RESEARCH ARTICLE

Harnessing silicon to bolster plant resilience against biotic and abiotic stresses

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Silicon (Si), though not traditionally considered essential for plant growth, exhibits profound benefits in enhancing crop yields and resilience to abiotic stresses. Its application, particularly in combination with other fertilizers, has demonstrated significant improvements in various crops, including sugar beet, potato, rice, sugarcane and canola. Silicon strengthens cell walls, bolstering resistance to pests and diseases while mitigating the impacts of environmental stressors such as drought, salinity and mineral deficiencies. This multifaceted role extends to radiation-induced injuries, where silicon supplementation has shown promise in mitigating damage and facilitating faster growth recovery in plants. Additionally, silicon deposition in plant tissues, particularly in leaves and hulls, contributes to reduced transpiration rates and enhanced membrane integrity, crucial for combating drought and climatic extremes. Furthermore, silicon alleviates chemical stressors like phosphorus deficiency and toxicity, as well as heavy metal toxicity, through various mechanisms including modulation of metal uptake and distribution. Its role in enhancing salt stress tolerance by decreasing transpiration and improving antioxidant activities underscores its potential in salt-stressed plants. Notably, silicon's beneficial effects vary across plant species, with genetic modifications aimed at enhancing root Si uptake abilities offering promise for widespread application. Overall, silicon emerges as a valuable growth regulator, enhancing plant growth and resilience to stressors, thereby offering significant potential for sustainable agricultural practices. Future research should focus on evaluating silicon's efficacy across a broader spectrum of crops and stress conditions to unlock its full potential in agricultural systems.

Key Words: *Silicon; Plant resilience; Biotic stress; Abiotic stress; Crop productivity*

INTRODUCTION

Silicon, the second most abundant mineral in the Earth's crust, primarily exists as H_4SiO_4. Despite not being classified as an essential mineral for plant growth, its application has been shown to enhance yields in various crops [1]. For instance, combining calcium and silicon foliar fertilizers has proven beneficial for sugar beet production, increasing both biological and sugar yields. Studies have demonstrated that silicon application can significantly boost yields in crops such as potato, rice, sugarcane and canola. Additionally, increased silicon doses have been linked to improved leaf structure. Silicon's role in strengthening cell walls enhances plant resistance to pests and diseases across a range of crops including wheat, rice, maize and vegetables [2,3]. Moreover, silicon aids in mitigating the effects of environmental stresses, such as deficiencies in manganese, cadmium, arsenic, aluminum, zinc and phosphorus, while also bolstering resistance to lodging, diseases and insects [4].

Furthermore, silicon enhances plant resilience to abiotic stresses like drought and salinity. It affects the nutrient composition of plants like sunflowers by increasing the accumulation of both macro and micronutrients. Silicon's presence within plant tissues, particularly in the endoplasmic reticulum, cell walls and intercellular spaces, contributes to overall growth and fertility [5]. Notably, silicon forms complexes with polyphenols, supporting cell wall structure and mitigating the toxic effects of heavy metals. Its presence in specialized cells like bulliform and dumbbell cells strengthens cell walls, enhancing resistance to diseases, pests and lodging, particularly in crops like rice.

Silicon's role as a dynamically active component in activating natural defense mechanisms has been recognized. The mechanisms of silicon transport in plants, particularly in silicon accumulators like rice, have been extensively reviewed. Silicon uptake occurs mainly as monosilicic acid in soil solution, followed by accumulation on the epidermis of various tissues as hydrated amorphous silica. Despite not meeting traditional criteria for essentiality, silicon has been reconsidered as essential due to its role in preventing abnormalities in plant growth and performance. Beneficial effects of silicon include increased photosynthetic activity, enhanced resistance to pests and diseases, reduced mineral toxicity, improved nutrient balance and increased tolerance to drought and frost. These effects vary among plant species and are more pronounced under stress conditions. Overall, silicon stands out for its ability to enhance plant resistance to multiple stresses.

MATERIALS AND METHODS

Fortifying the plant kingdom: How silicon combats abiotic stress

Silicon and physical stresses: Silicon has been identified as a potential protector of plants against radiation-induced injuries. Ma et al., [6] demonstrated that when rice seedlings were subjected to gamma-ray irradiation, those supplied with silicon exhibited a lesser decrease in dry weight compared to silicon-deficient plants, suggesting that silicon enhances rice resistance to radiation stress. Moreover, post-radiation treatment with silicon facilitated faster growth recovery in rice plants compared to those without silicon supplementation. Drought stress, characterized by stomatal closure and subsequent reduction in photosynthetic rates, poses significant challenges to plant growth. However, silicon has shown promise in alleviating water stress by reducing transpiration rates. Ma et al., [6] reported that silicon deposition beneath the cuticle of rice leaves forms a double layer, potentially decreasing transpiration through the cuticle by up to 30%. Interestingly, the beneficial effects of silicon on rice growth were more pronounced under water-stressed conditions compared to non-stressed conditions. Additionally, when rice leaves were exposed to Polyethylene Glycol (PEG), a solution mimicking drought stress, electrolyte leakage from leaf tissues decreased with higher silicon levels, indicating potential membrane protection conferred by silicon [7].

Furthermore, silicon's role in cell water relations, including mechanical properties and water permeability, has been implicated. Leaves containing silicon exhibited higher levels of polysaccharides in the cell wall compared to silicon-deficient leaves, suggesting a link between silicon and cell water dynamics. This association between silicon and water stress alleviation extends to yield components, particularly the percentage of ripened grains in rice and barley, with silicon potentially mitigating water stress effects on grain development.

Silicon deposition in the hull of rice and barley grains, forming a Cuticle-Si double layer, plays a crucial role in reducing transpiration from spikelet's. This deposition maintains a high moisture condition within the hull, which

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is essential for spikelet development, especially under water deficiency and adverse climatic conditions. Seo et al., [8] highlighted the importance of maintaining high moisture levels within the hull for normal spikelet development, with silicon content in rice hulls reaching as high as 7% and 1.5% in barley, respectively. In addition to drought stress, silicon has been shown to alleviate damage caused by climatic stresses such as typhoons, low temperatures and insufficient sunshine during the summer season. Ma et al., [6] demonstrated that silicon deposition in rice enhances stem strength by increasing culm wall thickness and vascular bundle size, thus preventing lodging-a common consequence of typhoon attacks. Moreover, silicon deposition on the hull helps prevent excess water loss from spikelets, reducing sterility caused by strong winds during typhoons. Silicon's positive effects extend to heat stress tolerance in rice plants, as observed by Agarie et al., [7], who noted reduced electrolyte leakage in silicon-supplemented leaves exposed to high temperatures. This suggests silicon's involvement in maintaining thermal stability of cell membrane lipids, although the precise mechanism remains unclear.

Overall, silicon emerges as a multifaceted ally in enhancing plant resilience to various abiotic stresses, including radiation, drought and climatic extremes. Its ability to modulate transpiration, improve membrane integrity and strengthen plant structures underscores its potential as a valuable tool in agricultural practices aimed at mitigating the adverse effects of environmental stressors on crop productivity.

Silicon and chemical stress: Phosphorus (P) deficiency in soil is a global issue. Numerous plants, including rice and barley, have been shown to benefit from silicon under P-deficiency stress. Early findings from a lengthy field trial at Rothamsted experimental station revealed that, in the absence of P fertilizers, barley output was higher in a field altered with Si than in a field without Si application. Si supply increased the dry weight of rice shoots more at a low P level (14 f.LM) than at a medium level (210 f.LM) in an experiment with a nutrient solution. These advantageous effects of Si were previously thought to be caused by either increasing P availability in soil or partially substituting Si for P. Subsequent tests, however, revealed that Si had no effect on the availability of P in soil. The P fixation capacity of a P-deficient soil was unaffected by the addition of silicic acid at different doses in the past. Various silicic acid concentrations did not desorb phosphorus fixed. The soil solution contains silicon in the form of silicic acid, which does not dissociate at pH values lower than 9. Consequently, the possibility of silicic acid and phosphate (an anionic form) interacting in soil is low. In both soil and solution culture, the Si supply at a low P level had no effect on the uptake of P [9]. On the other hand, the Si-treated plants showed a considerable drop in iron (Fe) and Manganese (Mn) uptake. Plants redistribute and translocate phosphorus in an inorganic form. Due to P's strong affinity for metals like Fe and Mn, the concentration of Mn, Fe and other metals may have an impact on P's internal availability at low P concentrations. Consequently, the increased availability of internal P due to the reduction of excess Fe and Mn uptake may be responsible for the greater favorable effect of Si on plant growth under P deficient stress. The finding that the availability of Si accelerated the rate of P translocation to the panicles in rice lends support to this [10]. Although excessive P stress is uncommon in natural soils, it has been noted in nutrient solution cultures that get high P concentrations or in certain greenhouse soils that have had extensive P fertilizer application. Leaf chlorosis or necrosis is caused by excess P, most likely as a result of the reduced availability of vital metals like Zinc (Zn) and Fe. By reducing the excessive intake of P, silicon can mitigate the harm caused by P excess by lowering the internal concentration of inorganic P. When the concentration of P in the medium is high, the reduced uptake of P may be caused by silicon deposited on the roots and/or Si-induced reduction of transpiration. Many plant species have been reported to have Si deposited in their endodermal cells, which may form apoplastic barriers that prevent P from moving radially across the root [11]. Certain Si non-accumulating plants, such as tomato, soybean, strawberry and cucumber, whose roots also deposit Si, have also shown the Si-induced reduction of P uptake.

Applying nitrogen fertilizers is a crucial technique for raising crop productivity. But too much N leads to lodging, mutual shading, illness susceptibility and other issues. As mentioned previously, silicon deposited on the stems and leaf blades inhibits lodging and mutual shadowing. Si application in the field greatly reduces the incidence of blast illness, particularly when Nitrogen (N) application is heavy. In agriculture systems with dense planting and strong N application, these functions of Si are particularly significant. Brown rice's high protein content is another result of over applying nitrogen fertilizers, which degrades the grain's quality. Rice may effectively produce low-protein rice if it receives a sufficient quantity of silicon (Figure 1).

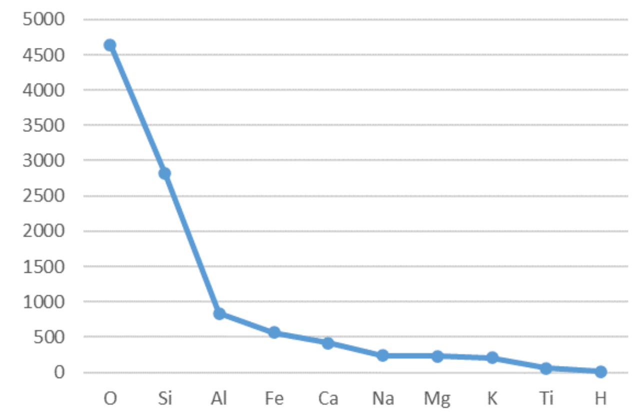

Figure 1) *Elements in the earth's crust*

RESULTS AND DISCUSSION

Si has been shown to have a mitigating effect on Mn toxicity in hydroponically grown rice, barley, beans and pumpkin. The involvement of three distinct systems appears to vary according on the kind of plant. Si decreased Mn absorption in rice by enhancing the roots ability to oxidize Mn. Si caused a uniform distribution of Mn in the leaf blade of barley and beans instead of lowering Mn uptake. Si was discovered to cause a reduced apoplasmic Mn content in cowpea, despite the fact that the mechanism underlying this homogenous distribution is still unknown. This finding suggests that Si alters the cell wall's ability to bind cations. Nevertheless, more recent research conducted by the same group has suggested that the Si-enhanced Mn tolerance in cowpea was also facilitated by soluble Si maintaining the apoplast in a decreased condition. Evidence demonstrating a negative link between the apoplastic Si concentration and the expression of Mn toxicity, but no correlation between the apoplastic Mn concentration and Mn toxicity expression, supports this. Si concentrations in Apoplastic Washing Fluid (AWF) were found to be negatively correlated with the activity of Apoplastic Guaiacol Peroxidase (POD). Silicon appears to have an impact on the POD-mediated oxidation of excess Mn *via* interacting with phenolic compounds during the apoplast's solution phase. On the other hand, in pumpkin, Si led to a localized build-up of Mn near the base of the trichomes. In this plant, Si had no effect on Mn uptake either. Reducing the toxicity of Fe excess in rice was another benefit of silicon. Rice roots oxidative capacity was increased by silicon, which led to a greater oxidation of iron from ferrous iron to insoluble ferric iron. Thus, administration of Si indirectly inhibited excess Fe absorption. Excessive Fe stress does not harm upland plants. Zn and Si coexisted in the cytoplasm of heavy metal-tolerant *Cardaminopsis halleri* cultivated on soil contaminated with Zn and Cadmium (Cd) [12]. It was found that Zn-silicate degrades slowly to SiO_2 and serves as a temporary storage compound for the metal. After then, zinc is translocated into the vacuoles where it accumulates in an unidentified way. It has been proposed that Zn-silicate production may mitigate Zn toxicity in *Cardaminopsis* and is a component of the heavy metal tolerance mechanism.

In rice, wheat and barley, the positive effects of silicon under salinity stress have been documented. For three weeks, exposure to 100 mM Sodium Chloride (NaCl) hindered the growth of rice shoots and roots by 60%; however, the addition of Si greatly reduced the damage caused by salt. Si addition reduced the concentration of Na in the shoot by around half. This effect of Si may be attributed to the reduction in transpiration caused by Si as well as the partial obstruction of the transpiration bypass flow, which is the route through which a significant amount of the Na uptake in rice happens. In barley, Si increased the leaf superoxide dismutase activity and suppressed the lipid peroxidation caused by salt stress and stimulated root H+ -ATPase in the membranes, suggesting that Si may affect the structure, integrity and functions of plasma membranes by influencing the stress-dependent peroxidation of membrane lipids, although these effects may be indirect. In many review and research articles, it was emphasized that water status of leaf and water-use efficiency of crops are increased by silicon application in many salt-stressed plants. Silicon application can improve antioxidant activities such as Superoxide Dismutase (SOD), Ascorbate Peroxidase (APX), Dehydroascorbate (DHAR), Guaiacol Peroxidase (GPX), Catalase (CAT) and Glutathione Reductase (GR) under salt stressed conditions. When the effects of silicon on cereals evaluated in terms of abiotic stress, application of silicon enhances plant growth in wheat under salt stress conditions [13]. Silicon application causes greater adaptation and, it alleviates salt stress, enhances chlorophyll content and photosynthetic activity in salt-stressed maize [14-17]. Although reports on the effects of silicon on dicots are very few, it was shown that silicon was effective to prevent salt stress in sunflower [13]. The effect was attributed to an increased antioxidant activity. Under salt stress, silicon may enhance the physiological traits and growth of cowpea and kidney beans [17,18]. In acid soils, one among the main factors limiting crop productivity is al toxicity. Root development and nutrient uptake are inhibited by ionic Aluminum (Al). Si has been shown to have an ameliorative effect on Al toxicity in sorghum, barley, soybean, rice and teosinte. Si supplementation as silicic acid considerably reduced Al-induced reduction of root growth in a maize experiment. As the concentration of Si increased, the alleviative impact became increasingly noticeable. It was discovered that adding silicic acid reduced the concentration of harmful Aluminum Phosphate (AP+). These findings imply that Si and Al interact in solution, most likely through the creation of non-toxic AI-Si complexes. Other theories, however, have also been put forth to explain the mitigating effect of Si. These include the plant's cytoplasm, the coding position of Al with Si, the impact on enzyme activity and indirect effects. Plant species differ in how much Si reduces Al toxicity, most likely as a result of variations in their tolerance to Al and/or in the mechanisms at work.

The positive impacts of Silicon (Si) under stressful conditions are depicted in Figure 2 [19]. It's evident that Si's beneficial effects primarily manifest through its deposition on leaves, stems and hulls, with the extent of effect correlating with Si accumulation in shoots. However, Si accumulation in shoots varies significantly across plant species, with most unable to accumulate high Si levels. This discrepancy in Si accumulation is attributed to differences in root Si uptake abilities. While soil Si abundance is prevalent, many plants, especially dicots, lack the capacity to absorb substantial Si from the soil, thus not reaping Si benefits. To enhance plant resistance to various stresses, one strategy involves genetically modifying Si uptake capabilities. Rice, known as a Si-accumulating plant, offers insight into Si uptake mechanisms, potentially informing genetic modifications to enhance root Si uptake abilities. Recent findings indicate that Si uptake in rice roots involves a transporter with low silicic acid affinity [19]. Rice's superior Si uptake ability likely stems from the absence of this transporter in other plants. Isolation and characterization of a rice mutant deficient in Si uptake offer promise in identifying the transporter gene, a pursuit underway in research laboratories.

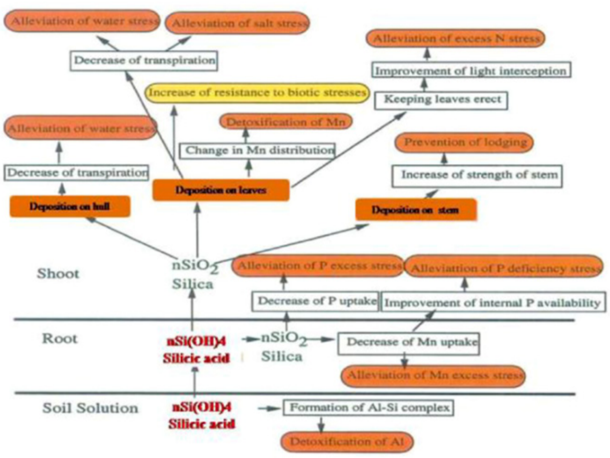

Figure 2) *Beneficial effects of Silicon (Si) under various stresses*

CONCLUSION

Silicon exerts multifaceted effects on plant physiology, with significant focus on the cell wall. Incorporation of silicon into cell walls bolsters their strength, salinity resistance, drought tolerance and photosynthetic activity. It fosters root and foliage growth and combats oxidative stress through antioxidant enzyme activation. Application of exogenous silicon effectively mitigates various biotic and abiotic stress responses by enhancing plant water uptake and transport. Additionally, silicon plays a pivotal role in ameliorating soil conditions, further reducing stress-induced damages. Hence, silicon emerges as a potential growth regulator to enhance plant growth and resilience under stress conditions. Applied research is warranted to assess water use efficiency, drought tolerance and resistance to diseases and pests across a broader range of crops.

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