REVIEW ARTICLE

Beneficial effects of silicon on salt and drought tolerance in plants

Yongxing Zhu · Haijun Gong

Abstract Soil salinity and drought are major abiotic factors that limit crop growth and productivity worldwide. Indeed, soil salinity and drought disrupt the cellular ionic and osmotic balance. Although silicon (Si) is generally considered nonessential for plant growth and developments, Si uptake by plants can alleviate both biotic and abiotic stresses. Silicon application could therefore improve crop production under adverse climate and soil conditions. Several reports have reviewed the benefits of silicon application on crop growth, but the mechanisms of silicon action have not been systematically discussed. Here, we review recent advances on silicon uptake, transport, and accumulation in plants and how silicon alleviates salinity toxicity and drought stress. The major points are the following: (1) both passive and active silicon uptake may coexist in plants; (2) although silicon transporters have been identified in some plants, more silicon transporters remain to be identified, and the process of silicon transport needs further clarification; (3) the mechanisms for silicon-mediated tolerance of salinity and drought have been extensively investigated at both physiological and biochemical levels. The physiological aspects include increasing water uptake by roots, maintaining nutrient balance, decreasing water loss from leaves, and promoting photosynthetic rate. At the biochemical level, silicon may improve antioxidant defense abilities by increasing the activities of antioxidant enzymes and the contents of non enzymatic antioxidants; silicon may also contribute to osmotic adjustment and increase photosynthetic enzymatic activities; and (4) silicon can regulate the levels of endogenous plant hormones under stress conditions, whereas silicon involvement in signaling and regulation of gene expression related to increasing stress tolerance remains to be explored.

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Keywords Environmental stress · Salinity · Drought · Silicon · Plant · Tolerance

Contents

1 Introduction

Soil salinity and drought are two of the major abiotic factors that limit crop growth and productivity worldwide. Approximately 7 % of the land on earth and 20 % of the total arable area are adversely affected by salinity (Fig. 1; Rasool et al. 2013). Man-made soil salinization is increasing owing to irrigation with salty water or ignoring the principles of soil drainage (Pisinaras et al. 2010). Such practices should be curtailed prior to spending any time, effort, and money restoring contaminated soil. High salinity causes ion imbalance and

hyperosmotic stress in plants and can result in plant death. Drought is another major limitation in crop production, especially in arid and semiarid regions (Fig. 1; Eneji et al. 2008). It is predicted that climate change may cause more severe and frequent droughts in the near future (Ye et al. 2012; Heffernan 2013). To maintain food supplies, it is thus urgent to increase the salt and drought tolerance of crops.

Silicon (Si) is the second most prevalent element after oxygen in the soil. However, pure silicon crystals are very rarely found in nature with silicon usually being found in the form of complex silicate minerals. It is such a ubiquitous element that it is difficult to verify its essentiality in higher plants (Epstein 1994) based on the criteria of essentiality of elements established by Arnon and Stout (1939). According to a more recent definition of the essentiality of elements proposed by Epstein and Bloom (2005), silicon should be considered an essential element for higher plants because silicon-deprived plants tend to grow abnormally, whereas silicon-supplemented plants grow normally (Agarie et al. 1992). Moreover, when present in excess, silicon is not detrimental to plants (Epstein 1994; Ma et al. 2001).

Regardless of its essentiality in higher plants, silicon has been reported to be beneficial in mitigating both biotic stresses (e.g., plant diseases and pest damage) and abiotic stresses such as salinity, drought, aluminum toxicity, heavy metal toxicity, nutrient imbalance, lodging, radiation, high temperature, wounding, and freezing (Richmond and Sussman 2003; Ma and Yamaji 2006; Liang et al. 2007; Kim et al. 2011; Van Bockhaven et al. 2013). In this regard, it has been suggested that silicate fertilizer could be a good soil amendment not only to sustain rice (*Oryza sativa* L.) production but also to decrease methane (a greenhouse gas) emission during rice cultivation. Because such emissions may contribute to climate/environmental change such as drought and flood (Ali 2013), application of silicate fertilizer may in fact help alleviate drought stress caused by global environmental changes (Ali et al. 2008).

Studies have shown that silicon application may increase tolerance to salinity and drought in plants (Liang et al. 2007; Bauer et al. 2011). Hence, application of silicon may be a facile means to increase crop yield during drought or in salty soils. Moreover, because silicon can improve drought tolerance of plants, its application may help reduce the need for irrigation, which in turn would reduce salinization of crop land. Moreover, silicon is noncorrosive and pollution-free, and therefore, silicon fertilizer is a high-quality fertilizer for developing ecologically green agriculture. Several researchers have reviewed recent advances on the beneficial roles of silicon on plant growth in adverse environmental conditions (Cooke and Leishman 2011; Guntzer et al. 2012; Van Bockhaven et al. 2013). For example, Guntzer et al. (2012) reviewed the mechanisms underlying the benefits of silicon supplementation for plants exposed to various biotic and

Fig. 1 Drought and salinity are two main constraints for agricultural production in northwest China. These photos were taken in Gansu, China. The *upper photo* depicts drought and desertification, and the *lower photo* depicts soil salinization

abiotic stresses. Van Bockhaven et al. (2013) summarized recent advances of silicon's roles in resisting plant diseases. To our knowledge, however, very few reviews have systematically discussed the roles and mechanisms of silicon in alleviating salinity and drought in plants. Here, we discuss recent advances regarding the mechanisms of silicon uptake, transport, and accumulation in plants. We then focus on the function of silicon in improving plant tolerance to salinity and drought stresses in detail.

2 Silicon uptake, transport, and accumulation in plants

The silicon content of soils can vary from <1 to 45 % dry weight (Sommer et al. 2006). Silicon can leach out, redistribute, or accumulate in soils during soil development (Sommer

et al. 2006). Although silicon is abundant in soil, most of it cannot be absorbed directly by plants. Plant root generally take up silicon in the form of soluble silicic acid [$Si(OH)_4$] (Mitani et al. 2005), an undissociated molecule that is normally present at 0.1–0.6 mM in the soil solution at most naturally occurring pHs (pH 1–9) (Takahashi and Hino 1978; Ma et al. 2006). Factors such as soil pH, temperature, water conditions, presence of cations, and organic compounds in solution influence the formation of soluble silicic acid and thus affect silicon accumulation in plants (Liu et al. 2003). Savant et al. (1997) proposed that depletion of plant-available silicon in soil could be a possible cause of declining yields for rice. In China, silicon-deficient soil accounts for more than 40 % of the total agricultural land (Ma et al. 2009), and application of silicon fertilizers is necessary to increase yields. Different types of silicon fertilizers exist, the most common being wollastonite (calcium silicate), residue of blast furnaces, and straw (Guntzer et al. 2012). The application rate of silicon fertilizers may depend on the content of available silicon in the fertilizer and the silicon level in the soil. Ma and Takahashi (2002) observed persistent increases in rice yield at the investigated rate of 75–135 kg sodium silicate per hectare. Ma et al. (2009) recommended an application rate of blast furnace residue of 1.5–4.5 tons/ha. According to statistics, in China, the demand for silicon fertilizer per year is 30–40 million tons, whereas the capacity of silicon production is only about 1 million tons (Zhou et al. 2006), illustrating the great challenge in addressing the soil silicon deficiency problem. From an economic viewpoint, silicon fertilizer is also cost effective, being 10–20 % of the cost of other fertilizers (Feng 2000). Therefore, it is necessary to apply silicon fertilizer in silicon-deficient areas to reap both economic and ecological benefits.

All plants grown in soil contain silicon in their tissues (Epstein 1994; Ma and Yamaji 2008), and silicon content in plants varies greatly among species and genotypes (Ma and Yamaji 2008). The process of silicon uptake and transport in plants can be classified as active, passive, or rejective. Accordingly, plants can be classified as high-, intermediate-, or nonsilicon accumulators (Henriet et al. 2006). Some species such as rice and barley (*Hordeum vulgare* L.) can take up silicon actively, whereas tomato (*Lycopersicon esculentum* Mill.) limits silicon transport from the root to the shoot (Nikolic et al. 2007). In cucumber (*Cucumis sativus* L.), Mitani and Ma (2005) and Liang et al. (2005a) obtained different results. Mitani and Ma suggested that different xylem loading of silicon in cucumber is mediated by passive diffusion, whereas Liang et al. reported that silicon uptake and transport are active processes in cucumber. In a later study, Liang et al. (2006a) investigated silicon uptake in rice, maize (*Zea mays* L.), sunflower (*Helianthus annuus* L.), and wax gourd (*Benincase hispida* L.), finding that both active and passive silicon-uptake components coexist in these species, with their contribution being dependent on species and silicon

concentrations in culture solution. Therefore, the difference in silicon uptake and xylem loading in cucumber may due to the difference in relative contribution of active and passive silicon-uptake among cultivars or differences in methods used to collect xylem sap and preculture of plants (Liang et al. 2007).

As mentioned above, it is commonly accepted that silicon is absorbed by plant roots in the form of soluble silicic acid. After being absorbed, silicic acid is then transported to the shoot via xylem (Ma and Yamaji 2008). Silicic acid finally polymerizes and precipitates at high concentration owing to water loss, forming "opal phytoliths" (also called "plant stones" or "plant opals" or "opaline silica") in the cell wall, intercellular space, and trichomes (Ma et al. 2006; Mazumdar 2011; Cooke and Leishman 2011). However, little information is available about the mechanisms that prevent silicic acid from polymerizing and precipitating in xylem. Still, some researchers believe that, in addition to silicic acid, SiO_2 in soil can be absorbed directly by plants. For example, Fu et al. (2002) reported that, in the cortex of a species of fern (*Matteuccia*), silica particles can be absorbed directly and selectively from soil; the soluble elements then leach from these silicate mineral particles and are carried to shoots as nutrients, leaving residual silica particles in the cortex.

Both passive and active silicon uptake may coexist in plants (Liang et al. 2006a; Henriet et al. 2006). Guntzer et al. (2012) suggested that silicon concentration in a given plant organ reflects of its transpiration rate. Raven (2001) found that the highest silicon concentrations in plants are in the major transpiration sites. The role of transpiration in silicon transport and deposition was further confirmed through silicon isotope studies, as Ding et al. (2005) observed that the $\delta^{30}Si$ values showed an increasing trend from rice roots, stems, and leaves, through husks, to grains. Active silicon uptake by root cells is mediated by transporters located in the plasma membrane (Ma et al. 2006, 2007).

Recent studies have shown that an efficient silicon uptake system mediated by both influx (Lsi1) and efflux (Lsi2) transporters accounts for silicon accumulation in monocots including rice (Ma et al. 2006, 2007), maize (Mitani et al. 2009a, b), barley (Chiba et al. 2009; Yamaji et al. 2012), and wheat (*Triticum aestivum* L.) (Montpetit et al. 2012) and in the dicot pumpkin (*Cucurbita moschata* Duch.) (Mitani et al. 2011). *Lsi1* encodes an aquaporin-like protein that functions as an influx transporter to transport silicon from the external solution to the exodermal cells and then to the endodermal cells (Ma et al. 2006; Ma 2010). Lsi2 is a plasma membrane-localized transporter that functions as an efflux transporter to release silicon from exodermal cells to the apoplast and then to the stele (Ma et al. 2007). The locations of these two types of transporters vary among species. For example, the efflux transporter Lis2 shows polar localization at the proximal side in rice, but it does not show polar localization in maize or barley (Mitani et al. 2009a; Ma 2010). The locations of Lsi1 and

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Lsi2 also differ between rice and pumpkin. In rice, Lsi1 and Lsi2 distribute on different parts of the same cell, namely, distal and proximal side of the root exodermis or endodermis. In pumpkin, Lsi1 is located in all root cells, and an alteration of a single amino acid (proline to leucine) at position 242 leads to the loss of silicon transport activity and a change in subcellular localization (Mitani et al. 2011). Rice plants lacking Lsi1 or Lsi2 transporter have significantly decreased silicon uptake (Ma et al. 2006, 2007). Thus, variations in plant silicon content among species and genotypes may be due to differences in expression levels of silicon transporter genes (Isa et al. 2010).

Silicon seems to mainly distribute in the outer layer and higher positions within a plant. Using X-ray analytical microscopy, silicon signals can be detected specially on the leaf sheath and midrib of leaf areas in rice, indicating that silicon deposition has the potential to maintain plant rigidity (Isa et al. 2010). This phenomenon also suggests that, in addition to transpiration, plants may have a special mechanism to regulate silicon distribution. Lsi6, a silicon transporter identified in rice, is a homolog of Lsi1 and permeable to silicic acid when expressed in *Xenopus laevis* oocytes (Yamaji et al. 2008). It mainly localizes in the adaxial side of xylem parenchyma cells in leaf sheaths and blades, and it is responsible for the release of silicic acid from the xylem and subsequently for the distribution of silicon (Yamaji et al. 2008; Ma 2010). Upon Lsi6 knockout in rice, silicon uptake by roots is not affected, but the pathway of silicon distribution between the panicles and flag leaf is selectively altered (Yamaji et al. 2008; Yamaji and Ma 2009), suggesting the involvement of Lsi6 in intervascular transfer. A similar transporter responsible for silicon unloading from xylem and distribution has also been identified recently in barley (Yamaji et al. 2012).

Although different types of silicon transporters for silicon uptake have been identified from several plant species, the transporter or channel protein responsible for silicon loading remains unknown. Moreover, the silicon transporters indentified so far are mostly from monocots. Therefore, more work is needed to compare and clarify the process of silicon absorption and transport (including silicon xylem loading) in different plant species/cultivars that exhibit different silicon accumulation (e.g., monocots versus dicots). More silicon transporters also need to be identified, especially from dicots. For example, potato (*Solanum tuberosum* L.) is an important grain crop in Northwest China, and drought is one of the serious limiting factors in potato production (Lin et al. 2010). However, the silicon transport and relevant transporters in this crop remain to be investigated.

3 Alleviative effects of silicon on salinity toxicity in plants

Salt stress is a major environmental limiting factor to plant growth and crop productivity (Hashemi et al. 2010). The consequent reduction in growth is a consequence of two factors: First, the relatively high osmotic potential of soil solution results in a water deficit within each plant, and second, the high concentration of certain ions (Na^+, Cl^-) causes ion toxicity and consequent secondary stresses such as nutritional deficiency and oxidative stress (Soylemezoglu et al. 2009; Yue et al. 2012). High salt concentration alters ion balance in plants. For example, the competition between Na^+ and K^+ uptake alters the K^+/Na^+ ratio. Under normal physiological conditions, the protoplasm maintains a high K^+/Na^+ ratio. However, the similarity of K^+ and Na^+ radii makes it difficult for plants to discriminate between them, so the normally high K^+/Na^+ ratio is altered upon the influx of Na^+ through K^+ pathways (Blumwald 2000).

Previous studies have shown that silicon application may increase salinity tolerance in some important crops, such as rice (Gong et al. 2006), barley (Liang 1999; Liang et al. 1996, 2003, 2005b), wheat (Ahmad et al. 1992; Tuna et al. 2008), sugarcane (*Saccharum officinarum* L.) (Ashraf et al. 2010a, b), soybean (*Glycine max* L.) (Lee et al. 2010), tomato (Al-aghabary et al. 2004; Romero-Aranda et al. 2006), and zucchini (*Cucurbita pepo* L.) (Savvas et al. 2009). Progress has been made on the mechanism for silicon-mediated alleviation of salt stress as summarized below.

3.1 Silicon reduces ion toxicity under salt stress

Increased salt concentration treatment usually results in an increase in Na^+ and Cl^- accumulation and a decrease in certain other cations like K^+ and Ca^{2+} (Guerrier 1996; Khan et al. 2000; Wang and Han 2007). High levels of Na^+ are injurious to plant cells, e.g., to cellular metabolism, and leads to reduced plant growth and overproduction of reactive oxygen species (Mahajan and Tuteja 2005). Under salt stress, plants must expend additional cellular resources to maintain a high concentration of cytosolic K^+ and low concentration of Na^+.

Application of silicon can decrease Na^+ accumulation in the roots and/or shoots. In salt-stressed barley roots, application of silicon decreases both Na^+ and Cl^- levels but increases K^+, with Na^+ and K^+ being more evenly distributed over the whole root section; this was proposed to be the key mechanism of silicon-enhanced salt tolerance in this species (Liang and Ding 2002). Similarly, compared with the NaCl treatment alone, exogenous silicon decreases Na^+ content in alfalfa (*Medicago sativa* L.) roots but not shoots; applying silicon to alfalfa notably increases K^+ content in the shoots (Wang and Han 2007). In rice, Gong et al. (2006) found that silicon dramatically reduces the Na^+ concentration in shoots but not roots of salt-stressed plants, which correlates with improved shoot growth in the presence of silicon. Gunes et al. (2007a) reported that silicon decreased the translocations of Na^+, Cl^-, and boron from roots to shoots of tomato plants grown in sodic-B toxic soil. In barley grown in sodic-B toxic soil, addition of silicon decreases the

concentrations of Na^+ and boron in shoots (Gunes et al. 2007b). Shahzad et al. (2013) demonstrated that high salinity causes the Na^+ concentration to increase in the leaf apoplast of the dicot field bean (*Vicia faba* L.) and that this is significantly ameliorated by addition of silicon. Tuna et al. (2008) found that, in salinized wheat, silicon addition decreases the Na^+ contents in both shoots and roots. In the two sugarcane genotypes tested by Ashraf et al. (2010a), silicon application significantly decreases Na^+ but increases K^+ concentration in shoots. Yin et al. (2013) reported that short-term application of silicon decreases leaf Na^+ concentration in the seedling of sorghum (*Sorghum bicolor* L.) but does not increase K^+ content, which is in agreement with observations in salt stressed rice (Gong et al. 2006). These studies indicate that silicon may mitigate the adverse effects of salinity by preventing root Na^+ uptake and/or its transport from roots to shoots.

The Na^+/H^+ antiporter plays an important role in maintaining a low Na^+ concentration by removing Na^+ from the cytosol or compartmentalizing it in vacuoles (Yue et al. 2012). The gene *SOS1*, which encodes a plasma membrane Na^+/H^+ antiporter, has been cloned from *Arabidopsis* (Shi et al. 2000). The plasma membrane H^+-ATPases use the energy of ATP hydrolysis to pump H^+ out of the cell, thereby generating an electrochemical H^+ gradient that is the main force for the operation of Na^+/H^+ antiporter. The tonoplast Na^+/H^+ antiporter is involved in Na^+ compartmentation, and it is driven by a H^+-ATPase and H^+-pyrophosphatase (H^+-PPase) in the tonoplast (Blumwald 2000; Shi et al. 2000; Zhu 2001). Liang (1999) observed decreased activities of plasma membrane H^+-ATPase in barley roots under salt stress, but the activities were increased significantly when silicon was added to plants. The increase in activities of plasma membrane H^+-ATPases may facilitate Na^+ export from the cell. Na^+ compartmentation is an important mechanism for plants to prevent Na^+ toxicity because Na^+ can be used as an osmoticum to help maintain osmotic homeostasis (Blumwald 2000; Zhu 2001). Liang et al. (2005b) reported that the activities of barley root tonoplast H^+-ATPase and H^+-PPase were also considerably stimulated by addition of silicon under salt stress, which may facilitate Na^+ compartmentation in vacuoles through the tonoplast Na^+/H^+ antiporter. According to Mali and Aery (2008), silicon improves K^+ uptake by increasing H^+-ATPase activity in both hydroponics and soil. Therefore, under saline conditions, silicon may decrease Na^+ level and increase K^+ level in the cytoplasm by stimulating H^+-ATPase activities on the plasma membrane and tonoplast and H^+-PPase activities on the tonoplast. However, whether silicon directly regulates the transport activity or expression of the Na^+/H^+ antiporter under salt stress remains unclear.

The silicon-induced physical barrier in roots is another mechanism by which silicon mediates salt tolerance in plants. Gong et al. (2006) observed that silicon is deposited on the exodermis and endodermis of rice roots, which dramatically decreases apoplastic transport (the so-called transpirational bypass flow) and therefore Na^+ accumulation. Similarly, silicon addition also decreases the Cl^- level in shoots (Shi et al. 2013). Faiyue et al. (2010) suggested that the lateral root may play a role in bypass flow because it lacks an exodermis, whereas silicon can enhance exodermal development in rice (Fleck et al. 2011). Therefore, in rice, both silicon-enhanced exodermal development and silicon deposition on the exodermis contribute to decreased loading of salt ions into the xylem of roots, resulting in decreased salt ion accumulation in shoots. Although silicon-induced reduction in transpirational bypass flow (and therefore Na^+ transport) contributes to salt tolerance in rice, this mechanism may not work in other plants such as grapevine (Gong et al. 2011).

Silicon-mediated salt tolerance in plants is not always accompanied by a decrease in tissue Na^+ or Cl^- levels (Table 1). In tomato, inclusion of silicon reportedly has no significant effect on Na^+ and Cl^- concentrations in leaves but improves water storage in plants (Romero-Aranda et al. 2006). This higher water content contributes to salt dilution, thereby reducing salt toxicity and improving plant growth (Romero-Aranda et al. 2006). Similarly, Tuna et al. (2008) found that silicon improves relative water content in salt-stressed wheat, whereas it has no such effect in unstressed plants. The hydrophilic nature of silicon may, to some extent, contribute to water restoration in salt-stressed plants (Romero-Aranda et al. 2006). Silicon may also improve cell-wall Na^+ bounding and thereby decrease potential Na^+ toxicity (Saqib et al. 2008). Additional experiments are needed to investigate whether and how exogenous silicon is involved in regulating water movement in whole plants under salt stress conditions.

It was thus concluded that silicon reduces ion toxicity in plants under salt stress by decreasing toxic ion accumulation and/or improving plant water status.

3.2 Silicon decreases oxidative damage under salt stress

Plants under salt stress usually suffer a water deficit that leads to overproduction of reactive oxygen species (Liang 1999) such as superoxide anion, hydroxyl radical, hydrogen peroxide, and singlet oxygen, each of which can disrupt normal metabolism (Zushi et al. 2009) and cause damage to the plasma membrane and endomembrane systems (Liang 1999; Gill and Tuteja 2010). Plants have complex antioxidant defense systems—having enzymatic or non-enzymatic constituents—to scavenge these reactive oxygen species. Antioxidant enzymes include superoxide dismutase, catalase, guaiacol peroxidase, ascorbate peroxidases, dehydroascorbate reductase, and glutathione reductase among others. Superoxide dismutase is a major scavenger that converts superoxide to hydrogen peroxide. Hydrogen peroxide is also cytotoxic and

Table 1 Different effects of silicon on ion accumulation, antioxidant enzyme activity, transpiration, and phosphorus uptake observed in different plant species and growth media under salt or drought conditions

Treatment	Parameters		Observed effects of silicon under stress conditions	Growth medium	Plant species (reference)
Salt stress	Na^+/Cl^- accumulation		Decreases root Na^+ concentration	Solution culture	Alfalfa (Wang and Han 2007), barely (Liang and Ding 2002)
			Decreases shoot Na^+ and/or Cl^- concentrations	Potting soil	Barley (Gunes et al. 2007b), tomato (Gunes et al. 2007a), sugarcane (Ashraf et al. 2010b)
				Solution culture	Rice (Gong et al. 2006; Shi et al. 2013), wheat (Saqib et al. 2008), field bean (Shahzad et al. 2013), sorghum (Yin et al. 2013)
			Decreases Na^+ concentrations in both shoot and root	Potting soil	Wheat (Tuna et al. 2008)
				Solution culture	Barley (Liang 1999)
			No effect on shoot Na^+ or Cl^- concentrations	Solution culture	Tomato (Romero-Aranda et al. 2006)
	Antioxidant enzyme activity	Superoxide dismutase	Increase	Solution culture	Barley (Liang et al. 2003), cucumber (Zhu et al. 2004), tomato (Al-aghabary et al. 2004), maize (Moussa 2006)
			No effect	Potting soil	Grapevine (Soylemezoglu et al. 2009)
		Catalase	Increase	Solution culture	Tomato (Al-aghabary et al. 2004), maize (Moussa 2006), canola (Hashemi et al. 2010)
			Increase or no effect depending on stress duration	Solution culture	Barley (Liang et al. 2003)
			No effect	Solution culture	Cucumber (Zhu et al. 2004)
			Decrease	Potting soil	Grapevine (Soylemezoglu et al. 2009)
		Ascorbate peroxidase	Increase or no effect depending on cultivars	Potting soil	Grapevine (Soylemezoglu et al. 2009)
			Decrease or no effect depending on stress duration	Solution culture	Tomato (Al-aghabary et al. 2004)
Drought	Transpiration		Decrease	Solution culture	Rice (Agarie et al. 1998a, b), maize (Gao et al. 2004, 2006)
			No effect	Solution culture	Cucumber (Hattori et al. 2008b)
			Increase	Potting soil	Wheat (Gong et al. 2005), sorghum (Hattori et al. 2005; Ahmed et al. 2011a), rice (Chen et al. 2011)
	Antioxidant enzyme activity	Superoxide dismutase	Increase	Potting soil	Wheat (Gong et al. 2005)
			Increase or no effect depending on stress intensity	Field	Wheat (Gong et al. 2008)
			Decrease or no effect depending on cultivars	Potting soil	Sunflower (Gunes et al. 2008)
		Catalase	Increase	Potting soil	Sunflower (Gunes et al. 2008), wheat (Gong et al. 2005)
				Potting soil	Sunflower (Gunes et al. 2008)

Table 1 (continued)

Treatment	Parameters	Observed effects of silicon under stress conditions	Growth medium	Plant species (reference)
	Peroxidase	Decrease, increase or no effect depending on cultivars	Field	Wheat (Gong et al. 2008)
		Decrease or no effect depending on stress intensity	Potting soil	Wheat (Gong et al. 2005)
		No effect	Field	Wheat (Gong et al. 2008)
	Ascorbate peroxidase	Decrease or no effect depending on stress intensity	Potting soil	Wheat (Gong et al. 2005)
		No effect	Potting soil	Sunflower (Gunes et al. 2008)
	Glutathione reductase	Decrease or no effect depending on cultivars	Potting soil	Wheat (Gong et al. 2005)
		Increase	Potting soil	Wheat (Gong et al. 2008)
		No effect	Field	Maize (Gao et al. 2004)
Phosphorus uptake		Decrease	Solution culture	Rhodes grass, Timothy grass, Sudan grass and Tall fescue (Eneji et al. 2008)
		Increase	Potting soil	Barley (Rothamsted 2013)
			Field	

can be further broken down by catalase and a variety of peroxidases (Zhu et al. 2004; Soylemezoglu et al. 2009). Ascorbate peroxidases reduce hydrogen peroxide in the ascorbate–glutathione cycle, using ascorbate as an electron donor (Gong et al. 2005; Gunes et al. 2008). Nonenzymatic antioxidants include glutathione, ascorbic acid, nonprotein amino acids, and phenolic compounds, among others (Al-aghabary et al. 2004; Kumar and Bandhu 2005; Hashemi et al. 2010; Gill and Tuteja 2010).

Reactive oxygen species-mediated lipid peroxidation is considered the most damaging process in living organisms (Gill and Tuteja 2010). Silicon reportedly decreases the concentration of madondialdehyde, the end-product of membrane lipid peroxidation, in barley (Liang et al. 2003), maize (Moussa 2006), and grapevine rootstocks (Soylemezoglu et al. 2009) under salinity, suggesting that addition of silicon can decrease lipid peroxidation. The silicon-mediated decrease in lipid peroxidation is attributed to its regulation of antioxidant defense in plants. Addition of silicon to growth media can affect the activities of antioxidant enzymes, and the effect is time and plant species dependent (Table 1). For example, Liang et al. (2003) observed that, in barley, catalase activity increased under salt stress at day 2 when compared with control (neither silicon nor NaCl added) regardless of whether silicon was incorporated or not. On days 4 and 6 of salt treatment, catalase activity decreased, but silicon addition significantly alleviated the decrease (Liang et al. 2003). Silicon addition enhanced the activity of superoxide dismutase and decreased hydrogen peroxide level in salt-stressed tomato, cucumber, and maize (Al-aghabary et al. 2004; Zhu et al. 2004; Moussa 2006). In salt-stressed cucumber, the activities of guaiacol peroxidase, ascorbate peroxidases, dehydroascorbate reductase, and glutathione reductase increased upon addition of silicon, but catalase activity was unchanged (Zhu et al. 2004). In salt-stressed grapevine, however, addition of silicon did not affect the activity of superoxide dismutase, and it decreased the catalase activity, whereas the activity of ascorbate peroxidase was increased or unchanged depending on cultivars (Soylemezoglu et al. 2009). The level of another important antioxidant—glutathione—could be increased by exogenous silicon when plants were exposed to salt stress (Saqib et al. 2008). We thus conclude that silicon can regulate the antioxidant defense to counteract overproduction of reactive oxygen species under salt stress.

The silicon-mediated decrease in lipid peroxidation helps maintain membrane integrity and decrease plasma membrane permeability under salt stress, as observed in barley (Liang et al. 1996, 2003) and cucumber (Zhu et al. 2004). Silicon application also enhances plasma membrane H^+-ATPase activity (Liang et al. 2006b), which may be related to the silicon-mediated decrease in oxidative damage to proteins under salt stress as observed in wheat under

drought stress (Gong et al. 2005). Liang et al. (2006b) proposed that silicon may affect membrane fluidity and enzyme activity indirectly or secondarily because addition of silicon does not affect membrane fluidity and H^+-ATPase activity in vitro in plants not treated with salt. The fact that silicon addition enhances antioxidant defense indicates that silicon may be involved in the physiological or metabolic activity in plants such as barley, tomato, cucumber, and canola (*Brassica napus* L.) exposed to salt stress (Liang et al. 2003; Al-aghabary et al. 2004; Zhu et al. 2004; Gunes et al. 2007a, b; Hashemi et al. 2010). It should be noted, however, that many of these results are obtained from hydroponics experiments, and thus, further trials under field conditions are needed.

Photosynthesis, the conversion of sunlight into energy by plants and other organisms that use the energy to fuel the organisms' activities, is one of the most fundamental biochemical processes to have evolved (Hohmann-Marriott and Blankenship 2012). Photosynthesis in plants occurs in chloroplasts, and NaCl treatment can change chloroplast ultrastructure, e.g., dilation of thylakoid membranes and reduction in the number of grana (Kumar and Bandhu 2005). The ability of silicon to alleviate salt damage is related to protection of the photosynthetic apparatus (Liang 1998), which may be partly attributed to the silicon-mediated decrease in Na^+ uptake and increase in K^+ uptake in salt-stressed plants (Liang 1998). Tuna et al. (2008) found that addition of silicon to salt-stressed wheat restored the chlorophyll level completely, and with optimal silicon supplementation, the chlorophyll level was even higher than that of controls. In barley, silicon reportedly increased chlorophyll content and photosynthetic activity of leaf cell organelles with or without salt stress (Liang et al. 1996; Liang 1998). The beneficial effects of silicon on the photochemical apparatus and photosynthetic pigment have also been observed in tomato and *Spartina densiflora* (Al-Aghabary et al. 2004; Mateos-Naranjo et al. 2013). In saline conditions, the silicon-mediated protective roles on the photosynthetic apparatus and increased photosynthetic activities may be partly attributed to a silicon-mediated decrease in Na^+ uptake and increase in K^+ uptake and enhanced antioxidant defense.

It can be concluded that silicon can alleviate oxidative damage in plants under salt stress by modulating the plant antioxidant defense systems comprised of enzymatic or non-enzymatic constituents.

3.3 Silicon regulates biosynthesis of compatible solutes

Under stress conditions, except for accumulating antioxidants, plants nearly always react by accumulating compatible solutes, mainly including proline (Gzik 1997), glycine betaine (Mansour 1998), carbohydrates (Balibrea et al. 1997), and polyols (Kumar and Bandhu 2005). A common feature of compatible solutes is that they can accumulate to high levels

without interfering with normal biochemical reactions (Zhang et al. 2004); indeed, they are hydrophilic and can replace water at the surface of proteins, protein complexes, or membranes without disturbing protein structure and function (Bohnert and Shen 1999). These compounds may alleviate the inhibitory effects of high ion concentrations on enzyme activity by stabilizing proteins, protein complexes, or membranes under environmental stresses (Bohnert and Shen 1999; Ashraf and Foolad 2007). Compatible solutes may also function as oxygen radical scavengers (Seckin et al. 2009; An and Liang 2013). Seckin et al. (2009) reported that exogenous application of mannitol could enhance antioxidant enzyme activities in roots of salt-sensitive wheat and thus alleviate salt-induced oxidative damage. In higher plants, proline, a nontoxic and protective osmolyte under osmotic stress, is frequently involved in osmotic protection and is reportedly associated with salt tolerance (Flowers et al. 1986). Watanabe et al. (2000) also found that the stressors NaCl and mannitol induce proline accumulation in *Populus euphratica* leaves. Several studies have reported that proline level is lowered by addition of silicon in different salt/sodic-B-stressed plant species such as grapevine (Soylemezoglu et al. 2009), soybean (Lee et al. 2010), wheat (Tuna et al. 2008), barley (Gunes et al. 2007b), and sorghum (Yin et al. 2013). The decrease in proline level in stressed plants upon silicon addition may reflect the alleviation of stress damage. Yin et al. (2013) also found that short-term application of silicon could significantly increase the levels of sucrose and fructose in sorghum under salt stress, suggesting that silicon can alleviate salt-induced osmotic stress. However, little is known about the relationship between silicon addition and compatible solute metabolism and water transport, which remains to be investigated.

3.4 Silicon affects lignin biosynthesis and regulates levels of plant hormones and polyamines

Salinity increases the activities of certain reactive oxygen species-scavenging enzymes related to greater lignin biosynthesis, which in turn hinders plant growth (Ortega et al. 2006). Hashemi et al. (2010) found that addition of silicon decreases the lignin content in canola. The ability of silicon to reduce lignification in tissues may facilitate cell-wall loosening and extensibility and promote further plant growth under stress conditions (Hattori et al. 2003; Maksimović et al. 2007). Fleck et al. (2011) studied the effect of silicon on rice root anatomy and found enhanced formation of casparian bands in the exodermis and endodermis and the deposition of lignin in sclerenchyma cells. All these changes help reduce radical oxygen loss (the diffusion of oxygen generated through photosynthesis from the root to rhizosphere via aerenchyma such as root and stem) (Kotula and Steudle 2008). Stronger barriers to radical oxygen loss are believed to reduce Na^+ uptake and improve salt tolerance in rice (Krishnamurthy et al. 2009). The

contradictory results obtained for canola and rice may be related to differences in their abilities to accumulate silicon, which needs further investigation.

High salt concentration affects the levels of plant growth substances (Kumar and Bandhu 2005). Abscisic acid, a "stress hormone," is usually upregulated under osmotic stress and involved in altering salt stress-induced gene expression (Kumar and Bandhu 2005) and helps plants survive under stress condition (Dodd and Davies 2004; Wang et al. 2001). Experimental evidence has shown that the presence of abscisic acid largely inhibits Na^+ and Cl^- transport to the shoot in intact bean seedlings (Karmoker and Von Steveninck 1979). Lee et al. (2010) found that abscisic acid content increases in soybean plants under salt stress but decreases upon addition of silicon. Gibberellins are essential phytohormones that regulate many aspects of plant growth. Exogenously applied gibberellins can alleviate the inhibitory effect of NaCl on plant growth (Chakrabarti and Mukherji 2003). Lee et al. (2010) reported that gibberellin level decreases under salt stress but increases upon silicon addition. Kim et al. (2013) found that silicon regulates the expression of genes responsible for the biosynthesis of abscisic acid and jasmonic acid, and these effects are time dependent. The relationship between silicon-mediated changes in the levels of these plant hormones and salt tolerance remains to be investigated.

Polyamines are involved in a wide range of plant processes such as growth promotion, cell division, DNA replication, and cell differentiation (Martin-Tanguy 2001). Polyamines also participate in the defense reaction of plants against abiotic stresses (Groppa and Benavides 2008; Gupta et al. 2013). Salt tolerance and accumulation of high levels of polyamines are positively correlated in a range of plant species. Zapata et al. (2004) studied the effect of salinity on polyamine levels during germination of different plant species and found that in most cases, the putrescine level decreases, whereas spermidine and/or spermine concentrations increase, suggesting that conversion of putrescine to spermidine and spermine is important for conferring salt tolerance (Zapata et al. 2004; Groppa and Benavides 2008). Chattopadhayay et al. (2002) also found that exogenous spermine and spermidine dramatically prevent the leakage of electrolytes and amino acids from roots and shoots of rice subjected to salt stress. Santa-Gruz et al. (1997) reported that total polyamines are reduced to a greater extent in the salt-sensitive tomato species (*L. esculentum*) than in the salt-tolerant species (*Lycopersicon pennellii*). These studies show that accumulation of poly-amines, especially spermidine and spermine, may contribute to salt tolerance. To our knowledge, few studies have addressed the effect of silicon on polyamine levels in plants. Liu and Xu (2007) reported that silicon alleviates the toxic effects of salt stress in *Zizyphus jujube* cv. Jinsixiaozao by regulating the levels of different polyamine types and forms. They found that addition of silicon significantly increased the

ratio of free spermine + spermidine to putrescine, total perchloric acid-soluble covalently conjugated polyamines, and perchloric acid-insoluble covalently conjugated spermidine and spermine, whereas the level of perchloric acid-insoluble covalently conjugated putrescine dropped. Further in-depth analyses are needed to enhance our understanding of the possible roles of silicon in polyamines metabolism.

We conclude that silicon is involved in regulating of lignin biosynthesis and levels of endogenous plant hormones and polyamines. Further investigations are needed to clarify the relationship between these changes and stress tolerance and the possible involvement of silicon in signaling. In addition, silicon may regulate plant water relations under stress conditions (Romero-Aranda et al. 2006), which is discussed below.

4 Alleviative effects of silicon on drought stress in plants

Drought is one of the most important environment stresses in agriculture, having several deleterious effects on plant growth and metabolic processes, including water relations, photosynthetic assimilation, and nutrient uptake (Cattivelli et al. 2008; Xiong et al. 2012). It has been widely reported that silicon increases drought tolerance in plants such as rice (Agarie et al. 1998b), sorghum (Hattori et al. 2005, 2008a; Ahmed et al. 2011a, b; Sonobe et al. 2011), cucumber (Hattori et al. 2008b), maize (Gao et al. 2004, 2006), wheat (Gong et al. 2005, 2008; Gong and Chen 2012), pepper (*Capsicum annuum* L.) (Lobato et al. 2009), and sunflower (Gunes et al. 2008). Moreover, silicon also increases tolerance to heat stress by maintaining membrane stability (Agarie et al. 1998a). Because drought is sometimes accompanied by high temperature (Halford 2011), application of silicon may be an alternative to alleviate the damage of both drought and heat stresses.

4.1 Silicon influences water relations and improves photosynthesis under drought stress

Leaf water potential and water content decrease substantially when plants are exposed to drought (Siddique et al. 2000; Farooq et al. 2009). Application of silicon can significantly improve water status in nonirrigated crops. Gong and Chen (2012) reported that the water potential of silicon-applied drought-stressed wheat leaves is maintained to a greater extent compared with stressed plants without silicon supplementation, suggesting that silicon can improve the water status of wheat plants during drought. A similar phenomenon was observed by Pei et al. (2010) in wheat exposed to polyethylene glycol-induced water stress.

Transpiration rate and stomatal conductance are important characteristics that influence plant water relations (Farooq et al. 2009). The beneficial effects of silicon on plant growth have been suggested to be associated with a change in transpiration.

Many researchers have postulated that the formation of a silica-cuticle double layer on leaf epidermal tissue may be responsible for the observed reduction in leaf transpiration from plants treated with silicon (Yoshida 1965; Wong et al. 1972; Matoh et al. 1991). Gong et al. (2003) reported that leaves of drought-stressed wheat become thicker upon addition of silicon and speculated that silicon might improve drought tolerance by reducing transpirational water loss. However, the cuticular transpiration rate is very low compared with the stomatal transpiration rate (Kerstiens 1996). In maize, Gao et al. (2006) found that the transpirational rate and conductance from the cuticula of leaves are not altered by added silicon, whereas the rate and conductance from stomata decrease upon silicon addition, suggesting the involvement of silicon in regulating stomatal movement. Therefore, reduction in transpiration—via cuticula or stomata—is one of the mechanisms for the observed silicon-mediated increase in drought tolerance.

Although decreased plant transpiration is an important mechanism for silicon-mediated drought tolerance, application of silicon does not always decrease transpiration. Hattori et al. (2005) observed that silicon increases the stomatal conductance and transpiration rate of leaves in potted sorghum under drought stress. Similar results were also observed in drought stressed wheat and rice (Gong et al. 2005; Chen et al. 2011). In cucumber, Hattori et al. (2008b) found that silicon addition does not affect transpiration rate or stomatal conductance of leaves regardless of whether osmotic stress was applied. Plants also need to adjust water uptake by roots to maintain water balance in the whole plant. In maize and sunflower seedlings, for example, Gao et al. (2004) found that addition of silicon decreases leaf transpiration and water flow rate in xylem vessels, resulting in more efficient use of water. They speculated that silicon deposition on the root cell wall might affect the wetting properties of xylem vessels and therefore water or solute transport. Although this speculation remains to be confirmed experimentally, these studies at least suggest that silicon can regulate water transport in plants.

Sonobe et al. (2011) suggested that inclusion of silicon in culture solution could enhance root water uptake by roots under water-deficit stress via active accumulation of soluble sugars and amino acids. A similar phenomenon was observed in rice (Ming et al. 2012). Proline is one of the important compatible solutes that accumulates under stress conditions and has been considered to play a substantive role in osmotic adjustment (Nayyar and Walia 2003). However, other researchers consider increased proline level as a symptom of injury rather than a cause for stress tolerance. Pei et al. (2010) observed that proline concentration increases in wheat leaves under water stress and that silicon addition decreases the proline accumulation. This result supports the view that proline accumulation is a symptom of stress-related injury. Therefore, the regulative role of silicon on the accumulations of different compatible solutes and their roles in drought tolerance need further investigation.

The differential impact of silicon on stomatal conductance and transpiration rate may be due to one of two reasons. First, different growth media conditions (soil culture vs. solution culture) may have an effect. In soil, plants subjected to drought generally have longer roots and a greater root surface area to increase access to water. While in solution culture, however, plants often respond to water stress by improving their internal hydraulic conductivity in the water flow pathway because roots are always in contact with water (Hattori et al. 2008b). Second, the contribution of cuticular transpiration to total transpiration may also have an effect. For example, the contribution of cuticular transpiration is ~25–39 % of total transpiration in rice (Matoh et al. 1991), 20–40 % in barley (Millar et al. 1968), and up to 50 % in *Acer syriacium* and *Rhododendron poticum* (Whiteman 1965). Considering the complexity of the relationship between silicon addition and transpiration in plants under drought conditions, further studies are needed to elucidate the regulative roles of silicon on water metabolism in whole plants. Besides, a reduced transpiration rate owing to water deficit reduces nutrient absorption and availability, which will be discussed later.

Closure of stomata is the first response of plants exposed to serious water deficit and has generally been accepted to be the main limiting factor of photosynthesis (Reddy et al. 2004; Farooq et al. 2009). Stomato closure decreases CO_2 influx and spares more electrons for the formation of active oxygen species (Farooq et al. 2009). In drought conditions, Meyer and Genty (1998) found that the decline of photosynthetic rate in *Rosa rubiginosa* was primarily due to CO_2 deficiency. However, Gong et al. (2005) found that the stomatal factor is not the main factor that inhibited the photosynthesis in drought-stressed wheat because neither drought nor silicon treatment significantly affected the internal CO_2 concentration significantly under their experimental conditions. In experiments with soil-grown rice, Chen et al. (2011) suggested that both stomatal and nonstomatal factors are involved in silicon-mediated improvement in photosynthesis under drought. In addition to stomatal movement, photosynthetic pigments have been reported to be affected by silicon addition. Lobato et al. (2009) demonstrated that silicon addition maintains the content of photosynthetic pigments (chlorophylls a, chlorophylls b, and carotenoids) in *Capsicum annuum* L. under water stress. This may be attributed to silicon-mediated improvement of chloroplast ultrastructure and increased activities of antioxidant enzymes such as superoxide dismutase and catalase (Liang 1998; Gong et al. 2005). Chen et al. (2011) found that added silicon not only increases the content of photosynthetic pigments but also increases the basal quantum yield (F_v/F_0) and maximum quantum efficiency of photosystemII photochemistry (F_v/F_m) of rice plants subjected to drought. Silicon can also regulate the activities of certain photosynthetic enzymes. Adatia and Besford (1986) found that the addition of silicon increased the activity of ribulose-bisphosphate

carboxylation in cucumber grown hydroponically. Gong and Chen (2012) reported that silicon application increased the activity of phosphoenolpyruvate carboxylase and the concentration of inorganic phosphorus in wheat leaves under drought conditions. These studies suggest that silicon is involved in both stomatal dynamics and photochemical reactions and therefore regulates photosynthesis. In conclusion, the beneficial effects of silicon in drought-stressed plants can be partially attributed to its positive impact on plant water status and photosynthesis.

4.2 Silicon decreases oxidative stress during drought

The silicon-mediated improvement of drought tolerance in plants is associated with increased antioxidant defense capability and alleviation of oxidative damage. Gong et al. (2005) reported that silicon partially offset the negative impacts of drought on wheat by increasing the activities of superoxide dismutase, catalase, and glutathione reductase and decreasing the hydrogen peroxide content, acid phospholipase activity, and oxidative damage of proteins. The observed decrease in activity of acid phospholipase, which hydrolyzes phospholipids, in silicon-treated plants under drought indicated that silicon alleviates phospholipid de-esterification in drought-stressed wheat (Gong et al. 2005). In addition, the ability of silicon to counter oxidative damage may be related to stress intensity, as observed in field tests of wheat under drought conditions (Gong et al. 2008). Gunes et al. (2008) reported that the superoxide dismutase activity decreased or was not affected by silicon application, whereas silicon's effect on catalase activity depended on cultivars.

The levels of nonenzymatic antioxidants are also affected by application of silicon (Gunes et al. 2008). Glutathione is one of several nonprotein thiols that mainly function as antioxidants in plant cells. Gong et al. (2005) observed that added silicon increased the activity of glutathione reductase in drought-stressed wheat. Pei et al. (2010) found that addition of silicon significantly increased glutathione concentration in water-stressed wheat leaves, which might be partly due to increased activity of glutathione reductase (Gong et al. 2005). Pei et al. (2010) also found that addition of silicon slightly increased ascorbic acid concentration in leaves of water-stressed wheat. Increases in the content of these nonenzymatic antioxidants may play important roles in alleviating the toxicity of reactive oxygen species induced by drought. These results suggest that silicon is involved in regulating of antioxidant defense and thus alleviates oxidative damage in drought-stressed plants. Further study is required to elucidate how silicon initiates these responses.

4.3 Silicon balances mineral uptake during drought

Water deficit limits nutrient uptake through roots and subsequent transport to shoots, thereby reducing nutrient availability and metabolism (Farooq et al. 2009). Furthermore, silicon may play an important role in balancing the uptake, transport, and distribution of minerals in drought-stressed plants.

Ca level is closely related to expression of osmotic stress-responsive genes (Zhu 2002; Mahajan and Tuteja 2005), and K^+ plays an important role in osmotic adjustment in plants (Ashraf et al. 2001). Kaya et al. (2006) observed that silicon addition increased Ca and K levels in water-stressed maize leaves. Pei et al. (2010) reported that silicon decreased the Ca, K, and Mg concentrations in wheat shoots under water-deficit stress induced by 20 % (w/v) polyethylene glycol; when the improvement of shoot dry matter by silicon was taken into consideration, however, the total content of each of these minerals in shoots actually increased. Chen et al. (2011) observed similar results in rice. The increased uptake of Ca and K may be attributed to a decrease in plasma membrane permeability and increase in plasma membrane H^+-ATP activity as a result of silicon addition (Liang 1999; Kaya et al. 2006). There are contradictory reports about the relationship between silicon application and P uptake (Table 1). Miyake (1993) reported that silicon supplementation decreased P uptake. Gao et al. (2004) also found that silicon addition decreased P concentration significantly in xylem sap of maize. As early as 1862, however, a classical Hoos barley experiment at Rothamsted, UK, showed that silicon fertilizer (as sodium silicate) increased the yields on plots not given P, suggesting that silicon increased P availability in these plots (Rothamsted 2013). Eneji et al. (2008) found a reasonable correlation between silicon and P uptake under both wet and dry conditions, and they suggested that this was due to silicon-induced increase in water-soluble P concentration in the soil. Ma and Takahashi (1990) suggested that improved P utilization in the presence of silicon might result from interactions with cationic metals such as Fe and Mn. Recently, Detmann et al. (2012) reported that silicon increased both rice grain yield and nitrogen use efficiency. More work is needed to identify factors that affect silicon's effects on P and N uptake.

Root traits (e.g., lateral spread, depth, length, and surface area) affect plant growth and development directly. Some studies have shown that silicon addition can enhance root growth under drought conditions. In drought-stressed sorghum, Hattori et al. (2005) observed a significantly lower shoot/root ratio and higher root dry mass accumulation in silicon-applied plants compared with plants not treated with silicon, indicating that silicon facilitates root growth during drought. Ahmed et al. (2011b) suggested that silicon application is mainly beneficial to the growth of sorghum root, allocating more matter to the plant root system grown hydroponically. The stimulative effect of silicon on root growth may be due to enhanced root elongation as a consequence of enhanced cell wall extensibility in the growth zone, as observed in sorghum (Hattori et al. 2003). However, the

beneficial effects of silicon on root growth under drought are not observed in certain plants such as wheat, cucumber, and sunflower (Gong et al. 2003; Gunes et al. 2008; Hattori et al. 2008b; Pei et al. 2010). These observed differences may be related to culture conditions and plant species/cultivars.

Nutrient uptake is related to root surface area and length (Barber 1984). An increase in surface area provides more exposed sites for uptake of diffusible ions (Barber 1984; and references therein). Silicon-mediated enhancement of root growth may therefore stimulate nutrient absorption and increase drought tolerance. In some studies, although silicon did not stimulate root growth under drought, silicon application in fact increased water uptake (Sonobe et al. 2011), thereby contributing to stimulation of nutrient uptake. The increased water uptake upon silicon addition under drought is due to improved hydraulic conductance of roots (Hattori et al. 2008a) and root activity (Chen et al. 2011).

These studies suggest that silicon application may improve plant growth under drought by balancing nutrient uptake. Further investigations will be needed to determine how silicon regulates water uptake by roots and affects root anatomical characteristics to better understand the mechanisms of silicon-promoted plant growth.

5 Future perspectives and conclusions

Silicon, albeit not essential, plays important roles in plant growth and development. Silicon accumulation in plants can improve the salt and drought tolerance by regulating both physiological and biochemical processes. Much work has been conducted to explore the influence of silicon on plants under stress conditions. Part of the work is summarized in Table 1. Based on current knowledge of the beneficial effects of silicon on salt and drought tolerance in higher plants, the possible mechanisms underlying silicon-enhanced osmotic stress tolerance are depicted in Fig. 2. There are many common aspects of the basic physiologies of drought stress and salt stress. For example, both drought and high-salt stress hinder water and nutrient acquisition (Mahajan and Tuteja 2005). Perhaps, this is why some of the basic mechanisms by which silicon alleviates salt and drought stress overlap with each other.

Fig. 2 Possible mechanisms for silicon-mediated tolerance to salinity and drought in plants
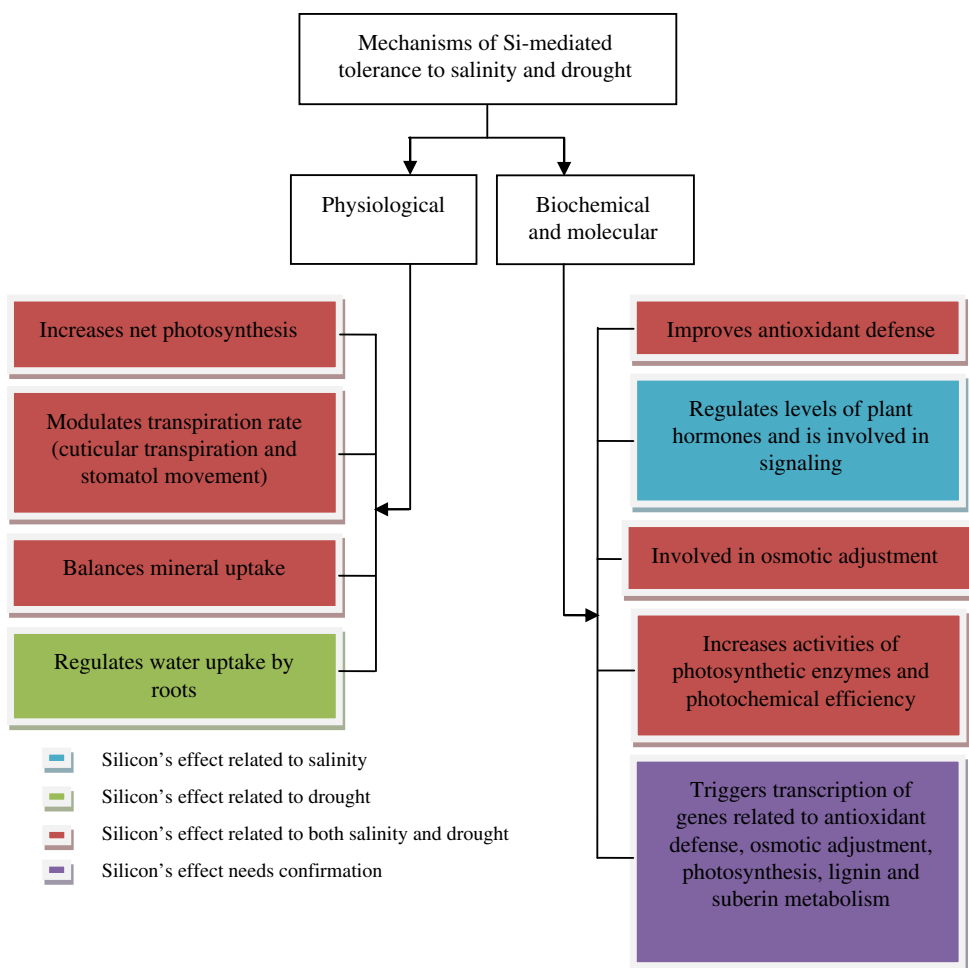
Although numerous studies have proved that silicon supplementation benefits the growth of many plant species—especially when they are subjected to environmental stresses—further research is needed to understand the mechanisms by which silicon alleviates environmental stresses. In-depth investigation should focus on how silicon regulates plant tolerance to salt and drought stresses at the molecular level, including molecular recognition, signal transduction, and gene expression, which may help us to better understand the physiological and biochemical functions of silicon. An increasing number of studies suggest that silicon application may induce stress resistance by affecting phytohormone homeostasis (Van Bockhaven et al. 2013). Lee et al. (2010) reported that addition of silicon to salt-stressed soybean enhanced the levels of endogenous gibberellins, whereas it reduced the levels of abscisic acid and proline. Microarray studies of the effect of silicon in rice infected with *Magnaporthe oryzae* showed that silicon induced the ethylene signaling pathway (De Vleesschauwer et al. 2006; Brunings et al. 2009). Fauteux et al. (2005) proposed that silicon may interact with several key components of plant stress signaling systems, ultimately leading to induced resistance. In view of the important roles of phytohormones and secondary metabolites in plant tolerance to environmental stresses, it would be interesting to investigate how silicon regulates their levels and initial adaptive responses. An in vitro experiment has shown that orthosilicic acid can bind hydroxyl groups on amino acids (Jugdaohsingh et al. 2008). However, it remains unclear whether silicon binds to proteins or has direct biochemical functions in plants. Fauteux et al. (2005) suggested that silicon may affect protein activity and/or conformation by binding hydroxyl groups on amino acid residues, thereby regulating the phosphorylation status of signaling proteins. Silicon could also be involved in signaling by interacting with phosphorus and/or metal cofactor Mn and Fe (Fauteux et al. 2005). However, these various hypotheses need further investigation.

Inclusion of silicon improves water storage in tomato plants (Romero-Aranda et al. 2006), and the resultant higher water content contributes to salt dilution, thereby reducing salt toxicity and improving growth (Romero-Aranda et al. 2006). Aquaporins are a major facilitator of water transport in plants (Maurel et al. 2008). A positive correlation between hydraulic conductivity and certain highly expressed *PIP* transcripts in roots has been observed in *Arabidopsis* (Sutka et al. 2011). However, studies are needed to investigate whether silicon can regulate *PIP* expression and how exogenous silicon is involved in regulating water movement in whole plants under water stress.

Silicon also enhances the formation of casparian bands in the exodermis and endodermis and lignin depositions in sclerenchyma cells (Fleck et al. 2011). Further study is required to clarify the details of the relationship between the impact of silicon on root anatomy (such as the development of casparian bands and suberization and lignification) and silicon-enhanced tolerance to salt and drought. At the subcellular level, most silicon-related research has concentrated on the cell wall. It would be interesting to investigate the distribution of silicon in the cell nucleus and organelles, which may help explain the biological roles of silicon in enhancing plant tolerance to environmental stress. Environmental stresses also affect the uptake and translocation of other elements (Kumar and Bandhu 2005), including P, K, Ca, and Mg and micronutrient such as Fe, Mn, Cu, B, and Zn in plants (Wang and Han 2007). The effects of silicon on mineral uptake vary between species and environmental stresses (Miyake 1993; Gao et al. 2004; Eneji et al. 2008). Isa et al. (2010) found that silicon stimulates the elongation of lateral roots in rice. Detmann et al. (2012) demonstrated that silicon increases nitrogen use efficiency and alters primary metabolism by stimulating amino acid remobilization. Further studies are needed to clarify how silicon regulates root development and nutrient uptake.

Although advances have been made in elucidating the importance of silicon in improving plant stress tolerance at the whole-plant level, information is lacking on the molecular mechanisms of silicon-induced stress tolerance. OMICS-based technologies are of great value for investigating physiological and metabolic processes (Zargar et al. 2011). Transcriptome and proteome platforms have been the main technologies to reveal mechanisms of tolerance in plants (Ahsan et al. 2009; Wang et al. 2009). Nwugo and Huerta (2011) investigated the rice leaf proteome and observed that silicon is actively involved in physiological processes of cadmium tolerance in rice. Hence, the use of transcriptome and proteome technologies will help shed light on the transcriptional and posttranscriptional regulatory mechanisms of silicon-mediated tolerance to salinity and drought in plants.

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