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REVIEW

Silicon fertilization as a sustainable approach to disease management of agricultural crops

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Abstract

Silicon (Si) is the second most abundant element present in the lithosphere, and it constitutes one of the major inorganic nutrient elements of many plants. Although Si is a nonessential nutrient element, its beneficial role in stimulating the growth and development of many plant species has been generally recognized. Silicon is known to effectively reduce disease severity in many plant pathosystems. The key mechanisms of Si-mediated increased plant disease resistance involve improving mechanical properties of cell walls, activating multiple signaling pathways leading to the expression of defense responsive genes and producing antimicrobial compounds. This article highlights the importance and applicability of Si fertilizers in integrated disease management for crops.

Keywords: plant disease management, silicon fertilization, sustainable agriculture

Introduction

Silicon journey from soil to plant cells

Silicon makes up 28% of the Earth's crust, by mass, and after oxygen it is the second most abundant element found in the Earth's hard outer layer (Epstein *et al.* 1994). The silicon content in soil ranges from 1 to 45% dry weight (Sommer *et al.* 2006). Silicon is released into soil through the weathering of silicate minerals, the biogeochemical cycle or by being recycled through vegetation. Factors that affect Si distribution in the soil include parent material, climate, vegetation, texture, pedogenesis and intensity of weathering (Hallmark *et al.* 1982). Silicon deficiency can occur in strongly weathered or acidic soils (Nanayakkara and Uddin 2008).

Plants can absorb Si in the form of silicic acid [H_4SiO_4], which is present in the soil as an uncharged monomeric molecule below pH 9 (Ma and Yamaji 2015) with the concentration in soil varying from 0.1 to 0.6 mM (Epstein *et al.* 1994). Approximately 0.1–10% of shoot dry weight in plants can consist of Si. Some plant families e.g. Poaceae, Equisetaceae and Cyperaceae, show high Si accumulation (>4% Si) (Currie and Perry 2007). According to Matichenkov and Calvert (2002), around 210 to 224 million tons of Si are adsorbed by plants and removed from cultivated areas annually. Among the Si accumulators in the Poaceae family, sugarcane (*Saccharum officinarum* L.) showed the highest rate of Si absorption (300–700 kg of Si · ha^{-1}), followed by rice (150–300 kg of Si · ha^{-1}), and wheat (50–150 kg of Si · ha^{-1}) (Barker and Pilbeam 2007).

Silicon is taken up by plants via the transpiration stream (i.e., passive uptake), however, active silicon uptake is exhibited by some plant species such as rice *Oryza sativa* L. In rice plants, Si is taken up by the root system through a NIP group of the aquaporin family transporters called low Si 1 (Lsi1), which are involved in the Si influx. The efflux transport of silicon is carried out by putative anion Si transporters called low

Si 2 (Lsi2). The Lsi1 and Lsi2 are involved in passive and active transport of Si, respectively (Ma and Yamaji 2015). Homologous proteins to the Lsi1 channel proteins have been identified and characterized in other plants (Vatansever *et al.* 2017). The various capabilities of plant species in Si uptake can be associated with Si transporters that differ in their expression levels in the cells and localization in plant tissues (Chiba *et al.* 2009).

Following the uptake of monosilicic acid (H_4SiO_4) by the roots, Si is transported from the roots to the shoots. It is then deposited into plant cell walls, middle lamellae and intercellular spaces of cells and bracts in the form of amorphous silica gel ($SiO_2 \cdot nH_2O$) (Kim *et al.* 2002). The presence of Si in cell walls and its firm linkages with the cell wall matrix are revealed by inductively coupled plasma mass spectrometry (ICP-MS) and X-ray photoelectron spectroscopy (XPS), suggesting the crucial role of this nutrient element in maintaining cell integrity (He *et al.* 2013). Silicon polymerization occurs if the concentration of silicic acid exceeds 2 mM, leading to precipitation of amorphous silica particles called phytoliths (Ma and Yamaji 2006). It has been shown that soil Si application was consistently more effective than foliar treatments in plant Si uptake in wheat plants (Shahrtash 2017). This might be in the light of the fact that Si transporters (Lsi1 and Lsi2) are mainly expressed in the root system.

The role of silicone in plant resistance

Silicon mode of action in plant cells

A wealth of studies has shown that Si supplementation increases plant tolerance to biotic and abiotic stresses. Silicon has been shown to contribute to cell wall reinforcement through silicifying epidermal cell walls and acts as a physical barrier against fungal penetration. It has been suggested that Si enhances not only plant cell-wall rigidity but also cell wall elasticity during cell expansion.

Silicon mediated cell wall fortification is not the only mechanism involved in Si-mediated plant disease resistance. Several reports indicate that Si supplementation significantly decreased the level of malondialdehyde (MDA), an indicator of oxidative stress, in plant cells under biotic or abiotic stress (Mohsenzadeh *et al.* 2011). Cherif *et al.* (1994) indicated that less infection with *Pythium* spp. following Si treatment was due to higher activity of defense enzymes such as peroxidase (POD), β-1,3-glucanase, and chitinase in cucumber plants. Silicon application increased the accumulation of plant defense metabolites leading to Si-induced resistance which has similarities with systemic acquired resistance (SAR) (Fawe *et al.* 1998). The difference between known SAR and Si-induced resistance is the fact that following the withdrawal of the Si supplement, Si starts to polymerize in the cells and cannot play a role as an inducer of defense responses (Fauteux *et al.* 2005). However, SAR lasts for a longer period of time. Silicon treatment increased phytoalexins in cucumber (*Cucumis sativus* L.) plants infected by powdery mildew (*Podosphaera xanthii*, Castagne) (Fawe *et al.* 1998). Silicon may reduce disease severity through other modes of actions. Silicon supplementation increased the production of phenolic compounds and phytoalexins (Shetty *et al.* 2011). Wheat plants infected with *Blumeria graminis* DC f. sp. *tritici* showed papilla formation, production of callose and production of glycosilated phenolics following Si treatment (Bélanger *et al.* 2003). It was shown that Si induces resistance to rice brown spot by impairing the production of ethylene as the virulence factor of the fungus *Cochliobolus miyabeanus*, the causal agent of the rice brown spot disease (Van Bockhaven *et al.* 2015).

Most common silicon fertilizers

Foliar and soil Si fertilizers are commercially available. The most common Si sources are calcium silicate materials which are the by-products of metallurgical smelting processes. They contain varying percentages of Si, have liming potential and positive effects on correcting soil acidity (Shahrtash 2017). Another commonly used Si fertilizer is wollastonite, which is a natural calcium silicate. Although silicate slags are cost-effective, they often contain only a small proportion of easily soluble Si compared to wollastonite. Torlon *et al.* (2016) observed that wollastonite was effective in reducing powdery mildew severity in pumpkin (*Cucurbita pepo* L.). Application of silicon fertilizers such as calcium silicate slag and wollastonite reduced gray leaf spot (*Magnaporthe oryzae* B.C. Couch) incidences and severity in perennial ryegrass (*Lolium perenne* L.) suggesting that the material may be considered in integrated management programs (Nanayakkara and Uddin 2008). It has been reported that Si soil amendments such as wollastonite and silicate slag (280 kg · ha^{-1}) were consistently more effective than foliar application of Si (4,000 ml · ha^{-1}) in reducing wheat leaf rust (*Puccinia triticina* Eriksson) disease development under tropical conditions (Shahrtash 2017). Scanning electron microscopy (SEM) images of silica body distribution at leaf epidermal regions of wheat plants treated with different Si fertilizers are shown in Figure 1. Each image shows the relative %Si at 400× magnification (A–D) The leaf %Si in control, wollastonite, slag, and foliar-applied silicon in wheat plants was 0.36%, 0.95%, 0.78% and 0.50%, respectively (Shahrtash 2017).

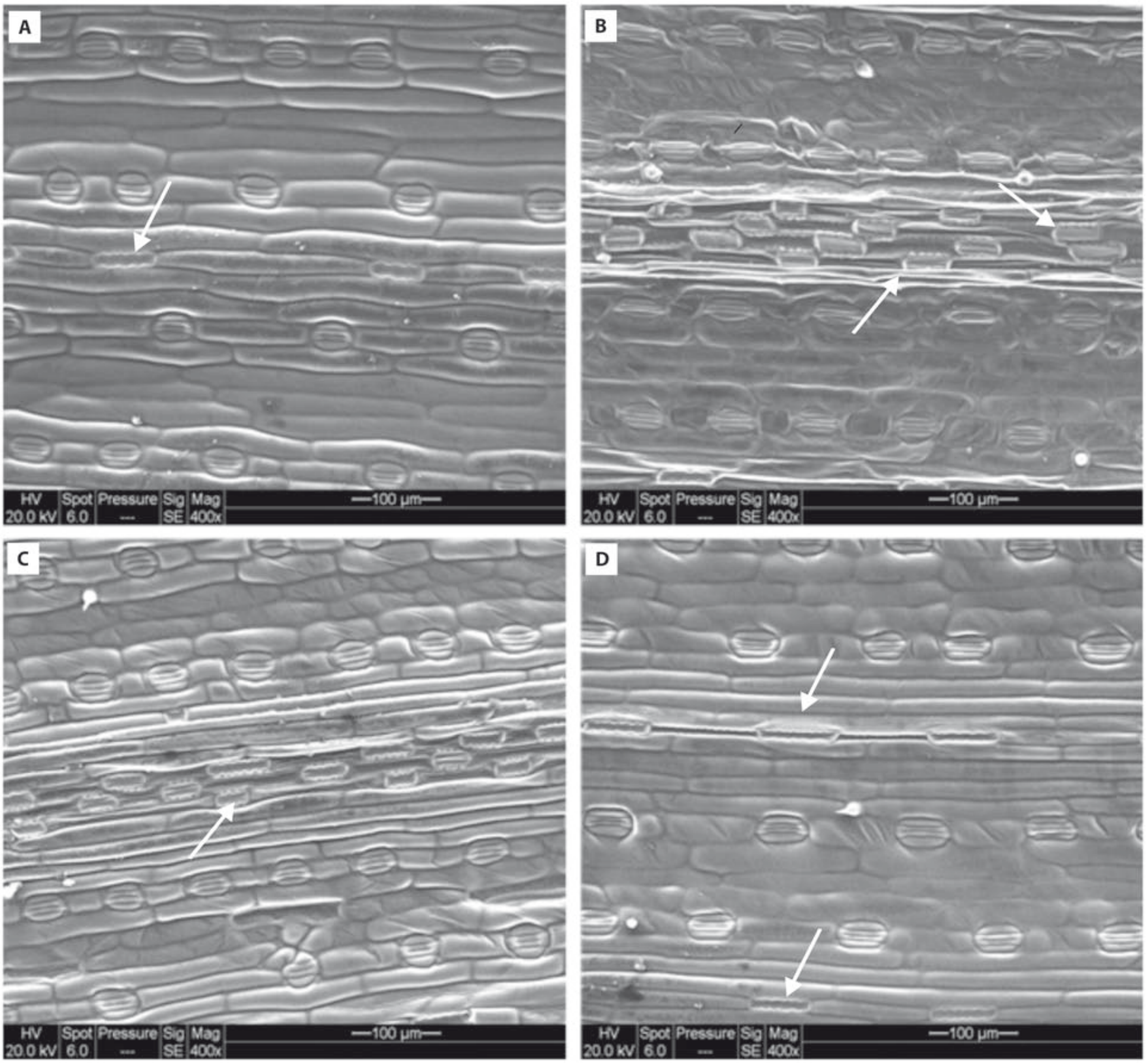

Fig. 1. Scanning electron microscopy of wheat leaf epidermal cells at 400× magnification. Arrows indicate the zigzag margin of silicified cells distributed among epidermal cells. (A) control plants, (B) wollastonite treated plants, (C) slag treated plants, (D) plants with foliar application of silicon (Si)

Conclusions and future perspectives

Plant diseases are considered to be major constraints in crop production and environmental health. Safety issues are among the biggest concerns in management practices using chemicals. Sustainable agricultural approaches focus on agronomic practices to improve production with minimal detrimental impact on the environment and on reducing chemical input. The beneficial effects of Si supplementation on plant growth, and plant resistance to pests and pathogens are widely accepted. A substantial number of studies reported the protective role of Si against plant fungal penetration through cell wall fortification and the triggering of induced systemic resistance (ISR) pathways. Since Si soil amendments exert priming in plants, and there has not been any report of negative effects of their application on the environment, they can be considered as an eco-friendly and cost-effective strategy to improve crop health. In the context of foliar application of Si and improved disease resistance, although there has been no report confirming that the influx of Si is carried out through the epidermal transporters, the potential role of Si as signaling molecules to stimulate pathogen recognition receptors (PRRs) certainly needs to be investigated. In-depth molecular investigation on a wide variety of crops will be helpful to elucidate the minimum concentration of Si that can trigger defense responses in each crop. Also, future research needs to look at Si fertilizer application rates and how those rates change soil chemistry and fertility.

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