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REVIEW

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Functions of silicon and phytolith in higher plants

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ABSTRACT
Silicon (Si) is abundant in the lithosphere, and previous studies have confirmed that silicon plays an important role in plant growth. Higher plants absorb soluble silicon from soil through roots which is deposited in plant tissues mainly in the form of phytoliths. Based on previous studies, the research progress in silicon and phytoliths in the structural protection, enhancement on photosynthesis and transpiration of plants and plant growth and stress resistance was reviewed. Meanwhile, gaps in phytolith research, including phytolith morphology and function, impact of diverse environmental factors coupling with phytoliths, phytolith characteristics at different stages of plant development and phytoliths in regional vegetation are identified. The paper intends to promote the wider application of phytolith research findings and provides reference for further research on phytoliths.

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Introduction

Silicon is the second richest element in the earth's crust, and it is one of the key elements in the cycle of earth's materials[1]. Silicon is absorbed by higher plant roots as soluble silica ($Si(OH)_4$) which was transported to different parts of the plant system through the vascular system. After a series of physiological and biochemical activities, it is silicified as phytoliths in various plant organs in specific forms depending on protocells and intercellular spaces[2–4]. Phytoliths are ubiquitous in the leaves, branches, shoots, flowers, fruits, stems and roots of higher plants. They are the main form of silicon in higher plants, accounting for more than 90% of total silicon in plant[5,6].

Due to the unique advantages of phytoliths, viz., wide spread presence, high temperature and corrosion resistance, morphological stability and in situ sedimentation, the phytolith analysis is irreplaceable and widely used in botany, zoology, archeology, geology, paleoecology, pedology, medicine and agriculture. Silicon research has expanded as an Earth-life science superdiscipline[7]. Phytoliths have attracted increasing attention in recent years, mainly involving plant morphology classification[8], plant community productivity[9], wildlife feeding habits[10], early evolution of plants and animals[11], topsoil phytolith analysis[12], stratum confirmation[13], evidence of forest and grassland fire history[14], reconstruction of ancient vegetation and environment[15], propagation routes of cultivated plants[16] and the origin of crops[17]. Based on previous research, this paper mainly summarized the positive effects of silicon and phytoliths on plant growth and physiological functions. In addition, the research trends and issues of the relationship between phytoliths and plants were summarized, which can provide a valuable reference for future research on phytoliths.

Structural protection function of silicon and phytoliths

Phytoliths play a structural protective role in plants. The sessile and almost immobile characteristics of plants make them in a passive state when being vulnerable to insects, herbivores or pathogens. The whole life of plants is fraught with crises, which directly affect their survival, forcing them to exhibit various unique survival strategies to cope with the adverse environment and predators to achieve the purpose of gaining advantages and avoiding disadvantages[18,19]. The expansion of grassland and the evolution of herbivores have also accelerated the evolution of phytoliths, and their co-evolution has formed a complex positive feedback network[20]. Silicon and phytoliths play a multitude of significant roles in plant and global ecology[21].

A large number of phytoliths produced significantly improve the mechanical stability of plants. Phytoliths exhibit better structural support performance than carbon-based compounds[22] which contributed to develop erect and hard defensive plant structures such as stems, branches and leaves through complex biochemical pathways[23]. Silicon deposition increases the number of phytoliths on the surface of stems, which significantly increases the cell wall thickness of stem sclerenchyma[24]. In the leaves of Gramineae plants, a large number of phytoliths are closely arranged, which better protect the vascular tissues of leaves and significantly enhance their

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resistance[25]. The uptake and accumulation of silicon by plants also affects the properties of plant communities and ecosystems, and thus affecting ecological functions and response to environmental changes[26].

In addition, phytolith has a relatively high hardness, which is even higher than that of enamel. It can wear the mouthparts of insects and the teeth of herbivores and increase their feeding pressure on plants in terms of food cost and digestion difficulty[10,27]. This effect of phytoliths in plants treated with higher silicon concentration is more obvious[28]. Another anti-herbivory defensive mechanism of silicon is the use of sharp silica needles. The needlelike phytoliths enter the tissues of herbivores through the oral cavity and digestive system, bringing in microscopic pathogens (bacteria, fungi, viruses) and causing infections and cancer. Internal micro spines can wound large herbivores, insects and other small herbivores[29–31]. Thus, silicon and phytoliths in plant tissue can act as a defense against vertebrate and invertebrate herbivores[32].

When plants are damaged to a certain extent by insects or herbivores, a large number of phytoliths are produced to resist the damage[33]. Structures such as micro hairs, bristles and hook hairs on the leaf epidermis of plants are frequently silicified. Hair density and hardness are used as physical defenses to directly "resist" herbivores, slow down or prevent the invasion of fungi and other pathogenic bacteria, and greatly enhance the ability of plants to resist erosion[34,35].

Generally, the deposition of phytoliths in vascular bundle and other conducting tissues and lignified cell wall in plants greatly enhance their mechanical strength and physical properties, decrease the mouthfeel of herbivores in feeding, thereby effectively reducing or avoiding the damage by herbivores and enhance the ability of plants to resist biotic and abiotic stresses in different ways.

Silicon and phytoliths enhance plant photosynthesis and transpiration

Photosynthesis and transpiration responsible for biomass production and overall growth and development are the most important physiological processes in plant. However, they are very sensitive to changes in environmental factors[36]. Silicon and phytoliths sustain normal photosynthesis and transpiration of plants under changing environment[37]. They regulate plant growth and physiological processes through photosynthesis and transpiration to alleviate the effects of stress on plants.

Exogenous silicon application increases the absorption and accumulation of silicon in plants, promotes the absorption of nutrient elements such as nitrogen, phosphorus, kalium, etc., thickens leaves and stems to enhance the average weight and significantly increases the chlorophyll concentration in leaves and the leaf arrangement, which has a positive effect on intercepting light energy, thereby improving the photosynthetic rate of rice, wheat, sugarcane, banana, cucumber, amaranth and other crops[38–41]. Wang et al.[42] found that the application of silicon fertilizer increases the volume of chloroplasts in mesophyll cells and increases the lamellar structure and grana of rice, which is conducive to the progress of photosynthetic phosphorylation, reduces the concentration of intercellular CO_2, delays the decline in chlorophyll content in rice, and increases the photosynthetic rate and stomatal conductance. The research of Detmann et al.[43] supported the above viewpoint. They found that the application of exogenous silicon in the reproductive growth stage of rice increased the photosynthetic rate, attributing to nonstomatal limitation. The increase in silicon enhanced the leaf thickness, chloroplast surface area and mesophyll cell wall thickness, thus enhancing mesophyll conductance and promoting photosynthesis. Avila et al.[44] found that silicon supplementation reduced the effects of water deficiency on leaf potential, instantaneous carboxylation efficiency and morphometry of the root system by increasing root growth, thus reducing the adverse effects of drought on photosynthesis. Silicon has been observed to ameliorate abiotic and biotic stresses in plants through gene regulation and interacting with other physiological processes to improve photosynthesis, such as absorption of macro and micronutrients, and phytohormones which also influence photosynthetic activity[45,46].

Silicon protects rice from overtranspiration under the stress conditions. Rice absorbs silicon and accumulates around the epidermis to form a special structure, which affects the permeability of plant tissues, reduces water loss from the epidermis. It precipitates in plant tissues and organs, responding to environmental stimulation in the form of stomatal movement to reduce transpiration and water evaporation on the plant surface[47–49]. Silicon deposition in the cell wall forms cuticle double layer in the epidermis of leaves; meanwhile, the stomatal conductance is reduced through the modification of the cell wall and reduces the transpiration of stratum corneum to improve the water status of plants under drought stress[50]. The application of exogenous silicon also significantly reduces the transpiration rate of maize under drought stress, and with the extension of stress time, the transpiration rate gradually decreased[51]. The silicon absorbed by plants is deposited in cell walls, which prevents plant tissue cells from swelling and cracking due to excessive water absorption and stabilizes the osmotic pressure of plant tissue cells to a certain extent. Meanwhile, the phytoliths formed by silicon deposition in plants contain water, which increases or decreases in response to environmental changes, thus playing a passive role in storing and regulating the water in plants[52].

Silicon promotes plant growth and fruit quality

The imperative role of silicon in triggering plant development has been identified. It is pivotal in regulating overall physiological and metabolic characteristics of the plants[53]. The yield of rice is significantly reduced due to the lack of silicon during its growth[54–56]. Supplementing silicon promotes the growth of rice roots, increases rooting sprouting (by 20%–30%), enhances the root vitality (by 1.12–1.13 times)[57,58] and prolongs the functional period of roots to avoid premature senescence. In addition, silicon supplementation increases the number of mitochondria in cells, which is conducive to oxidative phosphorylation, thus increasing the respiration rate and the content of ATP (adenosine triphosphate) in roots, and improving the absorption of water and nutrients by roots[59]. Some studies also show that silicon promotes cell elongation, significantly increases the length and cell wall extensibility of leaf epidermal cells, and promotes the growth of rice seedlings. Silicon supplementation increases the number of phytoliths on the surface of plant stems, which thickens vascular bundles, and increases the cell wall thickness and leaf thickness of stem sclerenchyma[60,61]. Silicon spraying on rice leaves activates and releases available soil nutrients, significantly increasing the total nitrogen content in rice leaves and the total phosphorus content in rice stems, sheaths, leaves and panicles, as well as the rice grain quality, e.g. the aspect ratio, brown rice rate and protein content[62]. Silicon enhances the nitrogen distribution in plants efficiently, reducing the nitrogen content in stems and leaves but increasing the nitrogen content in panicles, so as to promote the formation of fruits and seeds[63]. Through complex physiological and biochemical processes, silicon increases rice yield by increasing its height, root size, vascular bundle number in stems, leaf weight and nutrient content[64–66]. Silicon also affects the growth of wheat. Silicon promotes the germination of wheat, improves the activities of various enzymes in seed, and promotes the transformation of nutrients and development of wheat embryos[67]. In the growth stage of wheat seedlings, silicon application increases the root length, plant weight and chlorophyll content, enhances plant growth and development and increases the spike length, spikelet number and grain number to different degrees, thus increasing the wheat grain yield[68]. It also improves the tensile properties of wheat dough evaluated from dry and wet gluten content, flour water absorption, dough breaking time and other processing quality indicators[69]. Silicon application not only increases the photosynthetic pigment, biomass and growth of wheat but also improves the grain quality and yield[70]. Moreover, silicon application plays a positive role in the growth of wheat in all types of soil[71].

In addition, Suriyaprabha et al.[72] found that the silicon absorbed by maize roots was carried and accumulated in leaves and other parts of maize, which increased the total protein content in the maize leaves and significantly enhanced the absorption of trace elements (copper, iron, manganese, zinc, etc.), so as to improve the growth potential of maize. Pei et al.[73] found that foliar application of nanosilicon fertilizer promoted the absorption and utilization of nitrogen, phosphorus, potassium and other nutrient elements in amaranth, increased the chlorophyll content in leaves, and enhanced photosynthesis, thus promoting the growth of amaranth; The fresh weight, dry weight, biomass and soluble sugar content of amaranth were obviously increased, thus increasing the yield of amaranth (by 11%–31%). Zhang[74] found that silicon fertilizer application significantly increased the plant height and yield of tomato (*Solanum lycopersicum*), increased the soluble sugar and vitamin C content, but decreased the organic acid content in tomato fruit. Fitiyani and Haryanti[75] also reported that the growth potential of tomato seedlings treated with nanosilicon fertilizer was obviously improved, and the plant height, number of new leaves, root length and other indicators were significantly higher than those of the control. Gong et al.[76] applied silicon fertilizer to *Achnatherum extremiorientale* seedlings and found that the root length, plant height, fresh weight and relative water content of the seedlings were significantly increased. Alsaeedia et al.[77] found that silicon promoted the absorption of nutrient elements such as nitrogen and potassium by cucumber plants and regulated the cell ion and osmotic balance, thus not only retarding the damage caused by salt and alkali on cucumber seedlings but also promoting growth and increasing cucumber yield.

Silicon and phytoliths improve the abiotic and biotic stress resistance of plants

Plants may survive through various stress factors, including biological stresses viz., pests and diseases caused by both fungi and bacteria in different plant species, and abiotic stresses viz., temperature stress, water stress, light stress, metal toxicity, and soil salinization, etc. Previous studies have shown the beneficial effects of silicon for plant growth, particularly under stress conditions[78]. Silicon can alleviate the adverse impact of different abiotic and biotic stresses by different mechanisms including morphological, physiological, biochemical and genetic changes.

Silicon enhances the resistance to biotic stresses. Previous studies have shown that the improved mechanical strengthening of the plant as a result of silicon fertilization, thus directly improving plant constitutive defense ability against various folivores, borers, phloem and xylem feeder pests[79], including stem borer, brown planthopper, rice green leafhopper, and white-backed planthopper[80], greenbug *Schizaphis graminum* (Rondani)[81], *Thrips palmi* Karny[82], *Myzus persicae*[83], *Scirpophaga incertulas* (Walker)[84] and Asian citrus psyllid[85], etc. Silicon is as effective as conventional fungicides in resisting diseases. Under the condition of increasing silicon supply, the occurrence of stem rot, sheath brown rot, cucumber Fusarium wilt, crown spot disease, grain discoloration, gray leaf spot, dollar spot and brown patch besides rice blast and powdery mildew can be reduced[86]. Silicon is as effective as conventional fungicides in resisting diseases. Under the condition of increasing silicon supply, besides rice blast and powdery mildew, it can also reduce the occurrence of stem rot, leaf sheath brown rot, cucumber wilt, crown spot, grain discoloration, gray leaf spot, dollar spot and brown spot. The reduction in disease symptom expression is due to the effect of silicon on some components of host resistance, including incubation period, lesion size, and lesion number[87]. Silicon has also been proved to be mediated by signaling pathways during plant–pathogen interactions, viz., ET (ethylene), JA (jasmonic acid), SA (salicylic acid) and/or ROS (reactive oxygen species) (Ghareeb et al., 2011). Induced biochemical/molecular resistance stimulates the production of antibacterial compounds, regulates the complex signal pathway network, and activates the expression of defense-related genes to improve plant resistance[88]. The temperature regulation of silicon mainly acts on transpiration. It regulates the water use efficiency and thereby improving the drought resistance and high-temperature resistance of plants. Meanwhile, under high-temperature stress, silicon increases the diameter of pollen grains of rice and makes the anthers of crack normally, thus ensuring the fertilization rate and seed setting rate of rice flowers[89]. In the absence of silicon, the probability of rice suffering from rice blast is greatly increased[-90]. Silicon fertilizer application to cucumber effectively inhibits the probability of plant suffering from powdery mildew[24]. Silicon also significantly improves the resistance of plants to drought. Silicon application reduces the MDA (malondialdehyde) content and relative electric permeability of rice roots under water stress, thus increasing the stability of the plasma membrane of plant roots. Silicon application also inhibits the production of peroxide, enhances the antioxidant capacity of plant roots, and alleviates the degradation of ABA (abscisic acid) in plant root cells. Under the water stress, silicon weakens the influence on the physiological activity of plant roots and maintains certain activity of roots[51,91]. Silicon in sugarcane can reduce both freezing injury and water stress[92]. In addition, salt stress is the major threat for plant growth worldwide, and many studies have explained the regulation mechanism of silicon to alleviate salt stress from physiology, molecular genetics and genomic approaches[93]. Silicon inhibits the transport of soil salt to the aboveground parts, thus enhancing the salt tolerance of plants to a certain extent[94].

The relationship between silicon and other elements is synergism and antagonism. On the one hand, silicon promotes the absorption and utilization of the vast majority of nutrients or beneficial elements by plants[39,95,96]. On the other hand, silicon has an antagonistic effect on toxic and harmful elements and heavy metals to inhibit or reduce their harm to plants[97–99], and to some extent resists the adverse effects of radioactive elements (strontium, cesium, cadmium, etc.) on plant growth[100,101]. There is an interaction between silicon and phosphorus. Silicon promotes the absorption of phosphorus by plants, and silicate promotes the release of phosphorus in soil, thus improving the bioavailability of phosphorus[102]. The relationship between silicon and calcium is very close but complicated. Different plant species, soil components, ecological environments, etc., affect the content of silicon and calcium with significant variation[103]. Increasing the silicon absorption in plants reduces the stress of excessive iron and manganese. Silicon oxidizes iron and manganese ions in the roots of plants and turns them into hard-to-absorb deposits adhering to the surface of plant roots[104,105]. Silicon reduces the bioavailability of aluminum by adjusting the pH and absorbing silicic acid, thus reducing the toxicity of aluminum[106]. Silicon also precipitates heavy metals in plants, and improves the hardness of plants. Silicon promotes the precipitation of heavy metal ions in plants or precipitates in the form of silicate complexes, so as to reduce the concentration and mobility of active heavy metal ions in plant tissues. Moreover, silicon reacts with heavy metal ions in the outer cortex cells of plant roots to produce insoluble heavy metal salt complexes attached to the surface of roots, preventing the upward transportation of heavy metals in plants, thus weakening the damage of heavy metals to plants[97,107].

Summary and prospect

The silicon and phytoliths play a positive role in plant. They protect and support plant development by enhancing mechanical structure and their ability to resist herbivores and pathogens, adjusting the intensity of photosynthesis and transpiration and promoting the utilization of beneficial elements in soil by plants. They also inhibit the toxicity of heavy metals and alleviate the stress of soil salinization. Silicon reduces the damage to plants caused by water, temperature, light, air pollution and radiation and secures the transportation of water and nutrients, achieving physiological balance in plants from various aspects. Silicon enhances the ability of plants to resist biotic and abiotic stresses from different ways, thus promoting the growth and development. As an independent branch of micropaleontology, phytoliths provide a new perspective for extensive phytolith research. Gaps in the research on the relationship between silicon, phytoliths and plants remain to be filled:

(1) Different plants produce different morphotypes of phytoliths, and the phytoliths in different organs of the same plant species also differ. The morphotypes of phytoliths reflect the structure and function of plants to some extent. The development mechanism of phytoliths is worth exploring, viz., morphology, structure, and function of phytoliths in different life stages of plants.
(2) The responses of plants to different environmental factors differ. More attention needs to be addressed to the research of phytoliths in live plants and the variation of phytoliths type, size and yield from the perspective of single or complex environmental factors such as temperature, light, water and soil, etc.
(3) The demand for silicon differs in various stages of plant development. Systematic research on the silicon demand for plants at different development stages may provide practical support for crop cultivation, intensive agricultural production and the development of silicon fertilizers.
(4) Regional vegetation has different abilities to resist different biotic and abiotic stresses. Research on the physiological mechanism of silicon and phytoliths in plants, particularly the vegetation in ecologically fragile areas and its response to different stress may contribute to shaping the conservation strategies for vegetation restoration.

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