Chapter 8
Silicon-Mediated Tolerance to Other Abiotic Stresses

Abstract Silicon (Si) has been reported to mitigate some other abiotic stresses such as boron (B) toxicity, potassium (K) and phosphorus (P) deficiency, iron (Fe) deficiency, excess of nitrogen and phosphorus, UV radiation and flooding. In this chapter, current knowledge concerning the roles Si may play under such abiotic stresses is overviewed. More recently, rapid progress has been made at both the physiological and molecular levels in dissecting the mechanisms involved in Si-induced root mobilization of Fe from the rhizosphere and acquisition of root apoplastic Fe, thereby mitigating Fe-deficiency chlorosis in strategy 1 plants.

Keywords Boron toxicity • Excess of nitrogen and phosphorus • Flooding • Iron-deficiency chlorosis • Potassium and phosphorus deficiency • UV radiation

8.1 Boron Toxicity

Although boron (B) is an essential micronutrient for higher plants, there is only a narrow level between critical deficient and toxic concentrations of B in plant tissues, particularly in cereal species (Nable et al. 1990; Schnurbusch et al. 2010). Boron toxicity is a significant agronomic problem in a number of cereal-growing regions across the world, mostly in arid and semiarid climate conditions such as West Asia, Northern Africa and Southern Australia (Schnurbusch et al. 2010). Soil B excess is often accompanied by excessive salinity, the conditions conducive to multiple stresses such as osmotic stress and chlorine (Cl), sodium (Na) and B toxicity (Alpaslan and Gunes 2001). Boron is removed more slowly than salt ions during leaching (Yermiyahu et al. 2008), thereby remaining at excessive concentrations even after reclamation of saline soils (Ben-Gal and Shani 2002). Besides natural occurrence in the soil, B-contaminated irrigation water and mining pollution can also be a source of high soil B (Nable et al. 1997).

The mechanisms of B tolerance and B toxicity are not well understood. Within species, large genotypic differences exist in the capacity to tolerate high external B concentrations (Paull et al. 1992; Nable et al. 1997). These differences are based primarily on restrictions in B uptake by the roots, thereby restricting translocation of B to the shoot, rather than tolerance to high B in tissues (Nable et al. 1997). In wheat and barley, for instance, root B concentration is reduced in tolerant

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genotypes due to exudation of B from roots to soil (Reid 2007) via an efflux B transporter belonging to the BOR family (Miwa et al. 2007; Sutton et al. 2007). Recently, Schnurbusch et al. (2010) have proposed that tolerance to high soil B is mediated by reduced expression of *HvNIP2;1* to limit B uptake. This gene encoding HvNIP2;1, an aquaporin from the NIP subfamily, was previously described as a silicon (Si) influx transporter in barley (see Chap. 4). Moreover, differential expression of B toxicity tolerance among the genotypes, despite similarly high total concentration of B in leaves, seems to be related to a better redistribution of B by efflux transporters from sensitive symplastic compartments into the leaf apoplast (Reid and Fitzpatrick 2009). In general, species with high B demand may have also a higher capacity to sequester B in the cell walls (Broadley et al. 2011).

Silicon and B are elements with many similar chemical properties; in aqueous solutions both exist as weak, undissociated acids and can complex readily with polyhydroxy compounds (Brown et al. 1999; Kinrade et al. 1999). Plants take up Si as uncharged monosilicic acid (pK_a of 9.8) and B as boric acid (pK_a of 9.2), either passively or actively, which closely depends on the external concentration. Due to these similarities, interactions between Si and B are possible, but there is little information available regarding this aspect.

Dicots and graminaceous species differ not only in their capacity for Si shoot accumulation but also in their B demand, which is inversely related (Table 8.1). In barley, genotypical differences in restriction of uptake by roots and transport of B into the leaves are closely correlated with similar restrictions in uptake and transport of Si (Nable et al. 1990). Liang and Shen (1994) reported that under conditions of adequate or excess B concentrations, Si supply led to a decrease in B uptake, whereas under conditions of B deficiency, Si supply enhanced B uptake in oilseed rape. In *Lilium longiflorum*, Si supply increased the range between critical deficiency and toxicity for B (Polster and Schwenk 1992). However, in cucumber, Si supply had no effect on total B concentration of leaves, but influenced distribution of B between symplastic and apoplastic compartments, especially at high B supply (Wiese et al. 2007). In fact, more B was bound to the cell wall, and less B was in the cell sap of leaves of Si-treated plants, which was further correlated with a lower B concentration of the apoplastic fluid. Amendment of Si to high B soil effectively

Table 8.1 Shoot concentrations of Si and B in different graminaceous and dicotyledonous species

Plant species	Si concentration (mg g^{-1} dw)	B concentration (μg g^{-1} dw)
Rice	41	7
Barley	30	8
Wheat	26	7
Maize	23	10
Soybean	12	29
Sunflower	7	38
Grapevine	5	42
Tomato	3	60

mitigated B toxicity in spinach, wheat and barley by decreasing root-to-shoot translocation of B and in addition by preventing reactive oxygen species (ROS) membrane damages due to modulation of the activities of antioxidative enzymes (Karabal et al. 2003; Gunes et al. 2007a, b, c; Inal et al. 2009). Also, Si alleviates the concomitant adverse effects of salinity/sodicity (Na ions) and B toxicity on barley and grapevine (*Vitis vinifera*) rootstocks (Gunes et al. 2007a; Soylemezoglu et al. 2009).

8.2 Potassium and Phosphorus Deficiency

Potassium (K) deficiency reduces mechanical stability, nutritional quality, drought tolerance and crop resistance to pathogens (Liebersbach et al. 2004; Pettigrew 2008). Potassium deficiency also leads to oxidative stress, as evidenced by accumulation of ROS and membrane lipid peroxidation (Cakmak 1994, 2005). On the other hand, the ameliorative effect of Si on plants suffering from abiotic stresses often occurs through counteracting oxidative stress by modulating antioxidant enzymes (Liang et al. 2007). It has been reported that application of Si fertilizers improved growth, yield and quality as well as the overall nutritional status of different crops (see Chap. 10). Yet, a direct role of Si in mediating K deficiency has not been uncovered. The preliminary study of Miao et al. (2010) demonstrates that the application of Si- to K-deficient soybean (*Glycine max*) plants improved both internal K status and plant growth. In addition, Si also alleviated K-deficiency-induced membrane lipid peroxidation and oxidative stress by modulating antioxidant enzymes.

Soil-available phosphorus (P) is often low, especially in acid soils, because of its poor solubility, sorption and slow diffusion (Marschner 1995). Over 50 % of the cultivated land across the world is P deficient (Vance 2001). Most of the phosphate used in mineral fertilizers is derived from rock phosphate as a non-renewable resource; globally these resources are predicted for the next 50–100 years, assuming an increased use of P fertilizers to meet food requirements of a fast-growing world population (Cordell et al. 2009; Gilbert 2009).

The root exudation of carboxylates (mainly citrate and malate) and phenolic compounds (e.g. flavonoids) has been considered as the major root response to mobilize sparingly soluble P in the rhizosphere (for review see: Neumann and Römheld 2007; Cesco et al. 2010). However, the underlying mechanism involved in biosynthesis and subsequent exudation of organic acids in response to P deficiency and/or Al excess in acid soils remains unclear (e.g. Ryan et al. 1997; Li et al. 2000; Kochian et al. 2004; Neumann and Römheld 2007). The enhanced activity of phosphoenolpyruvate carboxylase (PEPC) appears to be a key Pi-independent metabolic bypass reaction of organic acid biosynthesis in P-deficient plants, to achieve a more economic internal P utilization under conditions of P limitation (Theodoru and Plaxton 1993; Plaxton 1998). However, this mechanism has not been proven in many plant species. For instance, unlike in white lupine, P deficiency did not enhance exudation of carboxylates by wheat roots despite an increased PEPC activity (Neumann and

Römheld 1999). Root P uptake is mediated by high-affinity plasma membrane (PM)-associated Pi transporters. In general, the expression of Pi transporter genes (*PHTs*, formerly known as *PTs*) is upregulated under P deprivation (e.g. Karthikeyan et al. 2002; Tittarelli et al. 2007), although some environmental factors may alter their expression (Catarecha et al. 2007; Glassop et al. 2005; Kostic et al. 2015).

Beneficial effects of Si under P-deficiency stress have been recorded on various graminaceous species such as wheat (*Triticum aestivum*), rice (*Oryza sativa*), maize (*Zea mays*), barley (*Hordeum vulgare*) and pasture grasses grown in both soil and hydroponic conditions (Rothbuhr and Scott 1957; Ma and Takahashi 1989, 1990a, b, 1991; Owino-Gerroh and Gascho 2004; Ma 2004; de Melo et al. 2007; Eneji et al. 2008; Yang et al. 2008; Abro et al. 2009). In a long-term field experiment conducted at the Rothamsted Experimental Station, when P fertilizers were not applied, yield of barley from a field fertilized with Si was higher than in a field without Si amendment (Fisher 1929). Such beneficial effects of Si have been attributed through the varied and even contradictory explanations, including competitive sportive interaction and exchange of these two elements (Smyth and Sanchez 1980), an enhancement of soil P availability by increasing soil pH (Roy et al. 1971; Owino-Gerroh and Gascho 2004) and decrease of metal uptake (e.g. Mn, Fe, Al, Cd), thus indirectly improving P utilization by plants (Ma and Takahashi 1990a; Liang et al. 2005). Different experimental materials and conditions could be an important reason for such varied explanations in the literature.

Phosphorus sorption is the major cause of P deficiency in acid soils. Phosphate ($H_2PO_4^-$) anions are specifically adsorbed onto hydrated Fe and Al oxides by replacing OH groups from the coordination sphere of the metals (Hingston et al. 1967; Obihara and Russell 1972). The chemical competition between $H_2PO_4^-$ and silicate ($H_3SiO_4^-$) anions for the sorption sites has been demonstrated in soils resulting in displacement of Si by P, and *vice versa* (Obihara and Russell 1972; Smyth and Sanchez 1980). Freshwater eutrophication, as a possible way of internal P loading under aerobic conditions, has been attributed to Si-induced mobilization of P from anion exchange sites in sediments (Tuominen et al. 1998; Tallberg et al. 2009). Although theoretically possible, the ability of Si to compete P for the sorption sites is highly pH dependent, since pK_a value of orthosilicic acid is much higher than that of orthophosphoric acid (9.8 and 2.1, respectively). Therefore, it is unlikely that such interaction between $H_3SiO_4^-$ and $H_2PO_4^-$ may occur in agriculture soils. Indeed, the experiments of Ma and Takahashi (1990b, 1991) did not confirm that increasing amount of applied Si could affect either fixation capacity or availability of soil P. Moreover, the uptake of P was also not affected by the Si supply at a low P level in both soil and solution culture (Ma and Takahashi 1990a, b, 1991). Therefore, Ma (2004) proposed that the larger beneficial effect of Si on plant growth under P-deficiency stress was attributed to the enhanced availability of internal P through the decrease of excess Fe and Mn uptake.

On the contrary, the recent experiments on acid soils showed that supply of different Si sources increased readily available P fraction followed by decreasing of Al- and Fe-bound fractions in wheat rhizosphere (Kostic et al. 2015). Moreover, application of Si in acid soil resulted in enhancement of the expressions of

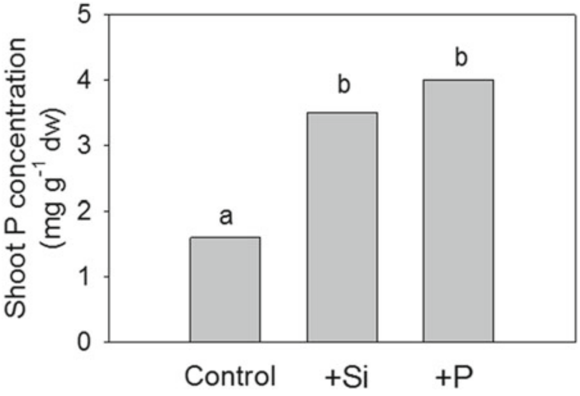


Fig. 8.1 Effect of Si supply on shoot P concentration of wheat plants grown in the acid soil (Based on Kostic-Kravljanac 2015)

P-deficiency-related genes encoding phosphoenolpyruvate carboxylase (PEPC), the organic anion efflux transport proteins, i.e. multidrug and toxic compound extrusion 1 (MATE1) and Al-activated malate transporter 1 (ALMT1), and high-affinity Pi transporters (PHT1.1 and PHT1.2) in wheat roots (L. Kostic and M. Nikolic, unpublished). Consequently, the leaf P concentration in Si-treated wheat plants without P application achieved the range of that in P-fertilized plants (Fig. 8.1).

8.3 Iron Deficiency

Despite being the fourth most abundant element in the Earth's crust, iron (Fe) deficiency is one of the major limiting factors for crop production in calcareous soils all over the world (Vose 1982). The overall processes of Fe acquisition by roots have been described in terms of two basic strategies to cope with Fe deficiency (Fig. 8.2; for review see Römheld and Nikolic 2007). Strategy 1 plant species (dicots and nongraminaceous species) respond to Fe deficit by undergoing both morphological and physiological changes. Morphological changes include an increase of the root surface characterized by the formation of lateral roots, root hairs in the apical zone, and the development of transfer cells (Schmidt 1999). All the components of strategy 1 root uptake machinery are upregulated proteins, i.e. PM-bound Fe^{III} chelate reductases [ferric reductase oxidase (FRO) family; Jeong and Connolly 2009], Fe^{II} PM transporter [iron-regulated transporter (IRT); Vert et al. 2002] and PM proton pump of the HA family P-type H^+-ATPase, which mediates acidification of the rhizosphere (Santi and Schmidt 2009). This acidification serves not only to make rhizosphere iron more available but also to facilitate the required FRO activity (Wu et al. 2005). Many strategy 1 species also enhance root exudation of low-molecular-weight compounds (e.g. carboxylates, phenolics and flavins), which can increase Fe availability due to chelation and potential reduction of Fe^{III}. Instead of the reduction-based Fe acquisition, graminaceous species (strategy 2 plants) developed the chelation-based mechanism of Fe uptake to cope with Fe-deficient conditions. This

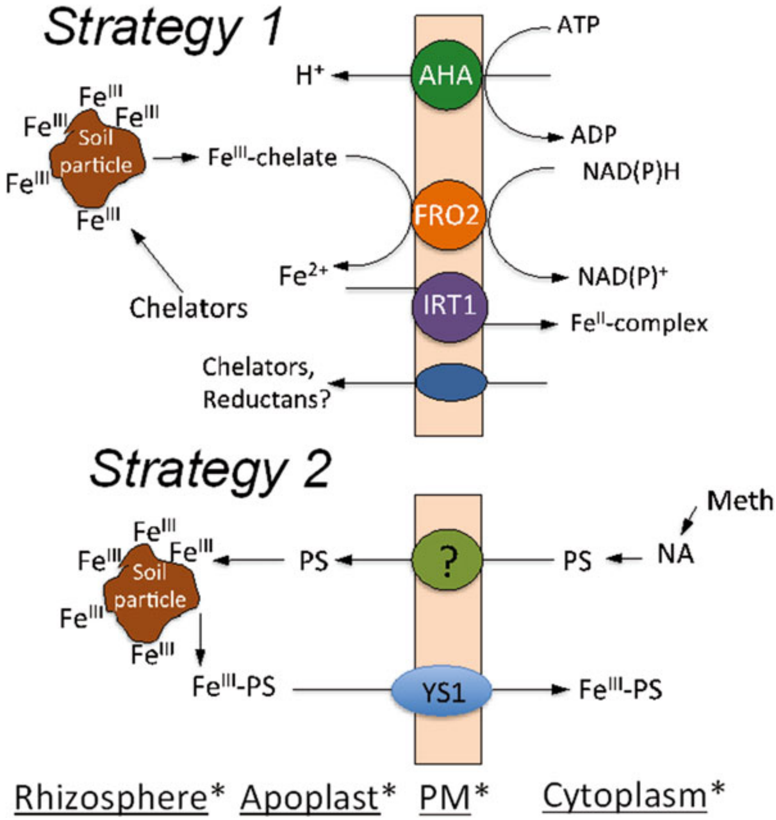


Fig. 8.2 Strategies for acquisition of Fe in response to Fe deficiency in strategy 1 (dicots and nongraminaceous species) and strategy 2 (graminaceous species) plants

includes the root biosynthesis and release of natural Fe(III) chelators such as the mugineic acid (MA) family of phytosiderophores (PSs) that chelate sparingly soluble Fe from the rhizosphere. The PS–Fe(III) complex is subsequently taken up by specific transporters belonging to yellow stripe-like (YSL) family of proteins, which also contribute to shoot transport and seed deposition of Fe (Curie et al. 2009). Nicotianamine (NA) is not only a precursor of PS biosynthesis (strategy 2 plants), but being a strong chelator of Fe(II), it plays a major role in symplastic homeostasis and phloem transport of Fe in plants (Haydon and Cobbett 2007).

Rapid progress has been made predominantly in elucidating the mechanisms of how Si mediates metal excess (see Chap. 5), whereas limited information is available on the relevance of Si nutrition under lack of Fe and other micronutrients. This is partly due to the fact that root responses to Fe deficiency have so far been studied and characterized mainly in nutrient solution experiments in which Si was omitted. Recently it has been reported that the addition of Si to the nutrient solution is able to mitigate Fe-deficiency chlorosis in strategy 1 plants such as cucumber, pumpkin

Fig. 8.3 Root application of Si mitigates symptoms of Fe-deficiency chlorosis in tomato, Si-excluding, Fe-strategy 1 species (Photograph by Miroslav Nikolic)

and soybean (Bityutskii et al. 2010; Pavlovic et al. 2011, 2013; Gonzalo et al. 2013). Interestingly, Si also prevented Fe chlorosis in tomato (*Lycopersicon esculentum*), which is known as a Si-excluder species (Fig. 8.3). However, Si supply had no effect on the nutritional status of zinc (Zn) and Mn, although it diminished leaf necrosis symptoms (Bityutskii et al. 2014), which is most probably due to an indirect effect of Si on enhancing antioxidant defence capacity in plant tissues.

Pavlovic et al. (2013) are the first to demonstrate Si-induced increase of the root apoplastic Fe pool, together with the enhanced expression levels of the proteins (FRO2, IRT1 and AHA1) involved in reduction-based Fe uptake (Fig. 8.4). Moreover, in Fe-deficient cucumber roots, Si influenced the genes involved in the carboxylate, shikimate and phenylpropanoid metabolism, thus resulting in enhanced accumulation of Fe-chelating compounds (organic acids and phenolics) for improved Fe mobilization from the rhizosphere and reutilization of root apoplastic Fe (Pavlovic et al. 2013). Application of Si also facilitated mobility and xylem translocation of Fe towards shoot, along with tissue accumulation of Fe-mobilizing compounds such as citrate (xylem sap, root and shoot tissues) or catechins (in roots) (Pavlovic et al. 2013; Bityutskii et al. 2014). Very recently, Nikolic's group has demonstrated that Si enhanced remobilization of labelled ^{57}Fe from old to younger leaves of cucumber, accompanied by Si-induced expression of genes encoding both NA biosynthesis and YSL transporters responsible for symplastic Fe unloading in leaves and phloem transport of the Fe–NA complex (Pavlovic et al. 2014). Based on these new findings, the alleviating effect of Si appears to be more indirect, by affecting activation of Fe-deficiency-associated genes responsible for enhanced root acquisition and tissue mobilization of Fe.

The alleviating effect of Si in strategy 2 plants is still under debate. Bityutskii et al. (2010) reported that addition of Si to the nutrient solution did not effectively mitigate Fe-deficiency chlorosis in maize and barley (strategy 2). In contrast, Nikolic's group has obtained opposite experimental evidence for maize plants (Fig. 8.5), even though this information is preliminary.

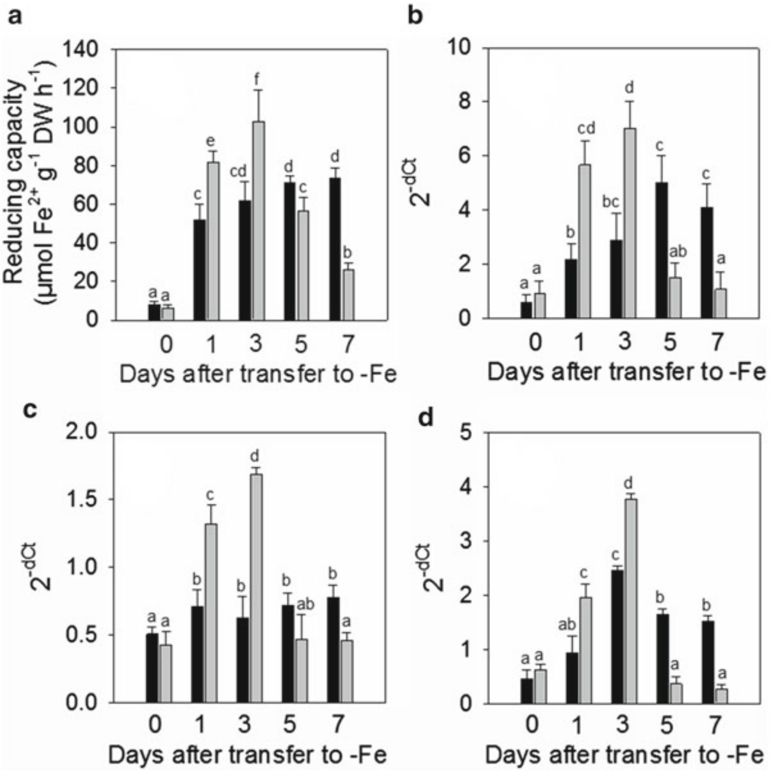


Fig. 8.4 Effect of Si supply on Fe-deficiency responses of cucumber roots during 7 days of Fe deprivation (From Pavlovic et al. 2013). FRO activity (**a**); *FRO2* relative expression (**b**); *IRT1* relative expression (**c**); *AHA1* relative expression (**d**). –Si (*black bars*); +Si (*grey bars*). Plants were pre-cultured in complete nutrient solution (10 µM Fe) –Si or + Si (1.5 mM) for 7 days and then transferred to Fe-free nutrient solution –Si or + Si (1.5 mM)

Although still in progress, these findings provide not only new evidence for the manifold beneficial role of Si in plant nutrition but, in perspective, can also be of practical importance in the development of new sustainable strategies for controlling Fe chlorosis in calcareous soils, which in general are low in available Si (Liang et al. 1994).

8.4 Excess of Nitrogen and Phosphorus

Overall, supply of Si is, in particular, of importance for the cultivation systems with dense planting and high nitrogen (N) application. To attain high yields, modern crop cultivars require large amounts of N fertilizers. However, excess N causes lodging, mutual shading and susceptibility to biotic stresses. Lodging is a major constraint to

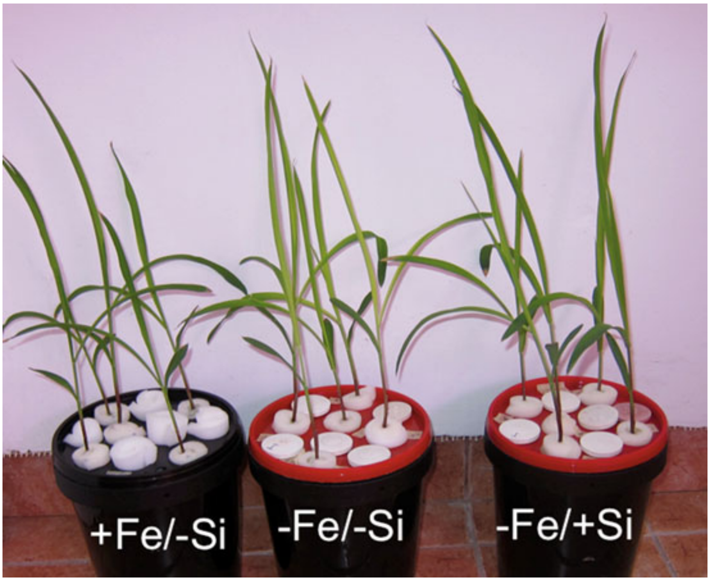


Fig. 8.5 Root application of Si mitigates symptoms of Fe-deficiency chlorosis in maize, Si-accumulating, Fe-strategy 2 species (Photograph by Dragana Nikolic)

rice production, especially in high-yielding cultivars, because it causes loss in grain yield and quality and has some indirect effects such as hindering harvesting operation (Fallah 2012). Deposition of silica in rice increases the thickness of the culm wall and the size of the vascular bundle, preventing lodging during typhoons in Japan (Ma et al. 2001). A lodging-resistant wheat cultivar has been shown to have a higher Si content in the culm epidermis than a lodging-sensitive one (Gartner and Paris-Pireyre 1984). Supply of Si counteracts the negative effects of an increasing nitrogen supply on stalk stability and lodging susceptibility of rice (Sadanandan and Varghes 1968; Idris et al. 1975; Balasta et al. 1989, also see Fig. 8.6). Also in dicotyledonous species, such as cucumber, Si increases the rigidity of mature leaves, which are held more horizontally, increases their chlorophyll content and delays their senescence (Adatia and Besford 1986). Leaf erectness is an important factor affecting light interception in dense plant stands. In rice, leaf erectness decreases with increasing N supply, while Si increases leaf erectness (Fig. 8.7) and thus to a large extent counteracts the negative effects of high N supply on light interception (Marschner 1995). The occurrence of blast disease is significantly inhibited by Si application in over-fertilized rice field (Ohyama 1985). These aspects are discussed in more detail in Chap. 9. Excessive application of N fertilizers also results in increase of protein content in rice, and thus adequate supply of Si is important in producing low-protein rice (Morimiya 1996).

Excess P stress can hardly occur in natural soils but was observed in some greenhouse soils where P fertilizer had been heavily applied or in hydroponic culture where a high P concentration was supplied (Ma 2004). It is well known that excess

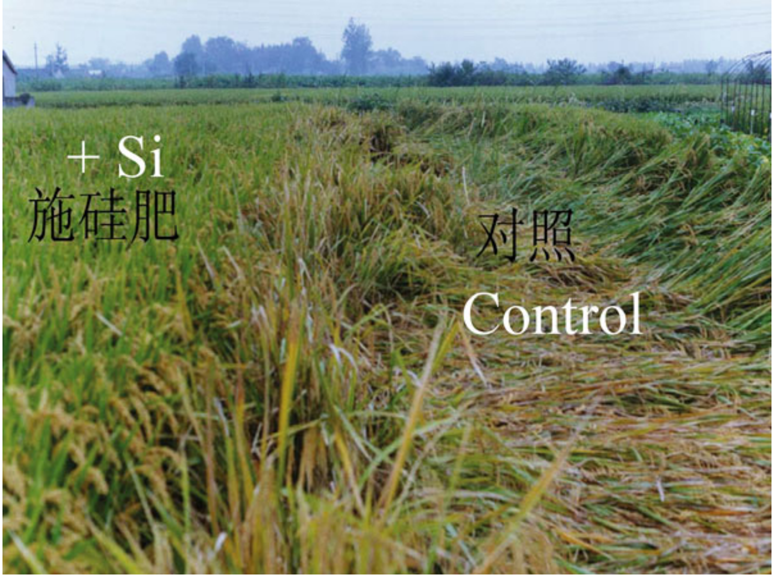
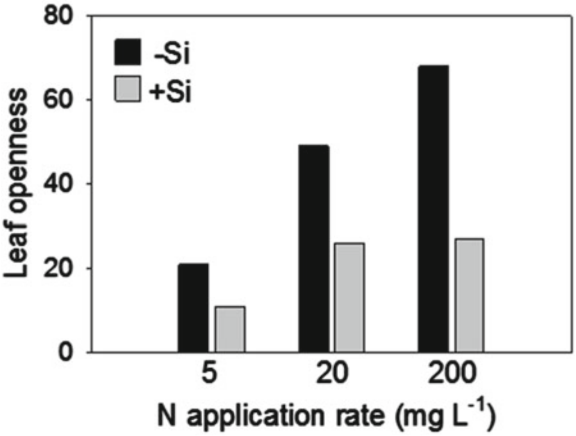


Fig. 8.6 Beneficial effect of Si fertilization on resistance against rice lodging in a calcareous paddy soil amended with heavy nitrogen (Photography by Yongchao Liang)

Fig. 8.7 Effect of Si supply of 3 mM on the leaf erectness (expressed as leaf openness; angle between the culm and the lamina) in rice plants at flowering grown at different *N* levels. Means of three rice cultivars recalculated from data of Yoshida (1969)



P might lead to P-induced Zn deficiency showing typical symptoms like leaf chlorosis and necrosis (Cakmak and Marschner 1987). In cucumber, application of Si alleviated the symptoms caused by P excess, resulting in an increase in the proportion of water-soluble to total Zn and an avoidance of toxic P accumulation (Marschner et al. 1990). Also, Marschner et al. (1990) demonstrated that a reduction of P supply as well as an increase in Zn supply prevented this disorder. They postulated that Si supply might increase Zn availability within the leaves and in particular in the leaf apoplast. However, an increase in the ratio of water-soluble to total Zn content by Si application has not been confirmed in the experiments of Rogalla (2001). Therefore, Si-mediated increase in internal Zn availability seems to be achieved only under very specific conditions (Wiese et al. 2007). Another explanation is that Si deposited in the endodermal cells of roots (e.g. Lux et al. 2003) may form apoplastic barriers against the radial movement of P across the root, thus decreasing the excessive uptake of P when the P concentration in the medium is high (Ma 2004). The Si-induced decrease of P uptake has been observed not only in rice (Ma and Takahashi 1990a) but also in some Si non-accumulating plants such as tomato, soybean, strawberry (*Fragaria vesca*) and cucumber (*Cucumis sativus*) (Ma et al. 2001 and references therein).

8.5 UV Radiation

The depletion of the stratospheric ozone layer is leading to more solar ultraviolet B (UV-B) radiation reaching the Earth (Madronich et al. 1998). In general, UV-B negatively affects plant cells, causing generation of ROS such as superoxide anion radicals (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals (·OH) and singlet oxygen (O_2). However, some plant species were unaffected, while in several species UV-B showed even stimulating effects on plant growth (Kakani et al. 2003). Plant sensitivity to UV radiation stress was influenced by water regime and nutrient status (Balakumar et al. 1993). Drought stress has been considered an important environmental factor to induce plant sensitivity to UV radiation (Alexieva et al. 2001). Under the exposure to high UV radiation, plants increase biosynthesis of phenolic compounds to absorb UV by the presence of carbonyl and hydroxyl groups, hence directly protecting their internal tissues from injury (Rozema et al. 1997; Winkel-Shirley 2002; Treutter 2005).

It is well documented that enhanced Si supply lowers stress induced by UV-B radiation in different plant species, including rice, soybean and wheat (Goto et al. 2003; Li et al. 2004; Fang et al. 2011; Shen et al. 2010; Yao et al. 2011). In leaves, Si is deposited in the space immediately beneath the cuticle layer, forming a cuticle–Si double layer in leaf blades (Hodson and Sangster 1988; Ma and Yamaji 2006; Currie and Perry 2007; Schaller et al. 2012). Such Si double layer may act like a glass layer and decrease the further transmission of UV radiation from the epidermis (Gatto et al. 1998). It still remains unclear whether the protective role of Si is associated with the plant's ability to increase formation of Si double layer in response to the UV-B or only a side effect of species-specific variations of Si accumulated in plants. Also, the role of Si in the metabolic response to UV radiation stress such as biosynthesis of low-molecular-weight UV-absorbing compounds (e.g. phenolic acids and flavonoids) is still not clear. For instance, Goto et al. (2003) reported that Si application increased Si deposits in rice leaves, but decreased cinnamyl alcohol hydrogenase activity and accumulation of ferulic and p-coumaric

Table 8.2 Effect of Si supply on chlorophyll content, net photosynthetic rate (*Ps*), lipid peroxidation, catalase (CAT) activity and H_2O_2 concentration in leaves of soybean exposed to high UV-B radiation

Treatment		Chlorophyll (mg g^{-1} fw)	*Ps* (μmol CO_2 m^{-2} s^{-1})	Lipid peroxidation (MDA nmol g^{-1} fw)	H_2O_2 (μmol g^{-1} fw)	CAT (u g^{-1} fw min^{-1})
Control	−Si	1.6	8.7	0.4	220	24
	+Si	1.8	9.2	0.5	240	26
UV	−Si	0.2	2.6	0.9	490	98
	+Si	1.4	3.0	0.6	360	36

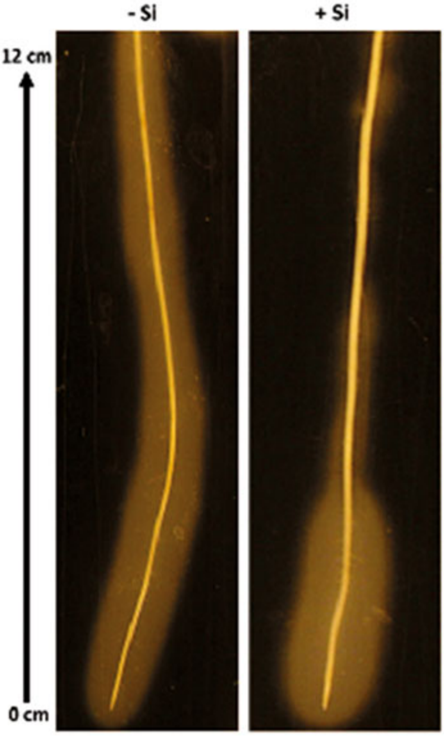
Based on Shen et al. (2010)

acids in leaf blades. Thus, Si-treated rice plants had lower UV absorbance around 320 nm via carbonyl groups or conjugated carbonyls of phenolic acids in the most cell types of leaf blades. It is possible that Si acts indirectly by enhancement of antioxidative enzyme activities and thereby contributes to higher ROS consumption. Furthermore, the experiment of Shen et al. (2010) showed that application of Si decreased lipid peroxidation, activities of the antioxidative enzymes and generation of H_2O_2 in soybean seedlings subjected to UV-B radiation stress (Table 8.2). Therefore, UV absorption due to the optical properties of accumulated Si might be an advantage with respect to the energy demand for producing UV-absorbing substances, as the alternative protection measure against UV radiation (Schaller et al. 2013).

8.6 Flooding

Despite the fact that rice normally grows under anaerobic soil conditions, the exact role of Si in alleviating flooding stress is still unclear. Wetland plants possess diverse anatomical, morphological and physiological features that maintain aerobic metabolism and growth and thereby survival in waterlogged soils under anaerobic and reductive conditions. Rice, like other wetland species, is adapted to a low-oxygen environment by the internal aeration of root via the aerenchyma, which provides a low-resistance pathway for the diffusion of oxygen within the root (Colmer 2003, 2006). To counteract the diffusion of oxygen from the root to the anaerobic rhizosphere, rice roots contain higher amounts of suberin and lignin in the outer root parts, forming a stronger barrier to radial oxygen loss (Kotula et al. 2009). Lignin and suberin metabolism in plants shares the phenylpropanoid pathway. Parts of this metabolic pathway were enhanced by Si supply in plants subjected to various stresses (e.g. Kidd et al. 2001; Cai et al. 2008; Führs et al. 2009; Pavlovic et al. 2013). The effects of Si on rice root anatomy (e.g. development of casparian bands in the exodermis and endodermis), and on the transcription of genes related to suberin and lignin biosynthesis, have recently been demonstrated (Fleck et al. 2011).

Fig. 8.8 Effect of Si supply on the oxidation power of adventitious rice roots (From Fleck et al. 2011)



In addition, under reductive conditions of flooded soils, the concentrations of readily available Fe(II) and Mn(II) are high, and plants can suffer from Fe and/or Mn toxicity (Marschner 1995). Silicon nutrition of rice plants also increased the oxidation power of submerged roots (Fig. 8.8), leading to an oxidation of Fe^{2+} and Mn^{2+} ions and their subsequent precipitation on the root surface, thereby decreasing Fe and Mn uptake (Okuda and Takahashi 1961). In plant tissues, excess Fe and Mn can induce production of ROS through nonenzymatic Fenton-like reaction (for details see Chap. 5). Indeed, under conditions of soil flooding, the application of Si decreases the intensity of ROS destruction in barley roots, however without significant changes in the activities of antioxidant enzymes (Balakhnina et al. 2012).

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