Review Article

Silicon uptake mechanism and its multidimensional influences on stress mitigation in rice (*Oryza sativa* L.)

ABSTRACT

Silicon (Si) is the second most abundant element in the earth crust. Si is a beneficial element for rice and has been recognized as a key nutrient to increase and stabilize rice yields (Savant *et al.*, 1997). The beneficial effects of Si includes mitigation of various forms of abiotic (e.g. metals toxicity, salinity stress, drought, mineral nutrient deficiency stress etc.) and biotic stress (e.g. plant disease and pest damage) (Meena *et al.*, 2014). Rice (*Oryza sativa)*, a typical Si accumulator, takes up Si actively (Ma *et al.*, 2001) in the form of silicic acid (Ma and Yamaji, 2006). The uptake mechanism of Si in rice is active. There are three transporters involved in the uptake of Si *viz*, LSi1, LSi2 and LSi3. Influx transporter (LSi1) takes silicic acid from soil solution up to the exodermis, followed by the efflux transporter (LSi2), which takes it further across the aerenchyma. Then, it is further moved up the aerial parts of the plants by another influx transporter, LSi6 and deposited as silica in the plant parts (Kaur and Greger, 2019). The key mechanisms of Si-mediated alleviation of abiotic stresses in rice include stimulation of antioxidants, complexation of toxic metal ions with Si, immobilization of toxic metal ions and compartmentation of metal ions within plants (Liang *et al.*, 2006). Si deposits in cell walls of xylem vessels prevent compression of the vessels under conditions of high transpiration caused by drought or heat stress. Results of Chen *et al.* (2011) showed that rice growth reduction upon expose to drought stress decrease with the application of 1.5 mM Si. Lodging has limited potential of increasing yield in rice. Fallah (2012) found that sufficient supply of Si has an effect on the stability of culms and serves to decrease the risk of lodging for rice plants. Rice is sensitive to metal toxicities like Fe, Mn and Al. Si application as calcium silicate showed significant reduction in these metal toxicities by decreasing available Fe, Mn, Al content in the soil (Nagula, 2014). Heavy metal toxicity of cadmium (Cd) and arsenic (As) can be alleviated along with reduction in accumulation of heavy metal (Cd & As) can be achieved by the supplementation of Si. Silicon ameliorates ionic toxicity by decreasing Na uptake and root-to-shoot translocation. Mitigation of salinity stress by regulating root morphological traits and osmotic potential (Guochao *et al.*, 2020). Silicon deposition in the plant tissues, which provides a mechanical barrier against the diseases and pests. The plants supplied with Si can produce phenolics and phytoalexins in response to fungal infection ((Datnoff and Rodrigues, 2005). Cuticle-Si double layer is less preferred by insect pests. Some studies reported that mandibles of stem borers fed on Si treated rice plants damaged and silicic acid in sap inhibits activity of the BPH (brown plant hopper) (Yang *et al.*, 2017).

Keywords: Silicon, Rice, Si uptake, abiotic stress, biotic stress

Introduction

Silicon is the second most abundant element constituting 27.7 per cent in the earth's crust occurring in diverse and complex mineral forms. Main forms of Si occur in dissolved forms such as polysilicic acids, monosilicic acid (H_4SiO_4), Si in adsorbed form and Si precipitated with oxides of Fe, Mn, Al, non-crystalline (amorphous or disordered) and crystalline silicate minerals (Savant *et al.*, 1997). Similarly, beneficial role of Si in plant growth and development has been reported (Farooq and Dietz, 2015). Silicon is considered as a wonder element and is reported to have promising impact on yield and quality of hyper-Si accumulator plants such as rice. Silicon also imparts various abiotic and biotic stress tolerance including drought stress, salinity stress, high temperature stress, chilling stress, flooding, nutrient deficiency and toxicity, and various fungal diseases which seriously marginalize the functioning of cellular proteins, lipids and elemental components of thylakoid membranes (Swain and Rout, 2017).

ROLE OF SILICON IN RICE

Rice (*Oryza sativa*) is an active absorber as well as an efficient Si accumulator (Ma *et al.*, 2001). Species variation and external Si concentrations influence Si uptake and transport in rice. Rice has a high Si demand, with straw containing 4-20 per cent SiO_2. Silicon can account for up to 10 per cent of shoot dry weight, which is many times more than the amount of critical macronutrients like N, P, and K. Rice crop has the capacity to uptake 150 to 300 kg ha^{-1} of Si (Bazilevich, 1993). It is estimated that nearly 20 kg of SiO_2 is being removed from the soil for the producing 100 kg of brown rice (Ma and Takahashi, 2002).

UPTAKE, TRANSPORT AND ACCUMULATION OF SILICON IN RICE

For Si accumulator, intermediate-type, and excluder plants, three mechanisms of Si uptake (active, passive, and rejective) have been proposed. Rice being a typical Si-accumulator follows an active process for Si uptake and transport (Kaur and Greger, 2019). In the solid phase of soil, Si exist mainly in the form of SiO_2 ranging from 50–70 per cent. The uptake of Si differs between plant species and appears to be dependent on the presence of particular Si transporters. Rice roots have a substantially better capacity for taking up Si than other gramineous species such as wheat, maize, sorghum, barley, and rye. It has been claimed that rice contains a particular absorption system that enhances silicic acid uptake and transport across the plasma membrane (Ma, 2004). Similar to aquaporins, membrane proteins namely Lsi 1, Lsi 2, and Lsi 3 are involved in Si uptake in rice. Lsi 1 act as Si influx transporter protein in rice roots while Lsi 2 is a member of the anion transport family that aids Si uptake from the roots to the vascular tissues (Ma *et al.,* 2007). The root hairs have no discernible role in Si uptake, while lateral roots play the major role (Ma *et al.*, 2001). Lsi 1 transporter protein show their expression only in the main roots and lateral roots but not in the root hairs.

Both Lsi 1 and Lsi 2 are located on the cell membrane. Lsi 2 is located on the proximal side of the membrane and are mostly accumulated in the mature root zone rather than the root tips. Furthermore, Lsi 2 exhibited complete efflux activity for silicic acid rather than influx activity. Expression of another Si transporter, Lsi 6 has been reported in parenchyma cells of rice leaves. Lsi 6 transports silicic acid through the vascular bundle sheath (Ma and Yamaji, 2006). Lack of Lsi 6 expression in the bundle sheath cells has no antagonistic effect on Si uptake, but it may result in silicified depositions on the epidermis and can result in outpouring the flow into the guttation fluid. Three of the above transporter proteins regulates the uptake and translocation of Si in the rice system. Lsi 1 controls the uptake of silicic acid from the soil solution and transports to the exodermis. Then the effux transporter (Lsi 2) transports silicic acid across the aerenchyma. Further transport to aerial parts of the plants is regulated by the influx transporter, Lsi 6 (Kaur and Greger, 2019).

In the plant system Si is translocated in the form of silicic acid [$Si(OH)_4$]. After transport from the root to shoot, silicic acid gets concentrated by loss of water through transpiration and then undergo polymerization. With increasing silicic acid concentration, the Si polymerization process transforms silicic acid to colloidal silicic acid and then to silica gel. This process is aided by loss of water through transpiration. Si thus get accumulated more in aged tissues within the plants as the element is not mobile in plant system. In leaves the deposition of Si occur below the cuticle layer (0.1 micro meter) forming a 2.5 micro meter thick layer and act as a first line of plant defence against various abiotic and biotic stresses (Savant *et al*., 1997). Rice leaf blades have two types of silicified cells: silica cells and silica bodies or silica motor cells. Silica cells are dumbbell-shaped and are found on vascular bundles, whereas silica bodies are found in rice leaf bulliform cells. Cellular silicification progresses from silica cells to silica bodies (Ma and Yamaji, 2006).

BENEFICIAL EFFECTS OF SILICON

Beneficial effects of Si on plants is observed during stress conditions. Silicon has the ability to impart plant resistance mechanisms during multiple abiotic (e.g. Al, Mn, Fe, salt and heavy metal toxicity) and biotic stresses (e.g. pest and diseases) (Savant *et al*., 1997). Various studies have confirmed the effectiveness of Si in controlling many major bacterial and fungal diseases in rice. Silicon also help to alleviate water stress by reducing water loss through transpiration and improves the photosynthetic efficiency by aligning the leaf blades upright and thereby resulting in better light interception. Pronouncing effect of Si on grain yield, in imparting lodging tolerance and in improving reproductive fertility has been reported.

Silica gel is deposited as a silica-cuticle double layer and a silica-cellulose double layer on cell wall of epidermal layer cells of stems, hulls and leaves. Bulliform cells present on the surface of leaves and hulls also have Si depositions. Silicon depositions on the cell walls will result in increased cell wall strength and rigidity, which in turn cause hindrance to the entry of pest and disease and provide lodging tolerance and decreased transpiration (Ma, 2004). These paramount influence of Si on rice makes silicate fertilizer application a suitable practice for improving rice productivity.

1. Alleviation of abiotic stress

Abiotic stress mainly includes chemical stress (salt, nutrient imbalance metal toxicity), physical stress (lodging, drought, high temperature, freezing, radiation, UV) and many others. Silicon is found to alleviate most of these stress conditions in the plant. The basic mechanism underlining these resistance is attributed to be the formation of Si depositions on the cell walls of leaves, stems, roots and hulls. In case of Si deposition in roots, the apoplastic bypass flow gets reduced and thereby providing metal ion binding sites. This results in reduced uptake and transport of toxic metals and salts into the plant vascular system. Similarly, the Si layer also reduces transpiration loss from the cuticle layers, strengthens the cell walls and thereby provide resistance to lodging, high and low temperature stress and resistance to drought. When the plant is subjected to drought and salt stresses Si favours the accumulation of antioxidants in the plants system and induces plant defence mechanisms (Ma and Yamaji, 2006). Other mechanisms of Si-mediated alleviation of abiotic stresses remains under explored. In case of rice five mechanisms are found to underline Si-mediated alleviation of abiotic stresses which includes: (1) co-precipitation or complexation of toxic metal ions with Si, (2) stimulation of antioxidant mediated defence mechanisms in plants, (3) immobilization of toxic metal ions in growth media, (4) regulation of uptake processes and (5) metal ion compartmentalization within plants (Liang *et al.*, 2006).

i. Lodging resistance

Lodging has substantial effect in declining rice yield and productivity. Lodging tolerance can be achieved by increasing the physical or mechanical strength of the rice culm. Silicon is found to improve cell strength, increases structural integrity and rigidity, increases culm thickness, increase the rigidity of rice stalk and provide mechanical strength to the plant (Dorairaj *et al.*, 2017). Increased culm stability and decrease of lodging in rice because of Si was also observed in hydroponic culture experiments. Along with reduction in lodging index, increasing Si levels up to 100 mg kg^{-1} has shown to have positive effects on internode length, culm thickness, increase of breaking resistance, plant height, fresh weight, green leaves, total dry weight and in controlling bending moments in rice (Fallah, 2012).

ii. Drought tolerance

Tolerance to drought stress during high transpiration rates are attributed to Si deposition in the cell walls of culms, hulls, roots and leaves. Increased depositions of Si prevent the compression of xylem vessels under high transpiration conditions while an epidermal cell wall with less silica gel will allow water to escape at an accelerated rate during heat and drought stress. Transpiration loss is also minimized by thick Si cellulose membrane of epidermal tissues. This action is a result of reduction in stomatal pore diameter, consequently, resulting in reduction in leaf transpiration. A reduction in transpiration loss as much as 30 per cent has been reported in rice due to the effect of Si (Agarie *et al.*, 1998). Similar deposition of Si in roots decreases the uptake and translocation of salts and toxic metals by reducing the metal ion binding sites. Several other hypothesis that help to combat drought stresses includes, (a) enhanced K/Na selectivity ratio, (b) increased concentration of soluble substances in the xylem, resulting in limited sodium adsorption (c) increased enzyme activity and (d) improved photosynthetic activity. An increase in antioxidant defence mechanism associated with enhanced Si concentration in the plant also has significant effect in alleviation of drought stress (Meena *et al.*, 2014).

Chen *et al.*, (2011) reported that during drought stress, significant decrease in growth occurred in rice, while exogenously applied 1.5 mM Si significantly increased plant dry matter, leaf water potential and water utilization efficiency (WUE) and increase in photosynthetic rate. Under drought stress, predominant Si accumulation occur in root which results in increased total root length, total root volume, total root surface area and increased root activity. So, Si supply can improve the root traits, enhance absorption of water and thereby imparting drought tolerance to rice plants.

iii. Alleviation of metal toxicity

a) Iron toxicity

Iron (Fe) toxicity occur due to the accumulation of oxidized polyphenols in the plant system. Increased polyphenol oxidase activity in turn increases the oxidized polyphenol levels. Iron toxicity can result in stunted growth, reduced tillering, chlorosis, iron plaque on roots, leaf bronzing and reduced root oxidation power and root elongation. Fe toxicity is widely reported in soils where lowland rice is practiced, where a condition of permanent flooding is observed. Fe toxicity effects persists throughout the growth cycle of the crop (IRRI, 2020).

Under moderate iron toxicity conditions, application Si results in increased activity of antioxidant enzymes like ascorbate peroxidase, catalase and soluble peroxidase (Chalmardi *et al.*, 2014). Such an increase in levels of antioxidant enzymes causes declined lipid peroxidation and greater hydrogen peroxide detoxification. Thus, a reduction in plant Fe concentration through Si fertilization can ameliorate the harmful effects of Fe toxicity. Fe toxicity has major impact on rice root system. Treatment of rice roots with 0.1 mmol L^{-1} Fe^{2+} caused severe necrosis and root distortion (You-Qiang *et al*., 2012). Application of Si to Fe^{2+} solution also decreased the occurrence of reddish iron plaques on the epidermal layers and root hairs.

b) Manganese toxicity

Magnesium (Mn) toxicity is not of major concern in lowland rice and in most of the irrigated rice systems. Generally, aluminium (Al) toxicity is accompanied by Mn toxicity in acidic upland soils were pH is less than 5.5. Mn toxicity symptoms include chlorosis of younger leaves, yellowish brown spots between leaf veins, reduced tillering and stunted plants (IRRI, 2020). Mn toxicity has also be reported to decrease the chlorophyll and carotenoid biosynthesis and thereby resulting in decrease of net photosynthesis (Li *et al.*, 2015).

Application of Si helps to mitigate Mn toxicity by stabilizing the structure of photosystem I, promoting CO_2 assimilation, increasing chlorophyll concentration and by increasing light-use efficiency. Che *et al.* (2016) also reported a decrease in root-to-shoot translocation rate of Mn due to formation of Si-Mn complex.

c) Aluminium toxicity

Aluminium toxicity in soil affects the uptake of several nutrients by plants. Aluminium toxicity induces Phosphorus (P), Calcium (Ca) and Magnesium (Mg) deficiencies to plants. Generally aluminium toxicity has less impact on rice in irrigated conditions. Major effect is mainly observed in acid upland soils (Ultisols, Oxisols) with high levels of exchangeable Al. Aluminium toxicity on rice results in interveinal chlorosis on leaves, scorching of leaf margins, necrosis of leaf tips, yellow to white mottling of interveinal regions, deformed root system and stunted growth of plants (IRRI, 2020).

Singh *et al.* (2011) reported that the symptoms of aluminium toxicity such as chlorosis and dwarfing of leaves can be reduced by the addition of Si. Aluminium treatment decreased the total chlorophyll and carotenoid control compared to its control and in that, chlorophyll was more affected compared to carotenoids. In contrast to this, addition of Si along with Al prevented the reduction in chlorophyll content, but it did not affect the carotenoid content in rice seedlings compared to the Al treatment alone. Silicon mitigated Al toxicity in the upland rice plants by decreasing Al transport to the plant shoots but, it did not reduce the Al uptake rate by roots (Freitas *et al*., 2017).

Pot culture experiment by Nagula *et al.* (2016) showed that foliar application of Si and B was reported to reduce the available Fe in laterite derived rice soils of Kerala. Effects of Fe toxicity in the soil significantly declined with the application of potassium silicate @ 0.5 per cent spray + borax 0.5 per cent. Silicon application improves the air passage from leaves to stem and finally to roots, thereby enhancing the oxidative power of rice roots. Oxidation of iron from ferrous iron to ferric form reduces the toxicity of iron in soil. Both foliar as well as soil application of calcium silicate @ 4 g kg^{-1} soil + borax @ 0.5 g kg^{-1} soil, also decreases the available Mn content of the soil. Similar findings were also recorded with respect to exchangeable Al in the soil, after the application of calcium silicate @ 4 g kg^{-1} soil, helping to mitigate Al toxicity. Foliar application of Si as 0.5 per cent potassium silicate along with borax 0.5 per cent reduced the iron toxicity in the soil in field conditions (Nagula, 2014). Application of calcium silicate 100 kg Si ha^{-1} and borax 10 kg ha^{-1} were proved to be more effective in reducing aluminium and manganese toxicity in the soil.

d) Alleviation of heavy metal toxicity

Toxic elements with relatively high risk of transfer to paddy grains from the soil includes cadmium (Cd) and Arsenic (As). Rice being the major dietary source for these two elements, reducing over accumulation of these elements in rice grain is important for human health and food safety. Toxicity of cadmium (Cd) and Arsenic (As) can leads to totally chlorotic and whitish leaves (Silva *et al*., 2014).

Jia-Wen *et al.* (2013) proposed a hypothetical mechanism of Si mediated heavy metal toxicity by which Si alleviate heavy metal toxicity through the mechanism of tolerance and avoidance. Avoidance mechanism includes increasing the pH of growth media, mediation of root exudate production to chelate heavy metals and regulates metal transporters. Tolerance is attained by restraining ion transport, chelation of metal ions with ligands, homogenising leaf distribution, stimulation of enzymatic and non-enzymatic antioxidants, compartmentation of heavy metals and by creating structural alterations in plants.

Presence of inorganic arsenic with carcinogenic property in rice grain is also a matter of concern regarding global food security. Under anaerobic soil conditions, rice plants efficiently assimilate arsenic in the form of arsenite, which is analogous to silicic acid. So, Si fertilization was found to reduce arsenic concentrations in rice grain by 22 per cent (Meharg and Meharg, 2015). Effect of paddy husk or mixed paddy husk and ash on uptake of As (arsenic) and Cd (cadmium) by rice and their accumulation in rice grain was investigated by Seyfferth *et al.* (2019). Results indicated that soil-incorporation of husk and ash is a promising strategy to decrease the mobility and bioavailability of Cd and As in rice ecosystems.

iv. Salt stress

Salinity stress drastically affects plant growth and development by causing ionic toxicity and osmotic constraints, inhibition of photosynthesis and result in low yield. Higher Na^+ uptake and transportation to shoots results in reduced uptake of other minerals such as K, P and Zn. Silicon application mitigates salt stress in rice through the regulation of osmotic constraints and by the alleviation of ionic toxicity. Ionic toxicity is decreased by reducing Na uptake and its root-to-shoot translocation. Regulation of osmotic constraints is achieved through root morphological changes and maintenance of osmotic potential at cellular level (Guochao, *et al*., 2020). Salt stress also affects rice seedling development and decreases the growth by 22 per cent (Gong *et al*., 2006). Silicon application during saline conditions improves shoot growth and help in maintenance of osmotic stability in plants.

2. Resistance to biotic stress

i. Tolerance to diseases

Rice crop is affected by a wide range of pathogens. Application of Si in paddy soils can reduce the incidence and severity of blast (caused by *Magnaportha grisea*) and other rice diseases such as sheath blight, brown spot, leaf scald and grain discoloration. Silicon impart resistance to these pathogens, mainly through two mechanisms *i.e.*, by acting as a physical barrier and also as a modulator of host resistance. In first mechanism, resistance is achieved through Si deposition beneath the cuticle layer to form a cuticle–Si double layer which act as a physical barrier. This layer mechanically impedes the entry of pathogen such as fungi and, thereby, disrupt the infection process (Fauteux *et al*., 2005). In the second mechanism, Si acts as a modulator of host resistance (Datnoff and Rodrigues, 2005). Here, application of Si to paddy soils and their uptake activates a series of biochemical responses resulting in production of phenolics and phytoalexins in response to fungal infection. Increased levels of these biochemicals strengthens the plant defence reactions, enhancing disease tolerance (Fauteux *et al*., 2005).

Silicon application in the form of calcium silicate and in combination with mercuric fungicides were compared by Datnoff *et al.* (2001). Significant reduction of neck blast incidence by 40 per cent was observed after calcium silicate application while its combination with mercuric fungicide (phenyl mercuric acetate) reduced neck blast by 75 to 90 per cent. Similarly, reduction in brown spot disease severity and decrease in rate of disease progress in rice plants was achieved with propiconazole applications (Datnoff and Rodrigues, 2005). Enhanced tolerance to *Rhizoctonia solani* due to the production of total soluble phenolics, flavonoids, and lignin and high activity of PAL (phenylalanine ammonia-lyase) and PPO (polyphenol oxidase) was also reported by Zhang *et al.* (2013).

ii. Tolerance to pest

There are more than 100 insect species are associated with the rice crop at one stage or the other, of which 20 are pests causing major economic loss. Silicon application enhances resistance to major pests such as brown plant hopper, green leaf hopper, stem borer, mites, and stem maggots (Ma, 2004). Silicon deposition in the plant tissues is attributed to act as a mechanical barrier against chewing and probing by insects. Silicon application also induces resistance to herbivore feeding habits two main resistance mechanisms including physical and chemical defences. In the case of physical defence, Si in plant system is deposited mainly as opaline phytoliths which causes increased hardness and abrasiveness of plant tissues, thereby reducing the digestibility. Soluble Si in rice plant also triggers chemical defences wherein production of defensive enzymes and enhanced release of plant volatile compounds counteracts insect herbivore attack (Reynolds *et al*., 2009).

Silicon fertilization in the form of Silixol granules at 37.5 kg ha^{-1} (along with 100% recommended dose of fertilizers) during critical stages such as tillering and flowering stages can reduce the per cent incidence of white ears (symptom of leaf folder) and dead heart (symptom of stem borer) in rice (Jawahar *et al.,* 2015). Silicon deposition in rice plant causes damage of mandibles of rice stem borers and the presence of silicic acid in plant sap inhibits the activity of the brown plant hoppers (Yang *et al.,* 2017). Wenqiang *et al.* (2015) also proposed a non-pesticide BPH management by treatment of susceptible plants with high Si solution. Silicon has pronounced impact in reducing feeding rate by BPH, in reducing population growth rates and in extending population doubling time in BPH (Yang *et al*., 2017).

CONCLUSION

Rice being a Si accumulator, Si nutrition and its management can play vital role in abiotic and biotic stress mitigation. In general, highly weathered soils of the tropics and subtropics are low in available Si mainly due to leaching process. The application of Si improves increases nutrient absorption capacity, agronomic performance and yield response quality in rice. Silicon primarily stimulates the production of secondary metabolites, protection of the photosynthetic machinery, ion homeostasis, antioxidant machinery, and the chelation of harmful metals. Si modifies the plant cell wall and controls gene expression. Thus si-amended rice crop show the ability to withstand or tolerate biotic and various abiotic stresses caused due to Al, Fe, and Mn soil toxicity and salinity. In short, application of Si in soil is necessary for both optimized soil fertility and improved plant nutrition.

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