Benefits of plant silicon for crops: a review

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REVIEW ARTICLE

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**Flore Guntzer · Catherine Keller ·
Jean-Dominique Meunier**

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

Contents

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

F. Guntzer · C. Keller · J.-D. Meunier (✉)
CEREGE CNRS/Aix-Marseille Université, Europôle
Méditerranéen de l'Arbois,
BP 80, 13545 Aix-en-Provence, cedex 4, France
e-mail: meunier@cerege.fr

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	Saccharum officinarum[b]	1.509
Maize	826	Zea mays[b]	0.827
Rice paddy	686	Oryza sativa[b]	4.167
Wheat	683	Triticum aestivum[b]	2.455
Potatoes	326	Solanaceae[c]	0.4
Cassava	232	_[d]	0.5
Soybeans	231	Glycine max[b]	1.399
Sugar beet	222	Malpighiales[e]	2.34–7
Barley	155	Hordeum vulgare[b]	1.824
Tomatoes	136	Lycopersicon esculentum[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, H_4SiO_4 (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 ^{30}Si 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 $[SiO_nOH_{(2n\ -\ 4)}]_m$ (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;
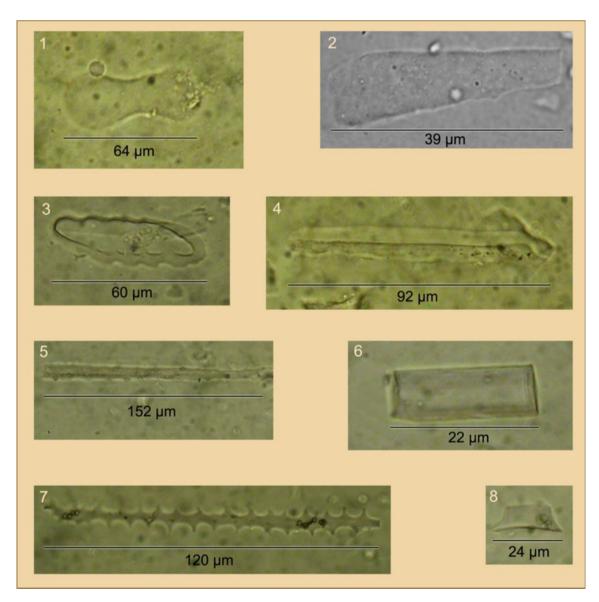

Fig. 1 Microphotographs of phytoliths from cultivated soils, France (Guntzer 2010); phytolith types are named according to the nomenclature of Madella et al. (2005): 1 Bilobate, 2 Clavate, 3 and 4 Trapeziform polylobate short cell, 5 Cylindric elongate, 6 Parallepipedal bulliform cell, 7 Elongate echinate 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).
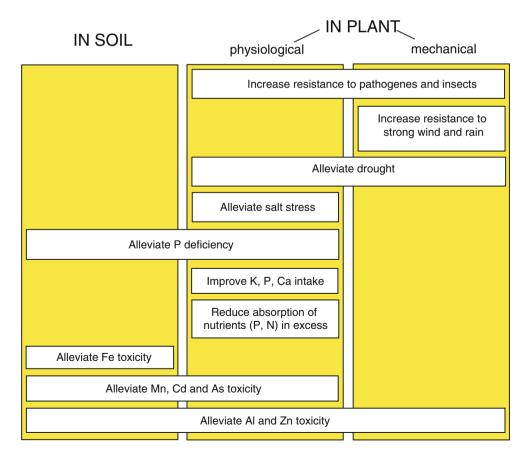
3 The benefits of Si under environmental stress

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).

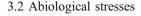The beneficial effects of Si have been thought to be due to the precipitation of amorphous silica in plants which acts as a mechanical barrier (Cheng 1982; Jones and Handreck 1967). It has since been shown that Si also protects the plant by other processes which can boost the

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 methyl-aconitate (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 suppresalis*), yellow borers (*Scirpophaga incertulas*), rice chlorops (*Chlorops oryzae*), rice leafhopper (*Nephotettix bipunctatus cinticeps*), 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 meta-silicate (50–800 mg Si kg^{-1}), as well as a better nodulation and apparently better N_2 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 SiO_2 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; Henriet 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 (Henriet 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 (Fraysse et al. 2006).
- The dissolution rate of phytoliths increases with pH (Fraysse et al. 2006). Fraysse 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 Fraysse et al. (2009).
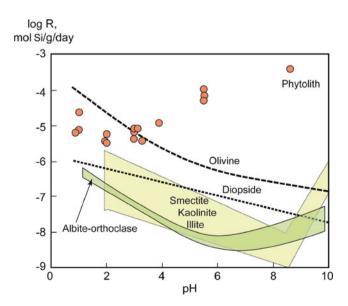

Fig. 3 Rate of dissolution (R) of frequent soil minerals and phytoliths as a function of pH (Fraysse et al. 2009)

- Batch experiments of litter degradation show that the rate of Si release is similar or higher than the one found for primary soil minerals (Fraysse 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 Na_2CO_3) originally used to quantify diatoms in marine sediments (Demaster 1981). Chemical and gravimetrical 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 gkg^{-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 ($\times 10^4$/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.

References

Ahmad R, Zaheer SH, Ismail S (1992) Role of silicon in salt tolerance of wheat (*Triticum aestivum* L.). Plant Science 85:43–50

Alexandre A, Meunier JD, Colin F, Koud JM (1997) Plant impact on the biogeochemical cycle of silicon and related weathering processes. Geochimica et Cosmochimica Acta 61(3):677–682

Alvarez J, Datnoff LE (2001) The economic potential of silicon for integrated management and sustainable rice productions. Crop Prot 20:43–48

Bartoli F (1983) The biogeochemical cycle of silicon in two temperate foresty ecosystems. In: Hallberg R (ed) Environmental biogeochemistry. Ecol Bull (Stockholm), vol 35, pp 469–476

Bartoli F (1985) Crystallochemistry and surface—properties of biogenic opal. Journal of Soil Science 36:335–350

Bélanger RR, Benhamou N, Menzies JG (2003) Cytological evidence of an active role of silicon in wheat resistance to powdery mildew (*Blumeria graminis* f. sp. *tritici*). Phytopathology 93(4):402–412

Berner EK, Berner RA (1996) Global environment: water, air, and geochemical cycles. Prentice Hall, New Jersey

Blecker SW, McCulley RL, Chadwick OA, Kelly EF (2006) Biological cycling of silica across a grassland bioclimosequence. Global Biogeochemical Cycles 20:1–11

Bouzoubaa Z (1991) Etude des rôles de la silice dans les mécanismes de tolérance à la sécheresse chez quelques espèces de grande culture. PhD thesis, Montpellier II University

Brenchley WE, Maskell EJ (1927) The inter-relation between silicon and other elements in plant nutrition. Ann Appl Biol 14:45–82

Cary L, Alexandre A, Meunier JD, Boeglin JL, Braun JJ (2005) Contribution of phytoliths to the suspended load of biogenic silica in the Nyong basin rivers (Cameroon). Biogeochemistry 74:101–114

Casey WH, Kinrade SD, Knight CTG, Rains DW, Epstein E (2004) Aqueous silicate complexes in wheat, *Triticum aestivum* L. Plant Cell and Environment 27:51–54

Cheng BT (1982) Some significant functions of silicon to higher-plants. Journal of Plant Nutrition 5:1345–1353

Cheong YWY, Chan PY (1973) Incorporation of P^{32} in phosphate esters of the sugar caneplant and the effect of Si and Al on the distribution of these esters. Plant and Soil 38:113–123

Clarke J (2003) The occurrence and significance of biogenic opal in the regolith. Earth-Science Reviews 60:175–194

Conley DJ (2002) Terrestrial ecosystems and the global biogeochemical silica cycle. Global Biogeochemical Cycles 16:1121. doi:10.1029/2002GB001894

Cornelis JT, Ranger J, Iserentant A, Delvaux B (2010) Tree species impact the terrestrial cycle of silicon through various uptakes. Biogeochemistry 97:231–245

Côté-Beaulieu C, Chain F, Menzies JG, Kinrade SD, Bélanger RR (2009) Absorption of aqueous inorganic and organic silicon compounds by wheat and their effect on growth and powdery mildew control. Environ Exp Bot 65:155–161

Cotterill JV, Watkins RW, Brennon CB, Cowan DP (2007) Boosting silica levels in wheat leaves reduces grazing by rabbits. Pest Management Science 63:247–253

da Cunha KPV, do Nascimento CWA (2009) Silicon effects on metal tolerance and structural changes in maize (*Zea mays* L.) grown

on a cadmium and zinc enriched soil. Water Air and Soil Pollution 197:323–330

da Cunha KPV, do Nascimento CWA, da Silva AJ (2008) Silicon alleviates the toxicity of cadmium and zinc for maize (*Zea mays* L.) grown on a contaminated soil. Journal of Plant Nutrition and Soil Science 171:849–853

Datnoff LE, Rodrigues FA (2005) The role of silicon in suppressing rice diseases. APS net Feature Story, 1–28. http://www.apsnet.org/online/feature/silicon/

Datnoff LE, Snyder GH, Korndorfer GH (eds) (2001) Silicon in agriculture. Studies in Plant Science 8. Elsevier, Amsterdam

De Saussure NT (1804) Recherches chimiques sur la végétation. Chez la veuve Nyon, Paris

Demaster DJ (1981) The supply and accumulation of silica in the marine environment. Geochimica et Cosmochimica Acta 45:1715–1732

Deren CW (2001) Plant genotype, silicon concentration, and silicon-related responses. In: Datnoff LE, Snyder GH, Korndorfer GH (eds) Silicon in agriculture. Studies in plant science, 8. Elsevier, Amsterdam, pp 149–158

Derry LA, Kurtz AC, Ziegler K, Chadwick OA (2005) Biological control of terrestrial silica cycling and export fluxes to watersheds. Nature 433:728–731

Desplanques V, Cary L, Mouret JC, Trolard F, Bourrié G, Grauby O, Meunier JD (2006) Silicon transfers in a rice field in Camargue (France). J Geochem Explor 88:190–193

Dietrich D, Hinke S, Baumann W, Fehlhaber R, Baucher E, Ruhle G, Wienhaus O, Marx G (2003) Silica accumulation in *Triticum aestivum* L. and *Dactylis glomerata* L. Anal Bioanal Chem 376:399–404

Ding TP, Ma GR, Shui MX, Wan DF, Li RH (2005) Silicon isotope study on rice plants from the Zhejiang province, China. Chem Geol 218:41–50

Ding TP, Zhou JX, Wan DF, Chen ZY, Wang CY, Zhang F (2008) Silicon isotope fractionation in bamboo and its significance to the biogeochemical cycle of silicon. Geochimica et Cosmochimica Acta 72:1381–1395

Draycott AP (ed) (2006) Sugar beet. World Agriculture Series, Blackwell Publishing, p 444

Eneji E, Inanaga S, Muranaka S, Li J, An P, Hattori T, Tsuji W (2005) Effect of calcium silicate on growth and dry matter yield of *Chloris gayana* and *Sorghum sudanense* under two soil water regimes. Grass and Forage Science 60:393–398

Eneji AE, Inanaga S, Muranaka S, Li J, Hattori T, An P, Tsuji W (2008) Growth and nutrient use in four grasses under drought stress as mediated by silicon fertilisers. Journal of Plant Nutrition 31:355–365

Epstein E (1994) The anomaly of silicon in plant biology. Proceedings of the National Academy of Sciences of the United States of America 91:11–17

Epstein E (1999) Silicon. Annual Review of Plant Physiology and Plant Molecular Biology 50:641–664

Fauteux F, Remus-Borel W, Menzies JG, Bélanger RR (2005) Silicon and plant disease resistance against pathogenic fungi. FEMS Microbiol Lett 249:1–6

Fawe A, Menzies JG, Cherif M, Bélanger RR (2001) Silicon and disease resistance in dicotyledons. In: Datnoff LE, Snyder GH, Korndorfer GH (eds) Silicon in agriculture. Studies in plant science, 8. Elsevier, Amsterdam, pp 159–169

Fisher RA (1929) A preliminary note on the effect of sodium silicate in increasing the yield of barley. J Agric Sci 19:132–139

Fraysse F, Pokrovsky OS, Schott J, Meunier JD (2006) Surface properties, solubility and dissolution kinetics of bamboo phytoliths. Geochimica et Cosmochimica Acta 70:1939–1951

Fraysse F, Pokrovsky OS, Schott J, Meunier JD (2009) Surface chemistry and reactivity of plant phytoliths in aqueous solutions. Chem Geol 258:197–206

Fraysse F, Pokrovsky OS, Meunier JD (2010) Experimental study of terrestrial plant litter interaction with aqueous solutions. Geochimica et Cosmochimica Acta 74:70–84

Fu FF, Akagi T, Yabuki S (2002) Origin of silica particles found in the cortex of *Matteuccia* roots. Soil Science Society of America Journal 66:1265–1271

Gascho GJ (2001) Silicon sources for agriculture. In: Datnoff LE, Snyder GH, Korndorfer GH (eds) Silicon in agriculture. Studies in plant science, 8. Elsevier, Amsterdam, pp 197–207

Gérard F, Mayer KU, Hodson MJ (2008) Modelling the biogeochemical cycle of silicon in soils: application to a temperate forest ecosystem. Geochimica et Cosmochimica Acta 72: A304–A304

Gérard F, François M, Ranger J (2002) Processes controlling silica concentration inleaching and capillary soil solutions of an acidic brown forest soil (Rhône, France). Geoderma 107:197–26

Ghanmi D, McNally DJ, Benhamou N, Menzies JG, Bélanger RR (2004) Powdery mildew of *Arabidopsis thaliana*: a pathosystem for exploring the role of silicon in plant–microbe interactions. Physiological and Molecular Plant Pathology 64:189–199

Gomes FB, de Moraes JC, dos Santos CD, Goussain MM (2005) Resistance induction in wheat plants by silicon and aphids. Sci Agric 62:547–551

Gong HJ, Chen KM, Chen GC, Wang SM, Zhang CL (2003) Effects of silicon on growth of wheat under drought. Journal of Plant Nutrition 26:1055–1063

Gong HJ, Zhu XY, Chen KM, Wang SM, Zhang CL (2005) Silicon alleviates oxidative damage of wheat plants in pots under drought. Plant Science 169:313–321

Goto M, Ehara H, Karita S, Takabe K, Ogawa N, Yamada Y, Ogawa S, Yahaya MS, Morita O (2003) Protective effect of silicon on phenolic biosynthesis and ultraviolet specral stress in rice crop. Plant Science 164:349–356

Goussain MM, Prado E, Moraes JC (2005) Effect of silicon applied to wheat plants on the biology and probing behaviour of the greenbug *Schizaphis graminum* (Rond.) (Hemiptera: Aphididae). Neotropical Entomology 34:807–813

Guevel MH, Menzies JG, Bélanger RR (2007) Effect of root and foliar applications of soluble silicon on powdery mildew control and growth of wheat plants. European Journal of Plant Pathology 119:429–436

Guntzer F., 2010. Impact de la culture intensive de céréales sur les stocks de silice biodisponible dans les sols européens. PhD thesis, Aix-Marseille University

Hall AD, Morison CGT (1906) On the function of silica in the nutrition of cereals—Part I. Proceedings of the Royal Society (B) 77:455–477

Hattori T, Inanaga S, Tanimoto E, Lux A, Luxova M, Sugimoto Y (2003) Silicon-induced changes in viscoelastic properties of sorghum root cell walls. Plant and Cell Physiology 44:743–749

Hattori T, Inanaga H, Araki H, An P, Morita S, Luxova M, Lux A (2005) Application of silicon enhanced drought tolerance in *Sorghum bicolor*. Physiol Plant 123:459–466

Heaney PJ, Prewitt CT, Gibbs GV (eds) (1994) Silica: physical behavior, geochemistry and materials applications. Reviews in mineralogy 29. Mineralogical Society of America.

Henriet C, Draye X, Oppitz I, Swennen R, Delvaux B (2006) Effects, distribution and uptake of silicon in banana (*Musa* spp.) under controlled conditions. Plant and Soil 287:359–374

Henriet C, Bodarwe L, Dorel M, Draye X, Delvaux B (2008) Leaf silicon content in banana (*Musa* spp.) reveals the weathering stage of volcanic ash soils in Guadeloupe. Plant and Soil 313:71–82

Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytologist 162(1):9–24

Hodson MJ, Sangster AG (1988) Observations on the distribution of mineral elements in the leaf of wheat (*Triticum aestivum* L.), with particular reference to silicon. Ann Bot 62:463–471

Hodson MJ, Sangster AG (1993) The interaction between silicon and aluminum in *Sorghum bicolor* (L.) Moench—growth analysis and X-ray microanalysis. Ann Bot 72:389–400

Hodson MJ, Sangster AG (2002) X-ray microanalytical studies of mineral localization in the needles of white pine (*Pinus strobus* L.). Ann Bot 89:367–374

Hodson MJ, White PJ, Mead A, Broadley MR (2005) Phylogenetic variation in the silicon composition of plants. Ann Bot 96:1027–1046

Horiguchi T, Morita S (1987) Mechanism of manganese toxicity and tolerance of plants. VI. Effect of silicon on alleviation of manganese toxicity of barley. Journal of Plant Nutrition 10:2299–2310

Horst WJ, Fecht M, Naumann A, Wissemeier AH, Maier P (1999) Physiology of manganese toxicity and tolerance in *Vigna unguiculata* (L.) Walp. Journal of Plant Nutrition and Soil Science 162:263–274

Hossain KA, Horiuchi T, Miyagawa S (2001) Effects of silicate materials on growth and grain yield of rice plants grown in clay loam and sandy loam soils. Journal of Plant Nutrition 24:1–13

Hunt JW, Dean AP, Webster RE, Johnson GN, Ennos AR (2008) A novel mechanism by which silica defends grasses against herbivory. Ann Bot 102:653–656

Inanaga S, Okasaka A, Tanaka S (1995) Does silicon exist in association with organic-compounds in rice plant? Soil Science and Plant Nutrition 41:111–117

Jones LHP, Handreck KA (1967) Silica in soils, plants, and animals. Adv Agron 19:104–149

Kelly EF (1990) Methods for extracting opal phytoliths from soil and plant material. Workshop on Biotic Indicators of Global Change, University of Washington, Seattle

Kidd PS, Llugany M, Poschenrieder C, Gunse B, Barcelo J (2001) The role of root exudates in aluminium resistance and silicon-induced amelioration of aluminium toxicity in three varieties of maize (*Zea mays* L.). J Exp Bot 52:1339–1352

Kirkham MB (2006) Cadmium in plants on polluted soils: effects of soil factors, hyperaccumulation, and amendments. Geoderma 137:19–32

Korndörfer GH, Lepsch I (2001) Effect of silicon on plant growth and crop yield. In: Datnoff LE, Snyder GH, Korndorfer GH (eds) Silicon in agriculture. Studies in plant science, 8. Elsevier, Amsterdam, pp 133–147

Korndörfer GH, Snyder GH, Ulloa M, Powell G, Datnoff LE (2001) Calibration of soil and plant silicon analysis for rice production. Journal of Plant Nutrition 24:1071–1084

Leng MJ, Swann GEA, Hodson MJ, Tyler JJ, Patwardhan SV, Sloane HJ (2009) The potential use of silicon isotope composition of biogenic silica as a proxy for environmental changes. Silicon 1:65–77

Li YC, Summer ME, Miller WP, Alva AK (1996) Mechanism of silicon induced alleviation of aluminum phytotoxicity. Journal of Plant Nutrition 19:1075–1087

Liang YC, Ma TS, Li FJ, Feng YJ (1994) Silicon availability and response of rice and wheat to silicon in calcareous soils. Communications in Soil Science and Plant Analysis 25:2285–2297

Liang YC, Shen QR, Shen ZG, Ma TS (1996) Effects of silicon on salinity tolerance of two barley cultivars. Journal of Plant Nutrition 19:173–183

Liang YC, Chen Q, Liu Q, Zhang WH, Ding RX (2003) Exogenous silicon (Si) increases antioxidant enzyme activity and reduces lipid peroxidation in roots of salt-stressed barley (*Hordeum vulgare* L.). Journal of Plant Physiology 160:1157–1164

Liang YC, Sun WC, Zhu YG, Christie P (2007) Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: a review. Environ Pollut 147:422–428

Liu C, Li F, Luo C, Liu X, Wang S, Liu T, Li X (2009) Foliar application of two silica sols reduced cadmium accumulation in rice grains. J Hazard Mater 161:1466–1472

Lovering TS, Engel C (1959) Significance of accumulator plants in rock weathering. Bulletin of the Geological Society of America 70:781–800

Lucas Y, Luizão FJ, Chauvel A, Rouiller J, Nahon D (1993) The relation between biological activity of the rain forest and mineral composition of soils. Science 260:521–523

Lux A, Luxová M, Abe J, Tanimoto E, Hattori T, Inanaga S (2003) The dynamics of silicon deposition in the sorghum root endodermis. New Phytologist 158:437–441

Ma JF, Takahashi E (1990) The effect of silicic acid on rice in a P-deficient soil. Plant and Soil 126:121–125

Ma JF, Takahashi E (2002) Soil, fertiliser, and plant silicon research in Japan. Elsevier, Amsterdam

Ma JF, Yamaji N (2006) Silicon uptake and accumulation in higher plants. Trends in Plant Science 11:392–397

Ma JF, Goto S, Tamai K, Ichii M (2001a) Role of root hairs and lateral roots in silicon uptake by rice. Plant Physiology 127:1773–1780

Ma JF, Miyake Y, Takahashi E (2001b) Silicon as a beneficial element for crop plants. In: Datnoff LE, Snyder GH, Korndorfer GH (eds) Silicon in agriculture. Studies in plant science, 8. Elsevier, Amsterdam, pp 17–39

Ma JF, Mitani N, Nagao S, Konishi S, Tamai K, Iwashita T, Yano M (2004) Characterization of the silicon uptake system and molecular mapping of the silicon transporter gene in rice. Plant Physiology 136:3284–3289

Ma JF, Yamaji N, Mitani N, Xu XX, Su YH, McGrath SP, Zhao FJ (2008) Transporters of arsenite in rice and their role in arsenic accumulation in rice grain. PNAS 105:9931–9935

Madella M, Alexandre A, Ball T (2005) International code for phytolith nomenclature 1.0. Ann Bot 96:253–260

Makabe S, Kakuda K, Sasaki Y, Ando T, Fujii H, Ando H (2009) Relationship between mineral composition or soil texture and available silicon in alluvial paddy soils on the Shounai Plain, Japan. Soil Science and Plant Nutrition 55:300–308

Mali M, Aery NC (2008a) Influence of silicon on growth, relative water contents and uptake of silicon, calcium and potassium in wheat grown in nutrient solution. Journal of Plant Nutrition 31:1867–1876

Mali M, Aery NC (2008b) Silicon effects on nodule growth, dry-matter production, and mineral nutrition of cowpea (*Vigna unguiculata*). Journal of Plant Nutrition and Soil Science 171:835–840

Matichenkov VV, Bocharnikova EA (2001) The relationship between silicon and soil physical and chemical properties. In: Datnoff LE, Snyder GH, Korndorfer GH (eds) Silicon in agriculture. Studies in plant science, 8. Elsevier, Amsterdam, pp 209–219

Mecfel J, Hinke S, Goedel WA, Marx G, Fehlhaber R, Baeucker E, Wienhaus O (2007) Effect of silicon fertilizers on silicon accumulation in wheat. Journal of Plant Nutrition and Soil Science 170:769–772

Meunier JD, Colin F, Alarcon C (1999) Biogenic silica storage in soils. Geology 27:835–838

Meunier JD, Guntzer F, Kirman S, Keller C (2008) Terrestrial plant-Si and environmental changes. Mineral Mag 72:263–267

Meyer JH, Keeping MG (2001) Past, present and future research of the role of silicon for sugarcane in southern Africa. In: Datnoff LE, Snyder GH, Korndorfer GH (eds) Silicon in agriculture. Studies in plant science, 8. Elsevier, Amsterdam, pp 257–275

Mitani N, Ma JF (2005) Uptake system of silicon in different plant species. J Exp Bot 56:1255–1261

Mitani N, Yamaji N, Ma JF (2009) Identification of maize silicon influx transporters. Plant and Cell Physiology 50:5–12

Moraes JC, Goussain MM, Basagli MAB, Carvalho GA, Ecole CC, Sampaio MV (2004) Silicon influence on the tritrophic interaction: wheat plants, the greenbug *Schizaphis graminum* (Rondani) (Hemiptera: Aphidiidae), and its natural enemies, *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae) and *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae). Neo-tropical Entomology 33:619–624

Motomura K, Fuji T, Suzuki M (2004) Silica deposition in relation to ageing of leaf tissues in *Sasa veitchii* (Carrière) Rehder (Poaceae: Bambusoideae). Ann Bot 93:235–248

Neumann D, zur Nieden U (2001) Silicon and heavy metal tolerance of higher plants. Phytochemistry 56:685–692

Neumann D, De Figueiredo C (2002) A novel mechanism of silicon uptake. Protoplasma 220:59–67

Neumann D, Lichtenberger O, Schwieger W, zur Nieden U (1997) Accumulation of silicon in *Deschampsia caespitosa*, *Festuca iehmannii* and *Schoenus nigricans*. Plant Biology 1:290–298

Pei ZF, Ming DF, Liu D, Wan GL, Geng XX, Gong HJ, Zhou WJ (2010) Silicon improves the tolerance of wter-deficit stress induced by polyethylene glycol in wheat (*Triticum aestivum* L.) seedlings. Journal of Plant Growth Regulation 29:106–115

Perry CC, Keeling-Tucker T (1998) Aspects of the bioinorganic chemistry of silicon in conjunction with the biometals calcium, iron and aluminium. J Inorg Biochem 69:181–191

Ponzi R, Pizzolongo P (2003) Morphology and distribution of epidermal phytoliths in *Triticum aestivum* L. Plant Biosystems 137:3–10

Prychid CJ, Rudall PJ, Gregory M (2003) Systematics and biology of silica bodies in monocotyledons. Bot Rev 69:377–440

Rains DW, Epstein E, Zasoski RJ, Aslam M (2006) Active silicon uptake by wheat. Plant and Soil 280:223–228

Raven JA (2001) Silicon transport at the cell and tissue level. In: Datnoff LE, Snyder GH, Korndorfer GH (eds) Silicon in agriculture. Studies in plant science, 8. Elsevier, Amsterdam, pp 41–55

Rémus-Borel W, Menzies JG, Bélanger RR (2005) Silicon induces antifungal compounds in powdery mildew-infected wheat. Physiological and Molecular Plant Pathology 66:108–115

Rémus-Borel W, Menzies JG, Bélanger RR (2009) Aconitate and methyl aconitate are modulated by silicon in powdery mildew-infected wheat plants. Journal of Plant Physiology 166:1413–1422

Ryder M, Gérard F, Evans DE, Hodson MJ (2003) The use of root growth and modelling data to investigate amelioration of aluminium toxicity by silicon in *Picea abies* seedlings. J Inorg Biochem 97:52–58

Rodgers-Gray BS, Shaw MW (2004) Effects of straw and silicon soil amendments on some foliar and stem-base diseases in pot-grown winter wheat. Plant Pathology 53:733–740

Rogalla H, Romheld V (2002) Role of leaf apoplast in silicon-mediated manganese tolerance of *Cucumis sativus* L. Plant Cell and Environment 25:549–555

Saccone L, Conley DJ, Koning E, Sauer D, Sommer M, Kaczorek D, Blecker SW, Kelly EF (2007) Assessing the extraction and quantification of amorphous silica in soils of forest and grassland ecosystems. European Journal of Soil Science 58:1446–1459

Sachs J (1862) Ergebnisse einiger neuerer Untersuchungen über die in Pflanzen enthaltene Kieselsäure. Flora 4:53–55

Sangster AG (1978) Silicon in roots of higher plants. Am J Bot 65:929–935

Sangster AG, Hodson MJ, Tubb HJ (2001) Silicon deposition in higher plants. In: Datnoff LE, Snyder GH, Korndorfer GH (eds) Silicon in agriculture. Studies in plant science, 8. Elsevier, Amsterdam, pp 85–113

Saqib M, Zorb C, Schubert S (2008) Silicon-mediated improvement in the salt resistance of wheat (*Triticum aestivum*) results from increased sodium exclusion and resistance to oxidative stress. Functional Plant Biology 35:633–639

Sarwar N, Saifullah, Malhi SS, Zia MH, Naeem A, Bibi S, Farid G (2010) Role of mineral nutrition in minimizing cadmium accumulation by plants. J Sci Food Agric 90:925–937

Sauer D, Saccone L, Conley DJ, Herrman L, Sommer M (2006) Review of methodologies for extracting plant-available and amorphous Si from soils and aquatic sediments. Biogeochemistry 80:89–108

Savant NK, Datnoff LE, Snyder GH (1997a) Depletion of plant-available silicon in soils: a possible cause of declining rice yields. Communications in Soil Science and Plant Analysis 28:1245–1252

Savant NK, Snyder GH, Datnoff LE (1997b) Silicon management and sustainable rice production. Adv Agron 58:151–199

Shen X, Zhou Y, Duan L, Eneji AE, Li J (2010) Silicon effects on photosynthesis and antioxidant parameters of soybean seedlings under drought and ultraviolet-B radiation. Journal of Plant Physiology 167:1248–1252

Shi XH, Zhang CC, Wang H, Zhang FS (2005) Effect of Si on the distribution of Cd in rice seedlings. Plant and Soil 272:53–60

Sommer M, Kaczorek D, Kuzyakov Y, Breuer J (2006) Silicon pools and fluxes in soils and landscapes—a review. Journal of Plant Nutrition and Soil Science 169:310–329

Tuna AL, Kaya C, Higgs D, Murillo-Amador B, Aydemir S, Girgin AR (2008) Silicon improves salinity tolerance in wheat plants. Environ Exp Bot 62:10–16

Wallace A (1993) Participation of silicon in cation–anion balance as a possible mechanism for aluminum and iron tolerance in some Gramineae. Journal of Plant Nutrition 16:547–553

Wang Y, Stass A, Horst WJ (2004) Apoplastic binding of aluminum is involved in silicon-induced amelioration of aluminum toxicity in maize. Plant Physiology 136:3762–3770

White AF, Brantley SL (eds) (1995) Chemical weathering rates of silicate minerals. Reviews in Mineralogy 31, Mineralogical Society of America

Williams DE, Vlamis J (1957) The effect of silicon on yield and manganese-54 uptake and distribution in the leaves of barley grown in culture solutions. Plant Physiology 32:404–409

Wonisch H, Gérard F, Dietzel M, Jaffrain J, Nestroy O, Boudot J-P (2008) Occurrence of polymerized silicic acid and aluminum species in two forest soil solutions with different acidity. Geoderma 144:435–445

Yoshida S, Navasero SA, Ramirez EA (1969) Effects of silica and nitrogen supply on some leaf characters of the rice plant. Plant and Soil 31:48–56