

Abiotic stress series

Silicon uptake and accumulation in higher plants

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Silicon (Si) accumulation differs greatly between plant species because of differences in Si uptake by the roots. Recently, a gene encoding a Si uptake transporter in rice, a typical Si-accumulating plant, was isolated. The beneficial effects of Si are mainly associated with its high deposition in plant tissues, enhancing their strength and rigidity. However, Si might play an active role in enhancing host resistance to plant diseases by stimulating defense reaction mechanisms. Because many plants are not able to accumulate Si at high enough levels to be beneficial, genetically manipulating the Si uptake capacity of the root might help plants to accumulate more Si and, hence, improve their ability to overcome biotic and abiotic stresses.

A brief history of silicon in plants

Silicon (Si) is the second most abundant element after oxygen in soil. Silicon dioxide comprises 50–70% of the soil mass. As a consequence, all plants rooting in soil contain some Si in their tissues. However, the role of Si in plant growth and development was overlooked until the beginning of the 20th century [1–3]. Because of the abundance of the element in nature and because visible symptoms of either Si deficiency or toxicity are not apparent, plant physiologists largely ignored it. However, repeated cropping and the constant application of chemical fertilizers such as nitrogen, phosphorus and potassium have depleted the amount of Si that is available to plants in the soil. An awareness of Si deficiency in soil is now recognized as being a limiting factor for crop production, particularly in soils that are deemed to be low or limiting in plant available Si and for known Si-accumulating plants such as rice and sugarcane. Today, Si still is not recognized as an essential element for plant growth but the beneficial effects of this element on the growth, development, yield and disease resistance have been observed in a wide variety of plant species [4]. Si fertilizers are routinely applied to several crops including rice and sugarcane to enhance high and sustainable crop yields. This review describes the progress in understanding the uptake and accumulation of Si, a gene recently identified in Si uptake in rice, and its important role in enhancing plant stress resistance.

Uptake, translocation and accumulation of silicon

Silicon is taken up by the roots in the form of silicic acid [$\text{Si}(\text{OH})_4$], an uncharged monomeric molecule, when the solution pH is below 9 (Figure 1) [2]. Plants differ greatly in their ability to accumulate Si, ranging from 0.1% to 10.0% Si (dry weight) [1–3]. Within the angiosperms, species from the commelinoid monocot orders Poales and Arecales accumulate substantially more Si in their shoots than do species from other monocot clades [2]. Among Poales, species from the *Gramineae* and *Cyperaceae* families accumulate high levels of Si [2]. Most plants, particularly dicots, are unable to accumulate high levels of Si in their shoots. The difference in Si accumulation between species has been attributed to differences in the Si uptake ability of the roots [2].

The uptake mechanisms differ between plant species. In a study using rice, cucumber and tomato, species that accumulate high, medium and low levels of Si, respectively, it was found that transportation of Si from the external solution to the cortical cells is mediated by a similar transporter with a K_m value of 0.15 mM in all three species [5]. However, the V_{max} differs with plant species (i.e. rice > cucumber > tomato), suggesting that the density of the transporter differs among plant species. It seems that this transport process is energy dependent because metabolic inhibitors and low temperature inhibit transport [5]. At the next step in the process – the transport of Si from cortical cells to the xylem (xylem loading) – the Si concentration in the xylem sap is much higher in rice than it is in cucumber and tomato. Furthermore, unlike in rice, where xylem loading of Si is mediated by a kind of transporter, xylem loading is mediated by diffusion in cucumber and tomato. These results indicate that xylem loading is the most important determinant for a high level of Si to accumulate in rice shoots. The much lower accumulation of Si in cucumber and tomato might be explained by a lower density of the transporter to transport Si from the external solution to the cortical cells, and a defective or absence of transporter to transport Si from cortical cells to the xylem.

Following uptake by the roots, Si is translocated to the shoot via the xylem. Chemically, silicic acid polymerizes to form silica gel ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$) when the concentration of silicic acid exceeds 2 mM. However, the concentration of Si in the xylem sap is usually much higher than 2 mM in rice and wheat, even though the major form of Si in the xylem has been identified as monomeric silicic acid in these plant species (Figure 1) [6,7]. It seems that a high

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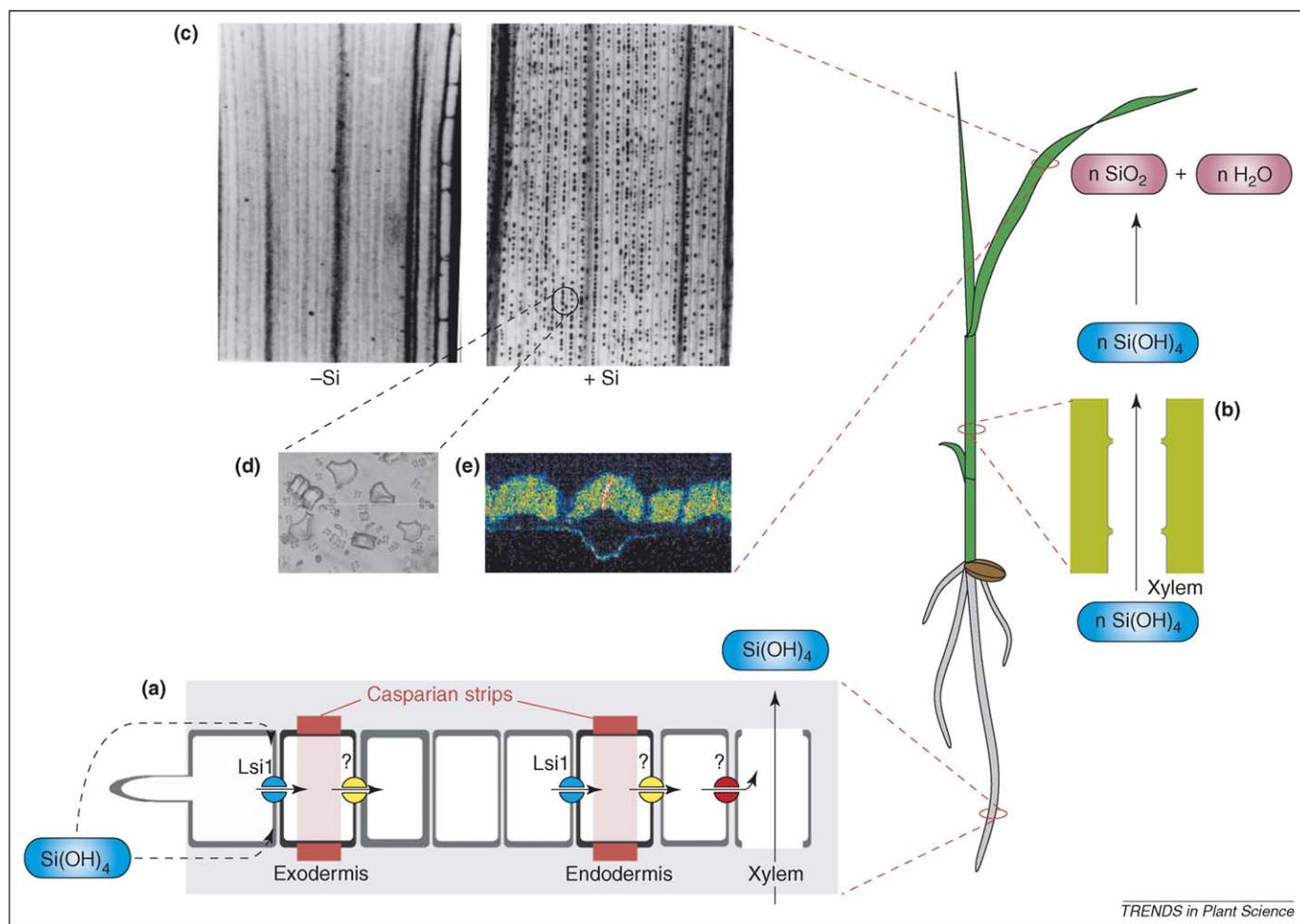


Figure 1. Uptake, distribution and accumulation of silicon (Si) in rice. Si is taken up via transporters in the form of silicic acid (a) and then translocated to the shoot in the same form (b). In the shoot, Si is polymerized into silica and deposited in the bulliform cells (silica body) (c,d) and under the cuticle (e). (c) Silicon detected by soft X-ray and (e) by SEM.

concentration of silicic acid is transiently present in the xylem sap because it starts to polymerize *in vitro* [7].

In the shoot, silicic acid is further concentrated through loss of water (transpiration) and is polymerized. The process of Si polymerization converts silicic acid to colloidal silicic acid and finally to silica gel with increasing silicic acid concentration [2]. In rice plants, >90% of total Si in the shoot is present in the form of silica gel, whereas the concentration of colloidal plus monomeric Si is kept below $140\text{--}230\text{ mg Si l}^{-1}$. A similar pattern of accumulation is observed in cucumber leaves, although the total Si concentration of cucumber is much lower than that of rice. The distribution of Si in the shoot is controlled by transpiration. More Si accumulates in older tissues because this element is not mobile within the plants.

Silicon is deposited as a $2.5\text{ }\mu\text{m}$ layer in the space immediately beneath the thin ($0.1\text{ }\mu\text{m}$) cuticle layer, forming a cuticle–Si double layer in leaf blades of rice (Figure 1) [2]. There are two types of silicified cells in rice leaf blades: silica cells, and silica bodies or silica motor cells (Figure 1) [2]. Silica cells are located on vascular bundles and are dumbbell-like in shape, whereas silica bodies are in bulliform cells of rice leaves. The silicification of cells proceeds from silica cells to silica bodies. In addition to leaf blades, silicified cells are also observed in the epidermis and

vascular tissues of the stem, leaf sheath and hull. These depositions of Si protect plants from multiple abiotic and biotic stresses. The silicified cells also provide useful palaeoecological and archaeological information known as plant opal or phytoliths [8].

Gene that controls silicon uptake in rice

Rice is a typical Si-accumulating plant – Si can make up to 10% of the shoot dry weight, which is several-fold higher than those of essential macronutrients such as N, P and K [2]. High levels of Si in rice tissues are attributed to the superior ability of the roots to take up this element. Physiological studies have shown that rice takes up Si actively; the uptake is much faster than that of water and is not affected by transpiration [2,9]. Among gramineous species, the ability of rice roots to take up Si is much higher than that of other gramineous species including barley, maize, rye, sorghum and wheat [10]. Therefore, a specific uptake system has been proposed to exist in rice that facilitates the transport of silicic acid across the plasma membrane. However, the molecular mechanisms underlying the system of Si uptake in rice are still poorly understood and genes responsible for Si uptake have not been identified so far in higher plants. A gene family encoding Si transporters has been identified in the marine diatom *Cylindrotheca*

fusiformis, which requires Si as an essential element [11,12]. However, there is no homolog of this gene in the rice genome. Furthermore, introducing one of the diatom Si transporter genes into tobacco did not increase Si uptake in tobacco, indicating that the Si uptake system in higher plants is different from that in diatoms.

Recently, a gene (*Lsi1*) that is responsible for active Si uptake has been identified from rice. This gene was cloned by using a rice mutant that is defective in Si uptake [13]. The gene is localized on chromosome 2 and comprises five exons and four introns [14,15]. The cDNA of this gene was 1409 bp and the deduced protein comprised 298 amino acids.

The gene is predicted to encode a membrane protein similar to aquaporins, the water channel proteins. The predicted amino acid sequence has six transmembrane domains and two Asn-Pro-Ala (NPA) motifs, which are well conserved in typical aquaporins (Figure 2a). Blast search and ClustalW analysis have revealed that *Lsi1* belongs to a Nod26-like major intrinsic protein (NIP) sub-family. There are three close homologs in maize (*ZmNIP2-1*, *ZmNIP2-2* and *ZmNIP2-3*) with 77–83% identity and one

homolog in rice (*Os06g12310*, named *Lsi6*) with 77% identity (Figure 2b).

Lsi1 is mainly expressed in the roots – supplying Si decreases its expression by a fourth. Interestingly, *Lsi1* is expressed in the main roots and lateral roots but not in root hairs (Figure 2c,d). This is consistent with the results of a previous physiological study that showed that root hairs do not play any demonstrable role in Si uptake, but that lateral roots contribute significantly to Si uptake [16]. Further investigations showed that the transport protein is localized on the plasma membrane of the distal side of both the exodermis and endodermis cells (Figure 2e), where Casparian strips exist. Because solutes are unable to pass through Casparian strips freely, transporters are needed to reach the stele for translocation from the roots to the shoot. When this gene is suppressed, Si uptake is also correspondingly reduced [15]. Furthermore, when the cRNA encoding *Lsi1* was injected into *Xenopus laevis* oocytes, an increased level of silicic acid transport activity was observed. All this evidence demonstrates that *Lsi1* is a major transporter of Si into rice roots.

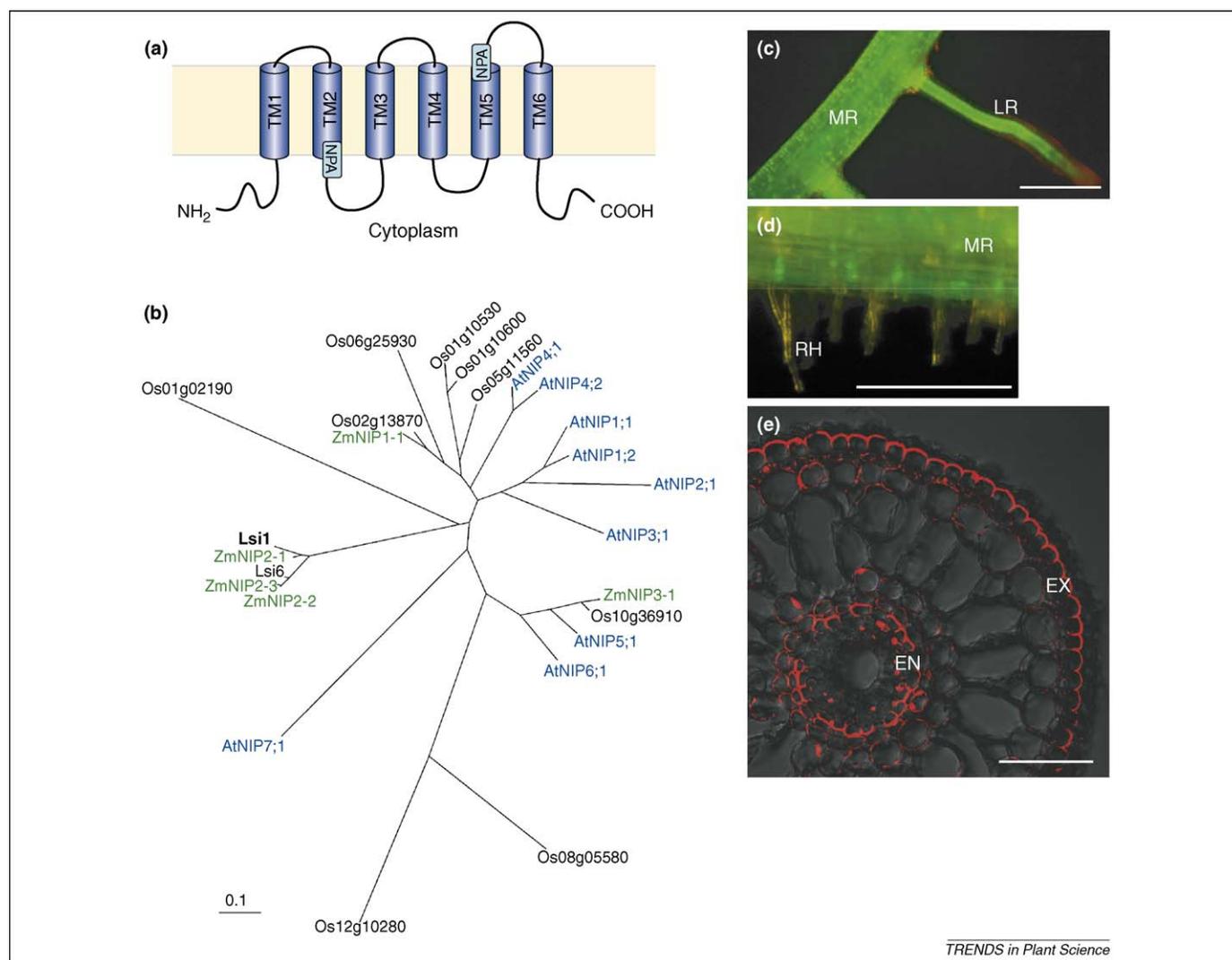


Figure 2. The *Lsi1* gene controlling silicon (Si) uptake in rice. (a) *Lsi1* is predicted to encode a plasma membrane protein with a six transmembrane domain. (b) Phylogenetic relationship of *Lsi1* proteins in rice (black), *Arabidopsis* (blue) and maize (green). (c,d) Localization of *Lsi1* in roots: main root (MR), lateral root (LR), root hair (RH). Scale bars = 500 μ m. (e) Subcellular localization of *Lsi1*. Cross section was stained with an antibody of *Lsi1*: endodermis (EN) and exodermis (EX). Scale bar = 50 μ m.

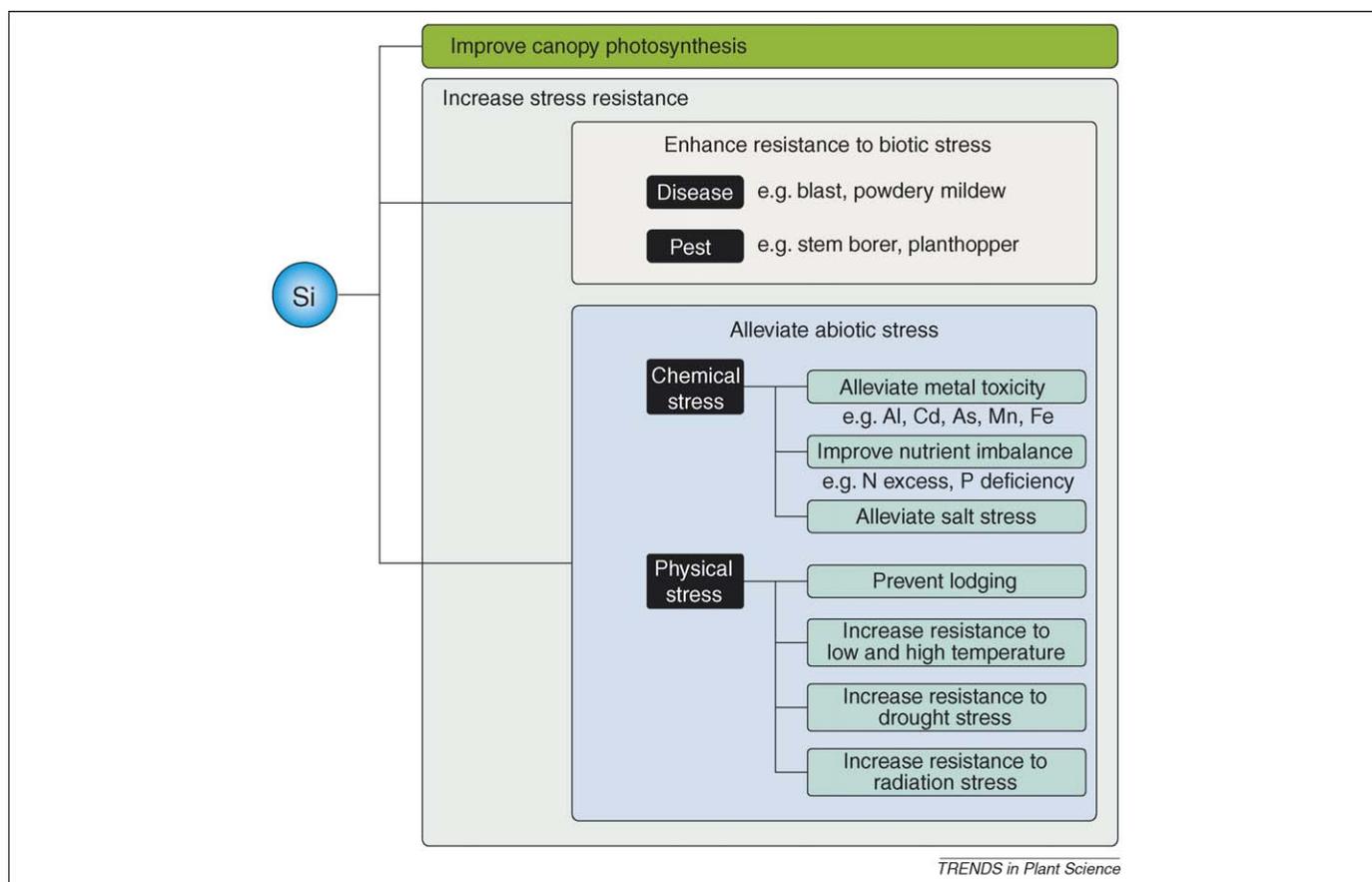


Figure 3. Beneficial effects of silicon on plant growth in relation to biotic and abiotic stresses.

Role of silicon in stress resistance

The beneficial effect of Si is more evident under stress conditions [2]. This is because Si is able to protect plants from multiple abiotic and biotic stresses (Figure 3). Numerous studies have shown that Si is effective in controlling diseases caused by both fungi and bacteria in different plant species. For example, Si increases rice resistance to leaf and neck blast, sheath blight, brown spot, leaf scald and stem rot [L.E. Datnoff and F.Á. Rodrigues (2005) *The Role of Silicon in Suppressing Rice Diseases*, APSnet feature <http://www.apsnet.org/online/feature/silicon/> [17,18]. Silicon also decreases the incidence of powdery mildew in cucumber, barley and wheat; ring spot in sugarcane; rust in cowpea; leaf spot in Bermuda grass (*Cynodon dactylon*) and gray leaf spot in St. Augustine grass (*Stenotaphrum secundatum*) and perennial ryegrass [18]. In a well-studied rice–*Magnaporthe grisea* pathosystem, the incubation period was lengthened by Si accumulation, whereas lesion length, rate of lesion expansion, and disease leaf area dramatically decreased [19].

Two mechanisms for Si-enhanced resistance to diseases have been proposed. One is that Si acts as a physical barrier. Si is deposited beneath the cuticle to form a cuticle–Si double layer [17]. This layer can mechanically impede penetration by fungi and, thereby, disrupt the infection process. Another mechanism proposed recently is that soluble Si acts as a modulator of host resistance to pathogens. Several studies in monocots (rice and wheat) and dicots (cucumber) have shown that plants supplied with Si can produce phenolics and phytoalexins in response to

fungal infection such as those causing rice blast and powdery mildew [20–23]. Silicon is also able to activate some defence mechanisms. For example, in roots of cucumber plants being infected and colonized by *Pythium*, Si enhanced the activity of chitinases, peroxidases and polyphenoloxidases [24]. In rice, differential accumulation of glucanase, peroxidase and PR-1 transcripts were associated with limited colonization by the fungus *M. grisea* in epidermal cells of a susceptible rice cultivar supplied with Si [25]. These biochemical responses are only induced by soluble Si, suggesting that soluble Si might play an active role in enhancing host resistance to diseases by stimulating some mechanisms of the defense reaction [17]. However, the exact nature of the interaction between the soluble Si and the biochemical pathways of the plant that leads to disease resistance remains unknown, although several possible mechanisms have been proposed [17]. A recent study shows that during the induction of systemic acquired resistance (SAR) in cucumber, the expression of a gene encoding a novel proline-rich protein was enhanced [26]. This protein has C-terminal repetitive sequences containing an unusually high amount of lysine and arginine. The synthetic peptide derived from the repetitive sequences was able to polymerize orthosilicic acid to insoluble silica, which is known to be involved in cell wall reinforcement at the site of the attempted penetration of fungi into epidermal cells. This study provided a biochemical and molecular basis for Si-enhanced disease resistance.

Silicon also enhances plant resistance to insect pests such as stem borer and planthopper [2]. This Si-enhanced

effect is attributed to Si deposition in the plant tissues, which provides a mechanical barrier against probing and chewing by insects.

Silicon also alleviates many abiotic stresses including chemical stress (salt, metal toxicity, nutrient imbalance) and physical stress (lodging, drought, radiation, high temperature, freezing, UV) and many others (Figure 3) [1–4]. Most of these beneficial effects are also attributed to Si deposition in cell walls of roots, leaves, stems and hulls. For example, deposition of Si in the roots reduces apoplastic bypass flow and provides binding sites for metals, resulting in decreased uptake and translocation of toxic metals and salts from the roots to the shoots. Deposition of Si in the culms, leaves and hulls enhances the strength and rigidity of cell walls and decreases transpiration from the cuticle and, thus, increases the resistance to lodging, low and high temperature, radiation, UV and drought stresses. Under drought and salt stresses, Si-alleviated effects have been associated with an increase in antioxidant defense abilities [27–29]. However, this might be a beneficial result of Si as opposed to a direct effect because it is unlikely that Si affects the activity of antioxidant enzymes.

In addition to the role of Si in alleviating various stresses, Si improves light interception by keeping leaves erect, thereby stimulating canopy photosynthesis in rice (Figure 3) [2]. This is particularly important in dense plant stands and when nitrogen fertilizers are heavily applied so as to minimize mutual shading. It has been reported that Si promotes cell elongation but not cell division, probably as a result of Si-enhanced extensibility of the cell wall in rice [30]. Recently, it was found that Si increased the extensibility of the cell wall in the growing zone and decreased cell-wall extensibility in the basal zone of isolated stellar tissues covered by endodermal inner tangential walls in the roots of sorghum, implying that Si has a role in enhancing root elongation and in protecting the stele as a mechanical barrier by hardening the cell wall of the stele and endodermal tissues [31,32].

Plants growing in the field are constantly subjected to an array of stresses that Si might alleviate. Plants that accumulate large quantities of Si benefit the most because this element enhances stress resistance. If plants are to benefit from Si they must be able to acquire the element in high concentrations regardless of whether they are monocots or dicots. This is particularly important for plants accumulating high levels of Si such as rice and sugarcane. For example, a high level of Si accumulation is required for growth and for the production of a high and sustainable yield of rice. Low Si accumulation results in a significant reduction in rice yield and quality (Figure 4).

Future prospects

Silicon accumulation in plants is controlled by the ability of roots to take up Si. Silicon uptake is probably a complicated process and might be controlled by multiple genes in rice. Subcellular localization of *Lsi1* shows that this transporter appears to be responsible for the transport of Si from an external solution to the root cell. Therefore, there is a possibility that genes responsible for Si efflux exist and these should be cloned and characterized in the near future. Some gramineous plants such as maize and wheat



Figure 4. Effect of silicon (Si) on rice growth and yield. (a) Rice with low levels of Si is susceptible to insect attack; (b) a low level of Si accumulation results in grain discoloration owing to infection by multiple fungal pathogens. The Si content of 'Low Si' rice is 0.48% in the shoot and 1.44% in the hull; the Si content of 'High Si' rice is 4.21% in the shoot and 8.05% in the hull.

also accumulate Si, although at a lower level compared with that of rice. Unfortunately, molecular mechanisms underlying Si uptake in these plants are unknown and, hence, Si uptake genes in other gramineous plant species need to be isolated and characterized. Furthermore, given that most plants, particularly dicots, cannot accumulate Si in large enough amounts to be beneficial, genetically manipulating the Si uptake capacity of the roots might help plants to accumulate more Si and, hence, more able to overcome both biotic and abiotic stresses.

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