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Benefits of plant silicon for crops: a review

Flore Guntzer · Catherine Keller ·
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Abstract Since the beginning of the nineteenth century, silicon (Si) has been found in significant concentrations in plants. Despite the abundant literature which demonstrates its benefits in agriculture, Si is generally not considered as an essential element. The integration of Si in agricultural practices is, however, effective in a few countries. Silicon fertilization by natural silicates has the potential to mitigate environmental stresses and soil nutrient depletion and as a consequence is an alternative to the extensive use of phytosanitary and NPK fertilizers for maintaining sustainable agriculture. This review focuses on recent advances on the mechanisms of Si accumulation in plants and its behavior in soil. Seven among the ten most important crops are considered to be Si accumulators, with concentration of Si above 1% dry weight. New approaches using isotopes and genetics have highlighted the mechanisms of uptake and transfer of Si *in planta*. There is a general agreement on an uptake of dissolved silica as H_4SiO_4 and precipitation as amorphous silica particles (the so-called phytoliths), but the mechanism, either active or passive, is still a matter of debate. The benefits of Si are well demonstrated when plants are exposed to abiotic and biotic stresses. The defense mechanisms provided by Si are far from being understood, but evidences for *ex planta* and *in planta* processes are given indicating multiple combined effects rather than one single effect. Phytoliths that are located mainly in shoots of monocots return to the soil through litterfall if the plants are not harvested and contribute to the biogeochemical cycle of Si. According to recent progress made on the understanding of the biogeochemical cycle of Si and the weathering process of silicate minerals, phytoliths may significantly contribute to the resupply of Si to plants. We suggest that straw of crops, which

contains large amounts of phytoliths, should be recycled in order to limit the depletion of soil bioavailable Si.

Keywords Nutrient cycling · Silica · Phytoliths · Wheat · Cereal · Environmental stress

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1 Introduction

Silicon is a major constituent of the Earth's crust, forming the silicate minerals. In soils, these minerals undergo chemical and physical weathering, resulting in the release of Si in solution, which is either combined with other elements to form clay minerals or released toward the streams and the oceans or absorbed by the vegetation. The

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impact of plant Si on soil development was firstly illustrated by Lovering and Engel (1959) who calculated that 1 ha of forest could extract nearly 5,000 tons of Si in 5,000 years, which is equivalent to a 30-cm-thick basalt layer. During litter decomposition, plant Si is re-injected into the soil and can constitute an important pool of Si in soil (Lucas et al. 1993). Conley (2002) estimated that the annual amount of silica stored in plants (60–200 Tmol/year) is of the same order of magnitude as the amount of Si fixed by diatoms in the oceans (240 Tmol/year). The amount of Si accumulated by plants is therefore a significant parameter in the natural functioning of soil development and in controlling the continental erosion rates.

In agronomy, Si is generally not considered an essential element. It is also currently assumed that Si is not limiting in soils. However, crops can take up Si at a much faster rate than in natural systems: 300 kg ha⁻¹ year⁻¹ for sugar cane (Meyer and Keeping 2001) and 500 kg ha⁻¹ year⁻¹ for rice (Makabe et al. 2009) compared with 41–67 kg ha⁻¹ year⁻¹ for tropical forests (Lucas et al. 1993; Alexandre et al. 1997), 22–67 kg ha⁻¹ year⁻¹ for US grasslands (Blecker et al. 2006), and 2.3–44 kg ha⁻¹ year⁻¹ for temperate forests (Bartoli 1983; Gérard et al. 2008; Cornelis et al. 2010). Matichenkov and Bocharnikova (2001) calculated that 210–224 million tons of Si are removed from cultivated soil every year. This figure is of the same order of magnitude as the annual flux of dissolved silica from rivers to oceans (Berner and Berner 1996) and shows that agriculture may have a significant impact at a global scale. Indeed, Savant et al. (1997a) suggested that the non-reincorporation of the straw to the field may lead to a depletion of plant-available Si in soils with a decline of cereal yields. The objective of this paper was to review recent advances on the mechanisms of Si uptake, transfer, and accumulation by crops as well as the role of plant Si on yields.

2 The lights and shadows of Si in crops

2.1 Variability and essentiality

As early as 1804, de Saussure (1804) analyzed Si in the ashes of plants and concluded that Si concentration in plants varied according to species, with higher amounts in Gramineae. Indeed, Si concentration in plants offers a large variability, ranging from 0.1% to 10% dry weight, depending on species (Epstein 1999; Hodson et al. 2005). The species which are the richest in Si are monocots. Dicots are generally poorer, but there are exceptions. Sangster et al. (2001) indicate that the following families show silicification processes:

- Among dicots: some Fabaceae (e.g., pea), Cucurbitaceae (e.g., cucumber), Rosales (e.g., elm), and Asteraceae (e.g. sunflower)

- Among monocots: Cyperaceae (e.g., sedge) and Gramineae (e.g., wheat)

Even if significant levels of Si are found in very different plants, Sangster (1978) and Hodson et al. (2005) consider that Si concentration in plants depends primarily on the phylogenetic position of the plant, more than on its environment (i.e., Si concentration in the soil and the soil solution, pH). Ma and Takahashi (2002) give the following explanation: unlike other elements, Si is abundant in nearly all soils, so environmental criteria do not impact Si accumulation in plants. The same authors present a phylogenetic tree of Si-accumulating plants and note that Si-rich species have generally low calcium concentrations, and vice versa. They propose criteria to differentiate non-accumulating plants from accumulating plants:

- “Accumulators” have a Si concentration over 1% and a [Si]/[Ca] ratio >1.
- “Excluders” have a Si concentration below 0.5% and a [Si]/[Ca] ratio <0.5.
- Plants that do not meet these criteria are called “intermediates.”

The critical value of 0.5% is considered to be the Si concentration obtained in a plant which would absorb 0.5 L of a solution containing 10 mg Si L⁻¹ and produce 1 g of dry matter. In addition, there are large differences among genotypes within the same species (Deren 2001). Several data compilations have reported the extent of this variation (Hodson et al. 2005; Ma and Takahashi 2002). However, a given species or cultivar grown in various Si concentrations will absorb different amounts of Si, as shown in banana, rice, or tomato (Henriet et al. 2006; Ma and Takahashi 2002). Thus, even though Si accumulation is a phylogenetic feature, the availability of Si will influence the amount of Si absorbed by plants.

The question of the essentiality of Si in plants was first highlighted by Sachs (1862): observing that two corn plants with respectively 0.3% and 9% Si in the shoot ashes showed no difference in their growth, he concluded that Si was not essential. In 1906, Hall and Morison (1906) raised the question of the role of Si in plants, doubting that an element forming up to 60% of the wheat ash had no metabolic role. More recently, Epstein (1994) found that the non-essentiality of Si had not been proven because of the difficulty to remove entirely Si from experimental nutrient solutions and thus obtain control plants. He suggested Si to be “quasi-essential for many of those plants for which its absolute essentiality has not been established.” Since the reviews by Epstein (1994, 1999), many studies have been conducted on the mechanisms of Si uptake, transport, and accumulation in plants that are useful to discuss the concept of Si essentiality.

Seven out of the ten most produced crops in the world (ranked by quantity) are accumulators (Table 1): understanding the role of Si in crop production is therefore a matter of

Table 1 Si concentration of some of the most important crops ranked by production

Name	Production (MT) ^a	Si concentration in shoots (% DW)	
Sugar cane	1.736	<i>Saccharum officinarum</i> ^b	1.509
Maize	826	<i>Zea mays</i> ^b	0.827
Rice paddy	686	<i>Oryza sativa</i> ^b	4.167
Wheat	683	<i>Triticum aestivum</i> ^b	2.455
Potatoes	326	Solanaceae ^c	0.4
Cassava	232	— ^d	0.5
Soybeans	231	<i>Glycine max</i> ^b	1.399
Sugar beet	222	Malpighiales ^c	2.34–7
Barley	155	<i>Hordeum vulgare</i> ^b	1.824
Tomatoes	136	<i>Lycopersicon esculentum</i> ^b	1.55

^a Source: FAO for 2008 at <http://faostat.fao.org/site/339/default.aspx>

^b Data compiled by Hodson et al. (2005)

^c Average estimated from the data compiled by Hodson et al. (2005)

^d Average estimated from the data compiled by Hodson et al. (2005)

^e Source: Draycott (2006)

global concern and justifies studies on mechanisms controlling Si uptake by plants both in the soil and *in planta*.

2.2 Root uptake

In soil solution and natural waters, pH is generally under 9.5, and Si is mainly present as uncharged monomeric orthosilicic acid, H₄SiO₄ (Casey et al. 2004), with concentrations generally within the range 0.1–0.6 mM (Epstein 1994). In soil solutions of acidic European soils, however, minor but significant (up to 20% of total Si) concentrations of polymerized silicic acid have been observed (Wonisch et al. 2008). Côté-Beaulieu et al. (2009) supplied wheat with organic compounds (as methyl silanols) that proved to be toxic. Therefore, it appears that orthosilicic acid remains the main form of Si absorbed by roots, although Fu et al. (2002) suggested that root uptake might occur via physical incorporation of Si soil particles.

Silicon uptake mechanisms have been mostly studied in rice, a Si accumulator. Estimating the permeability of the plasma membrane at 10⁻¹⁰ m.s⁻¹, Raven (2001) showed that high concentrations of Si found in rice could not be due to a simple flow caused by the permeability of the membrane and that the absorption of Si by rice required a metabolic control. In wheat, Rains et al. (2006) also proposed a metabolic control as Si uptake is inhibited by dinitrophenol or potassium cyanide. They concluded that the mechanisms involved in Si uptake by wheat, rice, or other species are similar, “differences being a matter of degree” and leading to various Si concentrations in plants.

By using a mutant cultivar that excludes Si, Ma et al. (2004) isolated two Si transporters: one called SIT1, responsible for the radial transport of Si from the external solution to the cortical cells, and the other called SIT2, responsible for the

transport of Si from the cortical cells to the xylem. The two transporters work oppositely to the concentration gradient, suggesting processes that consume energy. Also using rice mutants, Ma et al. (2001a) showed that Si uptake is performed by lateral roots, but not root hairs. Since this pioneer work on rice, Si influx transporters have been identified in maize (Mitani et al. 2009), but not in wheat yet.

Active and passive uptakes can coexist within the same plant (Henriet et al. 2006; Mitani and Ma 2005; Ding et al. 2008; Liang et al. 2007; Gérard et al. 2008). For example, Henriet et al. (2006) studied the Si uptake by bananas grown in hydroponics at different Si concentrations. On one hand, at higher Si supplies, Si absorption was proportional to the mass flow-driven supply, in good agreement with a passive uptake. On the other hand, at lower Si supplies, Si absorption was larger than the one expected if mass flow-driven supply had been the only mechanism, and Si in the nutrient solution was depleted, suggesting an active uptake.

2.3 Transfer to shoots

After penetrating the xylem, Si is transferred to the shoots. Transpiration is the most important factor regulating transport and deposition of Si in plant shoots. Generally, Si concentration of a plant organ directly reflects its rate of transpiration (Raven 2001). Henriet et al. (2006) measured Si concentrations in several parts of banana plants grown hydroponically with various Si concentrations in the nutrient solution; they found a concentration gradient within the plant that reflects the major role of transpiration in Si transport and this, whatever the Si concentration in solution. Silicon isotope studies have also been proven to be useful to evidence the role of transpiration. In rice for instance, Ding et al. (2005) found enrichment in the heavier isotope ³⁰Si from roots, to stem and leaves, then husk and grains, which is well explained by the Rayleigh distillation law. The potential use of Si isotopes in plants has been recently reviewed by Leng et al. (2009). As transpiration is the main driver for Si transport and deposition, the duration of plant growth plays an important role in the Si concentration: older leaves of a plant are richer in Si than younger ones (de Saussure 1804; Henriet et al. 2006). Besides all the evidences which demonstrate the role of transpiration, Mitani et al. (2009) have isolated a gene that mainly functions as a Si transporter for xylem uploading in maize. More work is therefore required to elucidate the importance of active vs. passive transfer of Si to the shoots.

2.4 Accumulation in shoots

In wheat sap, Casey et al. (2004) observed that the only forms of Si present were mono- and di-silicic acids, with a ratio of 7:1. But this part of soluble Si is minimal compared with the solid form. Sangster et al. (2001) studied the distribution of Si

in a wheat plant during its growth. After only 8–10 days, Si was almost exclusively found as a solid form in the aerial parts. Indeed, Si quickly precipitates as amorphous silica. Lux et al. (2003) observed the formation of silica aggregates in the root endodermis within 2 h following the transfer of a sorghum plant from a Si-poor environment to a Si-rich environment.

The presence of organo-silicon compounds in plants is not formally established. In rice, Inanaga et al. (1995) suggested that Si plays a role in the formation of links between lignin and carbohydrates, in association with phenolic acids. But there is no evidence of a Si–C bond, and the instability of Si–O–C bonds at physiological pH suggests that Si is probably regulated differently from the other nutrients (Perry and Keeling-Tucker 1998).

Amorphous silica is therefore virtually the only form of Si in plants (Ding et al. 2008). Amorphous silica particles that precipitate in plant cells are called phytoliths (Fig. 1). Phytoliths may contain impurities such as Al, Fe, Ti, Mn, P, Cu, N, and C (Clarke 2003), but are usually near-stoichiometric silica (Dietrich et al. 2003), the formula of which is $[\text{SiO}_n\text{OH}_{(2n-4)}]_m$ (with $n < 2$ and m large). Phytoliths can be assembled without any energy by polymerization of silicic acid when its concentration exceeds 2 mM (Ma and Yamaji 2006). Proportions and locations of phytoliths vary with the species, but also with the age of the plant (Ponzi and Pizzolongo 2003; Sangster et al. 2001). Phytoliths are not found evenly throughout the plant (Ponzi and Pizzolongo 2003; Prychid et al. 2003;

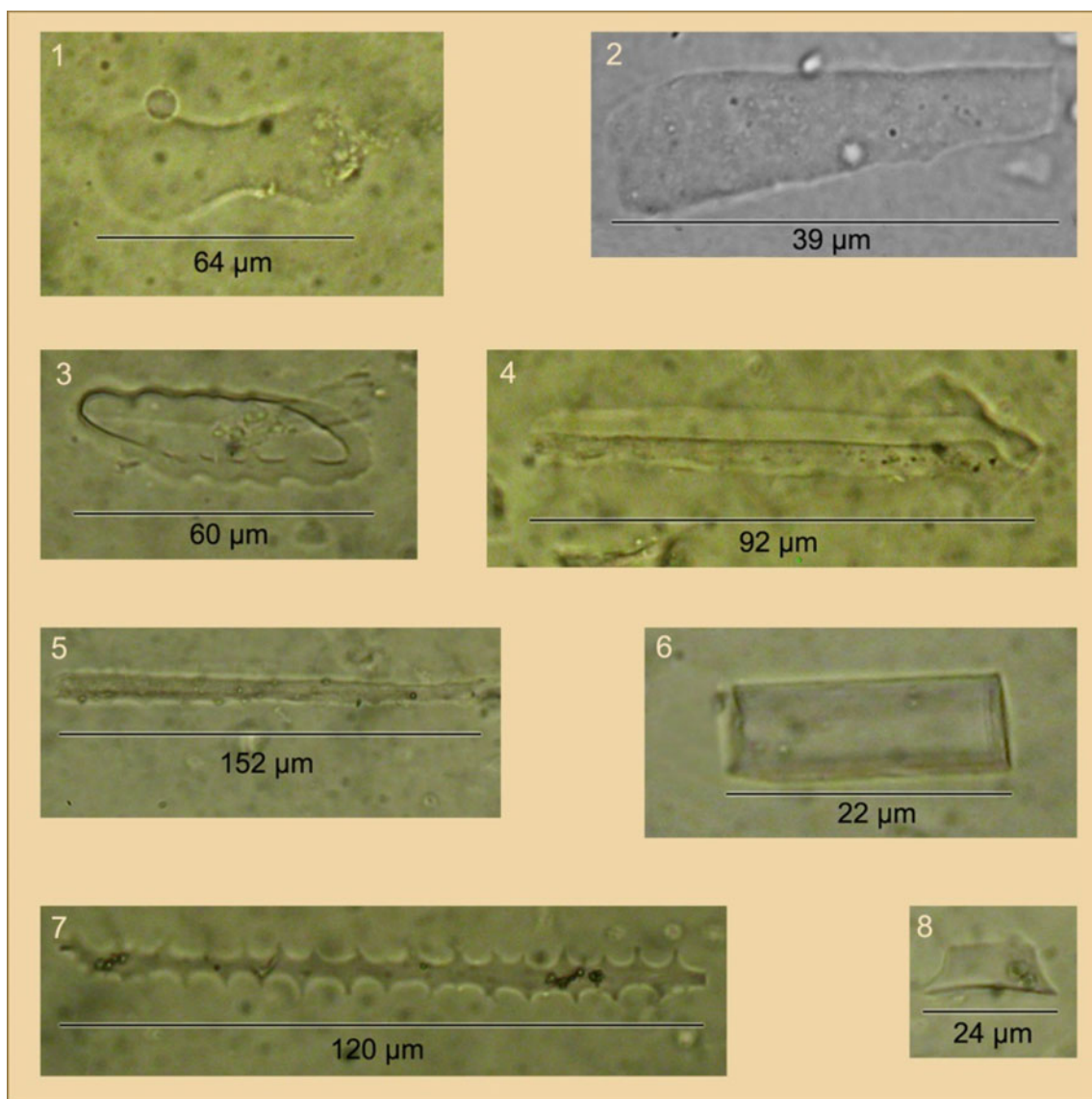


Fig. 1 Microphotographs of phytoliths from cultivated soils, France (Guntzer 2010); phytolith types are named according to the nomenclature of Madella et al. (2005): 1 Bilobate, 2 Clavate, 3 and 4

Trapeziform polylobate short cell, 5 Cylindric elongate, 6 Parallepedal bulliform cell, 7 Elongate echinate long cell, 8 Rondel

Sangster et al. 2001), but in leaf epidermis, in root endodermis, and in cell membranes of the vascular bundle (in relation with sclerenchyma) at transpiration sites.

In the case of wheat, Si is present in all tissues with higher levels in the inner tangential and radial walls of endodermis cells (Bouzoubaa 1991). In the leaves, Si is at first preferentially deposited in the abaxial epiderm, and then in both epiderms as the leaf grows (Hodson and Sangster 1988). Among those tissues, phytoliths are found in specific cells called silica cells located on vascular bundles and/or are present as silica bodies in bulliform cells, fusoid cells or prickle hairs in rice (Ma and Yamaji 2006), wheat (Dietrich et al. 2003), or bamboos (Motomura et al. 2004). These specific allocations observed in Poaceae have been taken both as proofs of passive or active Si transport, depending on the allocation (Motomura et al. 2004).

3 The benefits of Si under environmental stress

The beneficial effects of Si has been demonstrated by many studies using pots, hydroponic, and field experiments (see the reviews by Jones and Handreck 1967; Savant et al. 1997b; Epstein 1999; Datnoff et al. 2001; Datnoff and Rodrigues 2005). The benefits can be especially pointed out under environmental stresses because Si may act at several levels in

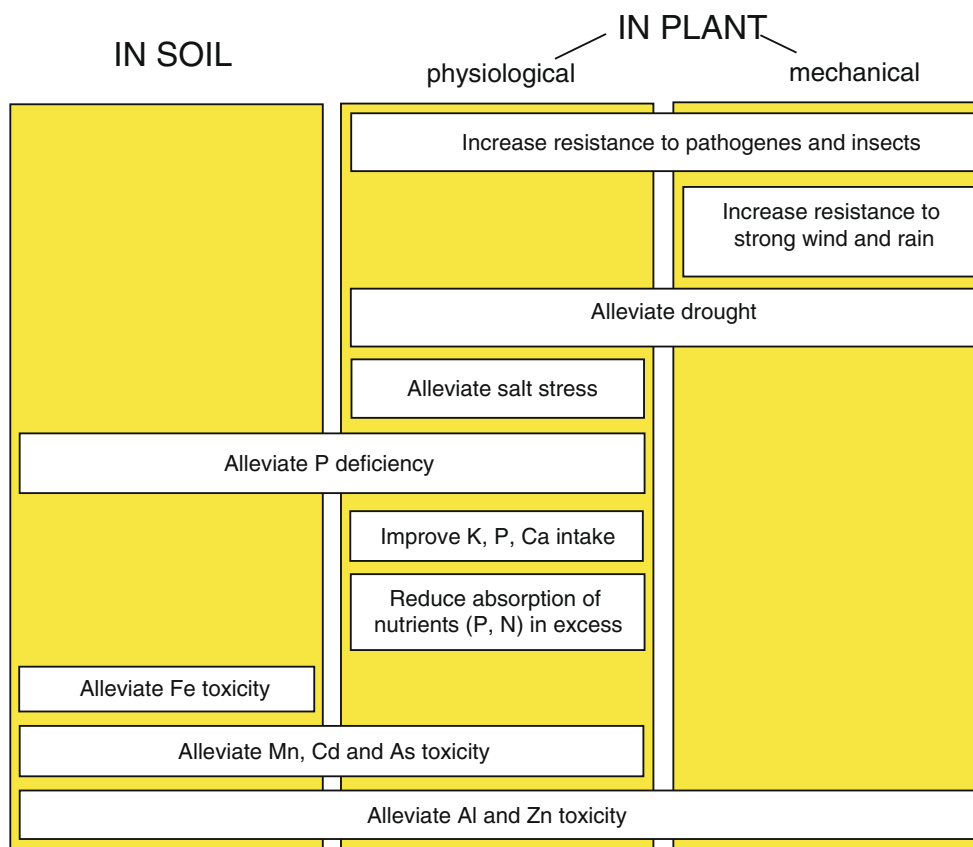
the plant functioning as well as in the soil (Fig. 2). Below, we present a few striking examples of the benefits of Si for plants based mostly on recent studies under various environmental stresses.

3.1 Biological stresses

The beneficial effects of Si intake have been shown for many pathogens on a wide range of plants, but are often based on empirical approaches. The mechanisms involved are poorly known. In the case of wheat, the beneficial effect of Si has been demonstrated on the following diseases and fungal attacks (Rodgers-Gray and Shaw 2004): powdery mildew (*Blumeria graminis*), septoria (*Phaeosphaeria nodorum* and *Mycosphaerella graminicola*), and eyespot (*Oculimacula yallundae*). In the case of rice, the effect of Si has been demonstrated on stalk rot (*Leptosphaeria salvinii*), rice blast (*Magnaporthe grisea*), fusarium wilt (*Fusarium*), tan spot (*Cochliobolus miyabeanus*), melting seedlings (*Thanatephorus cucumeris*), and leaf spots (*Monographella albescens*; Ma and Takahashi 2002; Savant et al. 1997b).

The beneficial effects of Si have been thought to be due to the precipitation of amorphous silica in plants which acts as a mechanical barrier (Cheng 1982; Jones and Handreck 1967). It has since been shown that Si also protects the plant by other processes which can boost the

Fig. 2 Synthesis of the benefits of Si for crops under various environmental stresses; the mechanical mechanism is due to the presence of phytoliths



defense mechanisms, including the accumulation of lignin, phenolic compounds, and phytoalexins (Epstein 1999; Fawe et al. 2001; Ma and Yamaji 2006). In the case of an attack by pathogenic fungi, Si triggers a rapid and extensive deployment of the natural defenses of the plant (Fauteux et al. 2005) either indirectly by sequestering cations or directly by increasing some protein activity. In the case of powdery mildew, it has been shown that when infection occurs after Si fertilization, the pathogen usually remains, but the development of the infection is minimal. Extensive research on epidermal cells have shown that in Si-fertilized plants, plant defenses were stimulated through the production of phenolic compounds, callose, or methylaconitate (phytoalexin) (Bélanger et al. 2003; Ghanmi et al. 2004; Rémus-Borel et al. 2005, 2009). Guevel et al. (2007) showed that foliar application of Si also reduced infection by powdery mildew, but did not propose a mechanism. The role of silicification may even be questioned as it has been shown for different pathogens that the prophylactic effect of Si is lost when the Si fertilization is stopped, whereas amorphous silica deposits are still present (Fauteux et al. 2005; Fawe et al. 2001).

Diseases are not the only biological stresses that Si helps to regulate: Si limits damages caused by animals, especially insects which are harmful to crops. Cotterill et al. (2007) and Hunt et al. (2008) showed that Si-fertilized grasses were less likely to be eaten by grazing animals, respectively wild rabbits and locusts, than unfertilized ones. Here, it is probably more a mechanical factor that plays a role as leaves containing Si are more difficult to graze. The beneficial effect of Si has been proven on attacks by many other species, among which are insect borers (*Chilo suppressalis*), yellow borers (*Scirpophaga incertulas*), rice chlorops (*Chlorops oryzae*), rice leafhopper (*Nephotettix bipunctatus cincticeps*), brown leafhoppers (*Nilaparvata lugens*), weavers spider mites (*Tetranychus* spp.), or mites (Savant et al. 1997b), but the effect of Si on aphid attacks has been mostly studied: Gomes et al. (2005) showed that Si fertilization decreased the number of aphids observed on an infested plant. Goussain et al. (2005), studying the penetration of aphids stylus, concluded that the silicification does not create a physical barrier to the penetration of the aphid stylus. However, the stylus is often removed and aphids excrete less honeydew, suggesting a lesser sap uptake, probably due to chemical processes within the plant. As in the case of powdery mildew, a foliar application of Si is effective on aphids (Moraes et al. 2004), but the mechanism in this case is not explained. Finally, although the beneficial effects of Si are observed empirically in many cases, the mechanisms behind these prophylactic effects are only beginning to be understood and have been proposed only for a limited number of plants and pathogens.

3.2 Abiological stresses

3.2.1 Regulation of nutrient uptake

Phosphorus The role of Si in P uptake by plants was one of the first effects of Si ever studied. Indeed, Brenchley and Maskell (1927) and Fisher (1929) found that Si fertilization increased the yields of barley crops mainly when phosphorus fertilization was limiting. They concluded that Si fertilization made soil phosphorus more available to plants. Eneji et al. (2008) also found correlations between Si and P uptake and concluded on an effect in soil. However, earlier studies had shown that the effect of Si under phosphorus deficiency could be due to an *in planta* mechanism, implying an improved utilization of phosphorus, probably through an increase in phosphorylation (Cheong and Chan 1973) or a decrease in Mn concentration (Ma and Takahashi 1990). In contrast, when phosphorus was supplied in excess, Si limited P uptake and the appearance of chlorosis, probably by reducing the transpiration rate (Ma et al. 2001b).

Potassium–nitrogen–calcium According to Mali and Aery (2008a), K uptake both in hydroponics and in soil is improved even at low Si concentrations through the activation of H-ATPase. Mali and Aery (2008a, 2008b) observed also a better absorption of N and Ca for cowpea and wheat fertilized with increasing doses of sodium metasilicate (50–800 mg Si kg⁻¹), as well as a better nodulation and apparently better N₂ fixation in cowpea. Yoshida et al. (1969) have shown that a decrease of erectness of rice leaves following excess of N application can be mitigated if Si is supplied to the nutrient solution.

3.2.2 Metal in excess

Soil contamination with trace elements due to human activities and excess of metals due to specific edaphic conditions are widespread. Contamination results in major physiological disturbances including reduced biomass production, photosynthesis inhibition, or disturbance of nutrient uptake. The number of studies, which tend to prove that Si may reduce toxicity symptoms, are steadily increasing, especially for metals of serious concern such as cadmium (Cd; Sarwar et al. 2010).

Iron In rice, it appears that Si increases the oxidizing capacity of roots, which converts ferrous iron into ferric iron, thereby preventing a large uptake of iron and limiting its toxicity (Ma and Takahashi 2002). It has been suggested that Si could regulate Fe uptake from acidic soils through the release of OH⁻ by roots when supplemented with Si (Wallace 1993).

Aluminum Several explanations have been given to explain the effect of Si on plants in the presence of an excess of aluminum. It was first assumed that Si and Al interact in the soil, creating subcolloidal and inert aluminosilicates, thereby reducing phytotoxic aluminum concentration in the soil solution (Li et al. 1996; Liang et al. 2007). It may also stimulate phenolic exudation by roots that would chelate and thus reduce Al absorption by corn roots (Kidd et al. 2001). In these cases, detoxification would be a mechanism external to the plant. It has also been shown that aluminum can be detoxified by *in planta* mechanisms either by forming hydroxyaluminumsilicates in the apoplast (Wang et al. 2004; Ryder et al. 2003) in roots or by a sequestration in phytoliths (Hodson and Sangster 1993; Hodson and Sangster 2002), which would reduce Al toxicity in the shoots.

Manganese, Cd, Cu, Zn, As Manganese toxicity is reduced in Si-fertilized plants because Si increases Mn binding to cell walls, which limits cytoplasmic concentrations (Liang et al. 2007; Rogalla and Romheld 2002). Horst et al. (1999) observed that Si application lowered the apoplastic Mn concentration (but not the vacuolar concentration) in cowpea leaves, suggesting that Si may modify the cation binding capacity of the cell walls. In addition, it induces a more homogenous distribution of Mn in leaves, limiting spot necrosis (Williams and Vlamis 1957; Horiguchi and Morita 1987; Ma et al. 2001b).

As for Al, Si has a “soil” and a “plant” effect on the uptake of trace metals like Cd, copper (Cu), or zinc (Zn; Liang et al. 2007). Metal concentrations in plant may either decrease or increase upon Si application depending on plant parts and metals. For example, reduced uptake of Cd after rice fertilization with furnace slag has been attributed to an increase in soil pH, thereby limiting Cd uptake, reduction of root–shoot translocation, and changes in compartmentation within the plant cell (Liang et al. 2007; Shi et al. 2005). Da Cunha and do Nascimento (2009) found that the decrease in Cd and Zn concentrations in maize shoots grown on Cd- or Zn-contaminated soil treated with calcium silicate, associated with an increase in shoot biomass, was due to changes in metal speciation in the soil rather than to pH increase (da Cunha et al. 2008). They also observed significant structural alterations in the shoots and suggested that the deposition of silica in the endodermis and pericycle of roots was responsible for maize tolerance to Cd and Zn stress. Hodge (2004) indicated that Si could change root plasticity, thereby increasing stress tolerance. Neumann and zur Nieden (2001) found that Si affected zinc inside the plant as zinc can co-precipitate with Si in cell walls (Neumann et al. 1997), leading to less soluble zinc in plants. In addition, foliar application of Si sol decreased Cd concentration in rice grains and shoots while increasing

their biomass (Liu et al. 2009). The authors suggested that alleviation of Cd toxicity and accumulation in rice would be related to Cd sequestration in the shoot cell walls. This indicates also that Si would be able to enter leaves through the stomatae. In metal-hyperaccumulating plants, Zn can be at least temporally associated to Si in vesicles or in the cytoplasm before Zn is being stored in vacuoles, leaving SiO₂ precipitates in the cytoplasm. Neumann and De Figueiredo (2002) suggested that this mechanism might be responsible for the high Zn tolerance of *Silene vulgaris*, *Thlaspi caerulescens*, or *Minuartia verna*.

Silicic acid also decreased arsenic (As) concentration in rice shoots grown in hydroponics, and arsenite transport in roots was shown to share the same highly efficient pathway as Si, indicating that sufficient available Si in soil would be efficient at reducing As accumulation in rice shoots (Ma et al. 2008). A whole range of mechanisms has been given that could explain the alleviating effect of Si on metal stress *in planta*, especially in shoots. In soil, however, the respective roles of soil and root factors in controlling metal uptake, and more precisely in alleviating metal stress when Si is applied to soil, have been still poorly investigated (Kirkham 2006).

3.2.3 Other stresses

Drought stress is of increasing concern because of its impact on crops production and its expected broadening worldwide. There is a general agreement on the positive effect of Si application on the biomass yield under deficit irrigation (Eneji et al. 2008). Indeed, increases of biomass and/or grain yields have been observed on a large set of crops (e.g., Eneji et al. 2008; Shen et al. 2010; Pei et al. 2010). Wheat plants subjected to drought and treated with Si maintained higher stomatal conductance, relative water content, and water potential than non-treated plants. Besides, leaves were larger and thicker, thereby limiting the loss of water through transpiration (Gong et al. 2003; Hattori et al. 2005) and reducing water consumption (Eneji et al. 2005). Along the same line, in the case of rice, Si increased resistance to typhoons (Ma et al. 2001b), probably because of the rigidity gained by the silicification of shoots. Silicon fertilization impacts also the development of secondary and tertiary cells of the endodermis, thus allowing better root resistance in dry soils and a faster growth of roots (Bouzoubaa 1991; Hattori et al. 2003, 2005). In addition, Eneji et al. (2008) observed that Si enhanced the uptake of major essential elements by various grasses exposed to a water deficit, while Pei et al. (2010) did not see any effect for wheat seedlings. The effects of Si in plants exposed to drought have also been observed at the physiological or metabolic

level: Gong et al. (2005) observed that Si increased antioxidant defenses and therefore maintained physiological processes such as photosynthesis. Pei et al. (2010) also found that in wheat under short-term water stress conditions, Si addition contributed to improved wheat growth by stimulating antioxidant defense rather than modifying osmotic pressure.

In the case of saline soils, Si increased the activity of antioxidant enzymes in wheat (Saqib et al. 2008), decreased plasma membrane permeability, and increased root activity, which allowed for a better absorption of nutrients in barley (Liang et al. 1996, 2003). Silicon also decreased sodium absorption when it was in excess (Ahmad et al. 1992; Ma et al. 2001b; Saqib et al. 2008). Comparing salt-sensitive and salt-tolerant wheat cultivars, Tuna et al. (2008) hypothesized that Si could alleviate salt stress through two mechanisms: either inhibition of transport of Na to the leaves and/or specific accumulation of Na in the roots.

Other effects of Si were observed empirically on abiotic stresses. Goto et al. (2003) showed that rice plants treated with Si absorbed less radiation than untreated plants. Ma and Takahashi (2002) reported that rice grew better after exposure to gamma rays if it had been previously fertilized with Si. Shen et al. (2010) showed that Si improved growth, photosynthesis, and antioxidant parameter response in soybean seedlings exposed to UV-B radiation.

4 Plant Si is a significant source for plant

4.1 Sources of plant Si

The Si concentration in plants depends primarily on the concentration of silicic acid in the soil solution (Ding et al. 2005; Henriot et al. 2008; Jones and Handreck 1967) and is not correlated to the total Si concentration of the soil (Brenchley and Maskell 1927). However, correlations were observed between the Si concentration in rice and the percentage of clay in soils (Cheng 1982), and between the Si concentration in rice or banana and the stock of weatherable minerals (Henriot et al. 2008; Makabe et al. 2009). The weatherability of silicate minerals, including phytoliths, depends on environmental factors such as temperature and pH as well as the physicochemical characteristics of the minerals which can be evaluated by thermodynamic and kinetic data (Gérard et al. 2002; White and Brantley 1995; Heaney et al. 1994).

Several studies have attempted to quantify the proportion of plant Si that is coming from the recycling of phytoliths, which are the main Si form in plants. Using a steady-state approach, Bartoli (1985) showed that about 85% of the Si uptake originated from the dissolution of phytoliths in a

deciduous forest ecosystem which is characterized by a strong Si biological cycle. Besides, only 15% of the Si uptake originated from the dissolution of phytoliths in a coniferous forest ecosystem which is characterized by a weak Si biological cycle. Using a similar approach for a rain forest developed above a latosol in Congo, Alexandre et al. (1997) showed that about 74% of the DSi in soil solution originates from the dissolution of phytoliths. Gérard et al. (2008) found that the proportion of plant recycling averaged 60% in an acidic brown soil covered by Douglas fir. These studies show that a strong Si biological cycle may control the biogeochemical cycle of Si of a given ecosystem through the production of phytoliths.

The role of phytoliths in controlling significantly the level of dissolved silicon (DSi) in soil solutions is based on several experimental evidences:

- Solubility data show that phytoliths are highly soluble, like other amorphous silica particles (Frayse et al. 2006).
- The dissolution rate of phytoliths increases with pH (Frayse et al. 2006). Frayse et al. (2009) also showed that soil phytoliths were among the minerals that dissolved the fastest in a range of pH relevant to most soil types (Fig. 3).
- At common pH values (4–8), phytoliths are as reactive as hydroxides or allophanes (Bartoli 1985) and are 100–10,000 times more reactive than primary clays or silicates. Bartoli (1985) suggested that between pH 8.9 and 9.8, the dissolution of phytoliths would be controlled by aluminum concentration, but this conclusion was not supported by the results obtained recently by Frayse et al. (2009).

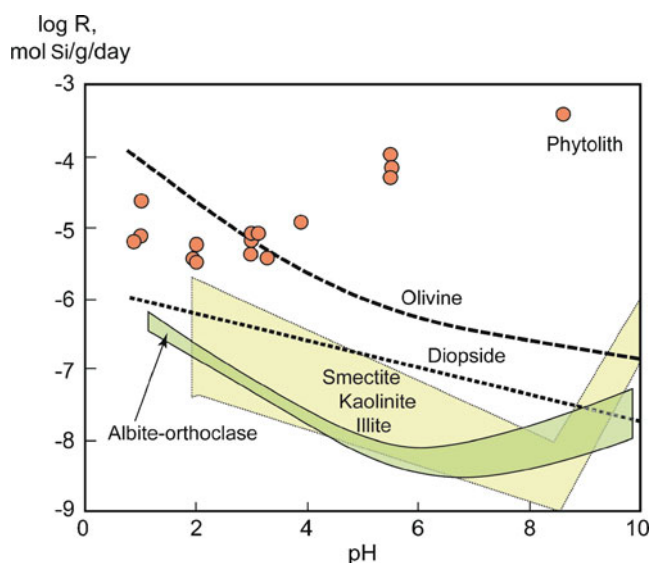


Fig. 3 Rate of dissolution (R) of frequent soil minerals and phytoliths as a function of pH (Frayse et al. 2009)

- Batch experiments of litter degradation show that the rate of Si release is similar or higher than the one found for primary soil minerals (Frayssé et al. 2010).
- The importance of biogenic amorphous silica as a source of dissolved Si in the soil solution is also supported by data from isotopic geochemistry. By studying Si isotopic ratios in different compartments of a bamboo field, Ding et al. (2008) showed that Si dissolved in the soil solution originated from phytoliths. Using Ge/Si ratios in Hawaiian soils waters, Derry et al. (2005) showed that surface samples characterized by high DSi values and low Ge/Si ratios were controlled by the dissolution of phytoliths.

The importance of plant Si (phytoliths) recycling in natural ecosystem is therefore well established, and it allows explaining the uptake of Si by plants even in soil depleted in primary weatherable minerals (Alexandre et al. 1997; Lucas et al. 1993) where they can become the major source of potentially available Si to plants.

4.2 The phytolith pool

The quantification of the phytolith pool in soils is based on the physical and chemical properties of amorphous opal A. Other biogenic amorphous silica particles can be found in soils such as diatoms frustules and the camoebian testates (Cary et al. 2005). Depending on the target (biogenic silica, plant-available Si, or amorphous Si as a whole), the aim of the study, and the scientific discipline, different approaches have been developed to identify and quantify amorphous silica in soils (Sauer et al. 2006).

The gravimetric method (Kelly 1990), which separates particles of amorphous silica from the rest of the soil using heavy liquid flotation, allows for the observation and quantification of amorphous silica particles and phytoliths. The phytoliths represent generally 0.7–3% of the forest soil dry weight (Bartoli 1985). Jones and Handreck (1967) observed 1–2% of phytoliths in grassland soil, while soil horizons resulting from phytolith accumulation have also been described (Meunier et al. 1999).

An alternative technique to quantify the phytoliths in soil is by solubilization. Contrary to the gravimetric method, this is a destructive method so that the proportion of phytoliths vs. other amorphous silica particles cannot be assessed. Saccone et al. (2007) used alkaline extractions (NaOH and Na₂CO₃) originally used to quantify diatoms in marine sediments (Demaster 1981). Chemical and gravimetric techniques on similar samples do not necessarily give good correlations (Saccone et al. 2007), indicating that the methodology should be improved if phytoliths are to be quantified. Other non-

alkaline extractants do not solubilize phytoliths and usually dissolve less than the alkaline ones (Saccone et al. 2007), but they may be used (or have been used) to quantify immediately plant-available Si in specific soils (e.g., Liang et al. 1994).

The depth distribution of soil phytoliths is variable, but generally, the highest concentrations are found in the topsoils of undisturbed soils (Saccone et al. 2007; Sommer et al. 2006) and decrease with depth. This distribution reflects the equilibrium between the rate of phytoliths input via litterfall and the rate of phytolith output via dissolution.

In cultivated soil, we can expect results different from those obtained in natural ecosystems depending whether the straw is exported or not. Indeed, repeated crop exports can reduce the concentration of potentially available Si present as phytoliths to the extent that Si fertilization is necessary (Datnoff and Rodrigues 2005; Eneji et al. 2005; Meunier et al. 2008; Savant et al. 1997a) because a fraction of plant Si does not return to the soil. For example, Desplanques et al. (2006) showed that if we consider amorphous silica as the only source of Si for plants, the stock of available Si from a rice field of Camargue (France) would be exhausted after 5 years of cultivation.

4.3 Fertilization

The addition of silicate materials to crops started in Japan in the early 1950s and is commonly used in many parts of the world such as Korea, Taiwan, Thailand, Ceylon (Liang et al. 1994), and the USA (Korndörfer and Lepsch 2001). An example from field trials conducted in Japan (Ma and Takahashi 2002) using Si fertilization on rice growth and yield is given in Table 2. The results show a slight increase in the panicle number, but up to a 17% yield increase. In the case of wheat, annual application of Si-containing materials (at a rate of 230 g kg⁻¹ of water-soluble Si) increased the grain yield by 4.1–9.3% during a 4-year field experiment (Liang et al. 1994). In general, farmers use about 900 kg Si ha⁻¹ year⁻¹ or more for rice cultivation (Korndörfer et al. 2001). Alvarez and Datnoff (2001) calculated the economic benefits expected from such

Table 2 Effect of Si fertilization (sodium silicate) on rice growth and yield in Japan (Ma and Takahashi 2002)

Application rate (kg ha ⁻¹)	Number of panicles (×10 ⁴ /ha)	Yield (ton.ha ⁻¹)
0	4.84	7.01
75	4.94	7.87
105	5.03	8.16
135	5.03	8.23

fertilization on the cultivation of rice in Florida and showed that the additional income would be on average US \$74 per hectare per year.

Different types of Si fertilizers exist, which have been compared in several studies (Gascho 2001; Mecfel et al. 2007; Meyer and Keeping 2001; Rodgers-Gray and Shaw 2004; Savant et al. 1997b). The most used are wollastonite (CaSiO_3), residues of blast furnaces, but also straw (mainly rice straw). By testing several types of Si fertilizers, including calcium silicate and rice straw, on rice crops in pots, Hossain et al. (2001) showed that rice straw offers better results in terms of Si concentration in plant. Yields are also larger when rice straw is added ground or combined with an organic matter decomposer. Experiments conducted in Japan showed that Si from rice straw used as a fertilizer is usually not fully available in the short term, but is available at more than 70% in the long term (40 years). Inorganic silicates affect the yields faster as they are used by plants in the crop following directly the fertilization. This has led to their wide use (Ma and Takahashi 2002). Foliar applications of inorganic silica have also been tested in order to gain in efficiency and in cost (Sarwar et al. 2010), but are not widely used. However, Savant et al. (1997a) calculated that in 1993, the world rice production had exported 33 million tons of Si as straw that could have been reused for fertilization. Savant et al. (1997a) suggested that intensive rice cultivation with straw export may deplete the plant-available silica, which could be a factor for explaining yield decline. The straw, which contains large amounts of phytoliths, should therefore be recycled because it is a source of bioavailable Si.

5 Conclusion

Most of the major crops are Si accumulators. Although not considered as an essential element, Si has a positive impact on plant development. The mechanisms that allow plant Si to alleviate many environmental stresses are still poorly known in details, but it is well established that *ex planta* and *in planta* processes may occur. Plant Si also has an impact on the Si cycle by providing a readily efficient source of Si to the soil.

In cultivated areas, the export of crops does not allow the recycling of Si by plants, and the biogeochemical cycle of Si is disturbed. More than a decade after the paper by Savant et al. (1997a), the assumption of the depletion of plant-available silica is still pertinent, but new evidences have proven that phytoliths are a significant source of Si for plant. This issue is fundamental as the decrease of bioavailable Si may have significant impacts on cereal yields.

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