Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: A review

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*This review article overviews roles Si plays in alleviating abiotic stress in
higher plants and discusses future research directions.*

Abstract

Although silicon (Si) is the second most abundant element both on the surface of the Earth's crust and in soils, it has not yet been listed among the essential elements for higher plants. However, the beneficial role of Si in stimulating the growth and development of many plant species has been generally recognized. Silicon is known to effectively mitigate various abiotic stresses such as manganese, aluminum and heavy metal toxicities, and salinity, drought, chilling and freezing stresses. However, mechanisms of Si-mediated alleviation of abiotic stresses remain poorly understood. The key mechanisms of Si-mediated alleviation of abiotic stresses in higher plants include: (1) stimulation of antioxidant systems in plants, (2) complexation or co-precipitation of toxic metal ions with Si, (3) immobilization of toxic metal ions in growth media, (4) uptake processes, and (5) compartmentation of metal ions within plants. Future research needs for Si-mediated alleviation of abiotic stresses are also discussed.

1. Introduction

Silicon (Si) is the second most abundant element both on the surface of the Earth's crust and in the soils. Silicon is present as silicic acid in the soil solution at concentrations normally ranging from 0.1 to 0.6 mM, roughly two orders of magnitude higher than the concentrations of phosphorus in soil solutions (Epstein, 1994, 1999).

Although Si has not been considered as an essential element for higher plants, it has been proved to be beneficial for the healthy growth and development of many plant species,

particularly graminaceous plants such as rice and sugarcane and some cyperaceous plants (Epstein, 1994, 1999; Liang, 1999; Ma et al., 2001a; Liang et al., 2005a). The beneficial effects of Si are particularly distinct in plants exposed to abiotic and biotic stresses (Epstein, 1994, 1999; Ma, 2004). However, Epstein and Bloom (2005) have recently modified the near-universally accepted definition of essentiality of elements established by Arnon and Stout (1939). Based on this newly-established definition, an element is essential that fulfils either one or both of the following criteria: (1) the element is part of a molecule which is an intrinsic component of the structure or metabolism of the plant, and (2) the plant can be so severely deficient in the element that it exhibits abnormalities in growth, development, or reproduction, i.e. 'performance', compared to plants with lower deficiency. Accordingly, Si

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will be an essential element for higher plants, which is to be generally accepted in the near future.

Over last two decades, more extensive and intensive studies have been performed aiming at better understanding of the possible mechanism(s) for Si-enhanced resistance and/or tolerance of higher plants to both abiotic and biotic stresses (Horst and Marschner, 1978; Horiguchi and Morita, 1987; Hodson and Evans, 1995; Liang, 1999; Epstein, 1999; Liang et al., 2003; 2005a,c; Gong et al., 2005; Guo et al., 2005). More recently, rapid progress has been made in Si uptake and transport in higher plants. In this paper we review current knowledge on the roles of Si in conferring tolerance to plants against abiotic stresses together with Si uptake mechanisms, and then discuss recommended future research directions.

2. Silicon uptake mechanisms

Silicon concentrations vary greatly in plant aboveground parts, ranging from 0.1 to 10.0% of dry weight. This wide variation in Si concentration in plant tissues is attributed mainly to differences in the characteristics of Si uptake and transport (Jones and Handreck, 1967; Jarvis, 1987; Epstein, 1994). In general, graminaceous plants take up much more Si than other species, while most dicotyledonous plants absorb Si passively and some dicots such as legumes exclude Si from uptake (Ma et al., 2001a; Liang et al., 2005b). Silicon uptake and transport in rice, a typical Si-accumulator, is an active process (Lewin and Reimann, 1969; Epstein, 1994; Ma et al., 2006), but some dicots such as cucumber, melon, strawberry and soybean (Takahashi et al., 1990; Ma et al., 2001a; Mitani and Ma, 2005) take up Si passively, and tomato (Takahashi et al., 1990; Mitani and Ma, 2005) and bean (Jones and Handreck, 1967; Liang et al., 2005b) exclude Si from uptake. Besides rice, other graminaceous plants such as wheat (Van der Vorm, 1980; Jarvis, 1987; Casey et al., 2003), ryegrass (Jarvis, 1987), and barley (Barber and Shone, 1966) and some cyperaceous plants take up Si actively, while certain other Gramineae such as oats take it up passively (Jones and Handreck, 1965). Rapid progress has recently been made in characterizing Si uptake and transport in rice by using rice mutants (Ma et al., 2002; Tamai and Ma, 2003). Ma and co-workers believe that lateral roots of rice play an important role in Si uptake while root hairs do not contribute to Si uptake (Ma et al., 2001b). Silicon uptake by rice is a specific transporter-mediated process and the transporter containing Cys residues but not Lys residues is not inducible and has a low affinity for Si ($K_m = 0.32$ mM) (Tamai and Ma, 2003). Furthermore, a gene responsible for xylem loading of Si has recently been mapped to chromosome 2 of rice using the Lsi1 mutant (formerly GR1 mutant) and is localized on the plasma membrane of the distal side of both exodermis and endodermis cells and constitutively expressed in the roots (Ma et al., 2006). The Si gene *Lsi1* is predicted to encode a membrane protein similar to water channel proteins (aquaporins) (Ma et al., 2006). In contrast to the rapid progress that has been made in characterizing Si uptake by rice, little information is available on Si uptake and transport in the other monocots and in dicots (Liang

et al., 2005b). More recently, Mitani and Ma (2005) have reported that the Si concentration was lower in the xylem sap of cucumber than in the external solution, suggesting that xylem loading of Si was mediated by a passive diffusion mechanism in cucumber. However, Liang and his colleagues have demonstrated that Si uptake and transport are also active processes in *Cucumis sativus* L. (Liang et al., 2005b). Such distinct discrepancy in Si uptake and xylem loading in *Cucumis sativus* might be caused by the different methods used for collecting xylem sap and the pre-culture of the plants, and/or by different cultivars studied. It appears that further investigation is needed to characterize Si uptake and transport in *Cucumis sativus*. More recently, it has been reported that both active and passive mechanisms are operating in Si uptake and transport in the same Si-accumulator such as rice and maize and intermediate type species such as sunflower and wax gourd with their contribution being dependent upon plant species and external Si concentrations (Liang et al., in press).

3. Mechanisms for silicon-mediated alleviation of metal toxicity

Silicon-mediated alleviation of (heavy) metal toxicity in higher plants is widely accepted. In 1957 Williams and Vlamis (1957a,b) discovered that Mn toxicity in barley in solution culture was alleviated by addition of a small amount of Si. Recently the role of silicon in mitigating Mn toxicity has been investigated extensively in barley (Horiguchi and Morita, 1987), rice (Okuda and Takahashi, 1962), bean (Horst and Marschner, 1978), pumpkin (Iwasaki and Matsumura, 1999), cowpea (Iwasaki et al., 2002a,b) and cucumber (Rogalla and Römheld, 2002; Shi et al., 2005b).

Williams and Vlamis (1957a,b) discovered for the first time that total Mn in the leaves was unaffected by Si but Si caused Mn to be more evenly distributed instead of being concentrated in discrete necrotic spots. This finding has been supported by subsequent experiments (Horst and Marschner, 1978; Horiguchi and Morita, 1987; Shi et al., 2005b). Horst et al. (1999) observed that Si lowered the apoplastic Mn concentration in cowpea, suggesting that Si may modify the cation binding capacity of the cell wall. Iwasaki et al. (2002a,b) found that the Mn concentration in the apoplastic washing fluids of plants with a continuous supply of 1.44 mM Si and 50 μM Mn and not showing Mn toxicity symptoms was higher than that of plants grown at 10 μM Mn without Si supply which showed distinct Mn toxicity symptoms, suggesting that Si supply alleviates 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 apoplast in the detoxicification of apoplastic Mn is indicated. Further research indicated that the severity of Mn toxicity symptoms and guaiacol-peroxidase (POD) activity in the apoplastic washing fluid (AWF) of these plants were not significantly correlated with the Mn concentrations in AWF, but were highly significantly correlated with the Si concentrations in AWF (Iwasaki et al., 2002b). These results suggest that Si may affect the oxidation process of excess Mn

mediated by POD through interaction with phenolic substances in the solution phase of the apoplast, maintaining the apoplast in a reduced state, which is thought to be a requirement for improved Mn tolerance of the leaf tissue. Almost at the same time, Rogalla and Römheld (2002) conducted similar experiments with cucumber. Their findings clearly showed that plants not treated with Si had higher Mn concentrations in the intercellular washing fluid (IWF) compared with plants treated with Si, especially in the BaCl$_2$- and DTPA-exchangeable fractions of the leaf apoplast despite approximately the same total Mn content in the leaves. The Mn concentration of the IWF was positively correlated with the severity of Mn-toxicity symptoms and negatively correlated with the Si supply (Rogalla and Römheld, 2002). Furthermore, in Si-treated plants less Mn was located in the symplast (<10%) and more Mn was bound to the cell wall (>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 (Rogalla and Römheld, 2002). These authors also drew the conclusion that Si-mediated tolerance of Mn in *C. sativus* is a consequence of stronger binding of Mn to cell walls and a lowering of the Mn concentration within the symplast.

More recently, it has been reported that the alleviation of Mn toxicity by Si in cucumber was attributed to a significant reduction in membrane lipid peroxidation caused by excess Mn and to a significant increase in enzymatic (e.g. SOD, APX, DHAR and GR) and non-enzymatic antioxidants (e.g. ascorbate and glutathione) (Shi et al., 2005b).

The discovery that Si alleviated Mn phytotoxicity in turn led to the finding that this role of Si can also be applied to other metal ions, particularly Al (Epstein, 1999). The alleviative effect on Al toxicity by Si and its possible mechanisms have been examined most extensively. Interactions of Al and Si have been studied in at least eight plant species but contradictory findings have been reported (Hodson and Evans, 1995). Half of the eight species investigated (sorghum [*Sorghum bicolor* L.], barley [*Hordeum vulgare* L.], teosinte [*Zea mays* L. ssp. Mexicana], and soybean [*Glycine max* (L.) Merr.]) showed significant alleviative effects of Si on Al toxicity and the others were demonstrated to exhibit little or no such effect (rice [*Oryza sativa* L.], wheat [*Triticum aestivum* L.], cotton [*Gossypium hirsutum*] and pea [*Pisum sativum* L.]). Applying Si has thus been suggested as an alternative approach to detoxifying Al toxicity in tomato (*Lycopersicum esculentum* L.) (Peaslee and Frink, 1969), sorghum (*Sorghum bicolor* L.) (Galvez et al., 1987; Galvez and Clark, 1991; Baylis et al., 1994), and barley (*Hordeum vugare* L.) (Hammond et al., 1995; Liang et al., 2001).

In an experiment with barley, Hammond et al. (1995) reported that Si exhibited significant ameliorative effects on Al toxicity and the amelioration was most marked where the toxic effects of Al were the greatest. As much as 80% amelioration of the decrease in root length was achieved using 2.8 mM Si and 50 μM Al, and the addition of Si reduced Al uptake into the roots (Hammond et al., 1995). Baylis et al.

(1994) found that Si ameliorated the effects of Al toxicity in soybean, but that this was dependent on pH. It has been established that interaction between Si and Al, reducing the activity of toxic metal ions in the medium, is one possible external mechanism for the detoxification of Al toxicity by Si (Hiradate et al., 1998). Such external effects are also supported by the finding that Si diminished the toxicity of Al to soybean (Baylis et al., 1994). The precipitation of subcolloidal, inert hydroxyaluminosilicate species seems to be responsible for the diminished concentration (activity) of phytotoxic Al in solution. In experiments with *Zea mays* in which Si afforded protection against the inhibition of root elongation by Al, Ma et al. (1997) also concluded that the formation of Al-Si complexes was responsible.

The co-deposition of Si with Al seems to occur not only in the growth media but also within plants (Birchall, 1990; Liang et al., 2001). It has been reported that added Si increased the shoot Al concentration, which may arise from the formation of hydroxyaluminosilicate complexes in shoots leading to enhanced Al transport from roots to shoots (Birchall, 1990). In a solution culture experiment in which a very small change in the concentration of Al and Si in solution was observed, Liang et al. (2001) believed that the co-deposition of Al and Si in solution was negligible because silicic acid rather than alkaline Na$_2$SiO$_3$ was used. However, co-deposition of Al and Si in the growth media using alkaline Na$_2$SiO$_3$ as Si source and within the plant is likely, which may be the mechanism for amelioration of Al toxicity by Si in plants grown with toxic levels of Al (Liang et al., 2001). Cocker et al. (1998a) have 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. In experiments with teosinte, Barceló et al. (1993) found that plants exposed to toxic Al concentrations (60 μM or 120 μM) were less inhibited in their growth when as little as 4 μM Si was added to the culture solution. The mechanism for this alleviative effect was attributed mainly to the inhibitory effect of Al uptake by the plants. It is notable that significantly higher concentrations of malic and formic acids were observed in the plants grown in the presence of added Si and Al. The same group, working with an Al-sensitive variety of corn, *Zea mays* var. BR 201 F, found that Si pretreatment was effective in counteracting the inhibition of root elongation by Al and diminished the absorption of Al by the plants (Corrales et al., 1997), suggesting a purely internal interaction between the two elements. In wheat, the mitigation of Al toxicity was also shown to be attributable to internal mechanisms or related to the physiological processes in plants (Cocker et al., 1998b). Silicon may have additional roles in increasing tolerance of aluminum by mediating the metabolism of phenolic compounds as it has been reported that silicon-treated maize plants release fifteen times more phenolics than untreated maize plants (Kidd et al., 2001). These flavonoid-phenolics (i.e. catechin and quercetin) have a strong Al-chelating ability and may provide metal tolerance in plants.

It is generally recognized that an external mechanism similar to Si-alleviated toxicity to Al applies to Si-mediated

detoxification of Cd in soil/plant systems, i.e. reduction in Cd availability via Cd immobilization arising from a rise in pH. This is true when sodium metasilicate, slag or alkaline Si-containing materials such as biosolids are incorporated into Cd-contaminated soils as Si sources (Chen et al., 2000; Liang et al., 2005a). Chen et al. (2000) reported that furnace slag was more effective in suppressing Cd uptake by rice and wheat than calcium carbonate or steel sludge. They speculated that the higher pH and increasing available Si arising from the furnace slag contributed to the reduced Cd uptake by plants (Chen et al., 2000). The role of Si in minimizing uptake and root-to-shoot transport of metal ions has recently been confirmed in seedlings of rice grown with toxic Cd (Shi et al., 2005a) and with arsenate (Guo et al., 2005). Si also significantly reduced the transport of the apoplastic fluorescence tracer PTS (trisodium-8-hydroxy-1,3,6-pyrenesulphonate) from roots to shoots (Shi et al., 2005a), suggested that the heavy deposition of silica in the vicinity of the endodermis might offer a possible mechanism by which silicon did at least partially physically block the apoplast bypass flow across the roots, and restrained the apoplastic transport of Cd.

In pot experiments with maize, Liang et al. (2005a) showed that Cd treatment significantly decreased shoot and root dry weights, while addition of Si significantly and greatly enhanced biomass. Silicon added at a high dosage (i.e. 400 mg kg^{-1} Si) significantly increased soil pH but decreased soil Cd availability, thereby reducing Cd concentrations in the shoots and roots and total Cd in the shoots. Moreover, more Cd was found to be in the form of specific adsorbed or Fe–Mn oxides-bound fraction in the Si-amended soil. These results suggest an external interaction between Si and Cd. By contrast, soil pH and available Cd were unaffected by addition of Si at a low dosage (i.e. 50 mg kg^{-1} Si), but shoot Cd concentration in the Si-amended Cd treatments was significantly decreased compared with the non-Si-amended Cd treatments, suggesting an internal mechanism for detoxification of Cd by Si occurring within plants (Liang et al., 2005a). The xylem exudates were significantly increased but the Cd concentration in the xylem exudates was significantly decreased in the Si-amended Cd treatments compared with the non-Si-amended Cd treatments irrespective of the Cd and Si levels used. The results suggest that Si-enhanced Cd tolerance can be attributed not only to Cd immobilization caused by silicate-enhanced pH in the soils but also to Si-mediated detoxification of Cd in the plants (Liang et al., 2005a). In a solution culture experiment with maize, Liang et al. found that more Cd was bound to the root cell walls but less to cytosols or symplast in +Si plants than in −Si plants under Cd stress (unpublished data), suggesting a root apoplastic role of Si in detoxification of excess Cd, a mechanism similar to that responsible for the Si-mediated Mn tolerance in plants (Iwasaki et al., 2002a,b; Rogalla and Römheld, 2002). However, contrasting results have recently been reported by Shi et al. (2005a), who have shown that most of the total root Cd (87%) was localized in the symplasm, whereas the apoplast Cd accounted for only 13% of the total in both −Si and +Si treatments. Furthermore, X-ray microanalysis (EDX) showed that Cd was deposited mainly in the vicinity of the endodermis

and epidermis, and Si deposition was heavier in the vicinity of the endodermis than of the epidermis (Shi et al., 2005a). The results from EDX, however, cannot explain the mechanisms underlying the Si-enhanced cadmium tolerance in rice seedlings because such low Cd concentrations (7.85 μmol Cd g^{-1} dry weight) in the roots were far below the detection limit of EDX (thousands of micrograms per gram) and could not thus have been detected by EDX (refer to Tables 1–4 and Fig. 3 of Shi et al., 2005a). We failed to detect Cd in maize roots containing Cd as high as 420 mg Cd kg^{-1} using EDX (unpublished data) in a pot experiment showing Si-mediated alleviation of Cd toxicity in maize (Liang et al., 2005a). Evidently, further in-depth studies are needed to re-examine the micro-distribution of Cd in plants as influenced by Si using more sensitive methods such as synchrotron radiation X-ray fluorescence analysis (SRXFA). Using electron-energy-loss spectroscopy (EELS) and other techniques such as electron spectroscopic image (ESI) and EDX, Neumann and zur Nieden (2001) have reported the occurrence of co-deposition of silicon and zinc in heavy metal tolerant Cardaminopsis halleri. The formation of Zn-silicate is part of the mechanism for tolerance to heavy metals and may be responsible for the amelioration of zinc toxicity in Cardaminopsis halleri.

Taken together, Si-mediated tolerance to metal (including Al and heavy metals) toxicity in plants can be summarized in Fig. 1, in which external and internal mechanisms are proposed to explain the alleviative effect of Si on metal toxicity.

4. Mechanisms for silicon-enhanced tolerance to salinity toxicity

Silicon has been shown to be effective in mitigating salinity in recent investigations. The mitigative effect of Si on salinity has been examined in rice (Matoh et al., 1986; Yeo et al., 1999), mesquite (Bradbury and Ahmad, 1990), wheat (Ahmad et al., 1992), barley (Liang et al., 1996, 2003, 2005c; Liang, 1998, 1999; Liang and Ding, 2002), cucumber (Zhu et al., 2004) and tomato (Al-Aghabary et al., 2004). Matoh et al. (1986) reported that shoot and root growth was severely inhibited in rice grown at 100 mM NaCl but was significantly ameliorated by addition of Si at 0.89 mM. Ahmad et al.
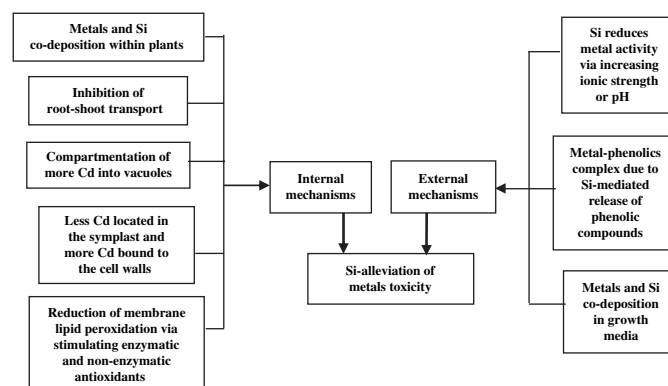

Fig. 1. Schematic hypotheses for Si-mediated tolerance to metal toxicity.

(1992) and Bradbury and Ahmad (1990) reported that salt tolerance of wheat (*Triticum aestivum*) and mesquite (*Prosopis juliflora*) could be markedly enhanced by the addition of small amounts of soluble silicon. Liang et al. (1996) demonstrated that added silicon increased salinity tolerance of barley grown hydroponically. The Na concentration in the shoots of rice (Matoh et al., 1986; Yeo et al., 1999) and barley (Liang et al., 1996; Liang, 1999) was decreased by addition of Si. This was attributed to Si-induced reduction in transpiration rate (Matoh et al., 1986) and to the partial blockage of the transpirational bypass flow (Yeo et al., 1999). The increased uptake and transport of K^+ and decreased uptake and transport of Na^+ from roots to shoots in barley was thought to be attributable to Si-induced stimulation of the root plasma membrane H^+-ATPase under salt stress (Liang et al., 1999, 2005c, 2006; Liang and Ding, 2002). Added Si decreased the permeability of the plasma membrane of leaf cells (Liang et al., 1996; Liang, 1999), and significantly improved the ultra-structure of chloroplasts which were badly damaged by the added NaCl with the double membranes disappearing and the grannae being disintegrated in the absence of Si (Liang, 1998). Silicon also increased leaf and root superoxide dismutase (SOD), peroxidase (POD), catalase (CAT) and glutathione reductase (GR) activities and the glutathione (GSH) concentration but suppressed the malondialdehyde (MDA) concentration in barley under salt stress and stimulated root H^+-ATPase and H^+-PPase activity in the plasma membranes and tonoplasts and mediated membrane fluidity, suggesting that Si may affect the structure, integrity and functions of plasma membranes by influencing the stress-dependent peroxidation of membrane lipids (Liang et al., 1996, 2003, 2005c, 2006; Liang, 1999). This hypothesis (Liang, 1999; Liang et al., 2003) that Si decreased lipid peroxidation in salt-stressed plants via enhancing antioxidant enzyme activity and non-enzymatic antioxidants has recently been corroborated in experiments with cucumber (Zhu et al., 2004) and tomato (Al-Aghabary et al., 2004).

Based on the knowledge of Si and salinity interactions in plants, the possible mechanisms underlying Si-enhanced salinity tolerance are illustrated in Fig. 2.

5. Perspectives

It may be expected that the essentiality for silicon will be finally recognized in higher plants according to the newly established definition of essentiality proposed by Epstein and Bloom (2005). The most important role of this element does not lie in its general acceptance of essentiality, but rather in its most striking and unique function or role in conferring tolerance in plants to various abiotic and/or biotic stresses. Again, the most important aspect for further studies on Si in plant biology should be focused not only on accumulating some direct lines of evidence to demonstrate that Si is part of plant constituents or metabolites but also on making full use of the role of Si in conferring tolerance in plants against abiotic stresses, and thus its role in environmental remediation. The former is vital to understanding the roles of Si in plant biology, while the latter is highly conducive to developing
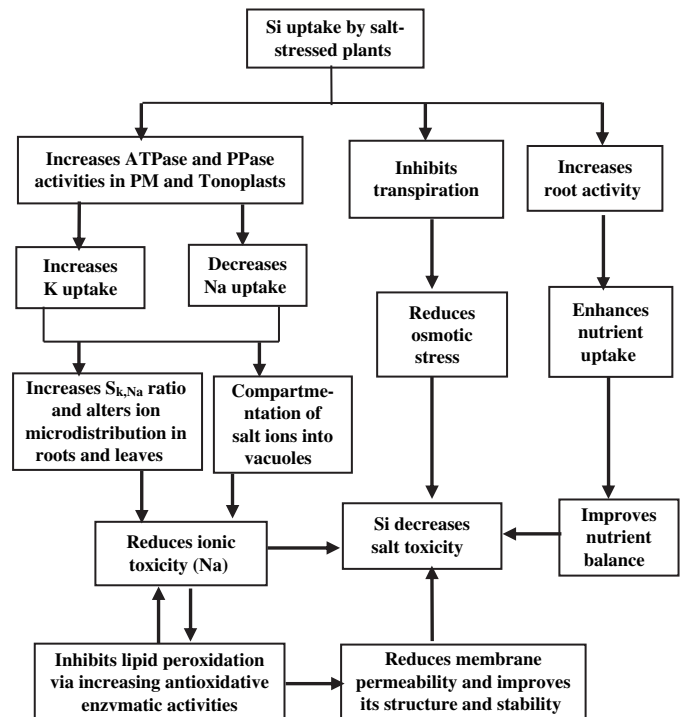
Fig. 2. Possible mechanisms for Si-mediated tolerance to salinity toxicity.

high yields and quality, and cost-effective and environmentally benign agriculture. The last but not the least will be the mechanism for Si uptake and xylem loading in higher plants, which is also the basis for better insight into the role Si plays in plant physiology (stress physiology in particular) and biochemistry. More recently, rapid progress has been made in cloning and characterization of the gene encoding Si-transporter in rice, a typical Si-accumulating plant (Ma et al., 2002, 2006; Tamai and Ma, 2003; Ma, 2004). However, no in-depth investigations have been performed on characterizing Si uptake and transport in root systems of Si-accumulating plants other than cucumber, in which Si uptake and transport has recently been reported to be an active process (Liang et al., 2005b).

Based on current knowledge, it can be concluded that Si is not inert, but acts as a physical or mechanical barrier in plants. It is not only deposited in the cell walls, but is also actively involved in the metabolic and/or physiological activities, especially in plants subject to multiple stresses.

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