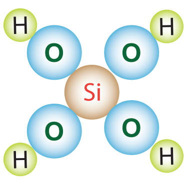
converge

collective impact solutions

The Importance of Silicon Nutrition on Plant Defense Systems

Extensive research has confirmed that silicon represents a natural activator of plant defense resistance to both abiotic and biotic induced stress in plants. Its activity is totally dependent on the accumulation and presence of silicon in its soluble form and is characterized by amplified expression of a number of plant defense reactions.



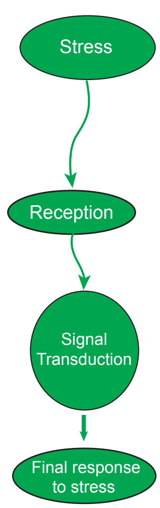
The majority of benefits associated with silicon are associated with the release of silicon (Si) species into the bulk solution -- the most important of which is monosilicic acid (silicon's plant available molecule).

Once absorbed by the plant, monosilicic acid is quite active and has been shown to consistently become involved in complex interactions with plant physiological processes and plant defense response components -- **particularly in plants subject to stress conditions**.

The beneficial role of silicon in reducing the vulnerability of plants to abiotic (non-living, environmental) stress is generally accepted. In addition, the effect of Si on promoting resistance to biotic (living) challenges is also well documented and **biochemical explanations for both observations have strong associations with silicon's integration within plant defense systems**.

Plant Signaling Networks

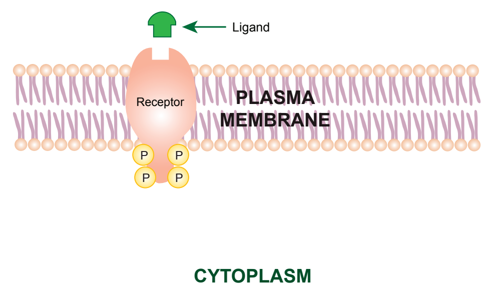
Plants are constantly subjected to a variety of abiotic (temperature, drought, UV-B rays, salinity and metal toxicity) and biotic (pathogens and herbivore attack) challenges. Because of their sessile nature, plants have evolved complicated defense mechanisms to survive such stressful conditions.



The ability of plants to recognize stress factors and signal an appropriate response is of paramount importance in plant defense systems. Recognition of stress factors is referred to as "**Reception**." The mechanisms on how the intracellular signaling molecules communicate and exhibit their responses on cells are known as "**Signal Transduction**."

Reception

Transmembrane Receptors (signal transducers). Transmembrane receptors (proteins) transfer information from the environment to the cell's interior (cytoplasm). These proteins have both extracellular and intracellular domains. A binding site on the extracellular domain specifically recognizes the extracellular signaling molecule (often referred to as the ligand or "**first messenger**").



The receptor protein changes shape when activated that in turn, gives rise to appropriate transduction pathway in the cytoplasm. Transduction pathways are chains of molecules that relay signals via molecular events inside a cell. In multi-cellular organisms such as plants, they have evolved to regulate cell communications.

It is becoming increasingly clear that plant signaling networks are not linear. Recent research indicate that signaling networks are actually part of a more dynamic and complicated network with substantial overlap among their branches. Different stresses or stimuli can activate overlapping receptors/sensors but produce distinct final outputs what are specific to each stimulus.

When signaling pathways interact with each other (often referred to as cross talk) they form networks which allow cellular responses to be coordinated.

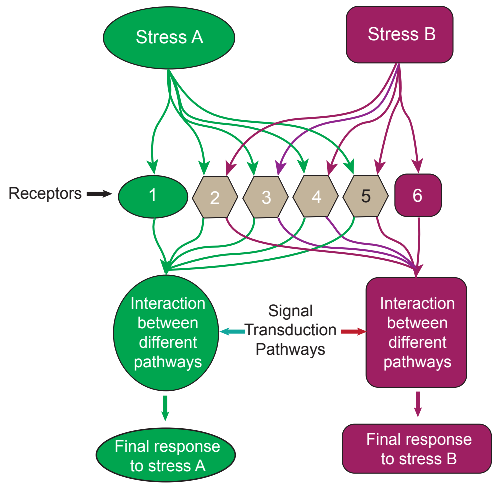
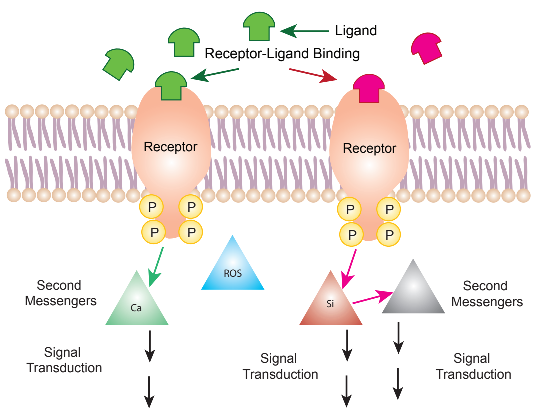


Illustration of simple, non-linear signaling network involving multiple receptors triggering more than one Signal Transduction Pathway.

Second Messengers. Although proteins are important constituents in signal transduction pathways, other types of molecules can participate as well. Many pathways involve second messengers, small, non-protein molecules that pass along or influence a signal initiated by the "first messenger."

Each sensor controls a branch of the signaling pathway activated by one aspect of the stress condition. However, recent research also suggests that initial stress is often perceived by multiple primary sensors and then a cascade of signaling events is initiated by "second messengers" (signals) such as hormones, reactive oxygen species (ROS), silicon and calcium which differ from the primary signal at points where they interact with the transduction pathway.



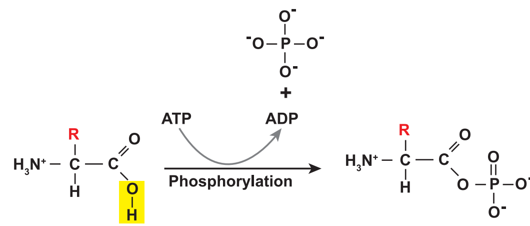
Illustraion showing role of Second Messengers that supplement and redirect intracellular signaling in cytoplasm.

The importance of second messengers to plant response cannot be understated. While second messengers are one of the initiating components of intracellular signal cascades, they are capable of migrating long distances from receptors to involve themselves in a number of transduction pathways.

Signal Transduction

Signals leading to the expression of plant defense responses are transmitted into the cell through the activation of chains of molecules that form a type of "circuit" called signal transduction pathways.

Transduction cascades are sequences of molecular reactions that add a phosphate group (via phosphorylation enzymes) at hydroxyl (-OH) sites of amino acids or subtract a phosphate group (via dephosphorylation enzymes) that induce conformational changes in the protein structure to regulate its activity.



Amino Acid

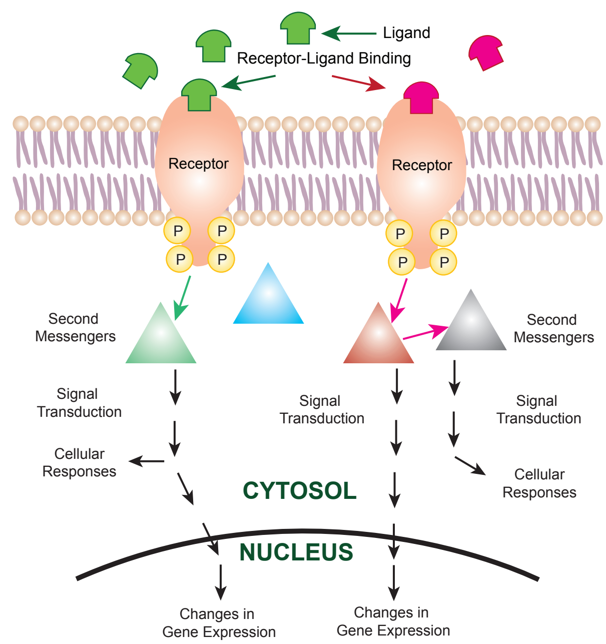
Illustraion showing role of Second Messengers that supplement and redirect intracellular signaling in cytoplasm.

Transduction cascades can be thought of as a row of dominoes. As a phosphate group is transferred to a domino it imparts energy to lean toward the next domino. If a phosphate group is removed, it acts to stop the motion of the domino stack or change its direction.

Response

Transduction downstream events can culminate at a number of sites that contribute to plant response such as:

- Metabolic enzymes creating altered metabolism
- Gene regulators resulting in altered gene expression and the redefinition of genetic machinery
- Hormones that involve nutrient signaling, cell cycle control and crosstalk between other pathways that affect regulation of plant growth and development
- Cytoskeleton proteins that alter cell shape or mobility.



Graphic showing the signal flow through plant defense system culminating in cellular responses and changes in gene expression resulting in protein-based defense molecules.

ROS as a Second Messenger

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.

Early Research

Early research with silicon fertilization of plants revealed that many plants (particularly dicots) did not absorb silicon (referred to as "non-accumulator" varieties). Those small number of varieties called "accumulators" appeared to absorb silicon and demonstrated improvement in plant growth and development.

Why the difference?

As researchers continued their work with silicon, information surfaced indicating that when plants previously considered as silicon non-accumulators were placed under stress (biotic or abiotic), they showed a significant increase in absorption of silicon (far different from previous work with non-stressed plants).

Moreover, these same plants that absorbed silicon under stress, demonstrated enhanced plant defense responses to stressors and plant growth and development was significantly better than the same varieties that were grown under the same stress conditions but not provided with silicon fertilization.

Recent molecular research conducted with silicon fertilization of plants under various stress led to the discoveries that specialized protein transporter genes in plants are involved in the molecular influx and efflux of silicon into and through cells in plants.

This is clearly an indication that absorption and transport of silicon in the majority of plants is the result of an energy dependent "active" system of molecular distribution. **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**.

<u>The impact of Si on secondary metabolism, like other Second Messengers, are significant only after elicitation</u>.

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***.

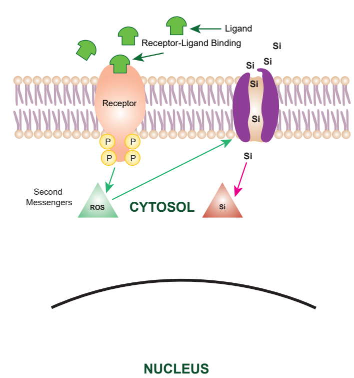


Illustration of potential for ROS to influence influx of silicon by activating transport genes.

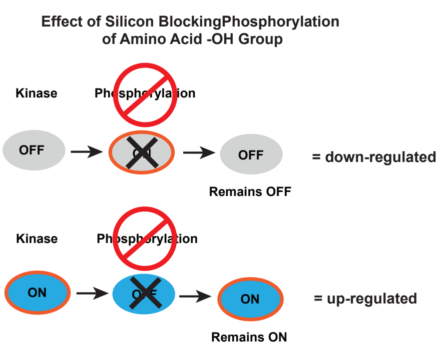
Robust Biological Inducer

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.

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 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.



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.

Silicon and Disease Resistance in Plants

Silicon's role in combating abiotic stress in plants is clear and pronounced. Literature is replete with data confirming **silicon is also an active participant in defense mechanisms targeted against biotic (living organisms) that cause diseases in plants**.

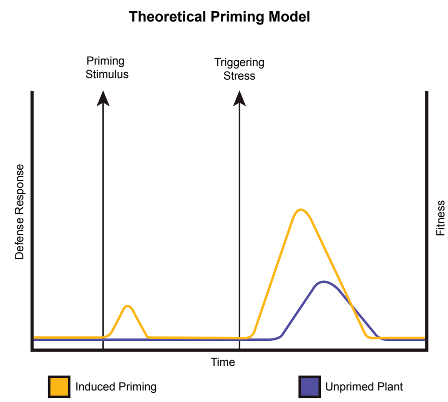
Biotic stressors may exist in the form of plant pathogens (including fungi), bacteria, viruses, insect herbivores and animals.

Plant disease resistance protects plants from biotic stressors in two ways: by pre-formed structures and chemicals, and by infection-induced responses of their defense response system. Inducible defensive strategies allow plants to manage energy reserves more efficiently by synthesizing defense compounds only when needed.

The timing of these defense responses is critical and can be the difference between being able to cope or succumbing to the challenge of a pathogen or parasite.

Biochemical Mechanisms – Priming

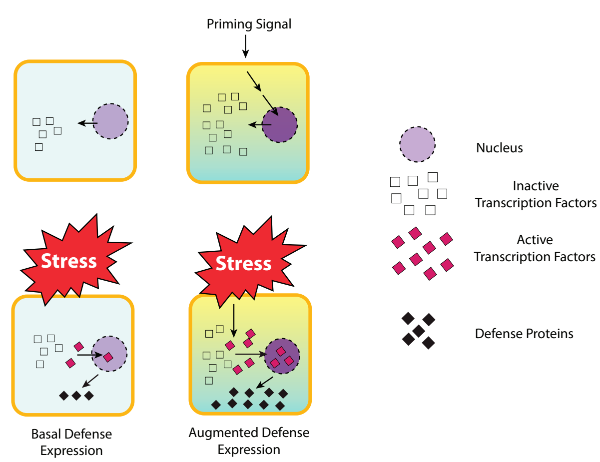
Over the course of evolution, plants have acquired the ability to 'prime' their immune system in response to specific signals that indicate an imminent threat. Upon exposure to a biotic or abiotic resistance-inducing agent, plants acquire an enhanced defensive capacity that results in a faster and/or stronger defense reaction at the moment the plant is exposed to biotic or abiotic stress. This phenomenon is commonly known as priming and has been associated with different forms of induced resistance.



Theoretical Priming Model depicting differences in enhanced defense response and fitness of plants following a biotic or abiotic triggering stress event. Note the difference in speed and degree of defense of expected response of "primed" plant versus "unprimed" plant.

Induction of the "primed" state may be brought about by an enhanced accumulation of signalling compounds, such as transcription factors (TFs) that remain inactive until the plant is exposed to stress. Transcription factors are proteins that regulate gene expression. They often contain features the help cells respond to the internal or external environment.

These are binding sites that interact with chemicals in the cell (ligands) that modulate the activity of the transcription factors. TFs may bind to hormones, chemicals or to other proteins in order to respond to the environment.



Plants have the ability to increase their level of basal resistance against future pathogen attack upon appropriate stimulation. This phenomenon is known as **induced resistance**. Based on differences in signalling pathways and spectra of effectiveness, different types of induced resistance have been defined.

Biotic Elicitation of Silicon Influx

Influx of silicon can certainly be attributed to biotic defense receptors initiating the need for additional silicon absorption to participate in induced systemic resistance.

The rapid release (respiratory "burst" or oxidative "burst") of reactive oxygen species (ROS) during even low levels of biotic elicitation, may also act as a primary (or a second messenger) to trigger silicon influx for priming.

Silicon's Prophylactic Role in Biotic Plant Defense

Both biological and transcriptional evidence exists that support plant biotic defense models where silicon plays a prophylactic role without a direct effect on metabolism. Silicon is used by the plant to modulate a more efficient and synchronized defense response to biotic stress.

The increased activity of phenolic compounds, polyphenol oxidases and peroxidases in plants treated with Si demonstrates the involvement of silicon in the induction of plant defense responses.

Silicon has also demonstrated its ability to orchestrate an up-regulation and down-regulation of regulatory genes, stress-related transcription factors and genes involved in signal transduction and influence the activity of enzymes related to defense such as chitinases and glucanases -- further "priming" the defense system for possible biotic attack.

Silicon can also act as a modulator influencing the amplitude of expression of hormonal defense responses able to induce resistance. This would be similar to its effect transduction cascades triggered by abiotic stresses. The effect of silicon is only visible once infection occurs and is characterized by an amplified expression of defense reactions.

It should be noted that silicon's effect on enhancing plant resistance against fungal pathogens is not limited to high silicon-accumulators as it has also been described in low silicon accumulators.

In summary, plants under silicon fertilization acquire an enhanced defensive capacity that results in a faster and/or stronger defense reaction at the moment the plant is exposed to biotic or abiotic stress. Silicon stands out for its potential to improve plant defense systems.

converge
collective impact solutions

NUMERATOR
TECHNOLOGIES, INC.
P.O. Box 868
Sarasota, Florida 34230
941.807.5333