REVIEW ARTICLE

Silicon in Plant Structure and Inorganic C-Sequestration

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Abstract

On the planet earth silicon is next only to oxygen in abundance. It is ubiquitous and is present in soil, water and air and biological systems from algae to human population. It is removed by crops in amounts larger than primary plant nutrients nitrogen, phosphorus and potassium and imparts several advantages to plants, such as, strength in straw in rice to prevent it from lodging and protection to crop plants against drought, salinity, toxicity of micronutrients and heavy elements, certain diseases, chewing insects and large herbivores yet it is not considered as an essential plant nutrient. However, Si is essential for diatoms and many other sea animals, which play a vital role in Si-cycle in the sea. Si helps in C-sequestration and plays an important role in maintaining the atmospheric CO_2 low, but this fact is not well realized.

Keywords: Drought, Lodging, Photosynthesis, Salinity, Silicon in air, Silicon in soil, Silicon in water, Toxicity to micronutrients.

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Introduction

Silicon (Si) with an atomic weight 28.0855 is in Group 14 of the Periodic table, the group that contains carbon (C, atomic weight 12.0107), the very essence of living and organic matter on the planet earth. Just like CO_2 in the case of C, SiO_2 is quite abundant form in the case of Si. Silicon is considered a bioessential element. It provides structural strength and resistance to attack by insect pests and herbivores and several other benefits to plants and is important for diatoms and other sea organisms (Kristiansen and Hoe1l, 2002). Si has been proved essential for diatoms (Lewin, 1961). Diatom cells are contained within a unique silica cell wall known as a frustule made up of two valves called thecae that typically overlap one another. A set of polyceticnic peptides (called silaffins isolated from diatom cell walls were demonstrated to generate silica nanospheres within seconds, when come in contact with silicic acid (Kröger *et al*., 1999). Diatoms constitute the largest group of silicifying organisms. The first proteins shown to directly intermingle with silicon were diatom silicon transporters (SITs). In addition to many partial SIT sequences, first full length SIT genes were identified from the pinnate diatom, *Nitzschia alba* and Centric diatom *Skeletonema costatum*, as a mechanistic model of silicon transport (Thamatrakoln *et al*., 2006). Diatoms form a major silicon pool in oceans (Yool and Tyrrell, 2003). Phytoplankton including diatom form the basis of the marine food web and are responsible for nearly half of global carbon dioxide (CO_2) fixation of about 50 Pg of carbon per year (Bristow *et al*., 2017). Field *et al*. *(*1998) observed *that* grasses fix ~15 Pg C per year out of total ~60 Pg C per year of net primary production on land, and diatoms fix >15 Pg C per year out of total ~50 Pg C per year of the net primary production in the ocean; both grasses and diatoms are rich in Si.

On the planet earth Si is next only to oxygen in abundance. Silicon is a ubiquitous element and is available everywhere in soil, water and some organisms.

Silicon in Soils

Silicon in the pedosphere of the earth's crust ranges from 0.52% to 47% with an average of 28% Si by weight and rocks such as basalt and orthoquartzite contain high concentrations of Si (23-47%) (Tubana *et al*., 2016). Silicon in soils occurs as liquid, adsorbed, and solid phase fractions. The solid Si phase consists of crystalline forms of Si (primary and secondary silicates, and silica), microcrystalline and amorphous (biogenic from plant residues and pedogenic from silicate minerals). The solubility of amorphous Si ranges between 1.8 and 2 mM (milli mol) compared with quartz's 0.10 to 0.25 mM Si (Monger and Kelly, 2002). Biogenic silica also contributes to the concentration of Si in soil solution, and with solubility 17 times higher than quartz, its contribution to the dynamics of plant-available Si in soil solution is rather significant (Frayesse *et al*., 2006). Si content in soil is higher in temperate soils than in tropical soils, because in tropical soils Si is mostly leached by desilification (Pal, 2017). Silica content in a temperate soil from USA is shown in Table 1, while chemical composition of clay fraction of an Oxisol from Indonesia is presented in Table 2.

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Table 1: Silica, alumina and iron oxide content in Orangeburg fine sandy loam, a temperate soil in USA.

Soil depth (cm)	*SiO_2 %*	*Al_2O_3 %*	*Fe_2O_3 %*
0-25 (A horizon)	96.16	1.85	0.63
40-75 (B horizon)	66.90	18.04	6.11
100-250 (C horizon)	83.22	9.67	2.38

Source: Holmes and Hearn (1938)

Table 2: Chemical composition of clay fraction of an Oxisol from Pleihari, Indonesia.

Soil depth (cm)	*SiO_2 %*	*Al_2O_3 %*	*Fe_2O_3 %*
0-10	6.72	37.90	47.91
10-30	6.67	44.23	55.23
30-70	7.31	37.29	57.62
70-105	7.09	44.73	58.37
105+	8.53	29.51	56.48

Source: Buurman and Soepraptohardjo (1980)

Fox *et al*. (1967) ranked different clay minerals with respect to Si-content and Si-solubility, as follows: 2:1 clays > 1:1 clays > Al and Fe oxides/hydroxides. In general, Si concentration in solution of highly weathered acid Oxisols soils is several times less than in less weathered neutral to alkaline Vertisols (Foy, 1992).

Despite the abundance of silica (SiO_2), soil solution concentration of Si is very low (0.1-0.6 mM), because the rate of dissolution of silica is very low (Raven, 1983). In soil solution Si is mostly present as monomeric silicic acid [$Si(OH)_4$], which is the plant-available form (Sposito, 1989).

Silicon in Water

Silicic acid content in some Tamil Nadu aquifers varied from 0.44 to 108.82 ppm (mg kg^{-1}), with an average of 30.38 ppm (Pradeep *et al*., 2016). Rivers are the main transporters of Si to ocean. Silica concentration in μmol (1000 μmol = 96 ppm Si $(OH)_4$ or 60 ppm of SiO_2 or 28 ppm of Si) some Indian rivers was as follows: *Northern Himalayan Region*: Ganges at Rishikesh 80, Ramganga 184, Ghaghara 85, Gandak 72, Kosi 98, Yamuna at Himalyan Front 154; *Alluvial Plain* Gomati 111, Buri Gandak 131; *Yamuna* and *Tributaries:* Yamuna at Allahabad 152, Chambal 208, Betwa 215, Ken 192; *Southern Peninsular* Tons 110, Son 157 (Frings *et al*., 2015). Using a Rayleigh isotope mass balance model they (Frings *et al*., 2015), predicted silica mobilization rates of 200, 150 and 107 kmol SiO_2 km^{-1} yr^{-1}, for the Himalaya, peninsular India and the alluvial plain, respectively. Among 380 rivers investigated in Japan, the lowest concentration of soluble SiO_2 was 4.1 ppm and the highest was 61.5 ppm with an average of 21.6 ppm (Kobayashi, 1960). In Jiulong River watershed in Southeast China, which is a subtropical region, DSi (dissolved silicon) flux was fairly high (246±76 μmol L^{-1}) due to granite lithology and increased human perturbation (Chen *et al*., 2014). From Egypt Abdel-Satar *et al*. (2017) reported silicate (mg L^{-1} or ppm) concentrations of 0.39-14.62 (2.48±2.89) in winter, 0.56-4.31 (2.45±0.84) in spring, 0.43-13.80 (4.83±2.68) in summer and 1.16-6.88 (2.75±1.23) in autumn. DSi in River Thames and its tributaries in UK varied from 2.4 to 7.0 mg L^{-1} or ppm (Bowes *et al*., 2018). DSi in Amazon River in South America ranged from 120 μmol L^{-1} in June 2010 to 145 μmol L^{-1} in November (Hughes *et al*., 2013). Turner *et al*. (2003) estimated riverine loading of the oceans for dissolved silica at 194 Tg yr^{-1} (million tons yr^{-1}), while (Tréguer *et al., 2013) estimated* total net inputs and outputs of silica in the ocean at 9.4±4.7 Tmol Si yr^{-1} (one Tmol of Si is 28 million metric tons) and 9.9±7.3 Tmol Si yr^{-1}, respectively. In the surface layers of oceans silicon concentrations are 30 ppb, whereas deeper water layers may contain 2 ppm silicon (https://www.lenntech.com/periodic/water/silicon/silicon-and-water.htm#ixzz5sFzCJdak).

Silicon in Air

Silica is very much in the air and dust storms are full of it. Quartz, an amorphous and crystalline silica, in dust sand, causes respiratory diseases (Al Kassimi, 1991; Ichinose *et al*., 2008; Kanatani *et al*., 2010). In a study at Raipur city, the concentration of SiO_2 in ambient air associated to the PM10 (particulate matter10) (10 μm diameter) ranged from 6.6 to 102 μg m^{-3} with a mean value of 30.0±6.0 μg m^{-3}, while in PM 2.5 (2.5 μm diameter) it ranged 0.2 to 15 μg m^{-3} with a mean value of and 4.3±0.8 μg m^{-3} (Patel *et al*., 2015). In a study in Iowa (USA) field measurements using the Nano Aerosol Mass Spectrometer (NAMS), which provides quantitative elemental composition of nanoparticles around 20 μm (microns) diameter, indicated that Si is a frequent component of nanoparticles (Bzdek *et al*., 2014). Nanoparticulate Si is most abundant in locations heavily impacted by anthropogenic activities. Wind direction correlations suggest the sources of Si are diffuse, and diurnal trends suggest nanoparticulate Si may result from photochemical processing of gas phase Si-containing compounds, such as cyclic siloxanes (oligomeric and polymeric hydrides with the formulae $H(OSiH_2)_n$ OH and ($OSiH_2$) (Bzdek *et al*., 2014). Silica concentration is very high in and around the factories manufacturing glass, where silica itself is the raw material. Bhagia (2009) reported that the average quartz concentrations in the vicinity of slate pencil industry was 41.07-57.22 μg m^{-3}, while at the control site it was only 3.51 μg m^{-3}.

Silicon in Plants

Plants form an important part of Si cycle. They take up Si from soil or water and return back to it either directly through leaf fall, after being cut, used and burned, being ploughed in fields or indirectly through manure and animal or human feces. Silicon concentration in plants may vary from 0.1 to 10% on dry weight basis (Currie and Perry 2007). Plants of the families Poaceae, Equisetaceae and Cyperaceae show high Si accumulation (>4% Si), the Cucurbitales, Urticales and Commelinaceae show intermediate Si accumulation (2-4% Si), while most other species demonstrate little accumulation (Hodson *et al*., 2005). Also different parts of the same plant can show large differences in Si accumulation, e.g., in rice, polished rice may have ~0·05%, rice bran may have ~5%, rice straw may have ~13% and rice hulls may have ~23% Si (Van Hoest, 2006). Cacti accumulate a lot of Si (Wright *et al*., 2014).

Irrigation water contributes a fair amount of Si taken up by crop plants. It is silicic acid form in which Si is absorbed by plants from soil solution. Three silicon transporter proteins (Lsi1 Lsi2 and Lsi6) have been identified from rice. Lsi1 (low silicon 1) is responsible for transport of Si from the external solution to the root cells (Ma *et al*., 2006), while Lsi2 (low silicon 2) is responsible for the transport of Si from the root cells to the apoplast (Ma *et al*., 2007). LSi6 (low silicon 6) is involved in transfer of Si from the large vascular bundles to the panicles (Yamaji *et al*., 2008; Babu Rao and Sushmita, 2017).

Despite considerable interest and reports in recent years of its benefits to plants as evidenced by several reviews (Epstein, 1999; Savant *et al*., 1999; Vasanthi *et al*., 2012) and even entire books (Datnoff *et al*., 2001; Prakash *et al*., 2018) on Si, it is still not considered an essential element for higher plants. It is only considered as a "beneficial" or "quasi-essential" element (Epstein and Bloom, 2005). One reason for this is its abundance in earth, while another reason is the fact that most plants can complete their life cycle without external addition of Si to the growing medium, although it is extremely difficult to completely exclude it from nutrient culture solution; even highly purified water contains about 20 nM Si (Werner and Roth, 1983). Most of the benefits attributed to Si are due to phytolithsor plant opal, which are amorphous silica particles that precipitate in plant cells. Phytoliths can be assembled without any energy by polymerization of silicic acid, when its concentration exceeds 2 mM. 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 (Babu Rao and Sushmita, 2017).

Concentration and silicon removal by crops

Draycott (2006) reported Si concentration in shoots (% DW) of some crops as follows: rice (*Oryza sativa*) 4.167 %, wheat (*Triticum aestivum*) 2.455%, sugar beet (*Beta vulgaris*) 2.340%, barley (*Hordeum vulgare*) 1.824%, sugar cane (*Saccharum officinarum*)

1.509%, soybeans (*Glycine max*) 1.399%, maize (*Zea mays*) 0.827% and potatoes (*Solanum tuberosum*) 0.400%. Crops remove large quantities of Si from soil. On a global perspective, the estimated amount of Si removed annually by different agricultural crops is between 210 and 224 million tons (Savant *et al*., 1997; Matichenkov *et al*., 2002; Tubana *et al*., 2016). Sugarcane removes approximately 300 kg ha^{-1} y^{-1} (Meyer and Keeping, 2001) whereas rice is as much as 500 kg Si ha^{-1} y^{-1} (Makabe-Sasaki *et al*., 2009). These amounts are much higher than the removal rates of primary essential nutrients such as nitrogen (N), phosphorus (P), and potassium (K). A study in Puerto Rico showed the above ground parts of a 12-month crop of sugarcane contained 379 kg ha^{-1} of Si, compared with 362 kg ha^{-1} of K and 140 kg ha^{-1} of N (Samuels, 1969). Si has become an important component of integrated nutrient management and sustainable agriculture across Asia, South America and the U.S., especially in rice and sugarcane (Snyder *et al*., 1986; Viator *et al*., 2004; Vasanthi *et al*., 2012; Prakash *et al*., 2018).

Silicon for a better growth and yield in crops

Rice (Oryza sativa)

Among the cultivated crops, rice, which grows in standing water is more affected by Si deficiency. Rice has the highest water requirement than other crops (~1000-2500 mm-ha for rice as compared to ~500-800 mm-ha for maize and 400-600 mm-ha for wheat). Japanese researchers, as early as 1930s (Okawa, 1936; Ishibashi, 1937) reported poor growth of rice with inadequate Si, but they did not identify any specific role of Si. Yoshida *et al*. (1962) also reported that rice (*Oryza sativa*) plants growing in nutrient solution significantly deficient in Si were physically inferior, prone to insects and disease attacks and produced less biomass than those growing in solution supplied with Si. Wagner (1940) also observed that Si was necessary for plant growth. Ma *et al*. (1989) reported 20 and 50% loss in straw and grain yields, respectively, when rice plants were denied Si during the reproductive stage, contrary to 24 and 30% increases in straw and grain yields obtained by those supplied with Si. Increase in rice yield due to Si fertilization has been reported from various countries like Sri Lanka (Radrigo, 1964), Thailand (Takahashi *et al*., 1900), Indonesia (Burbey *et al*., 1988), India (Subramaniam and Gopalswamy, 1991; Singh *et al*., 2006; Meena *et al*., 2014; Pati *et al*., 2016; Babu Rao *et al*., 2018), China (Liang *et al*., 1994) and U.S.A. (Datnoff *et al*., 1997). Snyder *et al*. (1986) noted that fields in Florida when farmed to irrigated rice showed Si deficiency and that the application of 1 tha^{-1} Ca silicate slag increased rice grain yields by greater than 30%. Narayanaswamy and Prakash (2009) also observed yield increases in rice growing in soils testing low for plant available Si when amended with Si fertilizer. Savant *et al*. (1997) suggested that the decline in yields of rice grown in many areas of the world was associated with soil depletion of plant-available Si. Silicon was first recognized as a fertilizer in 1955 in Japan and since then 1.5 to 2.0 tha^{-1} of silicate fertilizer has been applied to silicate deficient paddy soils resulting in a 5 to 15% increase in rice yield has been reported (Takahashi *et al.,* 1990).

Sugarcane (Saccharum officinarum)

Sugarcane is a 12 to 18 month tropical crop and has high water requirement (1500-2500 mm-ha) and is a Si accumulator. As early as 1960's Ayres (1966) in Hawaii, USA obtained responses to Si ranging from 9 to 18% in cane yield and 11 to 22% in sucrose yield for plant cane. Gascho and Andreis (1974) obtained significant positive responses to slag treatments ranging from 13 to 32% on the muck trial sites and two out of four sand sites Florida, USA. From Louisiana, USA, Viator *et al*. (2004) reported that sugar yield increased by a total of 3.7 tha^{-1} (P<0.05) for the whole crop cycle (three harvestings) of cane variety LCP 85-384 with a one-time application of 4.5 tha^{-1} Ca silicate slag at planting. Tubana *et al*. (2012) showed that Ca silicate application rate increased sugar yield by 1.45 tha^{-1} (P<0.01). Anderson *et al*. (1991) observed that an application of 20 $tha^{-1}$of slag increased cumulative cane yield by as much as 39% and sugar yield as much as 50% over three crop years. Raid *et al*. (1992) also from Florida, reported that yields of five varieties of sugarcane were increased on average by 17% and 21% during 1989 and 1990, respectively, following the addition of 6.7 tha^{-1} calcium silicate slag. There are several reports of increases in yield and sugar from Australia attributed to silicate based materials and mill wastes (Hurney, 1973; Haysom and Chapman, 1975; Rudd and Berthelsen, 1998). Ross *et al*. (1974) reported significant residual effects on sugarcane yield over a 6-year crop cycle from applications of calcium silicate, applied at a rate of 7 tha^{-1} to Si deficient soils.

Wheat (Triticum aestivum)

White *et al*. (2017) from Louisiana (USA) reported that Si fertilization increased spikes m^{-2}, grains $spike^{-1}$ and grain yield in wheat at high N application rates. In Idaho (USA) beneficial effects of applying silicon (140, 280, and 560 kg Si ha^{-1}) to the soil were observed in winter wheat (Walsh *et al*., 2018). Neu *et al*. (2017) from Germany reported an increase of biomass in winter wheat due to Si application, mostly in straw, but some also in grain. Silicon fertilization may reduce fertilization application to crops. In Albania, foliar application of marine calcite to wheat with a reduced (30%) application of NPK yielded grains with the same protein and fat content as at the full NPK dose (Prifti and Maçi, 2017). Foliar fertilization with silicon significantly increased wheat yield in Pakistan (Abro *et al*., 2009) and Egypt (Hellal *et al*., 2012).

Sugarbeet

Artyszak *et al*. (2014) from Poland reported an increase of 13-21% in the root yield of the sugar beet with foliar application of marine calcite (Herbagreen Basic). In Morocco soil application of Si using Agrisilica (26% of silicon) increased sugarbeet yield as the dose was increased from 150 to 250; application of 250 kg ha^{-1} recorded a significant increase in the sugar yield by 4.8 tha^{-1}, there was no significant increase in yield when the dose of Si was raised to 300 kg ha^{-1} (Prentice, 2017).

Potato (Solanum tuberosum)

Crusciol *et al*. (2009) reported from Brazil that silicon fertilization of the soil increased the average tuber weight, dry tuber weight, and tuber yield. In Poland the total yield of tubers increased, on average, by 14.8%, and the yield commercial grade tubers by 16.4% by foliar spraying of Si (Trawczyński, 2013). In India, application of diatomaceous earth @ 150 kg ha^{-1} with half the dose of the standard fertilizer (NPK + manure), increased the potato tuber yield by 12.9% (24.3 $Mg{\cdot}ha^{-1}$) as compared to the full dose of standard fertilizer (21.5 tha^{-1}) (Kadalli *et al*., 2017). Vulavala *et al*. (2016) from Israel reported that silicon fertilization improved potato quality by increasing skin cell area, lignification and suberization. In a study in Iran, effect of four different silicon compounds (nanosilica, sodium silicate, nanoclay, and bentonite) in two concentrations (1000 and 2000 ppm) was examined on the growth of potato plants (Soltani *et al*., 2018). Application of bentonite @1000 ppm increased leaf dry weight by 18% and both nanoclay and bentonite @1000 ppm increased stem diameter by 17%, while most root traits were improved by silicon fertilization. Sodium silicate @1000 ppm increased root area by 54%. There was no advantage in increasing the Si concentration from 1000 to 2000 ppm.

Corn (Maize) (Zea mays)

In north-east China Studies of silicon application to the soil increased corn yield by 5.6-10.4% (Liang *et al*., 2015). Jawahar *et al*. (2017) from India reported a significant increase in corn grain yield and improvement of grain quality when silicon in the form of monosilicic acid was applied to the soil or foliage.

Soybean (Glycine max)

In Poland, foliar application of Si as Optysil, a growth stimulator (94 g Si·dm^{-3}), increased number of pods in soybeans by 18%, and the average seed yield per plant by 21% (Ciecierski, 2016). In China soil application of silicon resulted in an increase in soybean yield by 7.5-13.6% (Liang *et al*., 2015). Shwethakumari and Prakash (2018) reported from India that foliar application of silicic acid (2%) soluble Si $(OH)_4$) significantly improved soybean growth and doubled or even tripled the grain yield.

Rapeseed (Brassica napus)

In Poland foliar Si fertilization with Optysil growth stimulator increased 1000-grain weight by 1.4 to 19% and rapeseed yield from 1.7 to 17% depending on the variety of rapeseed and location (Ciecierski and Kardasz, 2014).

Silicon and abiotic stress in plants

There are three kinds of abiotic stresses, namely, drought, salinity and toxicity of heavy elements and micronutrients.

Drought

In plants, water deficiency can result from a deficit of water from the soil, an obstacle to the uptake of water or the excess water loss. Silicon (Si) has been widely reported to alleviate the plant water status and water balance under variant stress conditions in both monocots and dicots, especially under drought and salt stresses (Chen *et al*., 2018). Drought stress can damage plant cell membranes, and cell wall architecture, as well as inhibit photosynthesis and cell division (Taiz and Zeiger, 2006). The deposition of Si in the outer walls of epidermal cells on both surfaces of leaves is reported to have reduced water loss by reducing transpiration and maintained normal growth under drought stress in rice (Agarie *et al*., 1998) and sugarcane (Savant *et al*., 1999).Silicon can reduce the transpiration rate by 30% in rice (Ma, 2004). Lux *et al*. (2002) reported that Sorghum is a silicon accumulating plant. In sorghum roots, Si is accumulated mostly in endodermal cells. Specialized silica aggregates are formed predominantly in a single row in the form of wall outgrowths on the inner tangential endodermal walls, while in the leaf epidermis, silicon deposits were present in the outer walls of all cells. In both the root and leaf epidermis, silicification was higher in a drought tolerant cultivar Gadambalia (3.5% in roots and 4.1% in leaves) compared with drought sensitive cultivar Tabat. This suggested that a high root endodermal silicification might be related to a higher drought resistance. Hattori *et al*. (2003) observed that silicon deposition might protect the stele as a mechanical barrier by hardening the cell walls of stele and endodermal tissues of the sorghum roots. A number of studies support the conclusion that Si application improves plant water status by increasing root water uptake, rather than by decreasing their water loss under conditions of water deficiency through the activation of osmotic adjustment, improving aquaporin activity and increasing the root/shoot ratio (Chen *et al*., 2018). Silicon deposits have also been found in guard cells around stomata in blueberry (Morikawa and Saigusa, 2004). Gong *et al*. (2003) observed that wheat plants treated with Si had thicker leaves and a better water use efficiency as compared to those without Si. Ciecierski (2016) from Poland reported that under laboratory conditions, application of Optysil (94 g Si·dm^{-3}) reduced the negative impact of drought stress on wheat. From India, Dinesh *et al.* (2017) reported the positive effect of soil fertilization with calcium silicate on the improvement of lodging resistance of wheat and increase in yield was confirmed. In several experiments with wheat in Mexico, foliar application of silicon twice, as well as soil application of Armurox (a complex of peptides with soluble silicon), had a positive effect on increasing plant resistance to lodging (Botta *et al*., 2014). Gunes *et al*. (2008) and Crusciol *et al*. (2009) found that silicon increased proline content in stressed plant tissue. Proline an amino acid, besides acting as an excellent osmolyte, plays three major roles during stress, i.e., as a metal chelator, an antioxidative defense molecule and a signaling molecule (Hayat *et al*., 2012). Kang *et al*. (2014) showed that application of silicic acid with sodium chloride could more effectively mitigate deleterious impacts of drought stress on the growth of *Haloxylon ammodendron*, a C_4 perennial woody species of the desert areas and the coexistence than silicic acid or sodium chloride alone.

Salinity

Rios *et al*. (2017) observed that plants treated with Si are able to maintain a high stomatal conductance and transpiration rate under salt stress, suggesting that a reduction in Na^+ uptake occurs due to deposition of Si in the root. They also reported Si-mediated upregulation of aquaporin (PIP) gene expression in relation to increased root hydraulic conductivity and water uptake. Tuna *et al*. (2008) reported that Si lowered significantly the concentrations of Na in both leaves and roots; bread wheat was more tolerant to salinity than durum wheat. In another study application of Si with the saline nutrient media significantly enhanced superoxide dismutase (SOD) and catalase (CAT) activities in plant leaves and increased salt tolerance in wheat at the booting stage compared to the other stages (Daoud *et al*., 2018). Addition of Si reduced the salinity effects of irrigation waters for melon (Gomes *et al*., 2018).

Toxicity of heavy elements and micronutrients

Si alleviates the toxic effects of heavy metals and micronutrients (Corrales *et al*., 1997). Clements (1965a,b) concluded that Si in calcium silicate reduced toxic levels of Al and Mn and cured freckling(rust-colored or brownish spots) in sugarcane leaves caused by excess Mn. Samuels and Alexander (1969) also reported that Mn uptake of the cane plant was suppressed as its Si supply was increased. Further, Halais and Parish (1963) observed that cane yield was inversely related to the Mn/SiO_2 ratio in the cane sheath. Silicon application is reported to reduce Mn toxicity in rice (Li *et al*., 2011) and in cucumber (Shi *et al*., 2005). Fleck *et al*. (2013) observed that application of Si to rice fields resulted in reduction of As^{3+} concentration in straw, shoot, flag leaves and husk up to 50% and also reduced the As^{3+} content of brown polished rice up to 22%. Other researches also indicated the role of silicon in amelioration of arsenic toxicity in rice (Bogdan and Schenk, 2008; Tripathi *et al*., 2013). Yuan and Chang (1978) reported that Si fertilization reduced the uptake of Fe^{2+} and Mn^{2+} by rice. Cocker *et al*. (1998) proposed that Si inhibits aluminum (Al) toxicity either by forming insoluble aluminosilicates or hydroxyaluminosilicates which reduces the concentration of free Al^{3+} in soil solution, or by blocking the apoplastic pathway. Bishop (1967) reported from South Africa that aluminum toxicity together with silicon deficiency were potential growth limiting factors in the highly weathered oxisols of the newly developed cane areas of the Natal Midlands. Silicon is reported to reduce Al toxicity in maize (Wang *et al*., 2004) and *Norway spruce* (Prabagar *et al*., 2011). Cunha *et al*. (2008) reported that addition of Si up to 200 mg kg^{-1} drastically reduced the bioavailability of heavy metals Cd and Zn in maize and led to an increased biomass production. Nwugo and Hueta (2008) reported that Si reduced Cd toxicity in rice, while Rizwan *et al*. (2012) reported that it did so in wheat and Song *et al*. (2009) reported the same in *Brassica chinensis* L.

Silicon and resistance to biotic stresses

Diseases

Si enhances resistance in plants to various diseases (Fauteux *et al*., 2005). Miyake and Takahashi (1983) observed that increasing the Si concentration of a solution in which a cucumber plant was grown led to an increase in shoot Si content and a subsequent reduction in the incidence of powdery mildew disease relative to plants growing in solution low in Si. Similar observation was made by Menzies *et al*. (1991), who reported reduced infection efficiency, colony size and germination of conidia when cucumbers were grown in nutrient solution containing high concentrations of Si. Datnoff *et al*. (1997) also reported decreased incidence of blast and sheath blight in rice under Si fertilization. The occurrences of leaf folders and rice blast disease were mitigated by increased Si uptake (Klotzbücher *et al*., 2017). Wheat plants treated with Si produced phytoalexins and inhibited powdery mildew infection (Remus-Borel *et al*., 2005). It is not only a physical barrier imparted by Si that reduces the incidence of diseases and pests in plants, but there is much more in the mechanism responsible for pathogen resistance. Several studies have reported the role of Si in disease resistance by activating defense-related enzyme activities such as chitinase, peroxidases, polyphenoloxidases, β-1,3-glucanase, phenylalanine ammonia-lyase, superoxide dismutase, phenylalanine ammonia lyase (PAL) etc. involved in the synthesis of plant secondary antimicrobial substances essential for plant disease resistance responses (Waewthongrak *et al*., 2015). The higher PAL activity after Si treatment contributes to an accumulation of total soluble phenolic and lignin-thioglycolic acid derivatives in the leaves of wheat, banana and coffee plants that lead to low disease incidence (Silva *et al*., 2010a,b; Fortunato *et al*., 2012). Wang *et al*. (2017) suggested the role of Si in plant resistance to pathogen infection as follows: 1. Si-induces resistance against a wide range of diseases by acting as a physical barrier in the cuticle, 2. Si-induced biochemical resistance during plant-pathogen interactions involves activating defense-related enzymes activation, stimulation of antimicrobial compound production, and regulation of the complex network of signal pathways, and 3. Si may act at a molecular level to regulate the expression of genes involved in the defense response. In Poland foliar application Si (Optysil) reduced the content of mycotoxins in corn grain (Ciecierski *et al*., 2017). In a pot study with wheat at Reading (UK), the silicon treatment reduced powdery mildew (*Blumeria graminis*) substantially but there were no effects on the slight infection by brown rust (*Puccinia recondita*) (Rodgers-Gray and Shaw, 2004).

Insect pests

Si-induced hardness in the cuticle offers resistance to insects. Soil application of Si-containing fertilizer resulted in increased rice Si uptake by as much as 32%, leading to a significant reduction in relative growth rate and the boring capacity of *Diatraea saccharalis* larvae (Sidhu *et al*., 2013). In sugarcane, Si accumulated in the stem epidermal tissue of the internode and root band increased the resistance to *Eldana saccharina* by reducing larval stalk penetration (Keeping *et al*., 2009). Si-treated rice plants revealed ladder-like structures of dumbbell-shaped silica and Si-enriched trichomes, which served as a mechanical barrier against stem borers and plant hoppers (Dorairaj and Ismail, 2017). In addition to silicon related hardness, plants emit chemical compounds in the form of herbivore induced plant volatiles (HIPVs), which can act either as attractants or repellents of insects and thus may be used as host-finding cues by entomophagous predators and parasitoids of insect pests (Van Poecke and Dicke, 2004; Van Oudenhove *et al*., 2017). Si may trigger different plant species to emit, amplify, and/or alter HIPVs. Furthermore, a high silica content in plant tissue reduces its digestibility and palatability, consequently slowing the insect growth rate (Massey *et al*., 2009). Si could damage the ultrastructure of the midgut epithelium, mainly through detachment of epithelial cells from the basement membrane as observed in larvae of the leaf miner *Tuta absoluta* fed Si-treated leaves of tomato (Dos Santos *et al*., 2015). Further, Si can reduce pest damage by enhancing the induced chemical defenses of plants following insect attack mediated by phytohormones. The common phytohormones salicylic acid (SA), jasmonic acid (JA) and ethylene play primary roles in orchestrating plant defense responses (De Vos *et al*., 2005). Rao (1967) reported that sugarcane varieties tolerant to a shoot borer had more of Si cells per unit area in the leaf sheath. In Taiwan, it was shown that the incidence of borer damage in Si treated cane was less than in untreated sugarcane (Pan *et al*., 1979). Elawad *et al*. (1985) observed that with improved Si nutrition there was a marked increase in the resistance of sugarcane to stem borer (*Diatraea saccharalis*) in Florida, USA. A large size pot trial, in which sugarcane was treated with calcium silicate and artificially infested with *E. saccharina*, showed significant reductions of 24% in borer damage and 20% in borer mass (Meyer and Keeping, 2000). Recently, Alhousari and Greger (2018) have reviewed the literature on role of Si in insect resistance in plants.

Frew *et al*. (2018) have suggested a holistic approach involving genomic, transcriptomic, proteomic and metabolomic techniques to assess the mode of action of Si between plant trait types (e.g. C_3, C_4 and CAM; Si accumulators and non-accumulators) and biotic and abiotic stressors (pathogens, herbivores, drought, salt).

Additional Benefits to Plants from Silicon

Preventing lodging

Idris *et al*. (1975), Fallah (2012) and Dorairaj *et al*. (2017) reported that addition of silica reduced lodging in rice and this increased rice yield. Liang *et al*. (1994) found practically no lodging in rice fields fertilized with calcium silicate, and more than 66% lodging in untreated control fields. Kim *et al*. (2012) reported that the lodging index of Si treated rice plants significantly decreased as compared with control and Si treated plants had 15.1% higher yield. In several experiments with wheat in Mexico, foliar application of silicon as well as soil application of Armurox (a complex of peptides with soluble silicon) had a positive effect on increasing plant resistance to lodging (Botta *et al*., 2014). From India, Dinesh *et al*. (2017) reported the positive effect of soil fertilization with calcium silicate on the improvement of lodging resistance of wheat resulting in an increase in yield.

Enhancing photosynthesis

Lau *et al*. (1978) proposed that under normal light, silica deposited in stomatal guard cells could serve as windows allowing more light to pass through the epidermis to the photosynthetic mesophyll tissue, thus enabling higher rates of photosynthesis. Mauad *et al*. (2003) suggested that Si improved cell wall thickness below the cuticle and improved the leaf angle, making them more erect and thus reduced shading, especially under high nitrogen rate. Song *et al*. (2014) reported that the leaf chloroplast structure was disordered under high-Zn stress, including uneven swelling, disintegrated and missing thylakoid membranes, and decreased starch granule size and number, which, however, were all counteracted by the addition of 1.5 mM Si. Furthermore, the expression levels of genes *Os08g02630* (*PsbY*), *Os05g48630 (PsaH)*, *Os07g37030* (*PetC), Os03g57120 (PetH)*, *Os09g26810* and *Os04g38410* decreased in Si-deprived plants under high-Zn stress. He reported that addition of 1.5 mM Si increased the expression levels of these genes in plants under high-Zn and concluded that Si alleviated Zn-induced damage to photosynthesis in rice.

Defense against grazing

Phytoliths present a powerful mechanical defense, especially in monocotyledons (grasses and sedges), which deposit more silica phytoliths than dicotyledons (Massey *et al*., 2009; Hunt *et al*., 2008). The phytoliths in plants prevent grazing by herbivorous animals. A rigid leaf surface caused by SiO_2 bodies in the leaf cuticle serves as a deterrent for herbivores (Herrera, 1985). Also grazing induces an increased concentration of silicon (Si) in leaves (Hartley, 2015), which reduces palatability and digestibility, which in turn lowers body mass and growth rate of grazing animals (Massey *et al*., 2007, 2009). Increased Si in foliage also increases abrasiveness resulting teeth tear in rabbits (Muller *et al*., 2014; Calandral *et al*., 2016).

Preventing freeze damage

Grape (*Vitis vinifera* L.) is one of the most important temperate fruit crops in the Mediterranean climate and is frequently damaged by freezing temperatures in many of the grape growing regions (Fennell, 2004). A study in Iran showed that foliar-applied Si (10 mM K_2SiO_3 with pH adjusted to 5.8 with phosphoric acid) can effectively alleviate adverse effects of freezing via maintenance of membrane integrity and alleviating photo-inhibition during recovery (Habibi, 2015). In Florida, it was observed that there is an increased tolerance to freeze damage of commercial sugarcane in areas treated with calcium silicate (Ulloa and Anderson, 1991). Beneficial effects of Si seed treatment with silicic acid on seedling establishment and the nutritional status of Zn and Mn were reported for a field-grown silage maize, exposed to chilling stress in Germany (Moradtalab *et al*., 2018). They observed that Si restored the hormonal balances to a level comparable with non-stressed plants and stimulated the production of hormones involved in stress adaptation (abscisic, salicylic, and jasmonic acids).

Silicon and Environment

On the earth's surface silicate minerals are abundant in rock formations all over the planet. Silicate minerals react with carbonic acid, which is available in plenty. The reaction is slow but steady. The reaction is as under:

$XSiO_3$ (silicate min.) + H_2O + $2CO_2 \rightarrow 2HCO_3 + SiO_2 \rightarrow XCO_3$ (Carbonate min.) + H_2O + CO_2

Where: X refers to a cation, generally Ca.

In this reaction 2 molecules of CO_2 are taken from the atmosphere and one is returned back to the atmosphere, so one molecule is sequestrated. This carbonate-silicate reaction is inorganic C-sequestration. Considering biogeochemical cycling within ecosystems, the import and export of silica to and from terrestrial ecosystems is small. The final stage of the process involves the movement of the seafloor, where the carbonate sediments are buried and under high pressure and temperature conditions combine with SiO_2 to form $CaSiO_3$ and CO_2, which is released back to the atmosphere by volcanism after a long interval of time, say millions of year.

The carbonate-silicate geochemical cycle, also known as the *inorganic carbon cycle*, as described by the long-term transformation of silicate rocks to carbonate rocks by weathering and sedimentation, and the transformation of carbonate rocks back into silicate rocks by metamorphism and volcanism (Berner *et al*., 1983; Walker *et al*., 1981), plays an important role in regulating CO_2 on the earth (Catling and Kasting, 2017). The global warming due to increased CO_2 in the atmosphere has recently received considerable attention. Atmospheric CO_2 concentration has increased from 280 ppm in the pre-industrial era of 1750s to 400 ppm in 2015, however, a major increase was observed in 20th century, which is the highest for the past 800 millennia (USEPA, 2017). Global warming is increasing at fairly fast rate in the 21st Century, since all but one of the 16 hottest years in NASA's 134-year record have occurred since 2000 CE (MacMillan, 2016). To combat this C-sequestration via photosynthesis by afforestation and vegetation is being attempted; this is known as *organic C-cycle*. Organic C-sequestration in the terrestrial biosphere, with a technical cumulative C sink capacity of 155 Pg C (158.6 billion tons C) in vegetation and 178 Pg C (182.1 billion tons C) in soil by 2100, is estimated to drawdown the atmospheric CO_2 to 156 ppm (Lal *et al*., 2018). As a contrast, 99.6% of all carbon (~10^8 billion tons of carbon) on earth is sequestered in the long term rock reservoir by silicate-carbonate formation and only 0.002% of carbon exists in the biosphere. Over tens to hundreds of millions of years, carbon dioxide levels in the atmosphere may vary due to natural perturbations in the silicate-carbonate cycle (Berner, 1991). On geological timescales, Earth's climate is regulated by a balance between silicate weathering reactions that consume atmospheric CO_2 and a continuous input of carbon from volcanic and metamorphic degassing (Walker *et al*., 1981). This would show how important Si is in the nature.

Conclusion

Silicon is a ubiquitous element, present in soil, water and air and organisms therefore its importance for plants is not realized. As a major component of soil, it provides anchorage to plants and as a component of plants themselves it provides structural strength to them. It protects plants against diseases, insect attacks and grazing by herbivores. It also saves plants from several abiotic stresses, such as, drought, freezing, salinity and toxicity from some elements (Al, As, Fe, Mn). Further field trials with silicon fertilization may be performed for reduction in arsenic contamination of rice grown in contaminated areas. However, many of these effects are physical in nature and Si has not been associated with a physiological or biochemical reaction in plants and thus has not been declared as an essential plant nutrient. Silicon is very much involved in inorganic C-sequestration and reduction of global warming. Further some studies have indicated that it enhances photosynthesis, so it also helps organic C-sequestering by plants. The break through researches of Si transporters in different parts of rice could be used as a genetic resource to develop transgenic crops to improve silicon uptake potential which would simultaneously enhance C-sequestration. Silicon therefore deserves special attention from the plant structure, plant protection and global warming viewpoint.

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