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Silicon and its Role in Crop Production

A LITERATURE REVIEW

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Abstract:

Silicon (Si) has long been known to provide beneficial effects on soil and plant growth. There is a significant collection of scientific literature that supports the beneficial effects of Si when incorporated into agricultural practices on a wide variety of crops. Most scientists and state regulators do not yet consider Si as an essential nutrient for plant growth. However, Si has recently been recognized as a Beneficial Substance by The Association of American Plant Food Control Officials (AAPFCO). This review of existing papers and research will outline the current knowledgebase surrounding the role that Si plays in plant nutrition, soil composition and quality, stress tolerance to abiotic and biotic factors and the metabolism of Si within the plant.

The application of Si derived from natural silicates has been shown to reduce the effects of environmental stresses on a plant as well as make more efficient use of soil and fertilizer nutrients such as nitrogen and phosphorous. Crops are divided into two groups when you discuss Si utilization by a plant. There are Si accumulators, where Si is greater than 1% of a plant's dry weight, and Si non-accumulators, where the Si is less than 1% of a plant's dry weight. Seven of the ten most planted crops in the world are Si accumulators. Most researchers believe Si is taken up as mono-silicic acid (H_4SiO_4) and moves in the xylem and the phloem of a plant's vascular tissue. Once in the plant the Si tends to form amorphous silica particles called phytoliths. The mode of action is still not completely understood and researchers are in disagreement as to the active or passive nature of phytolith formation.

The role that Si plays in reducing the impact on plants from abiotic and biotic stresses such as drought, disease, and insect stresses, has been well documented across a range of crops. Si functions in many different ways within a plant and most researchers believe it is a combination of multiple Si effects that allow plants to better tolerate the many stress factors a plant is exposed to in nature. Soil applications of Si have also been demonstrated to reduce the toxic impact from high levels of metals in the soil including manganese, cadmium, copper and arsenic. While much is known about Si and the impact Si has on plant growth factors there is

still much to be studied in regards to Si availability, Si levels in the soil and the role Si plays in plant metabolism and stress management.

Introduction

Silicon (Si) is the second most abundant element in the earth's crust. Silicon is present in the soil in many forms that vary with the pH of the soil solution. If the soil pH is below 9.0, Si is primarily in the monosilicic acid form, $Si(OH)_4$, and is found in soil solution at concentrations ranging from 14-20 mg Si/L. Even though Si has been found at significant concentrations within a range of plant species it is not currently considered an essential element for plant growth and development. Historically in most soils Si concentrations were not considered limiting to plant growth. However, as agriculture has become more intensive and yields have been dramatically increasing, the level of Si being removed from the soil has also been increasing resulting in depleted soil Si concentrations and limited plant growth and yields. Removal rates of Si varies with the plant species, for example sugar cane removes 300 kg ha/year (Meyer and Keeping 2001), rice removes 500 kg/ha/year (Makabe et al. 2009), grasslands in the U.S. remove 22-67 kg/ha/year (Blecker et al. 2006) while tropical forests remove 41-67 kg/ha/year (Lucas et al. 1993; Alexandre et al. 1997) and temperate forests remove 2.3-44 kg/ha/year (Bartoli 1983; Gérard et al. 2008; Cornelis et al. 2010). Crops remove Si faster than the natural soil system can mineralize and replace the utilized Si.

It has been calculated that 210–224 million tons of Si are removed from cultivated soil every year (Matichenkov and Bocharnikova 2001). This figure is roughly equivalent to the annual discharge of dissolved silica from rivers to oceans (Berner and Berner 1996) and indicates that agriculture may play a significant role in Si utilization and removal from the soil. Changes in farming practices have led to less incorporation of organic matter back into the soil which often results in lower Si levels. Savant et al. (1997a) suggested that not returning straw to the field soil might lead to a depletion of plant-available Si in soils with a resulting decline in cereal yields.

Variability and Essentiality

Work from the early 1800's by de Saussure (1804) looked at Si levels in ashed plant samples and concluded that Si concentration in plants varies according to the plant species. Plants from the Gramineae family had some of the higher Si concentrations. There is a large variability in Si concentration in plants, ranging from 0.1% to 10% dry weight, depending on species (Epstein 1999; Hodson et al. 2005). The species which have the highest concentration of Si are monocots or grass species. Dicots are typically lower in Si, but there are some exceptions. Sangster et al. (2001) suggested that the following families show higher levels of Si uptake and utilization:

- Dicots including: Fabaceae (e.g. peas), Cucurbitaceae (e.g. cucumber and squash), Rosales (e.g. elm trees), and Asteraceae (e.g. sunflower)
- Monocots including: Graminaceae (e.g. wheat) and Cyperaceae (e.g., sedges)

The level of Si in a plant may have more to do with its phylogenetic position in the evolutionary tree of plant development than the soil environment in which the plant is grown (Sangster 1978 and Hodson et al. 2005). To clarify, the evolutionary path of the plant may have more influence on Si concentrations in the plant compared to the effect of soil and soil solution Si concentration or the soil pH. Ma and Takahashi (2002) proposed that unlike other elements, Si is abundant in nearly all soils; so environmental criteria do not impact Si accumulation in plants. The same authors developed a phylogenetic tree of Si-accumulating plants and observed that Si-rich species typically have low calcium concentrations while Si-poor species have high calcium concentrations. They proposed a model that would differentiate Si accumulating plants from Si non-accumulating plants. In their proposed model:

- "Si-Accumulators" have a Si concentration over 1% and a [Si]/[Ca] ratio >1.
- "Si-Excluders" have a Si concentration below 0.5% and a [Si]/[Ca] ratio <0.5.
- Plants that do not meet any of these two criteria are called "Si-intermediates."

Deren (2001) noted that there is a significant difference among genotypes within the same species. These differences among genotypes have been substantiated by numerous other researchers (Hodson et al., 2005 and Ma and Takahashi, 2002). Researchers have also observed that the while Si-accumulation is mainly a phylogenetic feature, Si availability within the soil also will have a significant impact on the amount of Si a plant absorbs.

There have been conflicting opinions on the essentiality of Si in plant growth. Early work by Sachs (1892) did not show a difference in plant growth despite a large difference in Si concentration within the plant shoots. Epstein (1994) did a thorough review of all the work done on Si and concluded that there is not conclusive evidence to the non-essentiality of Si in plant growth and development. His position is based on the difficulty in removing all background levels of Si in the experimental nutrient solutions and as a result not having a true experimental control. His work suggests that Si is "quasi-essential to many of those plants for which its absolute essentiality has not been established." There have been significant amounts of additional work done on the Si uptake mechanism, Si transport and Si accumulation in plants since the Epstein (1994 and 1999) reviews that have contributed to the discussion of Si essentiality.

The American Association of Plant Food Control Officials (AAPFCO) regulates the products sold in the United States that claim to be fertilizers. They develop the rules and definitions for fertilizer products as well as soil and plant amendments. AAPFCO officials still consider Si to be a "beneficial substance" which they define as: "*any substance other than primary, secondary and micro plant nutrients that can be demonstrated by scientific research to be beneficial to one or more species of plant, when applied to the plant or soil*". Significant resources are being committed to scientific studies that will support the essential role that Si plays in plant metabolism. This would affect label claims for Si products that Si is an essential nutrient for plant growth.

Seven out of the top 10 crops grown in the world are designated as Si accumulators so understanding the role of Si and the mechanisms of Si uptake and translocation by the plant are justified.

Table 1. Si Concentration of some of the most important crops ranked by production.

Crop	**Production (MT)**	**Si Concentration in Shoots (% Dry Wt.)***
Sugar Cane	1.736	1.509
Corn	826	0.827
Rice	686	4.167
Wheat	683	2.455
Potatoes	326	0.4
Cassava	232	0.5
Soybeans	231	1.399
Sugar Beet	222	2.34-7
Barley	155	1.824
Tomatoes	136	1.55

- Data from Hodson et al. (2005)

Root Uptake

As mentioned earlier, when soil pH is below 9.5, Si is mostly present as the monomeric orthosilicic acid H_4SiO_4 (Casey et al. 2004). The primary form in which Si is taken up by plant roots is orthosilicic acid although there has been a suggestion from Fu et al. (2002) that root uptake of Si occurs through Si soil particles being incorporated physically into the root.

In rice (Raven, 2001) and wheat (Rains et al. 2006) it has been proposed that a metabolic mechanism was involved with the active uptake of Si. The uptake mechanisms are thought to be similar for rice and wheat as well as other crops with only minor differences based on plant species.

Ma et al. (2004) proposed two Si transporters; one named SIT1 is responsible for the transport of Si from the external solution to the cortical cells. The other, named SIT2, is responsible for the transport of Si from the cortical cells to the xylem. The transport systems work against the concentration gradient so it implies there is some type of energy consuming active transport system. Ma et al. (2001a) also suggested that the uptake of Si occurs in the lateral roots but does not involve the root hairs. Si influx transport mechanisms have been demonstrated in rice and corn (Mitani et al. 2009) but work is continuing in wheat to identify the transport mechanism.

Si transport more than likely involves both active and passive uptake mechanisms in the same plant (Henriet et al. 2006; Mitani and Ma 2005; Ding et al. 2008: Liang et al. 2007; Gerard et al. 2008). Work done in bananas grown hydroponically showed that when bananas were grown in solution with high Si concentrations, uptake was proportional to the mass flow-driven supply. At low Si concentrations, Si absorption was greater than you would expect with a mass flow-driven supply suggesting an active uptake mechanism.

Transfer to Shoots

Once Si has moved into the xylem it is moved to the shoots. This process is driven by transpiration within the plant and efficiently moves Si into the shoot tissue. The role of transpiration in Si movement to the shoot has been demonstrated in many studies (Henriet et al. 2006; Ding et al. 2005; Leng et al. 2009). Mitani et al. (2009) has isolated a gene that regulates the Si transport system for xylem loading in corn. Additional work is being dome to evaluate the relationship between active and passive transport of Si to the plant shoots.

Accumulation in Shoots

Studies in wheat by Casey et al. (2004) have shown that Si is present in mono- and di-silicic acids with the mono- silicic acid being the predominant form. The soluble form of Si is small compared to the solid form of Si in the plant. When Si is transported into the shoots it has been found to quickly precipitate to amorphous silica. Lux et al. (2003) observed solid Si aggregates in the root within 2 hours of moving a sorghum plant from a Si-poor nutrient solution to a Si-rich environment.

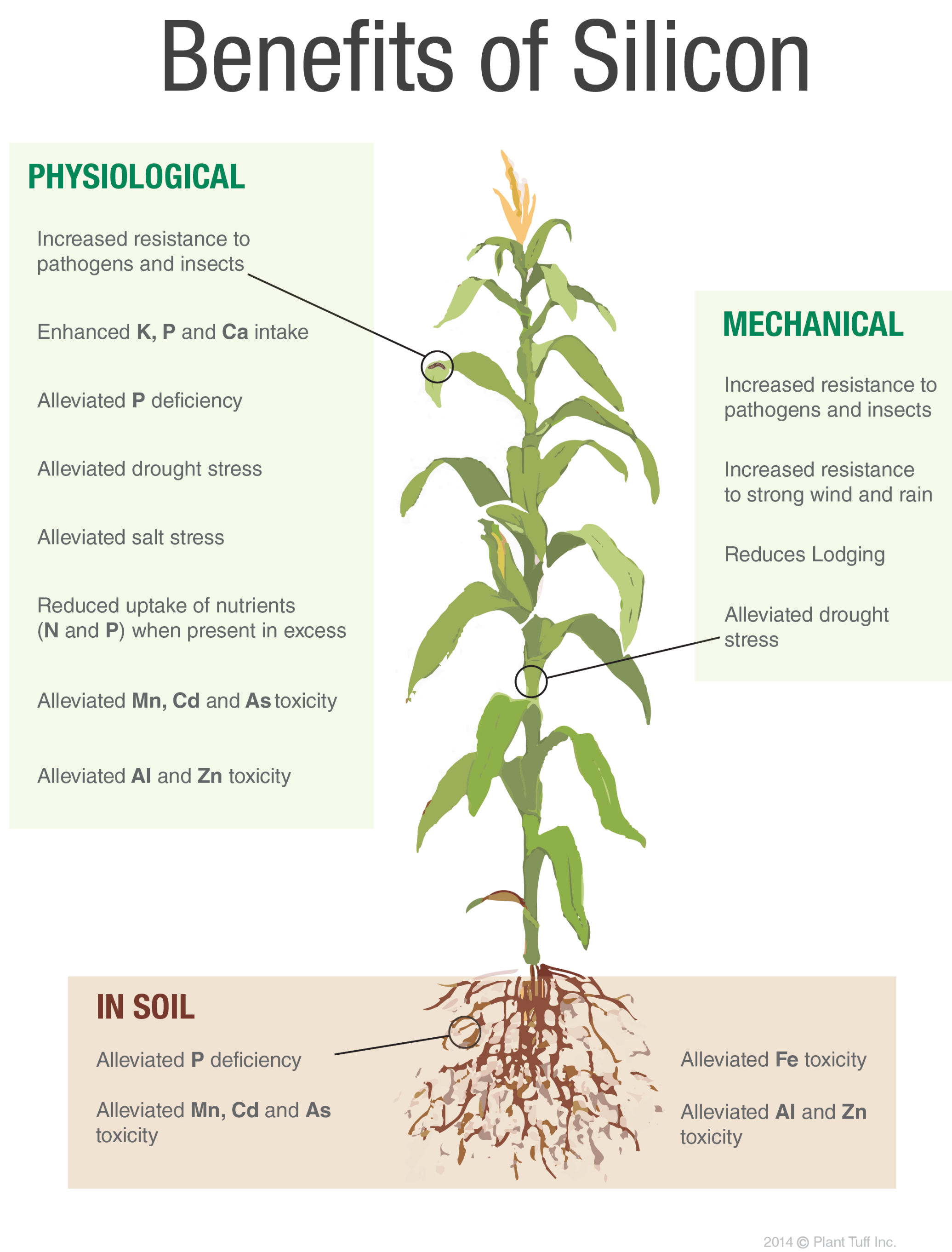
Organo-silicon compounds in Si treated plants have not been well documented. Inanaga et al. (1995) worked in rice and suggested that Si forms links between lignin compounds and carbohydrates. Si-C bonds have not been shown and the instability of the Si-O-C bond near neutral pH suggests that Si may be regulated in a different way from other nutrients (Perry and Keeling-Tucker 1998).

Ding et al. (2008) has shown that amorphous silica is the only form of Si within the plant. When amorphous silica precipitates in a plant cell they are called phytoliths. The polymerization of silicic acid forms the phytoliths and has been shown to take very little energy to polymerize. Phytoliths are not found uniformly throughout the plant (Ponzi and Pizzolomgo 2003; Prychid et al. 2003; Sangster et al. 2001) as they are sometimes found in the leaf or root epidermis and in the cellular membranes.

Beneficial Effects of Si

Managing Environmental Stresses

The numerous benefits that supplemental applications of Si can provide have been well documented in a range of studies including field, container and hydroponic trials (see the reviews by Jones and Handreck 1967; Savant et al. 1997b; Epstein 1999; Datnoff et al. 2001; Datnoff and Rodrigues 2005). The role that Si plays in alleviating environmental stresses on plant growth is due to the way Si functions in the soil as well as in the plant (See Fig 2). Si works at several different levels and can relieve stress from biotic as well as abiotic influences as described below.



Biotic Stresses

Si has been shown to enhance the resistance of plants to many disease organisms on a wide range of crops, including those caused by bacteria and fungi (Rodgers-Gray and Shaw

2004) and those diseases common to wheat such as powdery mildew (Blumeria graminis), septoria (Phaeosphaeria nodorum and Mycosphaerella graminicola), and eyespot (Oculimacula yallundae). The effect of Si has also been demonstrated in rice on stalk rot (Leptosphaeria salvinii), rice blast (Magnaporthe grisea), fusarium wilt (Fusarium), tan spot (Cochliobolus miyabeanus), melting seedlings (Thanatephorus cucumeris), and leaf spots (Monographella albescens; Ma and Takahashi 2002; Savant et al. 1997b). Datnoff et al., (1997) have shown that in soils deficient in Si, supplemental applications of Si is as effective as a fungicide application in controlling rice blast. Applications of Si also reduce the incidence of powdery mildew in cucumber, barley and wheat; sheath blight in rice, ring spot in sugar cane, rust in cowpea and leaf spot in Bermuda grass (Fauteux et al., 2005).

Applications of Si also appear to reduce insect activity on crops. This suppression includes pests such as stem borer and a range of leaf hopper and spider mites (Savant et al., 1997). Cotterill et al. (2007) and Hunt et al. (2008) showed that grasses treated with supplemental applications of Si were less likely to be fed on by animal pests including wild rabbits and locusts, than grasses that were unfertilized. It has been proposed that this may be more of a mechanical mechanism where Si leaves are tougher and more resistant to grazing. The beneficial effect of Si has been proven on attacks by many insect species, among which are insect borers (Chilo suppresalis), yellow borers (Scirpophaga incertulas), rice chlorops (Chlorops oryzae), rice leafhopper (Nephotettix bipunctatus cinticeps) and brown leafhoppers (Nilaparvata lugens),

Two mechanisms have been proposed to explain the Si-enhanced resistance to plant diseases and insects. The first proposed by Cheng (1982), Fauteux et al., (2005), Jones and Hendreck, (1967) and Ma and Yamaji (2006) states that Si behaves as a physical barrier where the Si is deposited beneath the leaf cuticle. This forms a cuticle-Si barrier that can mechanically inhibit the fungal or insect pest penetration, reducing the infections.

The second mechanism that explains Si-enhanced resistance to pathogens proposes that Si acts as a modulator in the host plant to the pathogen. Plants treated with Si increase the production of natural defense compounds including the elevated production of lignin, phenolic and phytoalexins (Epstein 1999; Fawe et al. 2001; Ma and Yamaji 2006). When a pathogenic fungus attacks a plant, the Si produces a broad quick response in the plant releasing natural defense compounds to deter the development of the pathogen (Fauteux et al. 2005). This is caused indirectly by binding specific cations or directly by increasing the activity of specific proteins.

Abiotic Stresses

Drought Stress

Si reduces the impact of abiotic stresses on plants. Attention to drought stress has increased with the extreme swings in rainfall patterns around the world in cultivated soils. Si applications have been shown to have a significant positive impact on a plant's ability to tolerate drought stress (Eneji et al., 2008). Yield increase has been observed in a variety of crops treated with Si when the crops are grown under moisture stress conditions (e.g., Eneji et al. 2008; Shen et al. 2010; Pei et al. 2010).

Drought stressed wheat plants that were treated with Si fertilizer retained greater stomatal conductance, relative water content, and water potential than un-treated plants. Treated leaves were larger and thicker, reducing the loss of water through transpiration (Gong et al. 2003; Hattori et al. 2005) and reducing overall water use efficiency (Eneji et al. 2005). In the case of rice, Si increased resistance to strong winds generated by typhoons (Ma et al. 2001b), related to the increased rigidity of the shoots through silification. Silicon fertilization enhances the development of secondary and tertiary cells of the endodermis which allows for increased root resistance in dry soils and a quicker growth of roots (Bouzoubaa 1991; Hattori et al. 2003, 2005). An additional benefit noted by Eneji et al. (2008) is that Si enhanced the uptake of major essential elements in a range of grass crops exposed to a water deficit.

Si applications also have an impact on other abiotic stresses including physical stresses such as lodging, temperature extremes, freezing and UV irradiation as well as chemical stresses from salt, metal toxicity and nutrient imbalance.

Salt Stress

Concern over quality of irrigation water and the salt toxicity that it causes in certain soils has heightened the awareness of the effect of Si on salt tolerance for a variety of crops. Matichenkov and Bocharnikova (2004) evaluated both dry and liquid forms of Si for the ability to mitigate stress to the plant brought on by drought as well as improving key soil properties. Their work in both the lab and greenhouse demonstrated that Si improved the soil water holding capacity and the basic chemical composition of the soil. Si applications also improved a plant's resistance to water or salt stress. It was also observed that Si could be used in conjunction with soil plastic-relief mapping to reduce the impact of irrigation water on salt build-up in the soil. In addition, a number of studies have demonstrated the direct benefit Si can have to increase yields in soils that are effected by salt stress including work by Ali et al., (2012) which showed when calcium silicate was applied to wheat plants grown in a hydroponic solution the wheat growth was enhanced as well as the K^+/Na^+ ratio. Na^+ uptake was reduced and K^+ uptake was increased.

Nutrient Regulation

Phosphorus

Si has been shown to affect the availability of phosphorus in the soil. Brenchley and Maskell (1927) and Fisher (1929) found that Si fertilization increased the yields of barley crops when soil phosphorus fertilization was limiting. It was observed that soil phosphorus was made more available to plants treated with Si.

Eneji et al. (2008) also observed the interaction between Si and P uptake and concluded that there was an effect in soil. Earlier studies had shown that the effect of Si applications under phosphorus deficient conditions could be due to an in-planta mechanism, suggesting an improved utilization of phosphorus, through an increase in phosphorylation (Cheong and Chan 1973) or a decrease in Mn concentration (Ma and Takahashi 1990). In contrast, when phosphorus was supplied in excess, Si limited P uptake and limited the appearance of chlorosis, likely related to reducing the transpiration rate (Ma et al. 2001b).

Potassium–nitrogen–calcium

Mali and Aery (2008a) studied the effect of Si on K uptake both in hydroponics and in soil. They observed that even when the concentration of Si was low there was an increase in uptake of K. This increase in K uptake was related to the activation of H-ATPase. Mali and Aery (2008a, 2008b) also reported an increase in absorption of N and Ca for cowpea and wheat fertilized with increasing doses of sodium metasilicate as well as an improvement in nodulation and N_2 fixation in cowpea. Yoshida et al. (1969) have shown that a decrease of erectness of rice leaves following excess of N application can be reduced if Si is applied as part of the nutrient solution.

Excess Metals

Contamination of soil with trace elements due to human activities and excess metals related to specific soil factors are common throughout the world. This pollution of the soil can affect physiological properties in plants including a decrease in plant biomass, an inhibition of photosynthesis and a disruption in the uptake of nutrients. There are numerous studies that support the positive impact of Si on the toxicity symptoms caused by the problem metals including heavy metals such as cadmium. The number of studies, which tend to prove that Si may reduce toxicity symptoms, are steadily increasing, especially for metals of serious concern such as cadmium (Sarwar et al. 2010).

Iron

Studies in rice suggest that Si applications increase a plant's root's ability to oxidize Fe, converting ferrous iron into ferric iron. The oxidation of iron reduces the uptake of iron which reduces its toxicity (Ma and Takahashi 2002). It has also been proposed that Si application to the soil could control Fe uptake from acidic soils by releasing OH- anions by roots after Si is supplemented (Wallace, 1993).It has also been proposed that Si application to the soil could control Fe uptake from acidic soils by releasing OH^- anions by roots after Si is supplemented (Wallace, 1993).

Aluminum

Several attempts have been made to explain the effect of Si when high levels of Al are present. Early work suggested that Si and Al interact in the soil to create subcolloidal and inert aluminosilicates. This will reduce phytotoxic aluminum concentrations in the soil solution (Li et al. 1996; Liang et al. 2007). Si may also promote the production of phenolic exudates from roots that would chelate free Al resulting in the reduction of Al absorption by corn roots (Kidd et al. 2001). In these situations, detoxification would be a mechanism external to the plant. It has also been shown that aluminum can be detoxified by in-planta mechanisms either by forming hydroxyl-aluminum silicates in the apoplast (Wang et al. 2004; Ryder et al. 2003) in roots or by a sequestration in phytoliths (Hodson and Sangster 1993; Hodson and Sangster 2002), resulting in a reduction of Al toxicity in the shoots.

Manganese, Cd, Cu, Zn

Manganese toxicity is reduced in Si-fertilized plants because Si increases Mn binding to cell wall limiting cytoplasmic concentrations (Liang et al. 2007; Rogalla and Romheld 2002). Horst et al. (1999) observed that Si application reduced the apoplastic Mn concentration in cowpea leaves, suggesting that Si may affect the cation binding capacity of the cell walls.

Additionally, it triggers a more homogenous distribution of Mn in leaves, limiting spot necrosis (Williams and Vlamis 1957; Horiguchi and Morita 1987; Ma et al. 2001b).

Si has effects in the soil and the plant impacting the uptake of trace metals like Cadmium (Cd), copper (Cu), or zinc (Zn) (Liang et al. 2007). Metal concentrations in plants may either decrease or increase upon Si application depending on the part of the plant and the specific metal. Reduced uptake of Cd following rice fertilization with furnace slag has been associated with an increase in soil pH which limits Cd uptake, reduction of root–shoot translocation, and changes in compartmentation within the plant cell (Liang et al. 2007; Shi et al. 2005). Da Cunha and Do Nascimento (2009) observed that the decrease in Cd and Zn concentrations in corn shoots grown on Cd- or Zn-contaminated soil that were treated with calcium silicate, resulted in an increase in shoot biomass due to changes in metal speciation in the soil rather than to pH increase (da Cunha et al. 2008). They also noted significant structural alterations in the shoots and suggested that the deposition of silica in the endodermis and pericycle of roots was responsible for corn tolerance to Cd and Zn stress. Hodge (2004) indicated that Si could affect root plasticity, thereby increasing stress tolerance. Neumann and zur Nieden (2001) found that Si affected zinc inside the plant as zinc can co-precipitate with Si in cell walls (Neumann et al. 1997), leading to less soluble zinc in plants. In addition, foliar application of Si decreased Cd concentration in rice grains and shoots while increasing plant biomass (Liu et al. 2009). The authors report that alleviation of Cd toxicity and accumulation in rice would be related to Cd sequestration in the shoot cell walls. This indicates also that Si would be able to enter leaves through the stomata. In metal-hyperaccumulating plants, Zn can be at least temporally associated to Si in vesicles or in the cytoplasm before Zn is being stored in vacuoles, leaving SiO_2 precipitates in the cytoplasm. Neumann and De Figueiredo (2002) suggested that this mechanism might be responsible for the high Zn tolerance of *Silene vulgaris*, *Thlaspi caerulescens*, or *Minuartia verna*.

Silicic acid also reduced the arsenic (As) concentration in rice shoots grown in hydroponics, and arsenic transport in roots was shown to share the same highly efficient pathway as Si, indicating that sufficient available Si in soil would be efficient at reducing As accumulation in rice shoots (Ma et al. 2008). A vast range of mechanisms has been proposed that could explain the alleviating effect of Si on metal stress in planta, especially in plant shoots. The role of soil and root factors in affecting metal uptake and reducing stress from metals on plants is still poorly understood and more work needs to be done (Kirkham, 2006).

Plant Growth Factors

Si applications have shown a significant effect on plant lodging and density of stands especially in cereal grain crops such as rice, wheat and barley. Deposits of Si in rice shoots enhanced the thickness of the culm wall and the size of the vascular bundles (Shimoyama, 1958) that results in a reduction in lodging. Strong winds that can increase lodging also act to desiccate the plant tissue. Si has be shown to be effective in preventing excess water loss by forming deposits on the hulls of rice.

Si also affects the erectness of plant leaves that can improve the amount of light a leaf can intercept, thereby improving photosynthesis. Work on specific plant cultivars has shown that as the amount of nitrogen added is increased the leaf erectness decreases. Si can counteract that negative effect of increasing N supply on light interception as well as reducing lodging (Idris et al., 1975).

Si has a beneficial effect on reducing stress caused by UV irradiation. Studies in rice indicate that Si applications reduces UV stress by increasing the biosynthesis of phenolic type compounds (Goto et al., 2003).

Summary

Seven out of the top ten crops are considered Si accumulators and Si applications have shown a range of beneficial effects to these plants, especially where the soil Si levels are low. Si has a significant impact on biotic and abiotic factors in plant growth and development including disease and insect resistance, drought stress, nutrient regulation, temperature stress, lodging and UV stress.

Current farming practices do not supplement soil Si levels as much of the grain and stover is removed through harvest. When Si is not returned to the soil through crop residue a net loss or reduction in soil Si levels occur. Si phytoliths are proving to be a valuable source of Si in the soil. The combination of the available Si coming from phytoliths and supplemental applications of Si from new sources will have a significant impact on crop yields around the world.

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