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The Role of Silicon in Strawberry Production

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Abstract

Silicon (Si) is among the most abundant elements in the Earth's crust, although most of it is in an insoluble form. Si is regarded as a beneficial nutrient for its ability to alleviate abiotic and biotic stress. Soluble Si plays a role in improving strawberry (*Fragaria x ananassa*) water use efficiency, activating defense enzymes, releasing volatile compounds, and developing resistance to powdery mildew and mite feeding. Si has also been implicated in the regulation of stomata closure, enhancement of drought tolerance, and mitigation of harmful reactive oxygen species produced under stress. Si fertilization has resulted in higher yield and fruit quality. Despite the documented role of Si in plant functioning defense and the existence of several genes involved in uptake and efflux, Si is not considered an essential element. However, as growers attempt to better control the growing environment through hydroponics, greenhouses, and enclosed structures, increased attention to this element is warranted.

Silicon is the second most abundant element in the Earth's crust. It is most readily available to plants via. the soil solution as a silicic acid—$Si(OH)_4$ (Epstein, 1994). Silicic acid is an uncharged monomeric molecule that is most readily assimilated by plants when the soil pH is below 9 (Ma and Yamaji, 2006). In most plants, including strawberry, Si travels to the Casparian strip through the roots (Naseer et al., 2012). Within the Casparian strip of the exodermis and endodermis, the complementary gene types *Lsi*1 (an NIP2 aquaporin homolog) and *Lsi*2 (an Ars-B complex) are responsible for the influx and efflux of $Si(OH)_4$, respectively (Ma and Yamaii, 2006; Wang et al., 2021). Both Lsi1 and Lsi2 were recently identified in strawberry (Ouellette et al., 2017). *Lsi*1 encodes a membrane protein which performs similarly to aquaporins and allows for $Si(OH)_4$ to enter the symplast via the plasma membrane. The protein encoded by *Lsi*2 is located on the proximal side of root cells. In the exodermis, *Lsi*2 facilitates Si movement into the apoplast from the symplast with active transport (Yamaji and Ma, 2011; Coskun et al., 2021).

Expression of Lsi1 and Lsi2 is dependent on the amount of internal soluble Si in the plant and externally on the soil solution (Ma and Yamaii, 2006). Once the Si passes through the Casparian strip, it is loaded into the xylem for transport throughout the plant as silicic acid. Upon reaching the shoots vascular tissue, the silicic acid is converted to a colloidal silic gel, and then to silica gel (SiO2 • nH2O) before it reaches the leaves (Ma and Yamaji, 2006). The recent identification of the transport gene *Lsi6* controls the movement of Si into the leaves from the xylem (Wang et al., 2021). Si is dependent on the xylem for movement in the plant, but is independent of transpirational flow (Gao et al., 2006). Si movement in the phloem is heavily constrained, however (Raven, 1983).

Functions of Si in plants

Si is involved in activating defense-related enzymes and regulating the complex network of signal pathways (Wang et al., 2017). It is responsible for controlling phytohormone homeostasis during stress, as well as priming the plant defenses to induce resistance (Wang et al., 2017). These are vital processes for plants to acclimate to a new environment by medi-

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ating growth, development, source/sink portioning and nutrient allocation (Fahad et al., 2015, Wang et al., 2017).

Si influences powdery mildew resistance. While all strawberry growers face pressure from powdery mildew (PM) (*Podosphaera aphanis*), greenhouse and high tunnel strawberry producers are at an even higher risk than those producing in the field (Pertot et al., 2007). While PM is most prominent outdoors in the field during the late summer/early fall for ever-bearing (day neutral) strawberries, the fungus presents a year-round problem for greenhouse producers (Ouellette et al., 2017). Without proper management, PM has the potential to decrease photosynthesis by disrupting the Calvin cycle along with chlorophyll synthesis, as evident in barley and cucumber (Scholes et al., 1994; Abo-Foul et al., 1996).

Si is responsible for the activation of plant defenses and is thought to impede the inoculation of fungi by one of the following mechanisms: 1) Si is mechanically deposited beneath the leaf cuticle or on the tissue surface as a mechanical barrier to inhibit the systemic penetration of fungal spores through the leaf (Samuels et al., 1991) and/or 2) Si activates several defense compounds, such as lignin, phenolic (secondary) compounds and phytoalexins (Ma and Yamaii, 2006), in addition to kinases, peroxidases and pathogenesis-related transcripts (Zargar et al., 2019). The exact mechanism between soluble Si and plant biochemical pathways related to disease resistance remains unknown (Ma and Yamaii, 2006).

Recent studies have explored the use of Si as a method to control PM in strawberries. Liu et al. (2020) reported that strawberries grown on a commercial farm in raised beds that were amended with Si via fertigation had less severe incidence of PM relative to the untreated control. Given Si's role in activating plant defenses, the researchers found that Si applications benefitted the strawberry plants to a greater extent when the severity of the disease was greater, and the most effective suppression of the disease came when Si was amended with a commercial fungicide. Kanto et al. (2006) obtained similar results when they treated field-grown strawberries with a potassium silicate fertilizer and observed that Si was most effective in reducing the overall severity of the PM infections as opposed to preventing their incidence completely.

Ouellette et al. (2017) found that applications of soluble Si fertilizers in a high tunnel setting greatly increased the Si content of strawberries. Generally, the Si content of strawberries is approximately 0.3% dry weight (Moradtalab *et* al., 2019) but Ouelette et al. (2017) reported much higher levels. The uptake of Si made the berries highly resistant to PM in high tunnels.

Kanto et al. (2004) found that strawberries grown hydroponically in 25 $mg \cdot l^{-1}$ K_2SiO_3 had greatly reduced severity of PM infections, and strawberries grown in 50 $mg \cdot l^{-1}$ were completely free of PM. The researchers speculate that the decrease in the infection incidence is due to an increase in leaf thickening with increasing levels of Si application. Wang and Galletta (1998) observed similar results when they foliarly applied potassium silicate to strawberries and measured decreased levels of PM. Variation in response to Si application by cultivar or species would be expected since leaf characteristics vary among genotypes. *F. chiloensis*, for example, has a much thicker cuticle than *F. ovalis* which is associated with a far greater resistance to PM infection (Kanto et al., 2004), and cultivars vary in the amount of *F. chiloensis* in their ancestry.

Si can reduce impacts from pests. There is some evidence that Si applications are effective against two spotted spider mites (*Tetranychus urticae,* TSSM). TSSM feed on over 1,100 plant species worldwide and can be problematic for strawberry growers (Bensoussan et al., 2016). The arthropod tends to interfere with plant growth and development by spinning webs over the leaf surface and reducing the photosynthetic capacity of the plant and crop yield (Livinali et al., 2014). Ribeiro et al. (2021) found the parental generation of TSSM had a shorter preoviposition, oviposition, and longevity when strawberry plants were treated with K_2SiO_3. In the F1 generation, the duration of the egg phase was longer in plants treated with nano-silicate particles relative to those treated with K_2SiO_3, and the larva phase duration was also longer in nano-silica plants in relation to the control. The delay of the pest's development could potentially be due to the increased leaf thickening and decreased palatability from Si application (Moraes et al., 2005). This would delay TSSM feeding ability and result in the increased larval stages. Liu et al. (2020) also reported decreased incidence of TSSM in plants fertigated with 70-80% (w/v) tetraethyl silicate. The average number of TSSM per strawberry leaf was two to three times greater in the untreated control than in the Si treatments in 2014 and more than three times greater in 2015.

Si also impacts plant-herbivore relationships through the modification of herbivore-induced plant volatiles where the parasitoids *Trathala flavo-orbitalis* and *Microplitis mediator* were more attracted to Si-treated rice (*Oryza sativa*) (Liu et al., 2017), suggesting that Si applications may have indirect benefits for plant production. Another report suggests that Si supplementation has proved effective in reducing the presence of fall armyworm [*Spodoptera frugiperda* (J. E. Smith)], causing high rates of mortality in the early stage of larvae (Ul Haq et al., 2022). Nevertheless, more research is required to understand the mechanism of Si in predator-prey dynamics as Si could be an environmentally friendly application in field settings (Deshmukh et al., 2017).

Si can mitigate the effects of abiotic stress. Strawberries under water stress often have decreased leaf area, chlorophyll content, net photosynthesis rate, and stomatal conductance, but foliar application of K_2SiO_3 can mitigate the transpiration rate and improve the water use efficiency (Dehghanipoodeh et al., 2018).

Applying Si, along with inoculating the strawberry plants with arbuscular-mycorrhizal fungi (AMF), improved the relative water content in leaves by increasing the capacity for water uptake that, in turn, allowed the maintenance of a high stomatal conductance and photosynthetic capacity for supporting growth and dry matter production (Moradtalab et al., 2019). Roots amended with both Si and AMF had increased levels of organic osmolytes, suggesting that this combination led to an increased influx of water into the root system (Moradtalab et al., 2019).

Si can increase salinity tolerance. Si plays a crucial role in alleviating salinity stress in strawberries. High levels of NaCl exposure caused necrosis, leaf burn and nutritional imbalances in strawberry leaves, resulting in decreased fruit yield and quality and increased rates of plant mortality (Avestan et al., 2019). The epicuticular wax layer (EWL) on strawberry leaves prevents water loss and serves as a barrier to abiotic stress (Jenks and Ashworth, 2010; González and Ayerbe, 2010). Since Si was linked with EWL formation, foliar application of the element as a nanoparticle has the potential to reduce salinity stress (Avestan et al., 2019). Strawberry plants growing in Si-amended soil had greater EWL than controls; the largest difference occurred at 100 $mg{\cdot}L^{-1}$ SiO_2 before flowering and 50 $mg{\cdot}L^{-1}$ after the flowering stage. Si nanoparticles reduced the relative water loss and improved the membrane stability index of strawberries grown under salinity stress, linking Si to improved water use efficiency in strawberry. The reinforcement of the cuticle layer is thought to lead to decreased leaf transpiration as the silica layers form a physical blockade through cell thickening (Wang et al., 2021).

Proline is often used as an indicator of salinity stress because it accumulates when the stress is applied (Hayat *et al*., 2012). Strawberries amended with Si had lower proline levels relative to the control plants; there was also a negative correlation between proline and the EWL. Root growth improved in strawberries amended with Si nanoparticles and this also contributed to improved water use efficiency (Avestan et al., 2019). The application of Si nanoparticles enhanced strawberry fruit set and yield as well. Strawberry plants amended with 100 mg·L^{-1} SiO_2 before flowering and 50 mg· L^{-1} after the flowering stage displayed the highest fruit set, and strawberry plants treated with SiO_2 nanoparticles had higher yields than the control (Avestan et al., 2019).

Si affects antioxidants. Reactive oxygen species (ROS) produced in plant leaves under stress have the potential to negatively impact plant metabolism (Muneer et al., 2017). Si application, in the form of K_2SiO_3 has been shown to activate enzymes involved in the antioxidant system such as superoxide dismutase, which effectively converts superoxide to hydrogen peroxide (H_2O_2) and then to water by ascorbate peroxidase and catalase (Muneer et al., 2017). Si is most effective when applied foliarly as K_2SiO_3 or when it is integrated into the dripline to scavenge ROS during extreme temperature stress. Park et al. (2018) found that the application of Si increased the expression of two superoxide dismutase isozymes during the plant's exposure to salt stress. They also confirmed that K_2SiO_3 is the most effective form of Si fertilizer. Catalase enzymes also were up-regulated in the presence of salinity-stressed strawberries amended with Si (Park et al., 2018).

Si fertilization can enhance yield and fruit quality. Foliar forms of supplemental Si increased the marketable yield, fruit size and firmness of strawberries (Weber et al., 2018; Ouellette et al., 2017). Potassium silicate applications in hydroponic solutions also increased yield and fruit firmness (Miyake and Takashi, 1986). Strawberries (cv. Paros) subject to Si-fertilization regimes showed increased levels of phenolic compounds. Pathways that synthesize phenolic acids–gallic acid, caffeic acid, chlorogenic acid, and ellagic acid–and pathways that produce flavonols and flavanols were both upregulated in plants amended with Si (Hajiboland et al., 2018). When plants were exposed to heat stress, the total sugar and anthocyanin concentration of Si-fertilized plants was higher than those not treated with Si (Weber et al., 2018). While Si supplementation can help strawberry cultivars reach their genetic potential, major changes in carbohydrate, enzyme activity, and secondary metabolite profiles are dictated by genotype (Topcu et al., 2022).

Despite some of the clear benefits associated with supplementing strawberry fertilizers with Si, some abnormalities have been reported, particularly the induction of albinism. Albinism was reported when the rate of soluble Si in the water source or nutrient solution was high (Lieten et al., 2002). Whether this is due directly to Si or an artifact of increased K and/or N is disputed. In albino fruit, the N:Ca ratio and K:Ca ratio tends to be higher relative to normal fruit (Sharma et al., 2006). Jun et al. (2006) also reported incidence of albino fruit in hydroponic solution when they applied over 200 mg·l^{-1} of K_2SiO_3. While considering these claims, Ouellette et al. (2017) refuted the notion that Si supplementation could directly result in albino fruit in strawberry. If growers use supplemental Si fertilizers, care should be used to avoid the induction of albinism from imbalances in nutrients.

Conclusion

Evidence suggests that Si is a critical element for optimal functioning of strawberry plants. Si fertilization can directly impact fruit size and quality, and indirectly enhance yield by mitigating abiotic and biotic stress. Both hydroponic and field-grown strawberry plants can benefit from regulated applications of Si, especially as it relates to the control of powdery mildew. Optimal application rates of appropriate forms of Si need to be determined for different production systems and the cultivars involved. Several associated underlying molecular mechanisms of Si functioning remain to be elucidated.

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