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Review Article

Importance of Silicon and Mechanisms of Biosilica Formation in Plants

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Silicon (Si) is one of the most prevalent macroelements, performing an essential function in healing plants in response to environmental stresses. The purpose of using Si is to induce resistance to distinct stresses, diseases, and pathogens. Additionally, Si can improve the condition of soils,which contain toxic levels of heavy metals alongwith other chemical elements. Silicon minimizes toxicity of Fe, Al, and Mn, increases the availability of P, and enhances drought along with salt tolerance in plants through the formation of silicified tissues in plants.However, the concentration of Si depends on the plants genotype and organisms.Hence, the physiological mechanisms and metabolic activities of plants may be affected by Si application. Peptides as well as amino acids can effectively create polysilicic species through interactions with different species of silicate inside solution. The carboxylic acid and the alcohol groups of serine and asparagine tend not to engage in any significant role in polysilicates formation, but the hydroxyl group side chain can be involved in the formation of hydrogen bond with $Si(OH)4$.The mechanisms and trend of Si absorption are different between plant species. Furthermore, the transportation of Si requires an energy mechanism; thus, low temperatures and metabolic repressors inhibit Si transportation.

2. Important Roles of Silicon

*2.1**. Forms of Si in Soil***. Each kilogram of soil usually contains Si ranging from50 to 400 grams. Silicon dioxide (SiO_2) is the common form of Si in soil. Vermiculite, smectite, kaolin (rich minerals in soils), orthoclase, feldspars, plagioclase (silicates in the form of crystal), amorphous silica, and quartz are the main Si components in most soils structures [25]. Solubility of all the above Si forms is low and biogeochemically immobile. The major soluble forms of Si in the soil are poly- and monosilicic acids [26]; however, monosilicic acid occurs mostly in a feebly adsorbed condition [27] and has low capability to migrate inside the soil [28]. By increasing the monosilicic acid concentration in the soil solution, plants are able to absorb phosphates (P) directly. The amount of monosilicic acid is increased because of chemical resemblance between phosphate and silicate anions causing a competitive reaction in the soil [29]. Insolubility of monosilicic acid decreases slightly through interactions with heavy metals, iron, aluminium, and manganese [30]. Essential soil components are polysilicic acids that commonly influence the physical properties of soils. In contrast, monosilicic acid is adsorbent and is chemically immobile and makes colloidal particles [31].Thus, polysilicic acids interferes with soil structure formation and soil water-holding [32]. In the biochemical processes which occur in the soil, the Si function is highlighted because this element possesses chemical properties that can create molecules with useful biological functions. The main drawback of Si is the disability of this element to form chemical bonds with different types of atoms that are necessary for the chemical versatility of metabolism. This disability is caused by the size and the molecular mass of the Si atom, which leads to limiting interaction with the other atoms and the formation of monotonous molecules.

*2.2. **Silicon and Plants***

2.2.1. Variability of Si Contents in Various Plant Species.

Among plants, sugarcane (*Saccharum officinarum*), rice (*Oryza sativa*), and wheat (*Triticum* spp.) absorb the largest amount of Si, with 300–700, 150–300, and 50–150 kg Si ha^{-1}, respectively [33]. Generally, Si uptake in graminaceous plants is much higher than its uptake in other plant species. For example, rice is a common Si-collector that absorbs Si in active progression [34], as other graminaceous plants do including wheat (*Triticum* spp.) [35], barley (*Hordeum vulgare* L.) [36], ryegrass (*Lolium perenne*) [37], maize (*Zea mays* subsp. *Mays*) [38], and some cyperaceous plants. The majority of dicotyledon plants, such as cucumbers (*Cucumis sativus*), melons, strawberries, and soybeans (*Glycine max* L.Merr) absorb Si inertly [39]. Nonetheless, some plants especially dicotyledon, such as tomatoes (*Solanum lycopersicum*), beans, and other plants, are not able to absorb Si from soil[39–42].

2.2.2. Absorption Forms of Si by Plants. Monosilicic acid or orthosilicic acid (H_4SiO_4) is the Si forms that are absorbed by plants root [43, 44]. Consequently, Si accumulates in the epidermal tissues, and a layer of cellulose membrane-Si is created when Ca and pectin ions are present [45], which provides protection to the plant [19, 46, 47]. Increasing of Si in the sap of plants leads to Si polymerisation [48], identified as Si gel hydrated with water molecules [49]. The process of mono- and polysilicic acids hydration is as follows (Figure 1). Recently, Nurul Mayzaitul Azwa (*personal commun*.) reported that mangrove plants can absorb large amounts of Si from the soil solution (Figure 2). Amorphous silica is the final form of 90% of absorbed and transformed Si in Si cellulose structures [50]. A nanometre level of biogenic silica is produced as intercell structures [51]. Concentration of Si differs significantly in the shoots and roots of plants, and this extensive variation in different plant tissues is related to differences in the mechanisms of Si uptake and transportation [52, 53].Nutrient uptake by plants depends on the potential of water and the solubility of elements in the soils. The nutrients uptake pathway is from the soil solution with a higher solute concentration to plant tissues with a lower solute concentration. Although Si is found plentifully in both silicate and oxidase forms in the soil, Si solubility in the soil solution is an obstacle for plant absorption because monosilicic acid is theonly form of Si that plants can absorb.

2.3. Silicon and Abiotic Stresses.

2.3. Silicon and Abiotic Stresses. It has been widely reported that Si is able to suppress both physical stress, such as drought, high temperature, UV, loading, and freezing, and chemical stress, including salinity, nutrient imbalance, and metal toxicity [54, 55].

2.3.1. Silicon and Salinity Stress. Salinity stress, a major yield restraining factor in dry and semidry areas, can be repressed by increasing Si [56]. Silicon indirectly reduces the oxidative damage of cucumber tissues under salt stress through the activities of guaiacol peroxidase, ascorbate peroxidase, superoxide dismutase, dehydroascorbate reductase, and glutathione reductase [16]. Oxidative damage in tomato leaves decreaseswith increasing Si [5], resulting in increased activity of catalase and superoxide dismutase enzymes, increased protein content in the tomato leaves, decreased ascorbate peroxidase enzyme, decreased malondialdehyde concentration, and decreased H_2O_2 levels [57]. The alleviative effect of Si over salinity stress has been demonstrated in wheat (*Triticum* spp.) [55, 58], rice (*Oryza sativa*) [55, 59], barley (*Hordeum vulgare* L.) [14, 40, 55, 60], mesquite [61], tomato (*Solanum lycopersicum*) [57, 62], cucumber (*Cucumis sativus*) [63], and maize (*Zea mays* subsp. *mays*) [64, 65].

The roots and shoots of Si-treated rice plants under salinity stress notably improved when compared to control plants [66]. It has been reported that the salt tolerance of mesquite and wheat can be increased significantly after supplying a Si nutrient solution at small amounts [58].Along with that, the salinity tolerance of hydroponically cultured rice can be increased by adding Si to the nutrient solution [67].Adding Si decreased the concentration of Na in barley shoots [68] and rice shoots [69].

The positive physiologic effects of silicon on improvement of plants are in conjunction with the endogenous stress responses of plants in different environmental condition [70]. Silicon is able to increase soluble protein content of plant leaves, which helps plants to overcome salt stress by replacing the lost soluble protein content under salinity stress [16]. Silicon can also increase the antioxidant enzyme activity of superoxide dismutase (SOD), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), and glutathione reductase (GR) in plants under salt-stress [14, 16, 68]. The induced oxidative damage by salt can be decreased through decreasing in level of electrolyte leakage percentage (ELP), lipid peroxidation (LPO), and H_2O_2 content [16]. This enzymatic protection mechanism helps plants to overcome salinity stress damage [71–73]. A considerable enhancement in the antioxidant enzyme activities in leaves of salt-stressed cucumber by additional Si treatment suggested that Si can be involved in physiological or metabolic cycles of plants [16]. The Si nutrition increased catalase activity significantly in all parts of plants and peroxidase activity in cell wall of plant's shoots [57, 74]. From the physical stand point, Si is able to decrease the plasma membrane permeability in leaf cells of plants which resulted in reducing the lipid peroxidation levels. The Si application of plants under stress condition leads to decreasing lignin content in cell walls of plant's shoots. It was reported that application of Si in canola plants resulted in decreasing Si content in shoot parts of plants by formatting complexes of Si-polyphenol or substitution of Si and lignin [75]. These physical changes in plants' cell wall could facilitate loosening process and promote cell extension, which results in plants' growth under salt stress [74, 76]. The Si protects plants from environmental stress, such as drought and heat, by providing more stable lipids involved in their cell membrane [16, 77]. It was considered that Si-induced motivation from plasma membrane of roots might increase absorption and transportation of K and decrease the uptake and transportation of Na from the roots to shoots of barley under salinity [60]. On the other hand, Na^+ ion concentration in canola tissues under salt stress is decreased with Si application.The Si accumulation in the endodermis and cell walls of plants could reduce the Na accumulation in roots and shoots *via* a diminution in apoplastic transportation [74, 78–81]. Plants under salinity stress encounter low water potential from the outside because of the high Na^+ and Cl^- content in the soil and salt deposition in the other plant cellular regions [82]. These ions move to the aerial parts of plants via transpiration, and when Na^+ and Cl^- are at a toxic threshold, different plant tissues can be harshly damaged. The hydrophilic nature of Si can decrease the poisonous levels of saline ions and reduce the osmotic effect of salt stress on the absorption and storage of water by plants. Additionally, Si treatment in plants results in enlarged leaf cells *via* cell wall expansion, which helps the plants to hold more water. Reportedly, Si treated plants grown under saline stress have a larger leaf weight ratio and a smaller specific leaf area than untreated plants, which have smaller leaf surface areas and loss of water transpiration [58]. It has been shown that when salinised plants were treated with Si, their water amounts increased up to 40%. Moreover, the turgor potential of plants treated with both NaCl and Si was 42% higher than that of NaCl-treated plants [62]. Silicon treated salinised plants showed 17%higher efficiency in using water than untreated plants [16]. This suggests that Si is able to alleviate the harmful effects of salinity stress. Silicon can decrease lipid peroxidation in plants exposed to salinity stress by enhancing the enzymatic and nonenzymatic activities of antioxidants [16, 57]. Silicon application to the plants under salt stress limits the transpiration ratio and increases root activities. Decreases in transpiration lead to reduced osmotic stresses in plant cells and improved root activities. As consequence of root activities, plants can increase the nutrients uptake and decrease salt toxicity. Silicon absorption by plants leads to increased PPase and ATPase activities in vacuoles, which reduces Na+ uptake and enhances K+ uptake by the cell membrane. Separation of salt ions into the vacuoles and increasing the K+/Na+ ratio in the cells of the roots and leaves decrease Na+ toxicity. Increasing antioxidative enzymatic activities cease electron losses from the lipids in cell membranes, which decreases lipid peroxidation and cell damage.

5. Conclusions

The primary purpose of this review is to provide comprehensive insight about the role of Si in plants and the effects of biomolecules that are involved in the biosilica formation mechanism. Silicon plays an important role in helping plants overcome different types of abiotic and biotic stresses. The macroelement also improves the soil conditions under toxic levels of heavy metals and several chemical elements. In addition, to the role of Si as a physical hindrance, the application of Si could affect the physiological and metabolic activities of plants. It is reasonable to recommend Si as a useful element involved in cellular processes. Understanding the roles of Si on higher plants may improve their growth and productivity yield and decrease their susceptibility to a wide range of diseases. Because of 3 hydroxypropanoic groups, serine is classified as a hydrophilic, polar amino acid. Serine plays an important role in the anabolism of pyrimidines and purines.The structure of serine helps this amino acid to participate in other metabolites by easily releasing one atom of carbon in biosynthesis. Hence, serine is an important component in the biosilica formation mechanism and improvement of plant metabolism. Most of plants, especially dicots, are not able to absorb large quantities of Si from the soil. Hence, genetically and biochemically manipulating the plant roots to increase their capacity of Si absorption and subsequently transferring of Si to the shoot parts could help plants to overcome a wide range of stresses and improve their metabolism.

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