

Silicon's Role in Improving Plant Salinity Tolerance

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ABSTRACT

Salinization is a main abiotic stress that affects crop growth and productivity all over the world, thus how to improve the resistance levels of crops to salinity has attracted worldwide attention. Silicon (Si) is the second most prevalent element in the earth's crust. When the solution pH is below 9, silicon is absorbed by higher plants in the form of silicic acid $[\text{Si}(\text{OH})_4]$. Although silicon has not been considered as essential element for higher plant, it is generally considered to be a 'beneficial element'. A number of studies have shown that silicon can increase plant resistance to multiple abiotic and biotic stresses, including drought, salt stress, heavy metal toxicity, freezing, and plant diseases.

INTRODUCTION

Salinization is a main abiotic stress that affects crop growth and productivity all over the world, thus how to improve the resistance levels of crops to salinity has attracted worldwide attention^[1]. Silicon (Si) is the second most prevalent element in the earth's crust. When the solution pH is below 9, silicon is absorbed by higher plants in the form of silicic acid $[\text{Si}(\text{OH})_4]$ ^[2]. Although silicon has not been considered as essential element for higher plant, it is generally considered to be a 'beneficial element'^[3]. A number of studies have shown that silicon can increase plant resistance to multiple abiotic and biotic stresses, including drought, salt stress, heavy metal toxicity, freezing, and plant diseases^[2-3]. In early years, studies suggested that silicon mainly exerts its protective action via the formation of a physical barrier by precipitating as SiO_2 and being incorporated into biological structures^[2]. With the in-depth research, more and more studies suggest that silicon also active involve in physiological and biochemical processes in plants^[4,5].

One important role of silicon is its alleviation effect of salt stress in plants, which has been reported in various species, including rice, barley, wheat, cucumber, tomato, and *Cicer arietinum*^[6-11]. Till now, investigations about the exact modulating mechanism(s) of silicon to plant physiology have been reported at both physiological and molecular (e.g. genomic and proteomic) levels, which significantly advanced our knowledge about the silicon in plants.

Three different modes of silicon uptake have been proposed for plants, that is, active, passive, and rejective uptake. Silicon transporters play important roles in silicon uptake and have been identified in both monocotyledon (e.g. rice, barley, maize, wheat) and dicot (e.g. pumpkin, cucumber)^[12-21]. The ability of plant to take up silicon may affect plant stress resistance ability^[22]. Therefore, more work is needed to investigate the silicon uptake and distribution in different plant species.

Salt stresses usually hinder plants growth in two ways: (i) osmotic stress that limits the water availability for plants and affects water status; and (ii) ion toxicity that disturbs essential biochemical reactions through impairing enzyme activities and protein functions^[23-24]. Most previous studies have focused on the mediation effect of silicon on ion balance under salt stress. To be specific, silicon application can decrease Na^+ uptake and its transport from roots to shoots and makes Na^+ being more evenly distributed over the whole root section^[25]. Besides, silicon affects the uptake of some other essential nutrients (e.g. Ca, K,

and N) to alleviate competition between salt ions and other essential nutrients uptake ^[2]. Most recently, studies suggested that polyamines may participate in the alleviation effect of silicon under salt stress through regulating Na⁺/K⁺ ratio ^[26].

DISCUSSION

Recently, more and more researchers showed that, under salt stress, silicon could improve plant water status through enhancing root water uptake and its transport to leaves, which mitigate ion toxicity by a dilution effect. In wheat, the alleviative effects of silicon have been found to be more pronounced in the osmotic stress phase than ion toxicity phase ^[23]. Besides, silicon-mediated up-regulating of aquaporin gene expression and silicon-induced accumulation of compatible solutes like soluble sugars play important roles in increasing water uptake ^[5,26].

Salt stress leads to the formation of reactive oxygen species (ROS) that seriously disrupt normal metabolism ^[24]. Silicon application alleviates oxidative stress by regulating the antioxidant defense and decreasing the production of ROS ^[9]. Meanwhile, silicon could ameliorate the damage of photosynthetic apparatus and pigment induced by salt stress and contributes to the improvement of the photosynthetic performance ^[27]. Salt stress inhibits photosynthesis through causing the accumulation of photosynthetic assimilates in the leaves and decreasing assimilates export to the roots. In cucumber, silicon has been reported to decrease the soluble sugar levels in leaves and increased starch content in the roots, which could alleviate photosynthetic feedback repression and provides more energy storage in the roots under salt stress condition ^[4]. However, the mechanisms by which silicon alleviates salinity stress via regulating carbohydrate metabolism need a deeper investigation in different species.

The molecular mechanism for silicon-mediated salt tolerance is still not very clear. Omics-based technologies, including transcriptome and proteome, provide a powerful tool to understand the mechanisms by which silicon alleviates environmental stresses at the molecular level. Transcriptome and proteome studies reveal that silicon could regulate the response of plants against salt stress through modulating the expression of transcription factors and hormone-related genes and the translation of associated protein ^[28,29]. Besides, there may be a crosstalk between silicon and signaling molecules including ethylene (ET), salicylic acid (SA), and polyamines (PAs) ^[30,32]. These researches empowered us the insight understanding about the alleviation mechanisms of silicon to environmental salinity stress, both at the physiological and molecular level.

CONCLUSION

In the future, the regulation effect of silicon on polyamines metabolisms and aquaporin expression need to be further experimentally tested. Sugars can function as compatible solutes, immediate substrates for intermediary metabolism, as well as signaling molecules in controlling metabolism, stress resistance, growth, and development in plants ^[24,33]. Thus further experiments are needed to reveal the specific mechanisms that silicon regulating carbohydrate metabolism. Meanwhile, molecular mechanisms of the alleviation effect of silicon under environmental stresses still needs to be investigated in more detail at the genomic, transcriptomic, epigenetics, proteomic, and metabolomic levels.

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