of water within plant tissue, due to reduced transpiration, allows higher growth rate and consequently mitigating detrimental effects of abiotic stresses. Si stimulates antioxidant defense system which helps the plants to maintain the desired level of reactive oxygen species in stress environment. Plants grown in the presence of Si show an erect growth, minimizing the amount of shade and allowing better distribution of light within the canopy. Si can lower electrolyte leakage, promoting photosynthetic activity in plants grown in stress environment. Si can positively affect the activities of certain enzymes and decrease the injury caused by abiotic stress factors. Si reduces the toxicity of elements such as iron, aluminum, manganese and cadmium through reduced uptake, complexation or immobilization and compartmentation or homogenous distribution of metal ions within the plant. This review deals with the current knowledge of beneficial effects of Si with focuses being on possible mechanisms of minimizing abiotic stress effects on plant growth and development.

Keywords: abiotic stress, drought, frost, heat, ion toxicity, salinity, Si

CONTENTS

INTRODUCTION

The world population is increasing very rapidly and is to be expected around 8.0 billion by the year 2025 (Pinstrup-Andersen *et al.* 1999). For sustaining food security, crop production must be increased by up to 100% over the next 25 years (Dyson 1999). But recent trends of crop production indicate that productivity and fertility of soils are globally declining due to intensive use of natural resources without proper management practices (Cakmak 2001).

Abiotic stresses, drought, salinity, high or low temperatures, excess light, inadequate mineral nutrient supply and ion toxicity, result from increasing world population and intensive use of natural resources (Gruhn *et al.* 2000; Cakmak 2001) contribute significantly to reduce crop yields well below the potential maximum yields (Cakmak 2005). According to Bray *et al.* (2000) the relative decrease in potential maximum crop yields because of abiotic stress factors are 54% in potato, 65.8% in corn, 69.3% in soybean and 82.1% in wheat. For sustaining food security and wellbeing of humankind, a high priority should be given to minimize detrimental effects of abiotic stresses through breeding, biological approaches and adequate and balanced supply of mineral nutrients (Marschner 1995).

Managing mineral nutrients properly offers both economic and environmental benefits to producers as well as rest of the society (Marschner 1995). There are actually 20 mineral elements necessary or beneficial for plant growth. Carbon (C), hydrogen (H), and oxygen (O) are supplied by air and water. The six macronutrients, nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S) are required by plants in large amounts. The rest of the elements are required in trace amounts (micronutrients). Essential trace elements include boron (B), chlorine (Cl), copper (Cu), iron (Fe), manganese (Mn), sodium (Na), zinc (Zn), molybdenum (Mo), and nickel (Ni). Beneficial mineral elements include silicon (Si) and cobalt (Co). The beneficial elements have not been deemed essential for all plants but may be essential for some (Matichenkov and Calvert 2002).

Si is found abundantly in healthy, rich soil and combines with oxygen to form silicon dioxide or sand (Epstein 1999). The role of Si in enhancing the tolerance of plants to various abiotic stresses, and its relevance to the world of agriculture has been widely recognized (Matichenkov *et al.* 1997; Epstein 1999; Guo *et al.* 2005; Gunes *et al.* 2007). It has been reported that Si treatment leads to alleviation of drought stress (Gong *et al.* 2005; Hattori *et al.* 2005), salt stress (Al-Aghabary *et al.* 2004; Romer-Aranda *et al.* 2006), heat stress (Ma 2004), oxidative damage (Liang *et al.* 2003;

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Zhu *et al*. 2004), frost damage (Ohyama 1985), Al toxicity (Ma *et al*. 1997; Liang *et al*. 2007), Mn toxicity (Rogalla and Romheld 2002), As toxicity (Guo *et al*. 2005), Cd toxicity (Liang *et al*. 2005), P deficiency and N excess (Ma and Takahashi 1990) and boron toxicity (Gunes *et al*. 2007).

The beneficial effects of Si are mostly attributed to its deposition in roots, leaves and stems. For example, deposition of Si in roots reduces apoplastic bypass flow and provides binding sites for salts, resulting in decreased uptake and translocation of salts from roots to shoots (Yeo *et al*. 1999). Deposition of Si in the clums, leaves and stems imparts mechanical strength and greatly improved light distribution within the canopy (Savant *et al*. 1997). Si deposition in leaves, clums and hulls reduces transpiration from the cuticle and hence salt accumulation (Romero-Aranda *et al*. 2006).

In this paper we intend to review the available literature and to summarize the potential benefits of Si in alleviating the detrimental effects of different abiotic stress factors on crop production.

SILICON IN SOIL

Si is the second most abundant mineral element in soil after oxygen and comprises approximately 28% of the earth's crust. 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 biogeochemically 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 9.0 (Hull 2004). At a higher pH (>9.0), silicic acid dissociates into silicate ions [$(OH)_3SiO^{-1}$]. The solubility of silicic acid in water is 2.0 mM at 25°C. When dissolved Si in soil solution exceeds 2.0 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). Polysilicic acid has a significant effect on soil texture, water holding capacity, adsorption capacity and soil erosion stability (Matichenkov and Ammosova 1996).

SILICON IN PLANTS

Plants absorb Si exclusively as monosilicic acid [$Si(OH)_4$] by diffusion and also by the influence of transpiration-induced root absorption known as mass flow (Ma *et al*. 2001; Liang *et al*. 2006). 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 (Takahashi 1995; Ma *et al*. 2001; Liang *et al*. 2005). Plants differ greatly in their ability to accumulate Si depending upon the mechanisms involved in Si uptake (Epstein 1999; Casey *et al*. 2003; Liang *et al*. 2007). Jones and Handreck (1967) classified the plants into accumulators (10-15% dry weight) including wetland 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 accumulator, intermediate and excluder plants, respectively (Takahashi *et al*. 1990; Epstein 1994; Ma *et al*. 2001, 2006). The difference in Si uptake among plant species could be explained on the basis of density of transporter and the mode of xylem loading (Epstein 1999; Tamai and Ma 2003). The xylem loading in rice was mediated by a kind of transporter whereas in cucumber and tomato xylem loading was mediated by diffusion (Ma *et al*. 2006).

Following uptake by the root, Si is translocated to the shoot via xylem. In shoot, monosilicic acid concentrated through the loss of water (transpiration) and is polymerized. The process of polymerization converts the monosilicic acid to colloidal silicic acid and finally to silica gel ($SiO_2{\cdot}nH_2O$) when the concentration of monosilicic acid exceeds 2 mM (Gao *et al*. 2004; Kaya *et al*. 2006). The amount of monosilicic acid in plant tissues varied depending upon plant species from 6 to 38%, polysilicic acid 10 to 70% of the total content of Si in plants. Si 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).

Si is deposited as a 2.5 µm layer in the space immediately beneath the thin (1.0 µm) cuticle layer forming a Si-cuticle double layer. Three loci of silicification are recognized: (i) the cell wall; (ii) the cell lumen, either wholly or partially infilled with silica and (iii) the intercellular spaces in root or shoot tissues or in an extracellular layer (Piperno 1988; Sangster and Hodson 1992).

Mechanisms for Si-mediated alleviation of abiotic stresses

1. Salinity stress

Soil salinization is one of the most significant abiotic stresses for crop plants (Chinnusamy *et al*. 2005). Approximately, 40% of irrigated lands worldwide show increased salt levels. Salts interfere with plant growth by ion cytotoxicity (Greenway and Munns 1980), osmotic effects (Munns and Termeat 1986), nutrient imbalances (Pessarakli *et al*. 1991; Khan *et al*. 2000) and/or oxidative damage (Hernandez *et al*. 2000). Plants have developed a wide range of adaptive/resistance mechanisms to maintain productivity and ensure plant survival under salinity stress (Foyer and Noctor 2000; Chinnusamy *et al*. 2005). Si has been reported to improve salt tolerance in a wide variety of crops (Adatia and Besford 1986; Romero-Aranda *et al*. 2006; Liang *et al*. 2007; Wang and Han 2007; Reezi *et al*. 2009; Ashraf *et al*. 2010) (**Table 1**).

Si interacts with Na^+, reduces its uptake and accumulation in plant tissues (Yeo *et al*. 1999; Zhu *et al*. 2004). Si, deposited as silica gel in the cell wall of the roots, provides binding sites for the salts and reduces their translocation to shoots which consequently improved plant growth and development (Yeo *et al*. 1999; Lux *et al*. 2003; Ashraf *et al*. 2010). Movement of salts into roots and shoots is a product of transpirational flux required to maintain the water status of plants. Si deposition and polymerization in leaves limits transpiration and hence salt accumulation (Bradbury and Ahmad 1990). Romero-Aranda *et al*. (2006) summarized that silica deposition in cell wall of leaves, clums and hulls increased the thickness and rigidity of the cell wall and decreased transpiration from the cuticle and improved water storage within plant tissues, which allowed higher growth rate that, in turn contributed to salt dilution within the plant, mitigating salt toxicity effects. Yeo *et al*. (1999) reported that Si deposition in the endodermis and rhizodermis blocks Na^+ influx through the apoplastic pathway in the roots. Restriction of Na^+ influx either into the root cells or into the xylem stream is one way of maintaining the optimum cytosolic K^+/Na^+ ratio of plants under salt stress. Similarly, Hashemi *et al*. (2010) demonstrated that Si nutrition ameliorated the deleterious effects of salinity on the growth of canola plants through lower tissue Na^+ contents, maintaining the membrane integrity of root cells, increased reactive oxygen species (ROS) scavenging capacity and reduced lignification.

Other authors (Liang *et al*. 2005; Wang and Han 2007) demonstrated that H^+-ATPase and H^+-PPase activities in the tonoplast were greatly inhibited under salt stress but considerably stimulated by the addition of Si. This Si-mediated elevated H^+-ATPase and H^+-PPase activities in the tonoplast may facilitate the compartmentation of Na^+ into the vacuole through tonoplast Na^+/H^+ antiport. They further reported that the added Si decreased tonoplast fluidity, membrane permeability and consequently the electrolyte leakage including Na^+ from the vacuole to cytoplasm under saline condi-

Table 1 Mechanisms for Si-enhanced plant tolerance to salinity.

Crop	**Silicon dose and form**	**Mechanism**	**References**
Sugarcane *Saccharum officinarum*	Si at 2 mM as calcium silicate	Reduced Na^+ uptake and translocation	Ashraf *et al.* 2010
Canola *Brassica napus* L.	Si at 2 mM as sodium silicate	Reduced tissue Na^+ content, maintained membrane integrity of root cells, increased reactive oxygen species scavenging capacity and reduced lignification	Hashemi *et al.* 2010
Rose *Rosa incida*	Si at 0.3 and 2 mM as potassium silicate	The suppression of Na^+ and Cl^- uptake as well as translocation to the photosynthetically active leaves	Sawas *et al.* 2007
Alfalfa *Medicago sativa* L.	Si at 1 mM as potassium silicate	Inhibition of Na^+ uptake by roots and affecting the uptake, translocation and/or distribution of K^+, Ca^{2+}, Mg^{2+} and Zn^{2+} within plants	Wang and Han 2007
Cowpea *Vigna unguiculata*	Si at 0.5 mM and 1 mM as calcium silicate	Contribution of Si to a more balanced nutrition under salt stress	Murillo-Amador *et al.* 2007
Tomato *Lycopersicon esculentum*	Si at 2.5 mM as potassium silicate	Increase plant water storage and plant water use efficiency	Romer-Aranda *et al.* 2006
Maize *Zea mays* L.	Si at 3 mM as sodium silicate	Enhanced chlorophyll content and photosynthetic activity	Moussa 2006
Barley *Hordeum vulgare* L.	Si at 1 mM as potassium silicate	Compartmentalization of Na^+ into the vacuole by stimulating the activities of H^+ATPase and H^+PPase in the tonoplast	Liang *et al.* 2005
Cucumber *Cucumis sativus* L.	Si at 1 mM as potassium silicate	Stimulation of antioxidant defense system	Zhu *et al.* 2004
Barley *Hordeum vulgare* L.	Si at 1 mM as silicic acid	Prevention of structural and functional deterioration of cell membrane	Liang *et al.* 2003
Rice *Oryza sativa*	Si at 3 mM as sodium silicate	Reduction in Na^+ uptake by blocking the transpirational bypass flow across the roots	Yea *et al.* 1999

tions.

Salinity affects nutrient uptake and nutrient balance in plant tissue (Pessarakli *et al.* 1991). Increasing salinity causes Na^+, Cl^-, SO_4^{2-} contents to rise and K^+, Ca^{2+} and Mg^{2+} contents to diminish in a number of crop species (Khan *et al.* 1999; John *et al.* 2003). Addition of Si to saline environment significantly decreased the Na^+ content but increased K^+ (Ashraf *et al.* 2010). The possible mechanism causing Si to stimulate the plants to absorb K^+ under salt stress was the activation of H^+-ATPase in the membranes (Liang 1999). The interaction between Si and Ca^{2+} varied with the plant species and the stressed environment to which plants were exposed (Ma and Takahashi 1993).

Salinity-induced accumulation of ROS including superoxide radical, hydroxyl radical, singlet oxygen ($1O_2$) and hydrogen peroxide (H_2O_2) which are detrimental to cells at higher concentration because they cause oxidative damage to membrane lipids, proteins, nucleic acids and chlorophyll (Mittler 2002; Karabal *et al.* 2003; Keles *et al.* 2004; Gunes *et al.* 2007). To scavenge these toxic species, plants employ antioxidants (e.g. ascorbate, glutathione, α-tocopherol and carotenoids) and detoxifying enzymes such as superoxide dismutase, catalase and ascorbate peroxidase (Liang 1999; Molassiotis *et al.* 2006). However, the efficiency of antioxidant defense system is greatly altered in stress environment including salt stress (Alscher *et al.* 2002; Sairam *et al.* 2005; Moussa 2006) and failed to maintain the ROS balance within the cell. The excess production of ROS during salinity stress results from impaired electron transport process in chloroplast and mitochondria as well as from pathways such as photosynthesis and photorespiration. The past studies demonstrated that application of Si under salt stress significantly increased superoxide dismutase activity and decreased malondialdehyde concentrations in plant leaves (Liang 1999) and increased superoxide dismutase, peroxidase, catalase and glutathione reductase activity and reduced lipid peroxidation in barley roots (Liang *et al.* 2003). Zhu *et al.* (2004) also demonstrated that the activities of superoxide dismutase, guaiacol peroxidase, ascorbate peroxidase, dehydroascorbate reductase and glutathione reductase in salt stressed cucumber were increased by Si application. Higher efficiency of antioxidant defense system in salt stressed plants with Si application coincided with decreases in their electrolyte leakage and lipid peroxidation level and H_2O_2 content, suggesting that oxidative damage induced by salinity stress could be alleviated by Si (Shalata and Tal 1998; Gossett *et al.* 1994; Al-Aghabary *et al.* 2004; Moussa 2006; Wang *et al.* 2010).

2. Drought stress

Drought is another important abiotic stress which limits plant growth and productivity (Gadallah 1995). Drought or water deficit leads to stomatal closure and reduced transpiration rates, a decrease in water potential of plant tissues, a decrease in photosynthesis and ultimately growth is inhibited (Lawson *et al.* 2003; Yordanov *et al.* 2003). Plants can adapt different morphological and physiological mechanisms such as drought avoidance and drought tolerance to acclimatize drought stress (Blum 1996; Sakamoto and Murata 2002). Recent studies (Gunes *et al.* 2007, 2008a, 2008b) indicated that Si could be used as a potential growth regulator, improving plant growth under drought conditions. The ameliorative effect of silicon on drought has been related to the depression of excess loss of water by transpiration (Romero-Aranda *et al.* 2006), osmotic adjustment (Trenholm *et al.* 2004), improved mineral nutrient uptake and accumulation (Gunes *et al.* 2008a) and/or activation of antioxidant defense system (Gunes *et al.* 2008b) (**Table 2**).

Si can alleviate drought stress by decreasing transpiration (Raven 2003; Gong *et al.* 2005). As Si is deposited beneath the cuticle of leaves forming Si-cuticle double layer that increases the rigidity of cell wall and reduces water loss through transpiration (Savant *et al.* 1999; Ma 2004). Agarie *et al.* (1998) also reported that deposition of Si in the cell wall reduced transpiration and increased internal storage of water under drought stress. According to Ma *et al.* (2001) Si can reduce transpiration by 30% in rice which has a thin cuticle. Si is known to absorb actively through the roots in the form of uncharged monosilicic acid, and is then passively transported by the transpiration stream, and irreversibly precipitated as $SiO_2.nH_2O$ in cell wall and cell lumens of all plant tissues (Richmond and Sussman 2003). Thus, another ameliorative effect of Si on drought could be related to the hydrophilic nature of $SiO_2.nH_2O$ which helps to keep water and to protect tissues from drought (Gong *et al.* 2005).

An important mechanism of drought tolerance is the osmotic adjustment as it helps to retain water despite low water potential (Romero-Aranda *et al.* 2006). Gunes *et al.* (2008b) described that Si deposited in the cytoplasm and high molecular weight Si complexes in the vacuoles could improve the efficiency of osmotic adjustment. Other authors (Gao *et al.* 2004; Hattori *et al.* 2005) also highlighted the role of Si on drought tolerance through osmotic regulation.

Decreasing water availability under drought generally resulted in reduced total mineral uptake and frequently

Table 2 Mechanisms for Si-induced resistance to drought stress in plants.

Crop	Silicon dose and form	Mechanism	Reference
Pepper *Capsicum annuum*	Si at 0.25, 1.0 and 1.75 μM as sodium metasilicate	Improved leaf water content by maintaining transpiration and stomatal conductance	Lobato *et al.* 2009
Potato *Solanum tubersum*	Si at 284.4 mg dm^{-3} as calcium silicate	Improved efficiency of osmotic adjustment	Crusciol *et al.* 2009
Sunflower *Helianthus annuus*	Si at 100 mg kg^{-1} as sodium silicate	Regulate the uptake and accumulation of essential and non-essential elements	Gunes *et al.* 2008a
Sunflower *Helianthus annuus*	Si at 100 mg kg^{-1} as sodium silicate	Enhanced efficiency of antioxidant defense system	Gunes *et al.* 2008b
Tomato *Lycopersicon esculentum*	Si at 2.5 mM as potassium silicate	Reduced transpiration, increased internal water storage and improved plant water use efficiency	Romer-Aranda *et al.* 2006
Wheat *Triticum aestivum*	Si at 0.1167 g m^{-2} as sodium silicate	Protection of plant tissue from membrane oxidative damage by stimulating antioxidant defense system	Gong *et al.* 2005
Sorghum *Sorgum bicolor*	Si at 1 mM as potassium silicate	Improved water uptake ability	Hattori *et al.* 2005
Barley *Hordeum vulgare*	1000-2000 kg ha^{-1} as amorphous silicon dioxide	Si-cellulose membrane in epidermal tissue reduced transpiration and improved tissue tolerance	Matichenkov and Bocharnikova 2004
Rice *Oryza sativa*	Si at 20, 40 and 100 ppm as silicon dioxide	Improved structure and integrity of plasma membrane and reduced electrolyte leakage	Agarie *et al.* 1998

reduced the concentration mineral nutrients in crop plants (Marschner 1995). The important effects of water deficits are on transport of mineral to the roots as well as reduced root growth and extension (Samarah *et al.* 2004). Reduced absorption of mineral elements can result from interference with mineral nutrient uptake, unloading mechanisms and reduced transpiration (Baligar *et al.* 2001). Xia (1997) reported that N, P and K uptake in faba bean was significantly reduced under drought conditions.

Si has been reported to alleviate drought stress in wide variety of crops (Gao *et al.* 2004; Hattori *et al.* 2005). Gunes *et al.* (2008a) demonstrated that application of Si under drought stress significantly improved the uptake of Si, K, S, Mg, Fe, Cu, Cl, Al, Na, Rb, Ti and Ba whereas Zn, Mo, Ni and Br uptake were not affected. Kaya *et al.* (2006) indicated that addition of Si increased Ca concentration which played a vital role in maintaining membrane stability and permeability. Liang (1999) reported that under water stress conditions, K concentration increased in the presence of Si possibly because of the activation of H^+-ATPase in the membranes. K is one of the primary osmotic substances which contribute to osmotic adjustment (Ashraf *et al.* 2001). Si-mediated maintenance of higher levels of K is essential in achieving better survival with improved growth under water stress (Umar 2002).

Drought stress also increases the production of ROS that damage the plants by oxidizing photosynthetic pigments, lipids, proteins and nucleic acids (Egert and Tevini 2002; Reddy *et al.* 2004). Increases in ROS production in drought stressed plants is well known and related to impairment in photosynthesis and associated disturbances in carbohydrate metabolism (Mishra and Choudhuri 1999; Jiang and Zhang 2002). Alleviation of detrimental effects of drought stress, particularly drought-induced oxidative damage, by Si application has been reported in wheat (Gong *et al.* 2005), bean (Zlatev *et al.* 2006), sorghum (Lux *et al.* 2002) and sunflower (Gunes *et al.* 2008a, 2008b). Reddy *et al.* (2004) suggested that effects of drought on antioxidant enzymes are very complex and depend on the duration of drought, plant species and varieties. However, application of Si regulated the activity of antioxidative systems and mitigated the deleterious effects of drought on plant growth (Gunes *et al.* 2008b).

Si can lower electrolyte leakage, promoting greater photosynthetic activity in plants grown under water deficit. According to Kaya *et al.* (2006), drought induced reduction in chlorophyll content could be alleviated by Si and hence improved photosynthesis under drought stress. Liang *et al.* (1996) showed that decrease in electrolyte leakage by Si application under water stress could be due to the effect of Si on structure and integrity of plasma membranes by influencing the stress-dependent peroxidation of membrane lipids. As cell membranes are one of the first targets of many abiotic stresses and it is generally accepted that the maintenance of their integrity and stability under drought stress is a major component of drought tolerance in plants (Liang 1999).

3. Heat stress

Temperature is one of the most important environmental factors governing plant growth and development (Monjardino *et al.* 2005). When grown near optimal temperature, plants are more likely to reach optimum yields. However, because of environmental fluctuation, temperature is often higher than optimum, thus increasing the probability of the plants being exposed to extended periods of supra-optimal temperature (Commuri and Jones 1999; Engelen-Eigles *et al.* 2000). Such temperature (heat stress) is detrimental to plant growth and dry matter accumulation because it inhibits protein synthesis, enzyme activity, chlorophyll formation, photosynthesis and increases transpiration (Gibson and Paulsen 1999). Commuri and Junes (2001) reported that extended periods of drought and high temperature lead to poor vigor and shallow rooting. A decrease in external water potential results in a reduction of cellular growth and thus root and shoot growth.

Application of Si has been reported to alleviate heat stress in different plant species (Martineau *et al.* 1979; Epstein 1999) (**Table 3**). According to Takahashi and Kurata (2007), Si deposited in the cell walls forms a protective layer reducing transpiration through the outer cells. Si deposited in the cell walls of the xylem vessels also prevents the compression of vessels under the conditions of high transpiration caused by drought or heat stress (Hattori *et al.* 2005; Liang *et al.* 2007). Heat stress causes the plants to virtually cease their metabolic functions because water is lost through transpiration faster than it can be replaced via plant's root system. This results in higher increase in cellular mineral concentration which inhibits plant functions (Stone and Nicolas 1998). However, increased levels of Si in cell walls reduce transpiration loss caused by higher temperature thus allowing continued metabolic functions under heat stress. According to Epstein (1999), plants wilt less, resist sunburn and are generally more tolerant to heat stress when Si is applied to growth medium. Agarie *et al.* (1998) observed that electrolyte leakage caused by the heat stress was particularly high in plants grown without Si and were minimal when sufficient Si was supplied. On the other hand, there is also evidence that heat stress induces the production of ROS which causes oxidative damage of cellular components (Epstein 1994). Addition of Si improves the efficiency of antioxidant defense system under various abiotic stresses and thus promotes the plant growth and development (Red-

Table 3 Mechanisms of Si-induced tolerance to temperature stress in plants.

Crop	Environmental stress	Mechanism	Reference
Seashore paspalum *Paspalum vaginatum* Swartz	Freezing stress	Maintenance of membrane stability to cope with chilling-induced oxidative stress	He *et al.* 2009
Cucumber *Cucumis sativus*	Freezing stress	Activation of antioxidant defense system	Liu *et al.* 2009
Wheat *Triticum aestivum*	Freezing stress	Higher antioxidant defense activity and lower lipid peroxidation through water retention in leaf tissue	Liang *et al.* 2008
Wheat *Triticum aestivum*	Freezing stress	Improved photosynthesis and water use efficiency	Zhu *et al.* 2006
Sorghum *Sorgum bicolor*	Heat stress	Si deposition in the cell walls of the xylem vessels prevents the compression of vessels under the conditions of high transpiration caused by heat stress	Hattori *et al.* 2005
Rice *Oryza sativa*	Heat stress	Reduced transpiration loss and, thereby, plants wilt less, resist sunburn and are generally more tolerant to heat stress	Epstein 1999
Rice *Oryza sativa*	Heat stress	Improved structural constituents and organization of cell membrane	Agarie *et al.* 1998
Sugarcane *Saccharum officinarum*	Freezing stress	Increased oxidative power of roots and decreased the injury caused by climatic stress such as frost damage	Savant *et al.* 1997
Alfalfa *Medicago sativa*	Freezing stress	Si-enhanced water retention in leaf tissues	Mckersie *et al.* 1993
Rice *Oryza sativa*	Freezing stress	Improved leaf and stem strength through deposition in the cuticle and by maintaining cell wall polysaccharides and lignin polymers	Ohyama 1985

dy *et al.* 2004; Gong *et al.* 2005; Zlatev *et al.* 2006; Crusciol *et al.* 2009).

Si has also been shown to result in higher concentrations of chlorophyll per unit area of leaf tissue. This means that a plant is able to tolerate both lower and higher light levels by using more of the available light. Moreover, supplemental levels of soluble Si have been shown to produce higher concentrations of enzymes RUBP carboxylase in leaf tissue which help in CO_2 metabolism in stress environment (Liang 1999; Sairam *et al.* 2005; Romer-Aranda *et al.* 2006; Gunes *et al.* 2008b).

4. Freezing stress

Like heat stress, both chilling and frost stresses can cause irreversible damage to plant cells due to mechanical forces generated by the formation of extracellular ice crystals as well as cellular dehydration and increased concentration of intracellular salts (Levitt 1980; Steponkus 1984). It has been reported that the major target of chilling injury is also cell membrane and the membrane damage is the primary damage induced by cellular dehydration in plants exposed to chilling or freezing (Levitt 1980). It has also been reported that freezing increases the level of ROS in plants and the increased lipid peroxidation arising from the accumulation of ROS is the major cause for membrane damage and the development of injury symptoms resulting from chilling (Senaratna *et al.* 1988) and freezing (McKersie *et al.* 1993). According to Marschner (1995), low temperature stress generally affects the fluidity of membrane lipids and hence alters membrane structure. Under low temperature stress, absorbed light energy exceeds the capacity of chloroplasts to use it in CO_2 fixation, and the excess energy is alternatively used for the activation of O_2 to ROS (Cakmak 2005). It has been reported that photosynthetic electron transport, CO_2 fixation, Rubisco activity and stomatal conductance are the major targets impaired by low temperature stress in plants. Numerous studies have shown that supply of Si under low temperature stress regulated the activity of antioxidant defense system and alleviated oxidative damage caused by chilling or frost (Savant *et al.* 1999; Ma *et al.* 2001) (**Table 3**). Si increased the oxidative power of rice roots, decreased the injury caused by climatic stress as typhoons and cool summer damage in rice, alleviated frost damage in sugarcane and favored super cooling of palm leaves (Savant *et al.* 1997; Liang *et al.* 2008). It has been reported that Si improves leaf and stem strength through deposition in the cuticle and by maintaining cell wall polysaccharide and lignin polymers (Takahashi *et al.* 1990; Hull 2004) and thus protected plants from low temperature and frost (Ohyama 1985). Application of Si under frost conditions resulted in higher concentration of chlorophyll (Schmidt *et al.* 1999) and the enzymes RUBP carboxylase in leaf tissue. This enzyme regulated the metabolism of CO_2 and enables the plants to make more efficient use of available levels of CO_2 under low temperature stress. In different experiments with cucumber, rice, maize, sunflower and wax gourd it has been found that the leaves of Si treated plants grown hydroponically at low temperature (0-4°C) were more tolerant to cold induced wilting and the root ability to absorb nutrients was higher. According to Liang *et al.* (2006) Si confers resistance and/or tolerance to chilling or freezing stress. Steponkus (1984) reported that photosynthesis and water use efficiency were significantly inhibited under freezing stress, but were significantly enhanced by added Si compared with non-Si amended freezing treatment. Based on the previous work (Liang 1999; Liang *et al.* 2003; Zhu *et al.* 2004; Gong *et al.* 2005) it could be concluded that the Si-mediated alleviation of freezing injury may be attributed to Si-enhanced antioxidant defense activities and consequent reduced membrane oxidative damage through better water retention in leaf tissues. Mckersie *et al.* (1993) also indicated that the possible mechanisms of Si-mediated freezing stress alleviation may be higher antioxidant defense activity and low lipid peroxidation and membrane permeability, which are acquired through Si-enhanced water retention in leaf tissues.

On the other hand, Liang *et al.* (2008) reported that the concentration of proline, one of the osmosis-regulated molecules in plant tissues was significantly higher in the freezing stressed plants than in the control plants, but was significantly lower when Si was added to these plants. This suggested that there was a general adaptive response to freezing stress in plants in the initial phase through the accumulation of osmosis-regulated compounds such as proline and that exogenous Si application induced resistance to freezing-driven water losses.

5. Mineral nutrient stress

Phosphorus deficiency stress: Phosphorus (P) deficiency is a typical abiotic stress, which has recognized as a limiting factor for crop growth and output in modern agricultural production (Wissuwa 2003). As atom radius, chemical properties and structures of Si and P are very similar, consequently they have certain interactions (Jiayu 1992; Kewei *et al.* 2002; 2004). Matichnkov and Calvert (2002) reported that Si fertilization influences the availability of P in two ways; the first process involves is that the increase in the concentration of monosilicic acid results in the transformation of slightly soluble phosphates into plant available phosphates. The equations for these reactions are as follows after Matichenkov and Ammosova (1996):

$$CaHPO_4 + Si(OH)_4 = CaSiO_3 + H_2O + H_3PO_4$$

$$2Al(H_2PO_4)_3 + 2Si(OH)_4 + 5H^+ = Al_2Si_2O_5 + 5H_3PO_4 + 5H_2O$$

$$2FePO_4 + Si(OH)_4 + 2H^+ = Fe_2SiO_4 + 2H_3PO_4$$

Secondly, Si adsorbs P, thereby decreasing P leaching by 40-90%. It is noteworthy that adsorbed P is kept in plant available form (Matichnkov and Calvert 2002). Kewei *et al.* (2002) indicated that Si had a significant effect on adsorption and desorption of P in soils. Matichenkov *et al.* (1997) and Datnoff *et al.* (2001) also demonstrated that the anion of monosilicic acid $[Si(OH)_3]^-$ can replace phosphate anion $[HPO_4]^{2-}$ from calcium, magnesium, aluminum and iron phosphates. Owino-Gerroh and Gascho (2004) demonstrated that application of soluble Si in acid soils could decrease adsorption of P in soils and increase the amount of bio-available P and soil pH.

Using a maize variety sensitive to low P stress, Yang *et al.* (2008) found that appropriate Si application to low P solution could enhance absorbability and utilization ability of P in maize seedling roots; increased content and accumulation of P and Si as well as dry matter accumulation in different organs, chlorophyll content and net photosynthetic rate. Datnoff *et al.* (2001) also reported that application of Si improved the growth and yield as well as P uptake and translocation to panicle in rice under P deficiency stress. It has been found that Si application under low P-stress could alleviate not only chlorophyll decomposition but also enhanced absorption of light in leaf. Scatter light transmittance of siliceous cells on leaf surface was 10 times higher than that of green cells (Savant *et al.* 1997), so it could promote photosynthesis and hence dry matter accumulation (Epstein 1999).

In an experiment using a nutrient solution, Si supply resulted in a larger increase of dry weight of rice shoot at lower P level (Ma and Takahashi 1990). Other investigators also indicated that barley yield was higher in a field amended with Si than field without Si application when P fertilizers were not applied (Ma 2004). Ma and Takahashi (1990) suggested that the beneficial effects of Si on plant growth under P-deficiency stress may be attributed to enhanced availability of internal P due to the reduced uptake of Fe and Mn. P is translocated and redistributed in plants in an inorganic form and showed high affinity for metals such as Fe and Mn. Thus, the reduction in uptake of Fe and Mn by Si application can increase the internal availability of P.

Excess nitrogen stress: Nitrogen (N) is essential for plant growth and development. However, the excessive application of N fertilizers cause lodging, mutual shading and susceptibility of plants to pests and diseases (Ma 2004). These effects could be minimized by the use of Si (Mauad *et al.* 2003). Deposition and polymerization of Si in plant tissues enhances the strength and rigidity of cell walls and hence increases plant resistance to lodging (Epstein 1999; Savant *et al.* 1999; Liang *et al.* 2005). It has been reported that plants become more susceptible to pests and diseases when N application is heavy because of N-induced succulence in plants (Mauad *et al.* 2003). However, the presence of silicate crystals in plant tissue provide mechanical barrier which hinders feeding of insects and inhibits fungal diseases by physically inhibiting fungal germ tube penetration of epidermis (Datnoff *et al.* 1997; Savant *et al.* 1999; Ma 2004).

Leaves, stems and clums in the presence of Si, show an erect growth thereby the distribution of light within the canopy is greatly improved. This is particularly important in dense plant shades and when N fertilizers are heavily applied so as to minimize the mutual shading (Epstein 1994; Savant *et al.* 1999).

Excessive application of N also causes high protein content in brown rice which affects its quality. However, sufficient supply of Si to rice is effective in producing low protein rice (Morimiya 1996). Mauad *et al.* (2003) indicated that high N rates stimulated tillering and the formation of new leaves, causing shading, a condition that favored diseases, lodging and reduction in productivity. However, Si fertilization increases cell wall thickness (Epstein 1999), imparting mechanical resistance to the penetration of fungi (Ma 2004), improvement of leaf angle, making leaves more erect and thus reducing self shading, especially under high N rates (Mauad *et al.* 2003).

6. Heavy metal toxicities

Metal toxicity has great impact and relevance not only to plants but also affects the ecosystem, of which the plant forms an integral component. Plants growing in metal polluted environment exhibit altered metabolism, growth reduction, lower biomass production and 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 thus disturbing physiological and molecular homeostasis (Christopher 2000). However, common remediation methods such as extraction of the polluted soils are too expensive to be practiced (Dong *et al.* 2004). One of the alternative mechanisms is the amelioration of metal toxicity by Si (Rogalla and Romheld 2002; Liang *et al.* 2005; Shi *et al.* 2005; Liang *et al.* 2007; da Cunha *et al.* 2009; Kaya *et al.* 2010). The relationship between Si and metal tolerance in plants has been largely studied. For instance, Neumann and Nieden (2001) regarded the accumulation of zinc silicate in the vacuole and cell wall of *Cardaminopsis halleri* leaves as a tolerance mechanism to cope with the metal toxicity. Rogalla and Romheld (2002) reported that cucumber (*Cucumis sativus*) plants treated with Si presented decreased Mn concentration in the cell wall. However, it is worth pointing out 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).

The key mechanisms of Si-mediated toxicities alleviation in higher plants include: 1) complexation or co-precipitation of toxic metal ions with Si, 2) immobilization of toxic metal ions in the growth media, 3) stimulation of antioxidant defense system, 4) uptake processes, and 5) compartmentation or homogenous distribution of metal ions within plants (Liang *et al.* 2005) (**Table 4**). However, these alleviative mechanisms may vary depending upon plant species (Epstein 1999).

Iron toxicity: Iron (Fe) toxicity, a common nutrition problem in wetland rice, is ascribed to the formation of ROS especially hydroxyl radical which is the most toxic ROS to aerobic cells (Cakmak 2005). Moreover, there are some Fe species which are also very toxic and produced by the reaction of Fe^{2+} with molecular O_2, forming ferryl ($Fe^{2+}O$) and perferryl ($Fe^{2+}O_2$) species (Cakmak 2000). Increasing evidence has suggested that Si is effective to alleviate Fe toxicity by enhancing oxidative power of roots which resulted in increased oxidation of Fe from ferrous iron to insoluble ferric iron (Ma 2004). Moreover, Si stimulated the activities of antioxidant enzymes which maintained the balance of ROS within the cell.

Aluminum toxicity: Aluminum (Al) is one of the most abundant elements in the earth's crust only after oxygen and Si, comprising about 7% of its mass (Kochian 1995). Most of the Al occurs as harmless oxides and aluminosilicates when soil pH is over 5.5. However, the solubility of Al increases greatly when soil pH falls below 5.5. Al toxicity is a major factor constraining the crop performance on acid soils (Cocker *et al.* 1998a). Micro molar concentration of Al

Table 4 Mechanisms for Si-mediated alleviation of metal toxicity in plants.

Crop	Silicon dose and form	Mechanism	References
Peanut *Arachis hypogaea*	Si at 1.8 mM as potassium silicate	Compartmentation of metal ions and stimulation of antioxidants systems	Shi *et al.* 2010
Maize *Zea mays*	Si at 50, 100, 150 and 200 mg Kg^{-1} as calcium silicate	Enhanced hydraulic status in plants caused by Si mediated increase in xylem diameter and mesophyll thickness	da Cunha and do Nascimento 2009
Pakchoi *Brassica chinensis*	Si at 1.5 mM as potassium silicate	Enhanced antioxidant defense capacity, membrane integrity and suppressed oxidative damage	Alin *et al.* 2009
Maize *Zea mays*	Si at 200 mg Kg^{-1} as calcium silicate	Reduced bioavailability of metal ions	da Cunha *et al.* 2008
Rice *Oryza sativa*	Si at 2 and 4 mM as silicic acid	Compartmentalization of Cd in cell walls and special silicified cells	Zhang *et al.* 2008
Rice *Oryza sativa*	Si at 0.2 and 0.6 mM as sodium silicate	Improved light use efficiency	Nwugo and Huerta 2008
Wheat *Triticum aestivum*	Si at 5 and 10 mM as sodium silicate	Prevention of oxidative membrane damage and translocation of B from root to shoot and/or soil to plant	Gunes *et al.* 2007
Rice *Oryza sativa*	1.8 mM as silicic acid	Uniform distribution of metal ions within plants	Shi *et al.* 2005
Maize *Zea mays*	Si at 1.4 mM as silicic acid	Formation of hydroxyaluminumsilicates in the apoplast, which transformed Al into a non-phytotoxic form	Wang *et al.* 2004
Cucumber *Cucumis sativus*	Si at 1.8 mM as sodium silicate	Binding of Mn to cell walls and thereby, lowering the Mn concentration within the symplast	Rogalla and Romheld 2002
Maize *Zea mays*	1000 μM as silicic acid	Chelation of metal ions with phenolic compounds	Kidd *et al.* 2001
Teosinte *Zea mays* ssp. *Mexicana*	4 μM as sodium silicate	Co-precipitation of aluminum with Si in the growth media as well as within plant	Baarcelo *et al.* 1993

can inhibit root growth within minutes or hours in many agriculturally important plant species (Guo *et al.* 2004). The major toxicity symptom of Al in plants is inhibition of root growth (Ma *et al.* 2001). There are increasing evidences of the Si role on ameliorating Al toxicity in cotton (Li *et al.* 1989), sorghum (Galvez and Clark 1991), soybean (Baylis *et al.* 1994), corn (Ma *et al.* 1997), maize (Kidd *et al.* 2001) and barley (Liang *et al.* 2001). According to Hodson and Evans (1995) interaction between Si and Al, reducing the activity of Al ion in the medium is one possible mechanism to alleviate Al toxicity. The precipitation of subcolloidal, inert hydroxyaluminosilicate species seems to have diminished the concentration of phytotoxic Al in solution.

$$2H_4SiO_4 + 2Al^{3+} = Al_2Si_2O_5 + 2H^+ + 3H_2O$$

$$2H_4SiO_4 + 2Al^{3+} + H_2O = Al_2Si_2O_5(OH)_4 + 6H^+$$

In an experiment with *Zea mays*, Barcelo *et al.* (1993) found that plants exposed to toxic concentration of Al (60 and 120 μM) were less affected in the presence of Si in solution as compared to Al-treated plants without Si. They suggested that possible mechanism by which Si minimized the toxic effects of Al on plant growth seemed to be co-precipitation of Al with Si in growth medium as well as within plant. Ma *et al.* (1997) also reported that Si significantly alleviated Al-induced inhibition of root elongation in maize, presumably by the formation of Si-Al complexes, a non toxic form. On the other hand, Corrales *et al* (1997) suggested a purely internal interaction between the two elements. This hypothesis was further supported by Cocker *et al.* (1998a) who demonstrated that the mitigation of Al toxicity in wheat by Si application was due the internal or physiological processes. In the subsequent study, Cocker *et al.* (1998b) proposed that low solubility aluminosilicates or hydroxyaluminosilicates or both are formed within the root cell wall (apoplastic) space, thereby reducing the concentration of free toxic Al^{3+} ions. Hammond *et al.* (1995) found that Al-toxicity in barley could be mitigated through Si application by reversing the inhibitory effect of Al on the absorption of Ca by roots and Ca transport to shoots. According to Wang *et al.* (2004), apoplastic binding of Al is involved in Si-induced amelioration of Al toxicity in maize.

Working with soybean, Baylis *et al.* (1994) found that Si alleviated the symptoms of Al toxicity, but the effective rate was dependent on pH. Greater concentrations of Si were required at lower pH where Al was more toxic. These results supported the hypothesis that pH dependent affinity of Si for Al in dilute solution, and the consequent formation of subcolloidal inert hydroxyaluminosilicate species, is the basis for the alleviation of Al toxicity by Si. Liang *et al.* (2007) reported that Si may have an additional role in increasing plant tolerance to Al toxicity by mediating the metabolism of phenolic compounds as it has been reported by Kidd *et al.* (2001) that Si treated maize plants released fifteen times more phenolics than untreated maize plants. These flavonoid phenolics have strong Al-chelating ability and may improve metal tolerance in plants.

Manganese toxicity: Manganese (Mn) toxicity in plants is often not a clearly identifiable disorder. The symptoms of Mn toxicity as well as the concentration of Mn that causes toxicity vary widely among plant species and varieties within species probably because phytotoxic mechanisms of Mn involve different biochemical pathways in different plant genotypes. Mn toxicity is likely with plants that fertilized with acid forming fertilizers, high rates of superphosphate or nitrate or plants that are low in Si or deficient in Ca, Fe, Mg or P (El-Jaoual and Cox 1998). Si is reported to detoxify Mn within plants, presumably by preventing localized accumulation of Mn associated with lesions on leaves (Foy *et al.* 1999). However, Okuda and Takahashi (1962) demonstrated that Si reduced Mn uptake in rice by promoting the Mn oxidizing power of roots. On the other hand, Williams and Vlamis (1957) in barley and Horst and Marschner (1978) in bean reported that Si did not reduce Mn uptake but led to a homogenous distribution of Mn in the leaf blade.

Horst *et al.* (1999) found that Si led to a lower apoplastic Mn concentration in cowpea and suggested that Si modified the cation binding properties of the cell wall. However, Iwasaki *et al.* (2002) indicated that Si alleviated Mn toxicity not only by decreasing the concentration of soluble apoplastic Mn through enhanced adsorption of Mn on the cell walls but also a role of soluble Si in the detoxification of apoplastic Mn. In an experiment with cucumber, Rogalla and Romheld (2002) found that plants not treated with Si had higher Mn concentrations in the intracellular washing fluid (IWF) as compared with plants treated with Si. The Mn concentration of IWF was positively correlated with the severity of Mn toxicity symptoms and negatively correlated with Si supply. Furthermore, in Si treated plants less Mn was located in the symplast (<10%) and more Mn was bound to the cell wall (>90%) as compared with untreated plants (about 50% in each compartment). More recently (Shi *et al.* 2005; Liang *et al.* 2007; Stoyanova *et al.* 2008) reported that the alleviation of Mn toxicity by Si was attributed to a significant reduction in membrane lipid peroxidation caused by excess Mn and to a significant increase in enzymatic (e.g. superoxide dismutase, guaiacol peroxidase, ascorbate peroxidase, dehydroascorbate reductase) and non-enzymatic antioxidants (e.g. ascorbate and glutathione).

Cadmium toxicity: Cadmium (Cd) toxicity is a widespread problem. In numerous plant species, including important crops, the exposure of plants, even, to low concentration of Cd causes growth inhibition and disturbs several metabolic processes (Zhang *et al.* 2008; Li *et al.* 2009). Moreover, Cd accumulation in plant organs, which are used as food or forage represents health risk and limits agricultural production on polluted soils. Vitoria *et al.* (2004) reported that 1 mmol L^{-1} of Cd provoked disintegration of epidermis and cortical parenchyma of radish (*Raphanus sativus*) roots; the plants displayed large intracellular spaces as well. According to authors, this was a consequence of the low cellular hydraulic potential owing to Cd toxicity. Nwugo and Huerta (2008) reported that Cd toxicity inhibited growth and photosynthesis. Guo *et al.* (2004) indicated a highly significant increase in malondialdehyde concentration and peroxidase activities in plants subjected to low pH and Cd toxicity.

It is well known that Si can increase the tolerance of many plant species to Cd toxicity (Liang *et al.* 2005; Nwugo and Huerta 2008). da Cunha and Nascimento (2009) reported that Si deposited as silica bodies and silica buliforms cells in the cell wall of epidermis, exodermis, endodermis, pericycle and xylem, precipitated Cd in these tissues. The co-precipitation of Si-metal complex seems to contribute to the cell detoxification, since the plant biomass was linearly increased as the result of Si addition to soil. The authors further indicated that xylem diameter was linearly increased by Si addition in Cd contaminated soil. As the decrease in size and number of xylem vessels is a common symptom of metal toxicity that strongly diminished the uptake and transport of water by plants (Barcello and Poschenrieder 1990; Gong *et al.* 2005). The increase observed for the xylem diameter paralleled the highest roots and shoots biomass of maize grown on Cd-contaminated soil (da Cunha and Nascimento 2009). These results suggested that Si effects on the plant hydraulic balance could play a role in increasing biomass under metal toxicity.

Zhang *et al.* (2008) reported that Si supply decreased shoot Cd concentration by 30-50% and Cd distribution ratio in shoot by 25.3-46% which led to an increase in shoot biomass by 131-171% and root biomass by 100-106% as compared with treatment without Si. According to Liang *et al.* (2005) addition of Si significantly increased soil pH but decreased soil Cd availability, thus reducing the concentration of Cd in the shoots and roots. Moreover, more Cd was found to be in the form of specific absorbed or Fe-Mn oxides bound fraction in the Si-amended soil. The xylem sap significantly increased but Cd concentration in the xylem sap significantly decreased in Si-amended Cd treatments as compared with non Si-amended Cd treatments. The authors concluded that Si-enhanced tolerance to Cd can be attributed not only to Cd immobilization caused by silicate-induced pH rise in the soils but also to Si-mediated detoxification of Cd in the plants. Shi *et al.* (2005) also indicated that the heavy deposition of silica in the vicinity of the endodermis might offer a possible mechanism by which Si did at least partially physically block the apoplastic bypass flow across the roots and restrained the transport of Cd to shoots. According to Feng *et al* (2010), Si nutrition stimulated the activities of antioxidant defense system and decreased the inhibiting effects of Cd.

PERSPECTIVES

The fact that Si plays an important role in mineral nutrition of many plant species is neither in doubt nor its ability to efficiently mitigate biotic and abiotic stresses in a wide variety of crops. Although, Si is not considered as an essential element because there is no evidence that Si is involved in the metabolism of plants. However, it may be expected that the essentiality for Si will be finally recognized in higher plants according new definition of essentiality as purposed by Epstein and Bloom (2005).

The most important role of Si lies in its potential to confer tolerance in plants to multiple stresses rather than its general acceptance of essentiality. Another important aspect for further studies on Si in plant biology should be focused not only to characterize its uptake and transport in plants but also demonstrate its role in metabolic and physiological activities of plants, especially in stress environment. Plant species and varieties may differ in their Si content and respond differently to Si application. One approach to enhance the resistance of plants to various biotic and abiotic stresses may be the genetic modification of root ability to take up Si. The strategic combination of a fine grade Si formulation with a Si accumulator plants also would reduce application rate, thereby minimizing the cost of Si amendment program.

As researchers and growers become aware of Si and its potential in agriculture, it is likely that this often overlooked element will be recognized as a viable means of sustainably managing abiotic stress effects in plants worldwide.

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