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Review Article

An Overview of the Uptake Mechanism of Silicon and Its Importance in Increasing Yield and Salt Stress Alleviation in Crops

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Abstract

Although present in huge abundance in the earth's crust, the availability of silicon (Si) is very low in soil. But it imparts manifolds benefits on soil and plant health like increasing the yield of crops, stabilization of soil characteristics *etc*. The uptake of Si in soil and plant is mediated by certain carrier proteins which are present in the root of the crops. Mostly, the *Poaceae* crops are the efficient users of Si. A major impact of Si in crops is the remediation of biotic and abiotic stress. Globally, salt stress poses a serious hazard to plant development. Numerous studies have been conducted utilizing physiological, molecular genetics and genomic-based techniques in order to investigate the possible mechanisms to regulate the salinity stress through Si application. These studies were carried out in order to get a better understanding of the processes involved. Clarifying silicon's mitigating effects on oxidative stress, Na toxicity and salt-induced osmotic stress has advanced recently. The behavior of silicon in the soil, the processes by which it is absorbed and the function that it plays in plants in the process of warding off salt stress in plants are the primary topics of discussion in this article.

Keywords: Crop, Remediation, Salt stress tolerance, Silicon, Uptake, Yield

Introduction

Rice is the major staple food consumed by people throughout the world. More than two-third of the people are supported by this crop and also it provides source of income for millions of people. With the rising population pressure to feed the growing demand for the food, it has a challenge to increase the productivity of the crop within the same land resource. The conventional use of primary nutrients like N, P and K along with secondary nutrients like Ca, B, Zn need to be additionally supported by some other beneficial nutrients. In this respect Silicon (Si) has come up with the promise of increasing the effectivity of the nutrients applied and increase the yield of the crop. It is found that with respect to the occurrence in the earth's chemical composition, Si is the second one to come (around 27.8%), next just to oxygen. Silicon is constituted up to 10% of the dry mass of rice straw and present with much higher quantities than the primary nutrients, including potassium (K), phosphorus (P) and nitrogen (N) (Tsujimoto *et al.*, 2014). The most prevalent forms of Si present in the soil are as mono- and poly-silicic acids, and in complexes with both inorganic and organic substances, like hydroxides and oxides of aluminium. Even with the larger availability, it is not found in the soil in the elemental form, rather it is present in the soil as silicates (SiO_3) and silica (SiO_2). Not only that, it is also found that silica accounts for around 50-70% of the total soil mass with a concentration that ranges from twenty percent to over one hundred percent (Sommer *et al.*, 2006). Several factors affect soil silicon solubility. These parameters include silicon fertilizer particle size, soil pH, organic complexes, phosphate, iron and aluminium ions, dissolving processes and soil pH. Si present in the soil has manifold implications in plant like it increases the nutrient uptake, increase the resistance mechanisms in the system against insect pests, draught, salinity, diseases *etc*. which in turn helps to accelerate the effectiveness of the nutrients applied in the soil, taken up by plats and efficiency in the photosynthetic activities of the plants, resulting in the higher yield generation. According to Rao *et al.* (2017), Si enhances the physical, chemical and biological qualities of soil. Not only in view of nutrient

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availability and stress resistance, Si has been found to show its impact on the amelioration of heavy metals toxicity.

In the context of current agricultural scenario, as much as 20% of the world's irrigated lands are facing the problems of elevated salt concentrations and the principle reasons behind this are increased industrial pollution, indiscriminate use of chemical fertilizers and inappropriate irrigation systems deployed (Zhu and Gong, 2014). Many factors are operating in the saline environment like poor water retention, nutrient imbalance, complex interactions of plant hormones and specific ion effects that result in the poor crop stand and poor crop yield. The occurrence of salt stress also causes detrimental effects on the plant physiological properties. Therefore, it is essential to find out the promising ways of reducing the adverse impacts of the salt stress in the plant. One of these efficient ways is the application of Si in the soil. Of late many studies have been done on the implications of silicon in remediation of the biotic and abiotic stresses (Wu *et al.*, 2015; Coskun *et al.*, 2016; Abinaya and Yul-Kuyn, 2017). Significant numbers of studies have been conducted so far for the understanding of the mechanisms of Si in remediation of the salinity and osmotic stress. Within the rice root, more investigations are done to identify the impacts that silicon has on the possibility of apoplastic cycling of sodium ions (Na^+). Researchers have discovered that Si has a direct impact on two genes in maize, SOS1 and HKT1, which are involved in the uptake of sodium. This is the first evidence that Si impacts these genes (Bosnic *et al.*, 2018). But the fact here is that being an unconventional soil conditioner, the application of Si in the soil for most of the country is a rare incident, particularly for the South-East Asian countries like India, Bangladesh, Pakistan, Nepal *etc*. With this view, this article is focused on the uptake mechanism by which Si can transport from soil to plant root and from root to the overall plant system and its importance in the remediation of the salinity stress in the plants.

Forms of Silicon in Soils

There are instances when soils have very low quantities of silicon, especially in the form that plants can use, even though most soils are rich in this element. These soils are primarily classified as Histosols, which have extremely high amounts of organic matter relative to the mineral components (Snyder *et al.*, 1986) and highly developed soils with low base saturation and acidic nature like Ultisols and Oxisols. Particularly beneficial are long-term cropped soils and those that have a high concentration of sand and quartz. While this is happening, plants have less access to silicon (Datnoff *et al.*, 1997). There are three main ways that soil silicon is often classified: as a liquid or solution, as adsorbed, or as solid (Sauer *et al.*, 2006; Matichenkov and Bocharnikova, 2001). Figure 1 shows the most thorough classification.

Crystalline forms of silicon, such as primary and secondary silicates, as well as silica solids, are mostly found in nature. According to Allen and Hajek (1989), the majority of soil silicate minerals are found in sand and silt particles. On the other hand, secondary silicates are generated by pedogenic processes that include phyllosilicates and iron-aluminium oxides of various forms. Short-range ordered silicates include soft-crystalline silicon, according to Allen and Hajek (1989). Chalcedony and secondary quartz are microcrystalline silicon formations. These forms of silicon are referred to as weakly crystalline. There are two types of amorphous silicon: biogenic and lithogenic/ pedogenic. These amorphous forms of silicon may be found in soil at concentrations ranging from less than one to thirty milligrams per gram, dependent on the total weight of the soil (Drees *et al.*, 1989; Jones, 1969). Biogenic silicon is derived from plant detritus and microbiological remains and is also known as biogenic opal. According to Aoki *et al.* (2007), Sauer *et al.* (2006) and Sommer *et al.* (2006), plants store silicon in the form of phytoliths or silica bodies in their leaves, stems and culms, whereas bacteria provide silicon in the form of microbial and protozoic silicon. The lithogenic and pedogenic forms result from the complexation of silicon with heavy metals, aluminium, iron and soil organic matter (Farmer *et al.*, 2005). The most available form of silicon mostly exists in the soil solution phase as mono-silicic acid (H_4SiO_4; the bioavailable form for plants), as well as in oligomeric or polysilicic acid forms. Plants primarily absorb monomeric silicic acid, whereas polymeric silicic acids are mostly linked to the soil aggregation process. Numerous studies (Norton, 1993; Matichenkov and Bocharnikova, 2001) indicate that polysilicic acid binds soil particles *via* silica bridges and in diverse soil types (ranging from light to heavy textures); the addition of silicon-rich materials enhances aggregate stability of soil, water holding capacity and buffering capacity. A portion of the dissolved silicic acid exists in an adsorbed state on soil solid phases, such as clay particles and sesquioxides (Hansen *et al.*, 1994; Dietzel, 2002). Silicate minerals, silicon dioxide and plant residues are the main sources of H_4SiO_4 in soil solution. Physico-chemical properties of SiO_2 determine their H_4SiO_4 release. But there is a fact that the concentration of this silicic acid is likely to be affected by the presence of SiO2 in the soil.

Mechanism for the Absorption and Transfer of Silicon

Silicon mostly exists in the soil solution as mono-silicic acid. This mono-silicic acid is absorbed by the lateral roots of the plant *via* the active transport mechanism (Ma *et al.*, 2001). The absorption of Si differs across many plant species (Table 1) and is regulated by particular transporter genes. Rice was the plant that provided the first evidence of the presence of silicon transporters in plants. LSi1, LSi2 and LSi6 are described as the three low silica genes (LSi) that are accountable for the transportation of silicon in rice, as shown by the study conducted by Yamaji and Ma (2009). According to the results of Blast and ClustalW analysis, the LSi1 transporter is a member of the aquaporins subfamily of the NIP3 major protein family (Gomes *et al.*, 2009). The root hairs do not express Lsi1, but the main and lateral roots do. In root basal zones, LSi1 is present more than at terminals. Exodermis and endodermis cells that have Casparian stripes have LSi1 attached to their plasma membranes. Study conducted by Yamaji and Ma (2011) reveals that the anion transporter LSi2 is responsible for transporting silicon from rice roots to vascular tissues.

Table 1: Uptake of silicon in different crops (Ma *et al.*, 2002)

Crop	Plant available Si (kg ha^{-1})	Major nutrients (kg ha^{-1})		
		N	P	K
Sugarcane	500-700	90	17	202
Potato	50-70	-	-	-
Rice	230-470	34	22	67
Cereals	100-300	-	-	-

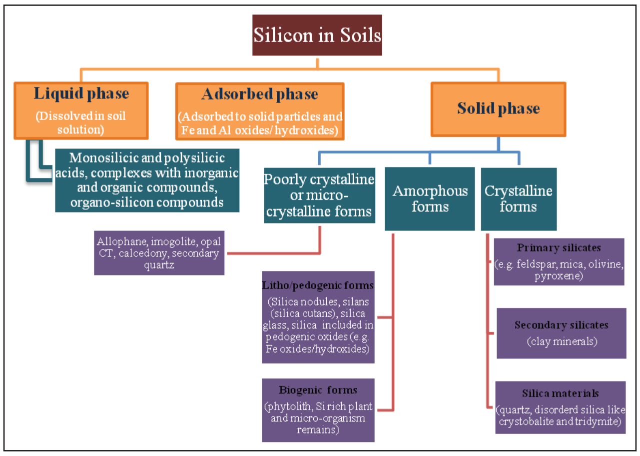

Figure 1: Forms of Silicon in soil (Matichenkov and Bocharnikova 2001; Sauer *et al.*, 2006)

Although they are found on the proximal side of the membrane, the LSi2 transporter is found in the same cells as the LSi1 transporter. For Si, LSi1 and LSi2 both display influx and efflux transport activities (Figure 2). While the inflow transporter (LSi1) is responsible for transporting silica acid from the soil solution to the exodermis, the other transporter (LSi2, known as the efflux transporter) is responsible for transporting it to the aerenchyma. This transporter is responsible for transporting all of the silicic acid that is flowing through the body as it travels through the body. Then, another influx transporter, LSi6, transports it to the aerial sections, or shoot (Figure 3 and 4). Not only that, LSi6 has also the role of transporting Si to the panicles, apart from carrying from root to shoot. According to Ma *et al.* (2011), LSi6 has a physiological function in the distribution of Si in plants by decreasing Si in panicles and increasing Si in flag leaves when it is knocked out.

Role of Silicon in Rice

More silica than plants require is absorbed, but it cannot be eliminated from tissues. It is primarily found in primitive *Urticaceae*, *Cucurbitaceae*, *Poaceae*, *Cyperaceae* and *Commenllinaceae* plants and animals. From grain crops to grasses, vegetables, fruit crops and legumes, silicon levels dropped. The aerial portions collect more silicon than the roots do. Compared to crops that do not accumulate silicon, rice is an efficient silicon-accumulating crop that takes up more silicon from the soil. Si absorption by rice crops ranges from 230 to 470 kg ha^{-1} (Rao *et al.*, 2017). Silicon improves soil nutrient availability and crop uptake. A study conducted by Pati *et al.* (2016) revealed that when Si was applied in the form of diatomaceous earth (DE), it resulted in significant increase in the total nitrogen, phosphorus and potassium content in straw and grain of rice. An increase in plant height, tiller count, panicle count and rice test weight were observed when straight fertilizer practices were combined with application of Si @ 600 kg DE ha^{-1}. This was in comparison to other treatments. Si also assisted stressed rice plants by raising the erectness of their leaves and decreasing the drop in filled grains, as stated by Ma *et*

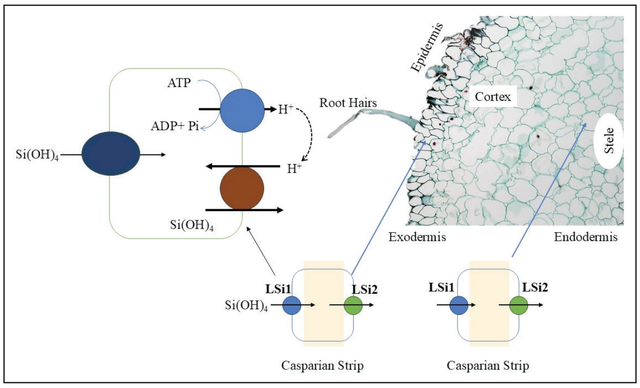

Figure 2: Influx (LSi1) and efflux (LSi2) transporter genes in rice root (Adopted from Ma and Yamaji, 2006; 2008)

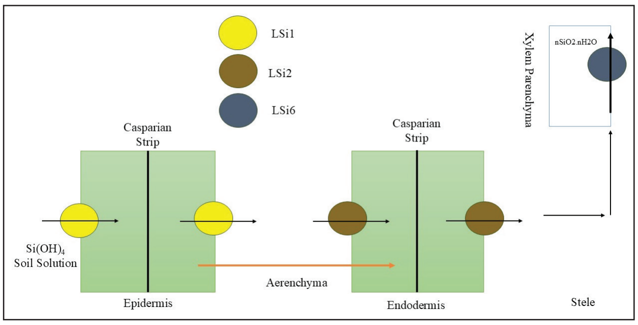

Figure 3: Si diffusion in rice via transporters. Si is taken up into the cell's exodermis by LSi1, the plasma membrane's influx transporter gene; by LSi2, an efflux transporter, over the aerenchyma; and by LSi6, which takes it up the plant's aerial parts. (Adapted from Ma *et al.*, 2011)

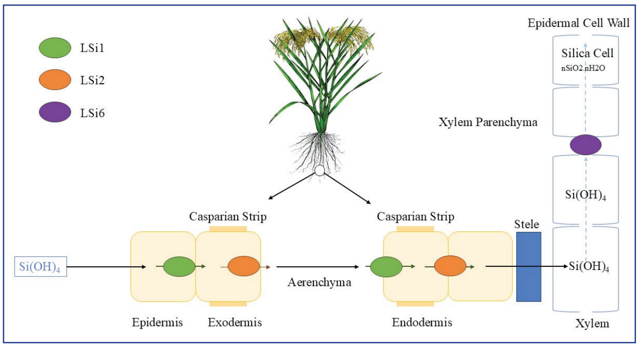

Figure 4: LSi6 mediated transfer of Si from root to shoot (Adapted from Rao and Susmitha, 2017)

al. (2004) for their research. This, in turn, decreased self-shading and accelerated photosynthesis, especially during the grain filling period, which was linked to the accumulation of starch in the grains. Similar research also indicated that using Si in conjunction with NPK fertilisers greatly enhanced rice's overall absorption of N, P and K (Singh *et al.*, 2005).

Role of Si in Remediation of Salinity Stress

The ability of silicon to stimulate the development of plant shoots and/or roots in response to salt stress has been shown to be beneficial to a broad variety of plant species, including rice, wheat, maize and others (Wu *et al.*, 2015). Upon subject to salt stress, it is generally found that the first occurrence always occurs in the root cells. In exposure of this salt stress, it is found that Si application can regulate the plant osmotic pressure and root growth (Kim *et al.*, 2014). Si may enhance root development in rice and sorghum by either enhancing cell wall extensibility in the growth area or by encouraging the establishment of Casparian bands and lignin and suberin production (Fleck *et al.*, 2015). The following is a summary of the ways that Si enhances plant photosynthesis in the presence of salt stress: (i) the addition of silicon under conditions of salt stress has the potential to minimize ion toxicity and the accumulation of reactive oxygen species (ROS), hence preserving the structure and activity of the organelles engaged in photosynthesis; (ii) Reduced stomatal conductance and non-stomatal inhibition also contribute to the lower photosynthetic rate by limiting the amount of CO_2 available for carboxylation processes (Liang *et al.*, 2003). The potential of Si in increasing the overall size and the number of stomata has been studied by Abbas *et al.* (2015). They have concluded in their research that silicon has the potential to increase the photosynthetic rate in plants even when subjected to salt stress condition. The maintenance of photosynthetic organs and pigment levels, in addition to the increase of plant carbon dioxide use, are the mechanisms by which this objective is achieved. Very limited resources are available relating to the mechanism by which Si increases the carbohydrate metabolism in the plants. Some evidences are there that shows that upon exposure to higher salt concentration, there is reduced uptake of nutrients like Ca and K and the ionic compounds like sodium and chloride play the most effective role here. Additionally, higher levels of salt ions increase the permeability of cell membranes, which may result in disregulation and metabolic disorders. The plant may decrease cytoplasmic ion toxicity by compartmentalizing Na^+ in the vacuole, increasing Na^+ efflux and decreasing Na^+ absorption in response to salt stress (Parida and Das, 2005; Xu *et al.*, 2015). This allows us to classify the potential mechanisms by which silicon responds to salt stress by regulating ion homeostasis into three broad groups. It is necessary that when the cell is subjected to salt stress condition, a quick detection of the excess Na^+ signals are essential for the initiation of cellular ionic homeostasis (Liang *et al.*, 2005; 2006). Upon the cellular breakdown of ATP by H^+ ATPases on cell membranes, H^+ ions are released out of the cells resulting into the formation of transmembrane proton gradient. The Na^+/H^+ antiporter protein in the plasma membrane is therefore driven by this situation. Liang *et al.* (2006) and Cheraghi *et al.* (2023) in their study have found that upon the injection of H^+ ions in the cels, Na^+ ions tend to release in the opposite direction of an electrochemical gradient. Earlier research by Liang *et al.* (2005) came out with the findings that the presence of Si in roots can result in the increased levels of plasma membrane H^+ ATPases and vacuolar membrane H^+ PPases. Furthermore, higher sequestration of sodium ions into vacuoles can also occur due to increased activities if the H^+ ATPases and H^+ PPases in vacuolar membranes, which results in reduced root damage caused by sodium ions (Liang *et al.*, 2005; 2006). Further studies are required to investigate the direct influence that Si exerts on the activities of Na^+/H^+ antiporters and H^+-ATPases in plasma membranes and vacuolar membranes. In addition, high soil salt concentrations reduce nitrogen and calcium uptake, causing ion imbalance. At the other end of the spectrum, it has been shown that silicon may increase the concentration of macro-elements like calcium, phosphorus and magnesium, as well as microelements like boron, iron, zinc and manganese, in diverse plant species (Zhu and Gong, 2014). Under salt stress situations, the quick detection of excess Na^+ signals are essential for restoring cellular ionic equilibrium (Yang and Guo, 2018a). Through the process of extruding sodium ions into the apoplast, the salt excessively sensitive (SOS) signalling system is often activated. This process is necessary for the maintenance of ionic homeostasis in plants (Yang and Guo, 2018b). The use of salt treatment is common. Less is known about how Si affects SOS1-mediated NaCl efflux. Silicon decreased salt accumulation in maize root apex and cortex, according to Bosnic *et al.* (2018). ZmSOS1 and ZmSOS2 were increased in the root cortex as a result of Si supplementation, whereas ZmHKT1 was down regulated. This encouraged the transfer of sodium ions to the leaves *via* the xylem. As a result of Si's upregulation of ZmNHX, which sequestered sodium ions into vacuoles, chloroplast sodium ions accumulated less. When plants are subjected to salt stress, they generate an excessive amount of reactive oxygen species (ROS), including H_2O_2, O_2^- and OH^-. ROS increases are responsible for oxidative damage to organelles and membranes, according to Gao *et al.* (2005). In this respect, two different antioxidant mechanisms exist and they are enzymatic and non-enzymatic. Ascorbate peroxidase (APX), catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD) are some of the primary enzymatic antioxidants that are found in plants. On the other hand, ascorbic acid, glutathione reductase (GR) and vitamin E are the examples of the non-enzymatic antioxidants (Choudhury *et al.*, 2017; Chongtham *et al*., 2024). It is found in different studies that Si helps in scavenging the ROS through the modification of the antioxidants and concentrations of non-enzymatic as well as enzymatic antioxidants. Although Si may have boosted SOD, CAT and GR activities in barley, it did not have any effect on APX (Liang *et al.*, 2003). Exogenous silicon may increase peroxidase (POD) activity and decrease malondialdehyde (MDA) more than salt stress alone, according to the findings of a study conducted on *Glycyrrhiza uralensis*. It was only *via* the use of 4 mM Si that a discernible increase in the SOD activity could be achieved (Li *et al.*, 2016). In spite of the variabilities in crop species as well as cultivars, treatment time, concentration and growth circumstances, silicon has the ability to modulate both enzymatic and non-enzymatic antioxidants in response to salt stress, therefore reducing the formation of reactive oxygen species (ROS). It is more cost-effective to do laboratory investigations as opposed to field trials; nonetheless, substantial field tests are required prior to administering silicon in field circumstances and offering suggestions for farmers. Although, it is to consider the fact that these short-term laboratory based outcomes may not always be well-fitted top the large scale field conditions under salt stress.

Conclusion

The richness of silicon in the crust of the earth and the beneficial effects that it has on the growth of plants has both contributed to the consolidation of silicon's relevance in the agricultural sector. Even though Si's ability to reduce salinity stress has been well investigated in both lab and field settings, little is known about the molecular and physiological processes underlying the Si-regulated salt stress response. The results of previous studies indicate that silicon governs the salt tolerance of plants in a manner that varies according to the species and cultivar. This may be mostly because different plants have varying capacities for absorbing Si. Silicon concentration, stress duration and intensity, soil culture and hydroponics cultivation, foliar and root silicon application, testing materials (root, leaf and stem) and silicon forms and concentrations (silicic acids, silicates and silica nanoparticles) are all factors that influence the degree to which plants are able to tolerate salt. It has been shown, for instance, that the application of foliar sprays that include silicates has a lesser impact on the development of plants in comparison to the applications of stabilized silicic acid (sSA), which is the only silicon molecule that plants are able to access. Additionally, sSA has a great deal of potential as an ecologically acceptable alternative to pesticides. Furthermore, new studies show that Si may reduce osmotic stress and salt-induced ion toxicity *via* several mechanisms. In operations that take place in the real world, it is difficult to differentiate between the two consequences. Plants of the same species may respond differently to Si addition during different treatment periods. Despite this, Si may considerably reduce salt stress damage in certain plant species.

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