International Journal of Agricultural Sciences ISSN: 2167-0447 Vol. 4 (2), pp. 111-120, February, 2014. Available online at www.internationalscholarsjournals.org © International Scholars Journals

Review

Silicon to silica bodies and their potential roles: An overview

Sheikh Abdul Shakoor

Systematics and Biodiversity Laboratory, Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar (Pb) India-143005. E-mail: shakoorshiekh9@gmail.com

Accepted 7 January, 2014

Plants have a unique capability to deposit Silicon (Si) within and between the cells as silica and thus creating casts of the cells commonly known as Silica bodies or Phytoliths (Plant stones). Silicon is present in plants in amounts equivalent to calcium, magnesium and phosphorus and is the second most abundant element after oxygen in soil. In Poaceae (Grass family) Si often is present in higher quantity than any other inorganic constituent. Yet except for certain algae, including prominently the diatoms and the Equisetaceae (horsetails or scouring rushes), it is not considered an essential element for plants. As a result it is being routinely omitted from formulations of culture solutions and considered a nonentity in much of plant nutrition research, which ultimately has lead to negative impacts on the proper growth and development of the plants. Silicon-deprived plants grown in conventional nutrient solutions to which silicon has not been added are in many ways experimental artifacts. They are often structurally weaker than silicon enriched plants, abnormal in growth, development, viability and reproduction. Furthermore, such plants are susceptible to biotic and abiotic stresses such as metal toxicities and prey easily to disease organisms and to herbivores ranging from phytophagous insects to mammals. Hence, the above mentioned points necessitate reviewing the background of silica in plants, its essentiality, cycling and potential roles in plant life.

Key words: Silicon, silicic acid, silica, silica bodies, phytoliths.

INTRODUCTION

The word silicon is derived from the Latin word silex, meaning flint. The word was originally used to denote any hard rock. In modern English, silicon refers to the element and silica refers to a compound in which each molecule of silicon is chemically bound to two oxygen molecules (SiO_2; silicon dioxide). The earth's crust contains a large proportion of silicon (Ingri, 1978; Iler, 1978). This silicon is mostly in the form of silicates and aluminosilicates. In soil solutions, silicon is found mostly in the form of silicic acid ($Si(OH)_4$) (Lindsay, 1979; Epstein, 1994). In plants, silicon is found mostly as silicon dioxide. Although silicon can be found in great abundance on this planet, its biological functions are not as well studied as those of other elements such as oxygen, hydrogen and carbon (Wainwright, 1997).

Silicon is considered an essential nutrient for a group of algae known as diatoms (Round et al., 1990; Kinrade et al., 2001, 2002). As for vascular plants, silicon is only considered essential for the Equisetaceae family (Chen and Lewin, 1969). However, silicon is absorbed by most plants, in greater or lesser quantities (Epstein and Bloom 2005). In particular, graminaceous crops are known to absorb silicon in higher amounts (Rafi and Epstein, 1999; Tamai and Ma, 2003). The interactions of silicon with crop plants have been of particular interest (Savant et al., 1997; Ma and Takahashi, 2002; Tamai and Ma, 2003; Rodrigues et al., 2004).

Silicon in Soil

Silicon constitutes a substantial percentage of majorities of the soil types, generally about 31% (Sposito, 1989). In soil solutions, silicon is found mostly as uncharged monomeric silicic acid at concentrations from about 0.1 mM to 0.6 mM (Epstein, 1994) or up to about 0.8 mM at equilibrium (Lindsay, 1979) when the solution pH is below 9 (Ma and Takahashi, 2002).

A few soil factors can affect the availability of silicon for plant uptake. According to Jones and Handreck (1967) "there is a marked effect of pH on the solubility of silica in soils," but this effect is not in the range of pH in which most plants are cultivated. Weathering is the main factor in the availability of silicon in soils. As weathering increases, available silicon is generally depleted. This phenomenon occurs mostly in tropical regions of the earth. Details of the speciation of silica in soils are provided by Lindsay (1979), but a brief review follows:

At a lower pH, silicic acid (H_4SiO_4) is more soluble and less likely to dissociate. Silicic acid (H_4SiO_4) is in equilibrium with soil SiO_2 at pH 3.10 and at a concentration of 0.794 mM. Silicic acid is in equilibrium with silicate ions that polymerize at pH 9.71 and at a concentration of 0.794 mM. A 1.0000 mM solution of H_4SiO_4 would dissociate into 0.9999 mM H_4SiO_4 and 0.0001 mM $H_3SiO_4^-$ at pH 6.00. The same solution would dissociate into 0.404 mM H_4SiO_4 and 0.596 mM $H_3SiO_4^-$ at pH 10.00. Uptake of silicon from soil increases with increasing soil water content (Hemmi, 1933; Williams and Shapter, 1955). The presence of aluminum and iron oxides in the soil has been shown to decrease the amount of soluble Si in the soil solution (Jones and Handreck, 1967). High concentration of silicic acid (for example >120–140 ppm or 1.2–1.5 mM) in the soil solution can lead to polymerization to colloidal silica (Jones and Handreck, 1967).

Some weathered acidic soils contain less available silicon than others. Lindsay (1979) states that "in highly weathered soils, free SiO_2 may become depleted from soils leaving sesquioxides of iron and aluminum as the major residual minerals." In such soils, silicon amendments can be important for optimal crop yields (Alvarez et al., 1988; Korndörfer and Lepsch, 2001).

Silicon Uptake and Deposition in Plants

The essentiality of silicon for plant growth has long been a question of interest to plant nutrition researchers. Uptake of silicon varies by species and by plant group (Jones and Handreck, 1967; Ma et al., 2001; Richmond and Sussman, 2003). In some plants, such as many species of the Gramineae family, uptake of silicon appears to be passive (Jones and Handreck, 1967). In other plants, such as dicotyledons, uptake of silicon appears to be excluded by the roots (Jones and Handreck, 1967). Originally, rice was considered a special case. Rice plants appear to perform active uptake of silicon (Ma and Yamaji, 2006; Van Soest, 2006) at least in hydroponic solutions. However, using modern analytical techniques, it is possible that many plants may soon be seen to have some form of silicon uptake or rejection mechanism in cortical cell membranes (Richmond and Sussman, 2003). Mitani and Ma (2005) note a silicon transporter in cortical cell membranes of several species of crops, noting also a greater density of the transporter in rice as compared to cucumber and tomato. Ma and Yamaji (2006) suggest that there is a gene that encodes "a Si uptake transporter in rice." Cornelis et al. (2010) suggest that silicon uptake is passive in forest trees.

Following root uptake from the rhizosphere, silicic acid is loaded into the xylem. Ma and Yamaji (2006) reported that xylem loading is "mediated by a kind of transporter" in rice, but not in cucumber and tomato. Hence, it appears that in dicotyledonous species xylem loading is passive. Other species are most likely to mediate xylem loading either by a transporter or by passive diffusion. Wiese et al. (2007) stated that xylem loading is of greater importance than uptake in the root symplast when it comes to silicon uptake. For most plants, the concentration and amount of silicon in the plant tends to increase with plant age (Jones and Handreck, 1967).

Once accumulated inside a plant, silicon can "lend rigidity and roughness to the walls" of plant cells (Epstein and Bloom, 2005) as well as provide other beneficial effects (Van Soest, 2006). Studies indicate that silicon is transported passively in the transpiration stream and is deposited at sites of high transpiration (Wiese et al., 2007). There is no evidence of silicon being mobile within plants. It is hypothesized that as water transpired from the plant, silicic acid accumulates and forms colloidal silicic acid, then amorphous silica ($SiO_2.nH_2O$) (also referred to as silica bodies, phytoliths, plant opal or biogenic opal), which polymerizes at high concentrations (> 2mM), thus creating a rigid polymer within the plant (Jones and Handreck, 1967; Gao et al., 2006; Ma and Yamaji, 2006). Silicon has been shown to enhance growth and yield, promote upright stature, prevent lodging, promote favorable exposure of leaves to light, provide resistance to bacterial and fungal diseases (Fawe et al., 2001; Voogt and Sonneveld, 2001) provide resistance to herbivores (Coors, 1987), low temperatures (Epstein, 1999; 2001), salinity (Hamayun et al., 2010; Lee et al., 2010), heavy metal toxicity (Liang et al., 2005) and aluminum toxicity (Cocker et al., 1998; Kidd et al., 2001) and influence nitrogen, phosphorus and the composition of other elements in plant tissue (Bollard and Butler, 1966; Epstein and Bloom, 2005) (Figure 2). Not only has rhizosphere supply of silicon been effective, but "silicon supplementation in the form of external foliar treatments has proven to increase the pathogen resistance of plant species that do not take up silicon efficiently" (Richmond and Sussman, 2003). Industrial by-products containing silicon have been used to benefit plants. "Siliceous blast-furnace slags" have been added to soils to increase rice disease resistance (Jones and Handreck, 1967; Savant et al., 1996; Pereira et al., 2004).

Silicon and Essentiality Criteria's

To date only two groups of plants are known to have an absolute and quantitatively major requirement for Si *viz.,* the diatoms and other members of the yellow-brown or golden algae, the Chrysophyceae (Simpson and Volcani, 1981; Werner and Roth, 1983) and the “scouring rushes,” Equisitaceae (Chen and Lewin, 1969). As for higher plants in general, however, essentiality of Si in the Arnon-Stout (1939) sense is yet to be justified (Asher, 1991; Takahashi et al., 1990). However, it is difficult to purge solution cultures thoroughly of Si. Woolley (1957) has done what still remains the most painstaking experimentation on this subject and reduced the Si content of tomato plant tops to a mere 0.0006% on a dry weight basis, but the growth of the plants was not diminished compared with that of plants supplied with Si. Japanese researchers, however, have led to the conclusion, in 1990, that further intensive research “should qualify silicon as an essential element for higher plants in the near future” (Takahashi et al., 1990). Werner and Roth (1983) are more sanguine and “consider it to be an essential element,” without, however, spelling out the criteria for this opinion. At this point we have to come to grips with the application of the Arnon and Stout (1939) definition of essentiality, already criticized above, to Si. This is not the place for a full-blown discussion of this subject, but a few points need to be made nevertheless. They have to do with (*a*) the limitations of purging elements from experimental cultures; (*b*) the genotypic variations in nutrient requirements; and (*c*) quantitative considerations. As for (*a*), when Woolley (1957), in the research already referred to, grew tomato plants in highly purified culture solutions and failed to find differences between their growth and that of plants deliberately supplied with Si, he concluded, correctly, that this did not show Si to be nonessential but only that, if it were essential, it would be required at tissue levels of less than 0.0006%. For demonstrating the essentiality of Si, it was necessary to purify the medium to the point where tissue levels were reduced to less than 0.00001%. Clearly, it has not been possible to reduce tissue levels of Si to comparably low values and the possibility of a micronutrient function for Si cannot be ruled out. This same point concerning the limitations of purification procedures has been made repeatedly (Asher, 1991; Epstein 1972; 1994). It applies to Si with particular force, because the uncharged H_4SiO_4 passes through the ion exchangers so widely used for preparing laboratory-grade water.

The second reservation about the definition of essentiality is that it conveys an impression of general applicability that is not warranted. Sodium is an example: It is a micronutrient for C4 plants (Brownell and Crossland, 1972) but not known to be a micronutrient for plants generally. For Si, equal care needs to be taken not to generalize, in view of its essentiality for some groups of plants. Finally, quantitative considerations. Chlorine is assuredly a micronutrient for higher plants (Broyer et al., 1954) but it may well play a macronutrient role not only in some halophytes but in some genotypes and conditions, for such a common crop as winter wheat (Engel et al., 1992). For Si, no micronutrient function has been shown; plants unable to grow without it have a quantitatively major requirement for the element. Thus it is necessary to go beyond mere listings of elements as essential or not known to be so and to give judicious interpretations of the complexities of the real world. In view of what follows, Si will be considered “quasi-essential” for many of those plants for which its absolute essentiality has not been established. An element is defined as quasi-essential if it is ubiquitous in plants and if a deficiency of it can be severe enough to result in demonstrable adverse effects or abnormalities in respect to growth, development, reproduction or viability. That deficient situation prevails for Si in many highly weathered tropical soils, such as Ultisols and Oxisols (Foy, 1992) and as already pointed out, in conventional, Hoagland-type solution cultures. By extension, these same considerations apply when plants are grown in commercial (or hobby) hydroponic systems (Belanger and Benyagoub, 1997). The addition of clay to soil less media promoted the growth of greenhouse crops (Ehret, 1998); might not that finding be due to Si having become available to the plants from the clay?

Plants and Silicon Cycle

Plants are not only involved with silicon in terms of growth, but are also major components of the global silicon cycle. Taking the land surface as a starting point, vascular plants play a major role in weathering silicate rocks. Plants and their associated microbiota directly affect silicate mineral weathering in several ways: by the generation of organic substances, known as chelates, that have the ability to decompose minerals and rocks by the removal of metallic cations; by modifying pH through the production of CO_2 or organic acids such as acetic, citric, phenolic and by altering the physical properties of the soil, particularly the exposed surface areas of minerals and the residence time of water. Primary silicates, secondary mineral phases containing silica and biogenic silica (Bartoli, 1985) weather in water to produce monomeric orthosilicic acid (Currie and Perry, 2007). Silicic acid concentration varies with soil type (Siever, 1957), but is generally between 0.1 and 0.6 mM silicic acid (Epstein, 1994). Silicon forms complexes with aluminium, iron, heavy metals and organic matter (Farmer et al., 2005). Silicic acid is the only known precursor of silicon compounds in biota (Exley, 1998) and plants take up aqueous, uncharged silicic acid through their roots (Raven, 1983) (Figure 1). In vascular land plants, the flux ratio (mol Si: m3 water) can be less than, equal to, or greater than the concentration of the soil solution and therefore, plants are considered to have restrictive, passive or active uptake of silicon, respectively (Mitani and Ma, 2005). Two different silicon transporters have been identified in the roots of rice, a high silicic acid accumulating species (Ma et al., 2006; 2007). Silicon is thought to be transported in the xylem rather than

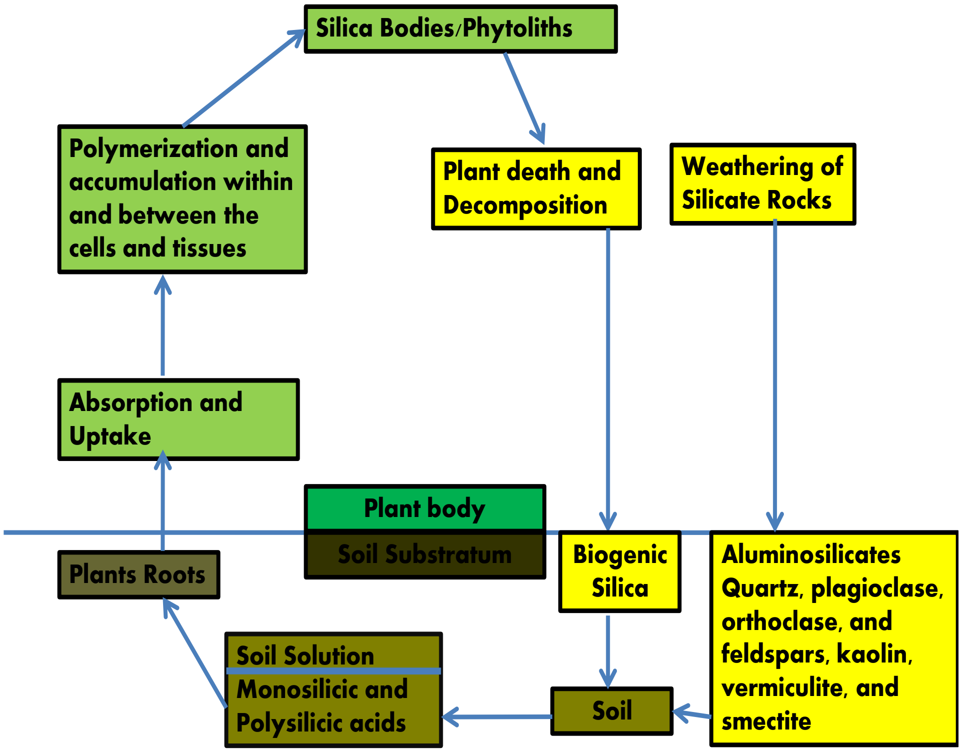

Figure 1. Silicon in plants. Silicic acid taken by plants from soil is deposited as biogenic, amorphous silica. When the plant dies, the silica is returned to the soil, where it can either persist for long periods or dissolve in the soil solution.

In the phloem and movement is apoplastic (Raven, 1983). Although transport around the plant is related to the transpiration stream, there is some active transport involved (Liang et al., 2006). Plasma membranes are permeable to silicon and high-molecular-weight silicon complexes can be transported into the vacuoles through endocytosis (Exley, 1998). Silicic acid saturates at 1.67 mM and then becomes highly polymerised, resulting in the deposition of solid, amorphous, hydrated silica ($SiO_2.nH_2O$) in the form of Silica (Currie and Perry, 2007). Plant silica is deposited in situ and once deposited, is not relocated (Raven, 1983). Silicon can be deposited in any plant part, within or between cells or as part of the cell wall, with discrete silica bodies known as phytoliths (Plant stones) (Piperno, 2006).

Following shedding of plant parts and subsequent plant senescence, much plant silicon dissolves in the soil solution and either cycles through biota or is leached into waterways. In some systems, most of the silicon entering streams have passed through the biogenic silica pool (Siever, 1962). However, some phytoliths can be preserved for long periods, although amorphous silica has a higher solubility than quartz which is crystalline silica. Figure 1 summarizes the cycling of silicon between plants and environment.

Soil-Plant Reactivity with Silicon

Soluble and plant available silicon compounds, such as monosilicic acid and polysilicic acid, affect many physico-chemical properties of soil. Monosilicic acid possesses high chemical activity (Lindsay, 1979; Iler, 1979). Monosilicic acid can react with aluminum, iron and manganese with the formation of slightly soluble silicates (Horiguchi, 1988; Lumsdon and Farmer, 1995):

$Al_2Si_2O_5 + 2H^+ + 3H_2O = 2Al^{3+} + 2H_4SiO_4$

$Al_2Si_2O_5 (OH)_4 + 6H^+ = 2Al^{3+} + 2H_4SiO_4 + H_2O$

$Fe_2SiO_4 + 4H^+ = 2Fe^{2+} + 2H_4SiO_4$

$MnSiO_3 + 2H^+ = H_2O + Mn^{2+} + 2H_4SiO_4$

$Mn_2SiO_4 + 4H^+ = 2Mn^{2+} + H_4SiO_4$

Monosilicic acid under variable concentrations is able to combine with heavy metals (Cd, Pb, Zn, Hg and others) forming soluble complex compounds if monosilicic acid concentration is less (Schindler et al., 1976), and slightly soluble heavy metal silicates when the concentration of monosilicic acid is greater in the system (Lindsay, 1979).

$ZnSiO_4 + 4H^+ = 2Zn^{2+} + H_4SiO_4$

$PbSiO_4 + 4H^+ = 2Pb^{2+} + H_4SiO_4$

Silicon may play a prominent part in the effects of aluminum on biological systems (Birchall et al., 1989).

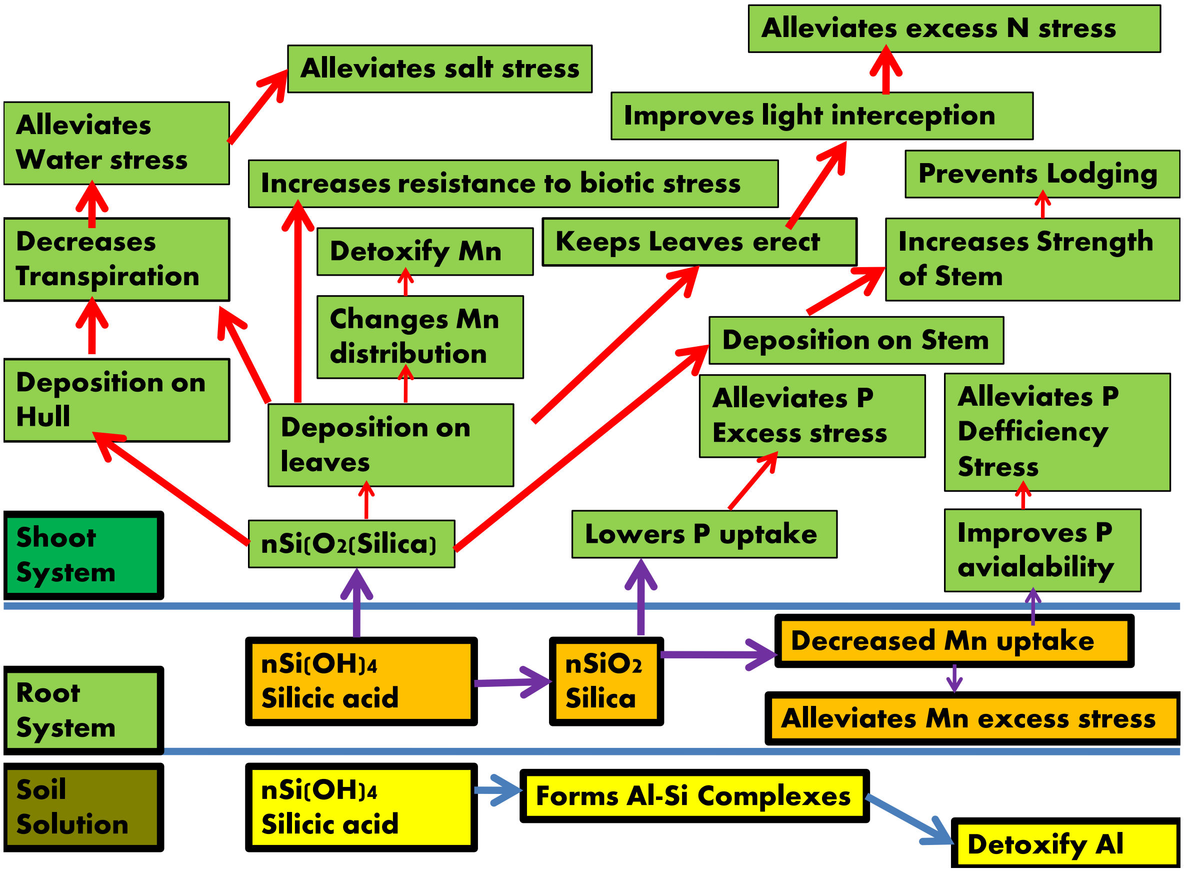

Figure 2. Beneficial effects of silica in relation to Biotic and Abiotic stress in plants.

Significant amelioration of aluminum toxicity by silicon has been noted by different groups and in different species (Hodson and Evans, 1995) (Figure 2). The main mechanism of the effect of silicon on aluminum toxicity is probably connected with the formation of nontoxic hydroxyaluminosilicate complexes (Exley and Birchall, 1993). The anion of monosilicic acid ($Si(OH)_3)^-$ can replace the phosphate anion $(HPO_4)^{2-}$ from calcium, magnesium, aluminum and iron phosphates (Matichenkov et al., 1997). Silicon may replace phosphate from DNA and RNA molecules. As a result, proper silicon nutrition is responsible for increasing the stability of DNA and RNA molecules (Adatia and Besford, 1986). Silicon has also been shown to result in higher concentrations of chlorophyll per unit area of leaf tissue. This action may mean that a plant can tolerate either low or high light levels by using light more efficiently. Moreover, supplemental levels of soluble silicon are responsible for producing higher concentrations of the enzyme ribulose bisphosphate carboxylase in leaf tissue (Adatia and Besford, 1986). This enzyme regulates the metabolism of CO_2 and promotes more efficient use of CO_2 by plants. The increase in the content of sugar in sugar beets (*Beta vulgaris* L.) (Leibig, 1840; Ayres, 1966) and sugar cane (Fox et al., 1967) as a result of silicon fertilizer application may be assessed as a biochemical influence of silicon as well. The optimization of silicon nutrition for orange resulted in a significant increase in fruit sugar (brix) (Matichenkov et al., 2002). There have been few investigations of the role and functions of polysilicic acid and phytoliths in higher plants.

In spite of numerous investigations and observed effects of silicon on plants and the considerable uptake and accumulation of silicon by plants, no evidence yet shows that silicon takes part directly in the metabolism of higher plants.

ROLES OF SILICON IN PLANTS

Protective Role of Silicon

As mentioned earlier, silicon is not traditionally considered as an essential element in plants, numerous studies have shown that it can influence positively plant growth and yield (Ahmed et al., 2011; Savant et al., 1997).

Figure 2 highlights the beneficial effects of silicon in plants. Silicon is applied to improve plant growth and yield, in particular, under stress conditions (Hattori et al., 2005). Silica may help to maintain rigidity in stems and linear leaves, although leaf stiffness may also be related to the degree of lignification (Matsuda et al., 1983). Silica has been shown to improve lodging resistance in wheat (Gartner et al., 1984). Silica content may be related to grazing of grasses by herbivores (Vicari and Bazely, 1993). McNaughton and Tarrants (1983) and McNaughton et al. (1985) found that silica content was higher in heavily grazed grasslands than in others and that more silica was present in plant tissues produced early in the growing season. In a feeding experiment, prairie voles (*Microtus ochrogaster*) preferentially ate grasses with low silica content (Gali Muhtasib et al., 1992). Wadham and Parry (1981) investigated the relationship between silica content and slug resistance. Djamin and Pathak (1967) tested several rice varieties and found that those with high silica content showed greater resistance to Asiatic stem borer (*Chilo suppressalis*) than others, prob-ably because the silica interfered with boring and feeding of the larvae; selecting rice varieties with a high silica content was more economical than applying silicate to the soil. Hanifa et al. (1974) studied the role of silica in the resistance of rice to the leaf roller (*Cnaphalocrocis medinalis*), and Moore (1984) examined the relationship of silica to stem-borer infection by *Oscinella* species in Lolium *tamulentum*. Plants uptake soluble Si from the soil and deposit it in apoplast in the epidermal cell walls thus restricting penetration of fungal germ tube into the epidermis. In fact, Si improves plant resistance against fungi by improving its defensive mechanisms. Plants, which are fed Si accumulate different phenolic compounds like fungitoxic which kills the fungal hyphae that penetrate the cells. In addition to inhibiting fungal diseases, silicon ameliorates mineral imbalances and other diseases caused by abiotic stresses in plants.

Several other functions have been attributed to silicon: improvement of nutrient imbalance, reduction of mineral toxicities, improvement of mechanical properties of plant tissues and enhancement of resistance to other various abiotic (salt, metal toxicity, nutrient imbalance, lodging, drought, radiation, high temperature, freezing, UV) and biotic stresses (Ma and Yamaji, 2006) (Figure 2). Biel et al. (2008) suggested that the protective role of silicon in plants may be connected with accumulation of polysilicic acids inside cells. This opinion found indirect support in the fact of increased stress tolerance accompanying an increase in the concentration of polysilicic acid in plant tissues (Matichenkov et al., 2000).

Salinity Stress

High salt concentrations normally impair the cellular electron transport within the different subcellular compartments and lead to generation of reactive oxygen species (ROS), which triggers phytotoxic reactions such as lipid peroxidation, protein degradation and DNA mutation (Ali and Alqurainy, 2006). Addition of Si decreased permeability of the plasma membrane of leaf cells and significantly improved the ultra structure of chloroplasts, which were badly damaged by NaCl addition with the double membranes disappearing and the grana being disintegrated in the absence of Si (Liang et al., 2003). It was shown in *Distichlis spicata* growing under soil salinity (Biel et al., 2008) that the plants accumulate bigger amounts of Si in their particular parts under stressful conditions. Al-Aghabary et al. (2004) results demonstrate that silicate partially offsets the negative impact of NaCl stress, which increases tolerance of tomato plants to NaCl salinity by raising superoxide dismutase (SOD) and catalase (CAT) activities. Liang et al. (2003) showed that exogenous Si significantly enhanced the activities of Superoxide dismutase, Catalase and Glutathione reductase (GR) in roots of salt-stressed plants. Molassiotis et al. (2005) reported increased SOD activity under salt stress. Zhu (2001) also observed that addition of Si increased the activities of SOD, guaiacol peroxidase (GPX) and Ascorbate peroxidase (APX) of salt-stressed cucumber. In Soylemezoglu et al. (2009) a study on the effect of silicon on antioxidant response of two grapevine (*Vitis vinifera* L.) rootstocks grown in boron toxic, saline and boron toxic-saline soil, application of Si lowered SOD and CAT but increased APX.

Heavy Metal Stress

Heavy metal stress negatively affects processes associated with biomass production and grain yield in almost all major field grown crops (Bednarek et al., 2006). Every metal and plant interact in a specific way, which depends on several factors such as the type of soil, growth conditions and the presence of other ions (Rana and Masood, 2002). Silicon alleviates metal toxicity by co-precipitation in the cell wall. Several studies have shown that Si can reduce or prevent manganese (Mn) and iron (Fe) toxicity and may also have beneficial effects on aluminum (Al) toxicity. Silicon does not seem to affect Mn uptake, but rather Mn distribution in plant tissues. When Si concentration in tissue is low, Mn tends to be distributed unevenly and accumulates to toxic levels in spots in leaves while adequate Si supply cause homogeneous distribution of Mn thereby preventing its accumulation in leaves. Silicon alleviates an otherwise detrimental nutrient imbalance between zinc and phosphorus. Hammond et al. (1995) showed that silicon treatments gave significant alleviation of the toxic effect of Al in barley plants. Aluminium uptake by roots was significantly diminished in the presence of Si. Silicon-mediated alleviation of heavy metal toxicity in higher plants is widely accepted (Figure 2).

Shi et al. (2005) reported that the alleviation of Mn toxicity by Si in cucumber was attributed to a significant reduction in lipid peroxidation (LPO) intensity caused by excess Mn and to a significant increase in enzymatic activity for example SOD, APX and GR and non-enzymatic antioxidants for example ascorbate and glutathione. In the study conducted by Gunes et al. (2007), unlike SOD and CAT activities, APX activity of barley was significantly higher, compared to plants growing without Si supplementation. It can be concluded from the APX results that APX was probably more important than CAT in H_2O_2 detoxification. Such coordinated responses of APX with H_2O_2 concentrations in tissues are believed to promote tolerance to oxidative stress (Gunes et al., 2007). Soylemezoglu et al. (2009) showed that the activities of SOD and CAT in boron stressed plants obviously increased, whereas that of APX was decreased. The results related to antioxidant enzyme responses under B toxicity were in agreement with the findings of Molassiotis et al., (2005) who reported increased SOD and CAT activity under B toxicity in apple rootstocks.

Water Stress/Drought

Water is vital to many biological systems and organisms. It supports many biological reactions by serving as a transport medium, a solvent and a fuel for the hydrolysis of photosystem II. Drought, one of the serious environmental stresses, is the most significant factor restricting plant growth and crop productivity in a majority of agricultural fields of the world (Devkota and Jha, 2011; Said-Al Ahl et al., 2009). Silicon plays a very important role in drought tolerance because silicon fed plants maintains higher leaf water potential. This is assumed to be due to the formation of silica-cutical double layer on the epidermis (Figure 2). In addition, endodermal tissue, which plays an important role in water transport across the root, accumulates large amounts of silicon in mature drought-tolerant plants. Numerous studies demonstrate that the antioxidant defense system improves the relationship between enhanced or constitutive antioxidant enzyme activities and increased resistance to drought stress. Compared with the non-silicon treatment, application of silicon under drought increased the activities of some antioxidant enzymes: SOD, CAT and GR as well as the fatty acid unsaturation of lipids and the content of photosynthetic pigments, whereas the content of H_2O_2 was decreased and the activities of GPX and APX showed no significant difference (Gong et al., 2005). Gong et al. (2005) suggest that the improvement of drought tolerance provided by silicon in wheat plants is associated with an increase in antioxidant defense abilities, thereby alleviating oxidative damage of cellular functional molecules induced by over production of ROS under drought and maintaining many physiological processes of stressed plants. The study by Schmidt et al. (1999) showed that foliar application of silicate stimulated the antioxidant activity of SOD in drought stressed bent grass. In the studies by Ma et al. (2004), silicon alleviated the physiological response of peroxidase (POD) to drought stress, maintained the SOD normal adaptation and increased the activity of CAT. Under severe stress, these physiological and biochemical reactions showed positive correlations with the amount of silicon supply. Gong et al. (2008) showed that the intensity of oxidative destruction tested by the concentration of thiobarbituric acid reactive substances (TBARs) in the leaves of wheat was increased by drought and there was a smaller increase upon application of silicon.

UV Radiation

Si has been attributed to prevent the plants by filtering the devastating Ultraviolet rays. In sugarcane, there is evidence that Si may play an important role in protecting leaves from ultraviolet radiation damage by filtering out harmful ultraviolet rays. Ultraviolet-B (UV-B) radiation negatively affects plant cells, causing generation of ROS such as superoxide anions ($O2^-$), hydrogen peroxide (H_2O_2), hydroxyl radicals (OH) and singlet oxygen (O_2) (Beckmann et al., 2012; Lizana et al., 2009; Zancan et al., 2008). Fang et al. (2011) also reported that Si increases plant tolerance to UV-B radiation. The experiment performed by Shen et al. (2010) showed that drought and UV-B radiation stresses caused intensification of (Lipid peroxidation) LPO in soybean seedlings, but Si application significantly reduced the membrane damage. The CAT and SOD activities increased under the effect of UV-B radiation and significantly decreased at Si application. The UV-B light had more adverse effects on growth than drought; the data also showed that Si could alleviate seedling damage under these stress conditions.

CONCLUSION

This survey has covered a great deal and ground regarding the biology surrounding the plant available silicates. As discussed early on, the ubiquitous and quantitatively prominent element, Si, plays significant roles in the growth and development as well as acts as a defense system thereby neutralizing the extremities of various biotic and abiotic stresses. Despite of this, Si has not received the attention it requires. Hence it is the need of hour to proceed wider and bring together not just strictly plant physiological evidence but to include findings and experiences gathered by botanists, agronomists, horticulturists, plant pathologists, plant biochemists and still others. There is no justification for the disregard of Si in so much science of plant biology. The evidence is forcing that in the real world of plant life, the presence and role of Si matters.

REFERENCES

Adatia MH, Besford RT (1986). The effects of silicon on cucumber plants grown in re-circulating nutrient solution. Annals of Botany 58 (3): 343-35.

Ahmed M, Hassen F, Qadeer U, Aslam MA. (2011). Silicon application and drought tolerance mechanism of sorghum. Afr. J. Agric. Res. 6: 594–607.

Al-aghabary K, Zhu Z, Shi Q (2004). Influence of silicon supply on chlorophyll content, chlorophyll fluorescence and antioxidative enzyme activities in tomato plants under salt stress. J. Plant Physiol. 27 (12): 2101-115.

Ali AA, Alqurainy F (2006**)**. Activities of antioxidants in plants under environmental stress. In: The Lutein-Prevention and Treatment for Diseases (Ed. N. Motohashi). Transworld Res. Network Press, India.

Alvarez J, Snyder GH, Anderson DL, Jones DB (1988). Economics of calcium silicate slag application in a rice-sugarcane rotation in the Everglades. Agric. Systems 28: 179–188.

Arnon DI, Stout PR (1939). The essentiality of certain elements in minute quantity for plants with special reference to copper. Plant Physiol. 14: 371–75.

Asher CJ (1991). Beneficial elements, functional nutrients and possible new essential elements. In Micronutrients in Agriculture. ed. JJ Mortvedt, FR Cox, LM Shuman, RM Welch, Madison: Soil Sci. Soc. Am. 2nd ed. 703–22.

Ayres AS (1966). Calcium silicate slag as a growth stimulator for sugarcane on low-silicon soils. Soil Sci. 101: 216–227.

Bartoli F (1985). Crystallochemistry and surface properties of biogenic opal. J. Soil Sci. 36: 335–350.

Beckmann M, Hock M, Bruelheide H, Erfmeier A (2012). The role of UV-B radiation in the invasion of *Hieracium pilosella* – A comparison of German and New Zealand plants. Environ. Exp. Bot. 75: 173-180.

Bednarek W, Tkaczyk P, Dresler S (2006). Heavy metals content as criterion for assessment of carrot root (in Polish). Acta Agrophysica. 142: 779-790.

Belanger RR, Benyagoub M (1997). Challenges and prospects for integrated control of powdery mildews in the greenhouse. Can. J. Plant Pathol. 19: 310–14.

Biel KY, Matichenkov VV, Fomina IR (2008). Protective role of silicon in living systems. In: Functional Foods for Chronic Diseases (Ed. D.M. Martirosyan). D and A Inc., Richardson Press, Dallas, USA.

Birchall JD, Exley C, Chappell JS (1989). Acute toxicity of aluminum to fish eliminated in silicon-rich acid waters. Nature 338: 146–148.

Bollard EG, Butler GW (1966). Mineral nutrition of plants. Annu. Rev. Plant Physiol. 17: 77–112.

Brownell PL, Crossland CJ (1972). The requirement for sodium as a micronutrient by species having the C4 dicarboxylic phytosynthetic pathway. Plant Physiol. 49: 794–97.

Broyer TC, Carlton AB, Johnson CM, Stout PR (1954). Chlorine-a micronutrient element for higher plants. Plant Physiol. 29: 526–32.

Chen CH, Lewin J (1969). Silicon as a nutrient element for *Equisetum arvense*. Can. J. Bot. 47: 125–131.

Cocker KM, Evans DE, Hodson MJ (1998). The amelioration of aluminum toxicity by silicon in higher plants: Solution chemistry or an *in planta* mechanism? Physiologia Planetarium 104: 608–614.

Coors JG (1987). Resistance to the European corn borer, Ostrinia nubilalis (Hubner), in maize, *Zea mays* L., as affected by soil silica, plant silica, structural carbohydrates and lignin. pp. 445–456. *In* H.W. Gabelman and B. Laughman (ed.) Genetic aspects of plant mineral nutrition. Martinus Nijhof, Dordrecht/Boston/Lancaster.

Cornelis JT, Delvaux B, Titeux H (2010). Contrasting silicon uptakes by coniferous trees: a hydroponic experiment on young seedlings. Plant Soil 336: 99–106.

Currie HA, Perry CC (2007). Silica in plants: biological, biochemical and chemical studies. Ann. Bot. 100: 1383–1389.

Devkota A, Jha PK (2011). Influence of water stress on growth and yield of *Centella asiatica*. Int. Agrophys. 25: 211-214.

Djamin A, Pathak M (1967). Role of silica in resistance to the Asiatic rice borer, *Chilo suppressalis* (Walker), in rice varieties. J. Econ. Entomol. 60: 347-351.

Ehret DL, Zebarth BJ, Portree J, Garland T (1998). Clay addition to soilless media promotes growth and yield of greenhouse crops. HortScience 33: 67–70.

Engel RE, Bruckner PL, Eckhoff J (1998). Critical tissue concentration and chloride requirements for wheat. Soil Sci. Soc. Am. J. 62: 401–5

Epstein E (1972). Mineral Nutrition of Plants: Principles and Perspectives. New York: Wiley. 412.

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. Annu. Rev. Plant Physiol. Plant Mol. Biol. 50: 641–664.

Epstein E (2001). Silicon in plants: Facts vs. concepts. *In* L.E. Datnoff, G.H. Snyder, and G.H. Korndörfer (ed.) Elsevier, New York. 1–15.

Epstein E, Bloom AJ (2005). Mineral nutrition of plants: principles and perspectives. 2nd ed. Sunderland (MA): Sinauer Associates, Sunderland, MA.

Exley C (1998) Silicon in life: a bioinorganic solution to bioorganic essentiality. J. Inorg. Biochem. 69: 139–144.

Exley C, Birchall JDA (1993). Mechanism of hydroxyaluminosilicate formation. Polyhedron 12: 1007–1017.

Fang Ch.-X, Wang Q-S, Yu Y, Huang L.-K, WuX-Ch, Lin W-X (2011**)**. Silicon and its uptaking gene Lsi1 in regulation of rice UV-B tolerance. Acta. Agron. Sin. 37 (06): 1005-1011.

Farmer VC, Delbos E, Miller JD (2005). The role of phytolith formation and dissolution in controlling concentrations of silica in soil solutions and streams. Geoderma 127: 71–79.

Fawe A, Menzies AJG, Chérif M, Bélanger RB (2001). Silicon and disease resistance in dicotyledons 1–15. *In* LE Datnoff, GH Snyder, GH Korndörfer (ed.) Silicon in agriculture. Elsevier, New York.

Fox RL, Silva JA, Younge OR, Plucknett DL, Sherman GD (1967). Soil and plant, silicon and silicate response by sugar cane. Soil Sci. Soc. Am. 31: 775-779.

Foy CD (1992). Soil chemical factors limiting plant growth. Adv. Soil Sci. 19: 97–149.

Gali Muhtasib HU, Smith CC, Higgins JJ (1992). The effect of silica in grasses on the feeding behavior of the prairie vole, *Microtus ochrogaster.* Ecology 73: 1724-1729.

Gao XC, Zou, Wang L, Zhang F (2006). Silicon decreases transpiration rate and conductance from stomata of maize plants. J. Plant Nutr. 29: 1637–1647.

Gong H, Zhu X, Chen K, Wang S, Zhang Ch (2005). Silicon alleviates oxidative damage of wheat plants in pots under drought. Plant Sci. 169: 313-321.

Gong HJ, Chen KM, Zhao ZG, Chen GC, Zhou WJ (2008). Effects of silicon on defense of wheat against oxidative stress under drought at different developmental stages. Biol. Plantarum. 52 (3): 592-596.

Gunes A, Inal A, Bagci EG, Coban S (2007). Silicon mediated changes on some physiological and enzymatic parameters symptomatic of oxidative stress in barley grown in sodic-B toxic soil. J. Plant Physiol. 164: 807-811.

Hamayun M, Sohn EY, Khan SA, Shinwari ZK, Khan AL, Lee IJ (2010). Silicon alleviates the adverse effects of salinity and drought stress on growth and endogenous plant growth hormones of soybean (*Glycine ma*x L.). Pak. J. Bot. 42: 1713–1722.

Hammond KE, Evans DE, Hodson MJ (1995**).** Aluminium/silicon interactions in barley (*Hordeum vulgare*L.) seedlings. Plant Soil. 173: 89-95.

Hanifa AM, Subramaniam TR, Ponnaiya BWX (1974). Role of silica in resistance to the leaf roller, *Cnaphalocrocis medinalis* Guenee, in rice. Indian J. Exp. Biol. 12: 463-465.

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

Hemmi T (1933). Experimental studies on the relation of environmental factors to the occurrence and severity of blast disease in rice plants. Phytopath. Zeit. 6: 305–324.

Hodson MJ, Evans DE (1995). Aluminium/silicon interactions in higher plants. J. Exp. Bot. 46: 161–171.

Horiguchi H (1988). Mechanism of manganese toxicity and tolerance of plant. IV. Effect of silicon on alleviation of manganese toxicity of rice plants. Soil Sci. Plant Nutr. 34: 65–73.

Iler RK (1978). Hydrogen-bonded complexes of silica with organic compounds. In: Bendz G, Lindquist J, editors. Biochemistry of silicon and related problems. New York: Plenum. 53–76.

Iler RK (1979). The chemistry of silica. Wiley, New York.

Ingri N (1978). Aqueous silicic acids, silicates and silicate complexes. 3–52. *In* G Bendz and J Lindquist (ed.) Biochemistry of silicon and related problems. Plenum, New York.

Jones LHP, Handreck KA (1967). Silica in soils, plants and animals, 107–149. In AG Norman (ed.) Advances in agronomy. Vol. 19. Academic Press, New York.

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

Kinrade SD, Gillson AME, Knight CTG (2002). Silicon-29 NMR evidence of a transient hexavalent silicon complex in the diatom *Navicula pelliculosa*. J. Chem. Soc. Dalton Tran. 307–309.

Kinrade SD, Hamilton RJ, Schach, Knight CTG (2001). Aqueous hypervalent silicon complexes with aliphatic sugar acids. J. Chem. Soc.-Dalton Tran. 961–963.

Korndörfer GH, Lepsch I (2001). Effect of silicon on plant growth and crop yield, 133–147. *In* LE Datnoff, GH Snyder and GH Korndörfer (ed.) Silicon in agriculture. Vol. 8 studies in plant science. Elsevier, Amsterdam.

Lee SK, Sohn EY, Hamayun M, Yoon JY, Lee IJ (2010). Effect of silicon on growth and salinity stress of soybean plant grown under hydroponic system. Agroforest. Syst. 80: 333–340.

Leibig J (1840). Organic Chemistry in Its Application to Agriculture and Physiology. From the manuscript of the author by Lyon Playfair. London: Taylor and Walton.

Liang YC, Chen QR, 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.). J. Plant Physiol. 160: 1157–1164.

Liang YC, Wong JWC, Wei L (2005). Silicon-mediated enhancement of cadmium tolerance in maize (Zea mays L.) grown in cadmium contaminated soil. Chemosphere58 (4): 475-483.

Liang YC, Wong JWC, Wei L (2006). Importance of plant species and external silicon concentration to active silicon uptake and transport. New Phytol. 172: 63–72.

Lindsay WL (1979). Chemical equilibria in soils, 51–54. John Wiley and Sons, New York.

Lizana C, Hess S, Calderini DF (2009). Crop phenology modifies wheat responses to increased UV-B radiation. Agr. Forest Meteorol. 149: 1964-1974.

Lumsdon DG, Farmer VC (1995). Solubility characteristics of proto-imogolite sols: how silicic acid can de-toxify aluminium solutions. Eur. Soil Sci. 46: 179–186.

Ma CC, Li QF, Gao Y, Xin TR (2004). Effects of silicon application on drought resistance of cucumber plants. Soil Sci. Plant Nutr. 50: 623-632.

Ma JF, Takahashi E (2002). Soil, fertilizer and plant silicon research in Japan, 1st ed. Elsevier, Amsterdam.

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

Ma JF, Miyaki Y, Takahashi (2007). An efflux transporter of silicon in rice. Nature 448: 209–212.

Ma JF, Miyaki Y, Takahashi Y (2001). Silicon as a beneficial element for crop plants. *In* LE Datnoff, GH Snyder and GH Korndörfer (ed.) Silicon in agriculture. Elsevier, New York. 17–39.

Ma Y, Miyaki Y, Takahashi E (2006). A silicon transporter in rice. Nature, 86: 688-691.

Matichenkov VV, Ammosova MY (1996). Effect of amorphous silica on soil properties of a sod-podzolic soil. Euras. Soil Sci. 28: 87–99.

Matichenkov VV, Bocharnikova EA, Calvert DV (2002). Response of citrus to silicon soil amendments. Proc. Florida State Hortic. Soc. 114: 94–97.

Matichenkov VV, Bocharnikova EA, Calvert DV, Snyder GH (2000). Comparison study of soil siliconstatus in sandysoils of south Florida. Soil Crop Sci. Florida Proc. 59: 132-137.

Matsuda TH, Kawahara, Chonan N (1983). Histological studies on breaking resistance of lower internodes in rice culm, II: Ultra structural and histochemical observations on the secondary wall formation. Jap. J. Crop Sci. 52: 84-93.

Mcnaughton SJ, Tarrants JL (1983). Grass leaf silicification: natural selection for an inducible defence against herbivores. Proceedings of the National Academy Sciences, USA 80: 790-1.

McNaughton SJ, Tarrants JL, McNaughton MM, Davis RH (1985). Silica as a defense against herbivory and a growth promotor in African grasses. Ecology. 66: 528-535.

Mitani N, Ma JF (2005). Uptake system of silicon in different plant species. J. Exp. Bot. 56 (414): 1255–1261.

Molassiotis A, Sotiropoulos T, Tanou G, Diamantidis G, Therios I (2005). Boron induced oxidative damage and antioxidant and nucleolytic responses in shoot tips culture of the apple rootstock EM9 (*Malus domestica* Borkh). Environ. Exp. Bot. 56: 54-62.

Moore D (1984). The role of silica in protecting Italian ryegrass *(Lolium multiflorum)* from attack by dipterous stem-boring larvae *(Oscinellafrit* and other related species). Ann. Appl. Biol. 104: 161- 166.

Pereira SH, Korndörfer GH, Vidal ADA, Camargo MSD (2004). Silicon sources for rice crop. Sci. Agric. 61: 522–528.

Piperno DR (2006). Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists, Rowman and Littlefield.

Rafi MM, Epstein E (1999). Silicon absorption by wheat (*Triticum aestivum* L.). Plant Soil 211: 223–230.

Rana A, Masood A (2002). Heavy metal toxicity: effect on plant growth and metal uptake by wheat and on free living Azotobacter. Water Air, Soil Pollut. 138: 165-180.

Raven JA (1983). The transport and function of silicon in plants. Biol. Rev. 58: 179–207.

Richmond KE, Sussman M (2003). Got silicon? The non-essential beneficial plant nutrient. Curr. Opin. Plant Biol. 6: 268–272.

Rodrigues FA, McNally DJ, Datnoff LE, Jones JB Labbé C, Benhamou N, Menzies JG, Bélanger RR (2004). Silicon enhances the accumulation of diterpenoid phytoalexins in rice: a potential mechanism for blast resistance. Phytopahology 94: 177–183.

Round FE, Crawford RM, Mann DG (1990). The diatoms: biology and morphology of the genera. Cambridge University Press, Cambridge, United Kingdom.

Said-Al Ahl HAH, Omer EA, Naguib NY (2009). Effect of water stress and nitrogen fertilizer on herb and essential oil of oregano. Int. Agrophys. 23: 269-275.

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

Savant NK, Snyder GH, Datnoff LE (1996). Silicon Management and Sustainable Rice Production. Adv Agron 58: 151–199.

Schindler PW, Furst B, Dick R, Wolf PO (1976). Ligand properties of surface silanol groups. I. Surface complex formation with Fe^{3+}, Cu^{2+}, Cd^{3+} and Pb^{2+}. J. Colloid Interface Sci. 55: 469–475.

Schmidt RE, Zhang X, Chalmers DR (1999). Response of photosynthesis and superoxide dismutase to silica applied to creeping bent grass grown under two fertility levels. J. Plant Nutr. 22: 1763-1773.

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

Shi QH, Bao ZY, Zhu ZJ, He Y, Qian QQ, Yu JQ (2005). Silicon mediated alleviation of Mn toxicity in *Cucumis sativus* in relation to activities of superoxide dismutase and ascorbate peroxidase. Phytochem. 66: 1551-1559.

Siever R (1957). The silica budget in the sedimentary cycle. Am. Minerol. 42: 821–841.

Siever R (1962). Silica solubility, 0–200 C and the diagenesis of siliceous sediments. J. Geol. 70: 127–150.

Simpson TL, Volcani BE (1981). Silicon and Siliceous Structures in Biological Systems. New York: Springer-Verlag. 587.

Soylemezoglu G, Demir K, Inal A, Gunes A (2009). Effect of silicon on antioxidant and stomatal response of two grapevine (*Vitis vinifera* L.) rootstocks grown in boron toxic, saline and boron toxic-saline soil. Sci. Hort. 123: 240-246.

Sposito G (1989). The chemistry of soils. Oxford University Press, New York.

Takahashi E, Ma JF, Miyake Y (1990). The possibility of silicon as an essential element for higher plants. Comments Agric. Food Chem. 2: 99–122.

Tamai K, Ma JF (2003). Characterization of silicon uptake by rice roots. New Phytologist 158: 431–436.

Van Soest PJ (2006). Rice straw, the role of silica and treatments to improve quality. Anim. Feed Sci. Technol. 130: 137–171.

Vicari M, Bazely DR (1993). Do grasses fight back-the case for antiherbivore defenses. Trends in Ecology and Evolution. 8: 137–141.

Voogt W, Sonneveld C (2001). Silicon in horticultural crops in soilless culture. *In* LE Datnoff, GH Snyder and GH Korndörfer (ed.) Silicon in agriculture. Elsevier, New York. pp. 115–131.

Wadham MD, Parry DW (1981). The silicon content of *Oryza sativa* L. and its effect on the grazing behavior of Agriolimax reticulatus Muller. Ann. Bot. 48: 399-402.

Wainwright M (1997). The neglected microbiology of silicon: from the origin of life to an explanation for what Henry Charlton Bastian saw. Soc. Gen. Microbiol. Quart. 24: 83–85.

Werner D, Roth R (1983). Silica metabolism. In Inorganic Plant Nutrition, Encyclopedia of Plant Physiology, New Ser., ed. A L¨auchli, RL Bieleski, Berlin: Springer-Verlag. 15B: 682–94.

Wiese H, Nikolic M, Römheld V (2007). Silicon in plant nutrition. In B. Sattelmacher and W.J. Horst (ed.) The apoplast of higher plants: compartment of storage, transport and reactions. Springer, The Netherlands. pp. 33–47.

Williams RF, Shapter RE (1955). A comparative study of growth and nutrition in barley and rye as affected by low-water treatment. Australian J. Biol. Sci. 8: 435–466.

Woolley JT (1957). Sodium and silicon as nutrients for the tomato plant. Plant Physiol. 32: 317–21.

Zancan S, Suglia I, La Rocca N, Ghisi R (2008). Effects of UV-B radiation on antioxidant parameters of iron-deficient barley plants. Environ. Exp. Bot. 63: 71-79.

Zhu JK (2001). Plant salt tolerance. Trends Plant Sci. 6: 66-71.