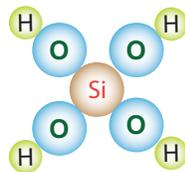


## The Importance of Silicon Nutrition on Plants

*Silicon is a bioactive element associated with a number of beneficial effects on the physical (mechanical) and physiological properties of plants. Silicon possesses very unique biochemical properties that allow the element to participate and influence a large number of diverse functions and processes in plants. The general body of research on silicon in plants indicate that its impacts of soil and plant function are the result of multiple combined effects rather than one single effect.*

Current research suggests that the beneficial effects of silicon (Si) are more universal among plant species than originally thought. Indeed, seven of the ten most important crops are now considered to be Si accumulators. Silicon has been found in grasses to an even greater extent.

There is a general agreement that the majority of benefits associated with silicon in plants initiate with the uptake of dissolved silicates from the bulk solution -- the most important of which is  $H_4SiO_4$  (orthosilicic acid).



Following absorption by the roots, upward movement of monosilicic acid in the xylem is transferred to the shoots. Transpiration has been identified as the primary force regulating transport and deposition of Si in plant shoots. Silicon is transported within the plant in its monomeric water soluble form, but can quickly polymerize into amorphous silica particles (phytoliths) via condensation reactions.

Silicon's functionality within plants is complex and multi-faceted but is generally associated with **mechanical protection** (by the polymerization of silicic acid) and its **ability to influence the timing and extent of plant defense responses** (via alteration of gene expression) and indirectly from **changes in cell responses**.

### Plant Mechanical Protection

The phytoprotective role of Si and the mechanisms of biosilicification in plants have been extensively reviewed and published. Its protective effects include the alleviation of abiotic / biotic stress damages and heavy metal toxicity.

Silicon has been shown to interact with several components of cell walls and provides increased mechanical support to the aerial parts. It has become clear that the organic environment of the cell wall, with its vast range of cellulose, pectin, hemicellulose and structural protein components, is

### CELL WALL POLYMERS

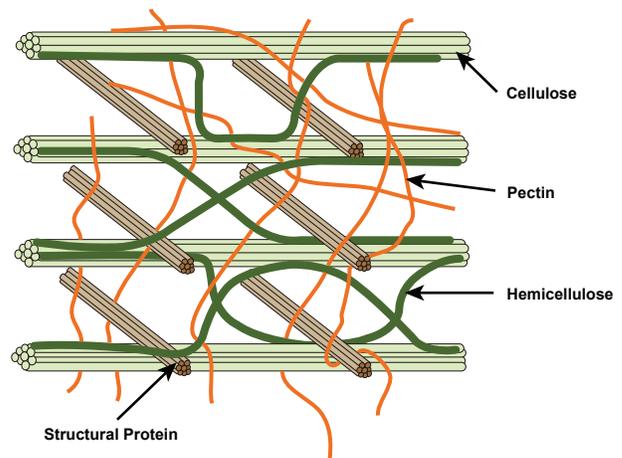


Illustration of plant cell wall polymer matrix

likely to play a fundamental role in the cell wall biosilicification process -- assisting in the "templating" of silicate placement, polymerization (via Si-O-C bonds) and cross linking within the cell wall polymer matrix.

It has been suggested that cell wall polysaccharides (non-cellulosic) such as callose might contribute to a sequestering of amorphous silica particles. Lignin has also been identified as a sequestering agent for Si polymers in plant cell walls.

Amino acids with positively charged side-chains can associate with the negatively charged silica species via electrostatic interactions, thereby favoring biosilicification.

The polymerization of monomeric silicic acid to form larger silica particles proceeds through various condensation reactions. The overall effect is a strengthening of the cell walls by increasing the length of macromolecule filaments and increasing microfibril density.

## BIOSILICIFICATION OF CELL WALL POLYMERS

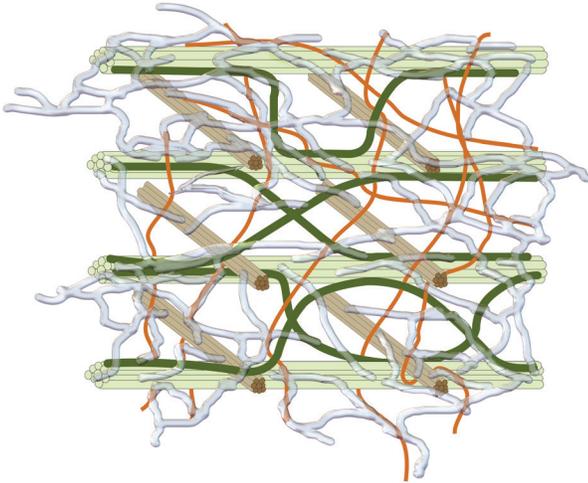


Illustration of biosilicification of plant cell wall polymer matrix

### Positive Effects of Biosilicification of Cell Walls

Silicification of cells is not restricted to the plant's leaf blades and silicified cells are also found within the epidermis and vascular tissue of the stem, leaf sheath and hull. Considered in total, biosilicified structures fulfill an infinite variety of crucial functions in biological systems. The following is a number of direct effects of biosilicification of cell walls but should not be considered the total array of positive effects:

- Improves the overall structural strength of the plant
- Biosilicified structures deposited in epidermal cells of plant leaves reduce the heat load of leaves and are remarkably effective in cooling leaves by virtue of the highly efficient mid-infrared thermal emission of plant silica
- Si treatment in plants results in enlarged leaf cells via cell wall expansion and strengthened vascular system, which helps the plants to transport and hold more water
- Provides Increased resistance to biotic challenges
- Amorphous silica in secondary and tertiary cells of the endodermis allows for enhanced root resistance in dry soils and has been show to promote faster growth of roots
- Provides physical protection of key photosynthetic functional machinery
- Silicon has been shown to improve root plasticity resulting in increased stress tolerance

### Plant Defense Responses

During normal growth and development, reactive oxygen species (ROS) are generated under normal metabolic processes with increased production under biotic and abiotic stress.

For decades, ROS has been characterized as toxic by-products of plant metabolism. **This traditional notion has changed.**

Plants are well adapted for minimizing the damage that could

be induced by ROS under natural growth conditions. ROS only reaches toxic levels when the production of ROS exceeds the quenching capacity of the protective systems due to biotic and/or abiotic stress conditions.

Sufficient data now exists worldwide to confirm that **ROS are also highly controlled signaling molecules that can exist as active second messengers well before they reach toxic levels.** The generation of ROS messengers is virtually instant following the onset of the stress event. As a result, ROS represent ideal signaling components.

Acting as signal molecules, ROS interact with a number of transduction pathways to control metabolic processes, optimize different cell functions, activate acclimation responses and control whole-plant signaling pathways.

**ROS are recognized to be produced by plants in response to both biotic and abiotic stresses.** They are now known to play a central signaling role alone as a second messenger via upstream or downstream interactions, or with other key signaling components. They often represent a point where various signaling pathways come together.

These recent discoveries as to the participation of ROS within intracellular communication in plants that offer additional clarification as to the physiological and molecular mechanisms underlying the beneficial role of silicon in plant defense systems.

### Silicon and Abiotic Stress Resistance in Plants

Literature is filled with reports verifying that silicon (monosilicic acid) promotes plant growth and development especially when the plant is under some form of stress.

Silicon applications have been proven to be effective against a suite of abiotic stresses including drought, heat, cold, salinity, UV-B rays and metal toxicity. Moreover, silicon enhances plant defense responses against an array of stresses (including multiple stress conditions) without the occurrence of resistance and/or growth and yield penalties.

However, reported findings are at times, confusing or contradictory when it comes to silicon's impact and proposed benefits to plants.

**It should be noted that biochemical or molecular defense responses (to include growth and yield responses) associated with silicon fertilization are usually not apparent unless in the presence of an abiotic or biotic stressor.**

**This is closely tied to the body of evidence that suggests that silicon is used by plants primarily as a defense/survival response mechanism to stress conditions.**

### Silicon's Modes-Of-Action

It has become clear that silicon takes on an active role as a source of influence on plant defense mechanisms. **Recent findings point to an important role of silicon as a *Second Messenger* signaling molecule capable of influencing the timing and extent of plant defense responses.**

**The impact of Si on secondary metabolism, like other Second Messengers, are significant only after elicitation.**

ROS are well-known for their immediate release following abiotic or biotic challenge. They serve a central signaling role through their evident interactions with other key signaling components.

It is likely that in addition to abiotic and biotic elicitation of receptor proteins (Primary Messengers), ROS also act as activators of silicon influx into plant cells. In this function ROS *serve as Secondary Messengers, directing silicon cellular influx from a number of stress origins.*

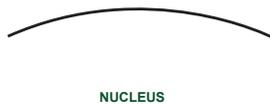
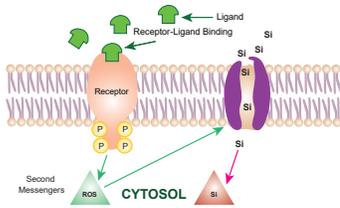
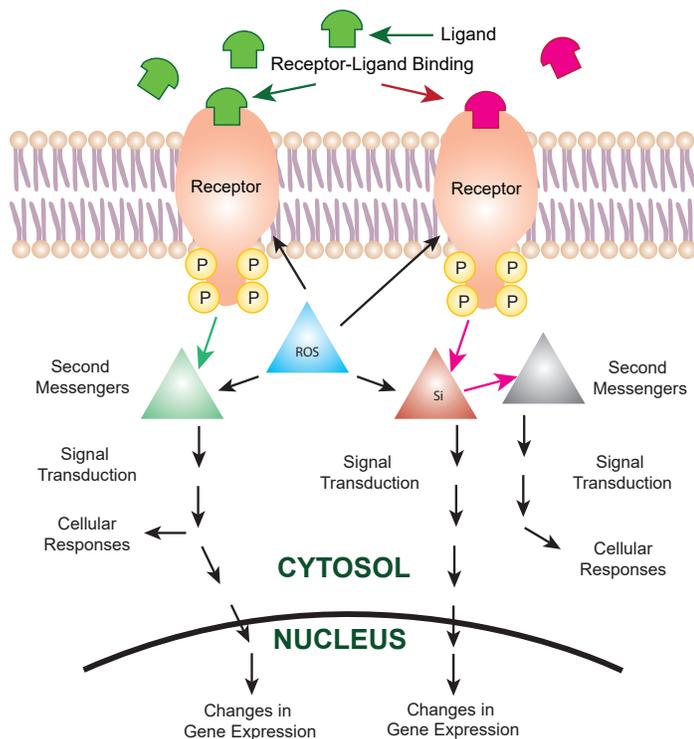


Illustration of potential for ROS to influence influx of silicon by activating transport genes.

### Robust Biological Inducer

Analyses of the affect of silicon fertilization of different plant species under stress show that silicon nutrition can enhance the expression of a large spectrum of inducible defense responses against both abiotic and biotic stresses.

The wide variety of responses influenced by silicon amendments offer a clear demonstration of its potential to act as a robust biological inducer with a broad defense footprint.

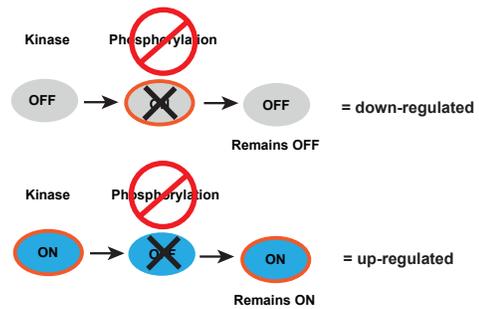


Graphic showing the signal flow through plant defense system (influenced by Si and ROS) culminating in cellular responses and changes in gene expression resulting in protein-based defense molecules.

There is convincing evidence that silicon's ability to modulate plant defense responses is mainly dictated by the hydrogen-bond (H-bond) interactions between both the COOH moiety and the side-chain functionalities of the considered amino acid and the terminal silanol groups of the surfaces. Evidence also exists that certain amino acids adsorb through their  $\text{NH}_3^+$  part of the amino acid molecule.

One of most compelling results supporting the beneficial properties of Si in stressed plants was the general observation that genes that normally would be down-regulated by pathogenesis were less severe as a result of silicon treatment preventing down-regulation gene being turned on by blocking phosphorylation. Moreover, these silicon protected genes belong to key classes of genes involved in primary metabolism.

Effect of Silicon Blocking Phosphorylation of Amino Acid -OH Group



Graphic showing the effect of silicon blocking -OH site on amino acid fragments. Genes that would be switched "on" or upregulated by phosphorylation under stress would remain "off" and be deemed "down-regulated" by effect of silicon on amino acid fragment.. The opposite effect, "up-regulation" occurs when a gene that would normally be switched "off" remains "on" as a result of -OH blockage by silicon.

### Photosynthesis

Photosynthesis is considered by most in the agriculture related industries as the major determinant factor for plant growth and development as its efficiency is directly correlated to optimization of basic and critical plant physiological processes.

Photosynthesis is also one of the most stress-sensitive plant processes, with stresses adversely affecting the important function of the photosynthetic electron transport chain.

Silicon's effect on the efficiency of photosynthesis under abiotic stress is an example of the impact silicon has on plant functions and processes when they are subjected to abiotic stress. It's effect is quite comprehensive inasmuch as both mechanical and a variety of defense responses come into play.

Stress conditions are known to confer serious damage on the photosynthetic machinery of plants. Photosystem II (PSII) is one of the most susceptible components of the photosynthetic machinery that bears the brunt of abiotic stress.

Abiotic stress caused by adverse environmental conditions, such as drought, heat, heavy metal toxicity, salinity and high light (HL), usually results in over-reduction of the electron transport chain (ETC), which in turn leads to the production of reactive oxygen species (ROS) such as superoxide radicals and single oxygen (photo-oxidation).

The overall effect of alteration of the electron transport chain by abiotic stresses are often associated with stress induced reductions in the levels of photosynthetic pigments, the inhibition of the formation or disintegration of PSI, PSII and light-harvesting pigment-protein complexes (LHCII).

Reactive oxygen species (ROS) have been identified as key players in degradation of photosynthetic processes such as PSII. Cellular responses to ROS formation often involve transcriptional downward regulation of key photosynthetic functions and processes such as PSII repair.

The leaf chloroplast ultrastructure is often disordered under high stress. Uneven swelling, fractured and missing thylakoid membranes, and decreased starch granule size and number are often the consequences of abiotic stress.

As a result, degradation of many photosynthetic parameters, including net photosynthetic rate, transpiration rate, stomatal conductance, intercellular CO<sub>2</sub> concentration, chlorophyll concentration and the chlorophyll fluorescence, are to be expected in plants exposed to abiotic stress.

### The Impact of Silicon on Photosynthesis

It has long been shown that applications of Si is a viable pathway to increase photosynthetic capacity and efficiency in plants. Silicon's positive impact on plant photosynthesis is particularly distinct in plants exposed to abiotic and biotic stress.

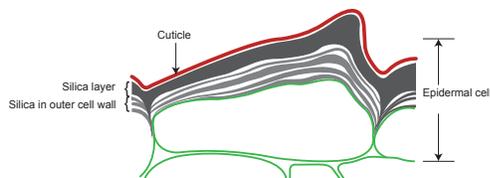
Benefits to enhanced/improved photosynthetic capability of Si-treated plants compared to untreated plants, will vary among plant type and the encountered abiotic/biotic stress(es).

**Commonly reported benefits include, but are not limited to:**

- Increases in contents of chlorophyll (a and b)
- Increases in shoot and root biomass
- Elevated net photosynthetic rate, stomatal conductance, transpiration rate and intercellular CO<sub>2</sub> concentration
- Alleviation/repair of damage to chloroplast ultrastructure
- Improved carbohydrate production

**The modes-of-action associated with the benefits that are associated with Si fertilization are complex but its effects are frequently links to physiological, morphological, nutritional and molecular aspects in plants.**

From a morphological perspective, Si can contribute to the protection of the photosynthetic apparatus through the deposition of silica in cell walls of leaves and vascular structures. This adds to the strength and stability of the cell wall surrounding the chloroplasts, reduces water loss due to transpiration and decreases damage to vascular system caused by water restriction.



Cuticle Silica Double Layer. Yoshida et al., 1962

Nitrogen absorption, an essential element necessary for the formation of chlorophyll, is increased with Si fertilization. As the vascular system is strengthened by silicon deposition in cell walls, conduction of water, necessary to transport nitrogen and other nutrients to critical regions of the plant, is improved.

Further photosynthetic protection is provided by enhanced antioxidant production and protein activity (reducing resistance to stress and providing repair potential) modulated by silicon's role as a secondary messenger in plant defense response systems (described earlier in this bulletin).

For example, under stress, the expression level of the *PsbY* gene (a polypeptide of photosystem II) is down-regulated under stress, but up-regulated by the addition of Si.

The light harvesting complex II (LHCII) structure, an array of protein chlorophyll molecules embedded in the thylakoid membrane of chloroplasts, represents a highly important element of photosynthesis. The expression levels genes associated with light harvesting often decrease under stress, but have been shown to be up-regulated by the addition of Si to protect them from high stress inhibition.

**Without questions, high stress conditions are capable of destroying the structure and/or function of the photosystem in plants. The addition of Si has been shown to protect the photosynthetic pigments in leaves, reduce the damage to chloroplast ultrastructure, and increase the expression of genes associated with photosynthesis.**

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