Although crops depend on a multitude of physiological, biochemical, and molecular processes, it is photosynthesis that is recognized as a major limiting factor in crop growth, development and survival. Photosynthetic capacity and efficiency directly affect turfgrass health and bioenergetic status. The operation of the photosynthetic machinery is severely affected in all its phases by abiotic stresses such as drought, temperature extremes, salinity, UVB light and metal toxicity.

It is well documented that the element silicon can play important roles in increasing crop tolerance or resistance to these abiotic stresses. Silicon is known to effectively mitigate various stress factors that include salinity, drought, heat, UVB rays, chilling and toxic metals.

Non-structural and structural carbohydrates, produced by photosynthesis, provide the source of fuel needed by crops to grow and develop. Carbohydrates are also used by the crops to survive during, and recover following, periods of abiotic stress.

Abiotic Stress

Effects on Photosynthesis

Abiotic stress occurs when non-living factors create conditions outside ranges favorable for growth and development of an organism. Plants may experience physiological stress when an abiotic factor is excessive or deficient (often referred to as an imbalance). Research also shows that abiotic stressors are most harmful when they occur in combination. These unfavorable conditions create stresses that can cause alterations in a wide range of physiological, biochemical and molecular processes in plants. The major plant abiotic stresses of agronomic importance worldwide are drought, cold (chilling and freezing), heat, salinity, UVB light and soil mineral and metal deficiency or toxicity.

Abiotic stresses have been reported to severely affect components and reactions within the plant’s photosynthetic machinery (pigments and photosystems, the electron transport system and CO₂ reduction pathways).

It should be noted that any damage to the photosynthetic apparatus caused by a stress event, may result in the reduction of the overall photosynthetic capacity, bioenergetic status and yield of crops.

Drought Stress

Crops are often subjected to soil and atmospheric water deficits during their life cycle. Drought stress usually prompts a reduction overall photosynthetic capacity. Drought stress has been shown to cause severe damage to photosynthetic pigments as well as result in deterioration of thylakoid membranes within chloroplasts. Decreases in chlorophyll (Chl) are also common occurrences under drought stress.

Direct effects of drought on photosynthesis are CO₂ diffusion limitation through the stomata and mesophyll and alterations in photosynthetic metabolism.
Secondary effects include oxidative stress caused by the production of Reactive Oxygen Species (ROS).

Even under mild or moderate drought stress, plants appear to quickly recognize drought stress and respond rapidly by altering (usually a down regulation) photosynthetic related gene expression in concert with physiological and biochemical alterations. The severity of drought condition and the ability of turfgrass to recover from drought conditions often determine the impact of photosynthesis decay and the loss of carbohydrate production capacity and efficiency.

Salt Stress

Salinity is a major limiting factor to agronomic productivity in the world. Salt stress causes decreases in plant growth and productivity by disrupting physiological and biochemical processes, especially photosynthesis -- even at low to moderate salt levels.

Soil salt prevents plants from taking up water, exposing them to what is commonly referred to as “physiological drought.” As a result, many of the direct and indirect effects of salt stress on photosynthesis are common to what is expected from drought stress.

However, when compared with drought, salt stress has been show to affect more genes and with more intensity.

Salt stress results in the breakdown of both chlorophyll and the reduction of carotenoids. Carotenoids are necessary for photoprotection of photosynthesis and serve as a precursor in signaling during abiotic stress.

Temperature Stress

Photosynthesis is highly sensitive to high temperature stress and it is often inhibited before many other cell functions are impaired.

The primary site of targets of high temperature stress are Photosystem II (the primary site of targets of high temperature stress and it is often inhibited before many other cell functions are impaired. The primary site of targets of high temperature stress are Photosystem II (the first protein complex in the light-dependent reactions of oxygenic photosynthesis. It is located in the thylakoid membrane of plants).

Plants exposed to high and low temperature stress often exhibit reduced chlorophyll biosynthesis (occurs in plastids), as key enzymes involved with chlorophyll biosynthesis are damaged or altered.

ROS production, generation of heat shock proteins, production of secondary metabolites are some of the consequences of high temperature stress. Photosynthetic capacity may not recover completely.

Under low temperatures, reduction of leaf chlorophyll, carotenoid content and net photosynthesis should be expected.

UVB Radiation

Often overlooked as a major stressor, UVB radiation can inflict major damage to the photosynthetic apparatus of plants at multiple sites resulting in the erosion of photosynthetic efficiency and the productivity of plants.

UVB rays inactivate light harvesting complex proteins. Key reaction center proteins on the donor and acceptor side of PS II are altered. Damage to Rubisco has been reported.

Of significance to crop production is that UVB radiation creates impaired photosynthetic function that render crops susceptible to other environmental factors.

Toxic Metals

Inhibition of photosynthesis by heavy metals is well documented. Heavy metals affect both light and dark reactions of photosynthesis directly or indirectly.

Heavy metals directly affect the photosynthetic machinery by binding to the various sensitive sites of the photosynthetic apparatus. Metals are known for their strong binding affinity to sulfhydryl groups, which are essential for enzymatic activity and protein structure.

In chloroplasts, heavy metals disturb the architecture of thylakoid membranes, which in turn, change some light reaction processes.

Toxic effects of metals on phototrophic organisms strongly appears to be related to the increase in the levels of lipid peroxidation and protein carbonylation. This occurs as the result of highly destructive hydroxyl radicals (•OH) that are produced from the Fenton Reaction. Hydroxyl radicals damage cell membranes which consist mainly of lipids.

Fenton Reaction

\[ \text{Metal}^{2+} + H_2O_2 \rightarrow \text{Metal}^{3+} + OH^- + OH \]

Secondary Effects - Oxidative Stress

Reactive Oxygen Species. Reactive oxygen species (ROS) in plants are produced as normal by-products of many metabolic pathways, including photosynthesis.

The production of ROS is also an unavoidable outcome of aerobic respiration. It is estimated that 1-2% of atmospheric oxygen consumed by plants is inevitably converted to ROS in forms such as the superoxide radical, perhydroxyl radical and hydroxyl radicals. Non-radical (molecular) forms, hydrogen peroxide and singlet oxygen, are also produced and can participate in destructive and toxic “chain reactions.”

Oxidative Stress. Under steady state conditions (normal metabolism), plant cells have evolved a complex system of enzymatic and non-enzymatic antioxidants which serve to maintain a delicate equilibrium between ROS production and their conversion to non-harmful molecules (scavenging).

The components of the antioxidant defense system in plants are enzymatic and non-enzymatic antioxidants. Common enzymatic antioxidants include superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione peroxidase (GPX), glutathione-S-transferase (GST), and catalase (CAT). Examples of non-enzymatic low molecular metabolites include ascorbic acid (ASH), glutathione (GSH), a-tocopherol, carotenoids and flavonoids.

A common result of abiotic stress in plants is the overproduction of ROS, which frequently results in oxidative stress. Oxidative stress often occurs when the production of ROS overwhelms the plant’s ability to maintain ROS at steady state levels.

Unfortunately in many plants, their antioxidant systems, which are tuned to maintain steady state levels, are insufficient to counteract increased production of ROS due to abiotic stresses, particularly under multiple stress conditions.

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Many “symptoms” of stress such as weakened plants and diminished crop quality caused by abiotic factors (drought, heat, salts, chilling, metal toxicity and ultraviolet rays) are for the most part, actually indicators of oxidative stress.

Abiotic Stress

Drought • Heat • Cold • Salinity • UV

Plant Processes • Injury • Metal Toxicity

ROS production: Mitochondria Chloroplasts Cell Wall Peroxisome Membrane

Oxidative Stress

Silicon is not inert. It has been found to be a biologically active element, participating in highly complex interactions with key components of the plant’s defense response system.

Plant available silicon, released by CrossOver Agriculture and CrossOver G, plays key roles in activating processes that enhance and improve the efficiency and effectiveness of defense response systems under abiotic stress conditions.

Silicon Mediation of Abiotic Stress Factors

Many plants, particularly turfgrasses, have developed a predisposition for the uptake and use of silicon in conferring tolerance to abiotic stresses. Improved plant tolerance with silicon can be seen as a quicker and more efficient response at the onset of stress as well as enhanced recovery once the stress has abated.

Silicon actively participates in a number of response mechanisms to effectively mitigate various abiotic stress factors such as salinity, drought, heat, cold, UVB and metal toxicities.

Silicon’s ability to address different stressors makes it a valuable tool in combatting abiotic stress inasmuch as most turfgrasses encounter multiple stresses during the year.

Silicon and Photosynthesis

It is well documented that plants under abiotic stress demonstrate improvement in photosynthetic efficiency and capacity once applications of silicon are applied.

Silicon mediation of abiotic stress factors that affect photosynthesis in plants is understandably quite complicated and involves a complex of responses at molecular, cellular, metabolic, physiological, and whole-plant levels.

Areas of silicon-influenced mediation include but are not limited to:

- Gene Expression
- Altering Antioxidant Activity
- Immobilization of toxic metals in the soil or in planta
- Anatomical Alterations

Gene Expression

Researchers have found that silicon influences expression levels of a number of photosynthesis-related genes by either up-regulating and down-regulating the production of specific gene products (protein or RNA) to counteract the negative effects of abiotic stress.

Reported results of silicon’s influence on gene expression levels and its impact on various stress-related damage to plant photosynthetic apparatus include but are not limited to:

- Increased values of chlorophyll (a+b)
- Up-regulation of genes involved in photosystem I (PSI) and photosystem II (PS II) that were down-regulated by stressors
- Reversal of down-regulated cytochrome biological processes
- Alleviation (moderated damage) of chloroplast ultrastructures
- Enhanced electron transport chain of plants
- Prevention of damage to Light Harvesting Complex II (LHC II) structure that is critical to photosynthesis

Altering Antioxidant Activity

Silicon is a bioactive molecule that has preferential attraction to the hydroxyl unit amino acids found in proteins, enzymes and hormones. This may explain its bioactivity as a regulator of plant defense mechanisms.

Enzymes, proteins and hormones are major constituents of relay mechanisms, signaling pathways and cascades that drive defense and response mechanisms in plants.

Silicon’s biochemical properties enable it to interact with a host of enzymes, proteins and hormones and act as a modulator influencing the amplitude, timing and duration of stress transmission signals and protein activated plant defense response pathways.

Immobilization of Toxic Metals in Soils

Through its ability to interact with several key components of plant stress signaling systems silicon increases the production of important enzymatic and non-enzymatic antioxidants in plants (i.e., SOD, POD, CAT, GPX, APX, MDHAR, GR, ASA, and GSH).

It is generally accepted that this over production of ROS scavenging antioxidants (via upregulation of many ROS-scavenging genes) by silicon improves plant tolerance and resistance to various abiotic stresses.

Please refer to the CrossOver Granulated Liming Material label for use directions where soils may benefit from use of silicon to immobilize toxic metals.

In the soil profile, when silicon (Si) is released from CrossOver Agriculture formulations as mono- and polymeric acids, it is capable of complexing with inorganic and organic compounds.

Soluble silicates act to ameliorate heavy metal accumulation and toxic metal ions in four general ways:

1. Formation of insoluble metal silicates
2. Adsorption of metals onto polymerized silicate colloids and flocculants
3. Adsorption of metals onto polymerized silicates on exchange sites
4. Encapsulation of metals within silicate polymers

Formation of insoluble metal silicates

The dominant mechanism by which free metal ions are immobilized from the soil solution is by precipitation.

Silicates react rapidly with multivalent metal cations to form a number of insoluble metal silicate precipitates than are rendered incapable of entering into further reactions (neutralizing effect) and can be removed from the soil profile via leaching.
**Adsorption of metals onto polymerized silicate colloids**

Example of monosilicic acid forming inorganic ligand silicate precipitate with multivalent metal ion.

A second example of monosilicic acid forming inorganic ligand silicate complex with multivalent metal ions.

Monosilicic acid in the presence of metal oxides in solution reacts to form colloidal complexes with neutral or negative charges. These colloidal complexes create an electrostatic repulsion with each other resulting in the precipitation of the metal silicate flocculants.

**Adsorption of metals onto polymerized silicates on exchange sites**

The negative sites on soil surfaces are important exchange sites for cations. Fe, Al and Mn oxides embedded in the soil surface are known to strongly retain heavy metals.

Monosilicic acid interacts with Fe, Al, and Mn oxide surface OH groups through ligand exchange to form silicate inner sphere complexes.

This is highly significant because the silicate complexes formed serve two purposes. They neutralize the metal oxides on the particle surface and also establish stable adsorption sites for heavy metals that are less susceptible to desorption via pH or decomposition.

**Encapsulation of metals within silicate polymer**

Calcium silicate is unique in that it can undergo a number of very distinct geochemical reactions. These reactions allow silicates to form polymer/layered silicate compositions ("gels" or "binders) of varying complexity that are known to have the capacity to encapsulate or harbor potentially toxic metals within, or onto, their polymer structures.

**Immobilization of Toxic Metals in planta**

Under stress conditions, plants often significantly increase their absorption of silicon (monosilicic acid) molecules.

The build-up of monosilicic acid in the apoplast of the roots serves two important defense mechanisms against the absorption and transport of toxic metal ions into the plant.

Since the plants prefer silicate entry, they outnumber metal ions and “block” entry to the xylem. This is particularly effective even with roots that have underdeveloped or damaged casparian strips.

As the monosilicic molecules come in contact with free metals, they are also capable of forming complexes with the metals.

When monosilicic acid complexes with metal molecules, the metal silicate complex attaches to the extracellular walls of the apoplast or deposits as a precipitate.

These complexed metals are now neutralized and rendered non-exchangeable and they cannot engage in chemical reactions that produce reactive oxygen species. Moreover, this co-deposition process effectively removes metal ions from entering the Fenton equation.

**Fenton Reaction**

\[ \text{Metal}^{2+} + \text{H}_2\text{O}_2 \rightarrow \text{Metal}^{3+} + \text{OH}^- + \text{OH} \]

Silicon therefore indirectly contributes to a decrease in -OH ion production by decreasing the availability of many free cationic metals – preventing the Fenton reaction from acquiring required metal catalysts.

Silicon has also been found to stimulate the production of flavonoid-phenolics (i.e. catechin and quercetin) that have a strong metal-chelating ability and may provide metal tolerance in plants.

**Anatomical Alterations**

Silicon is absorbed by plant roots and moves upward in the transpiration stream to sites of strong evapotranspiration in epidermal regions of stems and leaves. In these areas, the silica forms solid, hydrated gels between the cuticle and the cell walls.

Silicon is also deposited within cell walls where it improves cell wall strength, plant rigidity, root development, linear growth, water efficiency and presents barriers to environmental stresses.