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# Role of silicon in counteracting abiotic and biotic plant stresses

**Divya Bhatt and Geeta Sharma**

### Abstract

Food security has been a major concern in India so to fulfil the nutritional needs of the people, numerous attempts are being made to defeat hunger. Since ages, the use of pesticides is thought of as an immediate solution to increase crop productivity but this strategy is leading to a drastic environmental stresses faced both by man and plants. So the need of the hour is to rely on eco-friendly approaches so as to be in harmony with nature. One of such approach is use of Silicon in our agricultural practices to combat various stresses as Silicon is continuously gaining serious attention since last few years due to its abundance and non-hazardous nature. Silicon nutrition is found to be helpful in abating many abiotic stresses including physical stresses such as drought, high temperature, flood, lodging, freezing, UV-radiation and chemical stresses such as salt, metal toxicity and nutrient deficiency. In context of biotic stresses, Silicon provides resistance to plants against diseases either due to an accumulation of absorbed Silicon in the epidermal tissue, or expression of pathogenesis-induced host defence responses. A better molecular understanding of Si uptake in plants is important to maximize the benefits derived from Silicon fertilization.

**Keywords:** silicon, biotic stress, abiotic stress, UV radiation, nutrient deficiency

### Introduction

Silicon is an element with symbol Si and atomic number 14. Due to its high chemical affinity for oxygen it widely occurs in the various forms of silica ( $\text{SiO}_2$ ) and silicates ( $\text{SiO}_3$ ) but rarely in its elemental form in nature. It was first prepared and characterized in pure form only in 1824 by Jöns Berzelius. The presence of Silicon as silica or silicates is widely found in dusts, sands, planetoids, and planets. Over 90 percent of the Earth's crust is composed of silicate minerals, making silicon the second most abundant element in the Earth's crust (about 27.7% by mass) after oxygen. Although silicon is readily available in the form of silicates, very few organisms use it directly. Diatoms and siliceous sponges use biogenic silica as a structural material for their skeletons. Their cell wall is made up of Silica and hence their essentiality has been found only in case of lower organisms. In more advanced plants, the silica are rigid microscopic bodies occurring in the cells for example in case of rice it has been observed through Scanning electron microscopy that Silica is prevalent all over the leaf surface while X-ray microanalysis showed that the quantity of Silicon was comparatively very high as compared to other elements present on the rice leaf surface, as rice needs silicon for their growth and development and hence found to be an essential element. Its beneficial effects on plant growth and yields have been repeatedly demonstrated particularly for rice crop (*Oryza sativa*) (Savant *et al.* 1997) <sup>[80]</sup>. Plants absorb silicon from the soil solution in the form of monosilicic acid (0.1-0.6 mM), and it can be regarded as a plant nutrient (Epstein 2009) <sup>[24]</sup>. Silicon is absorbed by the plant roots through a passive process regulated by transpiration stream, which occurs via the xylem along with water or by inactive process through transporters located in the plasma membrane of root cells. The absorbed silicon accumulates in the old tissues of the plants mainly in the walls of epidermal cells as polymerized monosilicic acid or amorphous silica ( $\text{SiO}_2 \cdot n\text{H}_2\text{O}$ ), which strengthens cell wall and increases the structural rigidity of tissues. Accumulation of silicon occurs in regions of maximum transpiration such as leaf epidermis near the stomatal guard cells, trichomes and thorns which mitigates the adverse effects of abiotic and biotic stresses (Dayanandam *et al.* 1983) <sup>[18]</sup>. For soil nutrient management, the abundance of silicon in the soil is interpreted differently. Because the agronomic value of silicon fertilization is well recognized in production agriculture, the research interest shifted in recent years, and many methodologies were established to

determine the plant-available silicon (Datnoff *et al.* 2001) [15]. Plants differ markedly in their ability to absorb silicon and concentration of Silicon in plants on the basis of dry weight varies between 0.1 – 10 percent (Liang *et al.* 2007) [52]. Silica concentration is found to be higher in monocotyledons (10-15%) as compared to dicotyledons (0.5% or less) and its level shows an increase from: legumes <fruit <vegetables <grasses <grain crops (Thiagalingam *et al.* 1977) [95]. The aerial plant parts accumulate more silicon than roots. The absorption capacity of different plant species may vary such as sugarcane can absorb 300-700 kg of silicon/hectare, rice can absorb 150-300 kg of silicon/ hectare whereas wheat plants can absorb 50-150kg of Silicon/ hectare from the soil (Bazilevich 1993) [2].

#### Categories of plant based on silicon accumulation

Silicon accumulation in plant tissues leads to the categorization of plants like (i) Accumulator- those plants that accumulate more than 1.5 percent Silicon content in their tissues (Rice, Sugarcane, Lentil) (ii) Intermediate Accumulator- those having Silicon in the range of 0.5-1.5 percent (Cucumber, Pumpkin, Rose, Marigold) and (iii) Non-Accumulator- those plants having less than (0.5 percent Silicon content in their tissues (Tomato and Sunflower) (Takahashi *et al.* 1990) [91].

For the high silicon-accumulator crops the removal of silicon from the soil is significantly higher than the removal in natural systems. With years of continuous and intensive cropping, the harvest of silicon-accumulator crops results in a significant reduction in the amount of plant-available silicon in soils (Meunier *et al.* 2008) [60].

#### Role of Silicon in Plants

Silicon promotes the growth of plants. In many instances the growth stimulation was due to the protection that Si afforded plants can withstand against the detrimental effects of abiotic and biotic stresses. Silicon provides strength and rigidity to the cell wall, improves growth, health and productivity (Rafi *et al.* 1997) [69], develop potential to withstand drought, frost and salt stresses and decreases lodging, boosts the plant's resistance against insects, pests and disease causing pathogens (Guntzer *et al.* 2012) [33]. Its beneficial effects on plant growth and yields have been repeatedly demonstrated particularly for rice crop (*Oryza sativa*) (Savant *et al.* 1997) [80].

Although Silicon is considered as non-essential for plant growth, but it helps in alleviation of biotic and abiotic stresses faced by the plants (Fautex *et al.* 2005, Fautex *et al.* 2006 and Vivancos *et al.* 2015) [25, 26, 99]. Abiotic stresses like water stress, salt/ion toxicity, air pollution and biotic stresses like pathogen and insects that cause heavy losses in the crops. Many studies have found that abiotic stresses cause heavy losses as compared to biotic factors as former are not under control of humans. Although there are various types of abiotic stresses but studies have found that silicon is able to alleviate only a few of them.

Plant responses to different stresses are highly complex and involve changes at the transcriptome, cellular, and physiological levels. Recent evidence shows that plants respond to multiple stresses differently from how they do to individual stresses, activating a specific programme of gene expression relating to the exact environmental conditions encountered. Rather than being additive, the presence of an abiotic stress can have the effect of reducing or enhancing susceptibility to a biotic pest or pathogen, and vice versa.

#### Silicon in Alleviation of Abiotic Stress

Silicon nutrition alleviates many abiotic stresses including physical stress like lodging, drought, UV-radiation, high temperatures, freezing and chemical stresses like salt, metal toxicity, nutrient imbalance (Epstein 1994 and Ma and Yamaji 2006) [22, 54].

#### Alleviation of Metal Toxicity

Use of acid fertilizers results in soil acidification, decrease soil pH and fertility and it also enhances metal toxicity by increasing the availability of manganese (Mn). Thus silicon fertilizers being slightly basic in nature will be able to reduce the acidification of the soil. Toxicity of heavy metals such as cadmium (Cd), copper (Cu), zinc (Zn) and manganese (Mn) was reduced in silicon fertilized plants because silicon increased metal binding capacity to the cell walls which limits cytoplasmic concentration of the heavy metals (Liang *et al.* 2007) [52]. Silicon and aluminium (Al) interact in the soil and form subcolloidal and inert alumino-silicates and reduces the concentration of phytotoxic aluminium in soil solution (Liang *et al.* 2007) [52]. Silicon binds with different metals and prevents their concentration to toxic levels at localized sites. Iron, manganese and aluminium are found to be less toxic in the presence of silicon as observed in silicon accumulator plants. Silicon facilitates the uptake of P, Mg, K, Fe, Cu and Zn (Chen *et al.* 2000) [9].

#### Alleviation of Drought Stress

Drought stress is of increasing concern because of its adverse impact on crop production. The positive effect of silicon utilization on biomass and yield under deficit irrigation has been observed in various crops (Pei *et al.* 2010, Shen *et al.* 2010) [68, 84]. Silicon deposited in the plant tissues helps to alleviate water stress by decreasing transpiration and improves light interception by keeping the leaf blade erect in position (Epstein 1999) [23]. Wheat plants which were subjected to drought stress and treated with silicon maintained higher stomatal conductance, relative water content, water potential and leaves were also larger, thicker and thereby show reduced water loss through transpiration (Hattori *et al.* 2005) [34]. Ma *et al.* (2001) [53] found that silicon increased resistance in rice plants because of the rigidity gained by the silicification of shoots. It has been found that silicon fertilization helps in the development of secondary and tertiary cells of the endodermis and allows better root resistance in dry soils and faster growth of roots (Hattori *et al.* 2005) [34]. Eneji *et al.* (2008) [21] observed that silicon enhanced uptake of major essential elements by various grasses exposed to drought conditions. Silicon fertilizer has been reported to increase frost tolerance capacity in lemon and sugarcane (Matichenkov and Calvert 2002) [57]. Si has also been shown to decrease drought stress in plants through different mechanisms, which include an increase in mineral nutrient uptake, modification of gas exchange attributes, osmotic adjustment, reduction in oxidative stress, modification of gene expression, and regulation of compatible solutes and phytohormone synthesis (Rizwan *et al.* 2015) [75].

#### Alleviation of Salt Stress

Silicon may alleviate salt stress by inhibition of transport of Sodium ions to the leaves and specific accumulation of these ions in the roots (Tuna *et al.* 2008) [97]. It alleviates salinity stress in tomato seedlings by increasing photosynthesis, leaf transpiration rate and stomatal conductance and by decreasing the concentrations of Na<sup>+</sup> and Cl<sup>-</sup> in the leaves, stem and

roots (Li *et al.* 2015)<sup>[50]</sup>. One of the mechanisms of silicon was its improvement to activity of plasma membrane H<sup>+</sup>-ATPase, tonoplast membrane H<sup>+</sup>-ATPase and H<sup>+</sup>-pyrophosphates of Aloe root under salt stress. When under salt stress, plants maintain a high concentration of K<sup>+</sup> and a low concentration of Na<sup>+</sup> in the cytosol. They do this by regulating the expression and activity of K<sup>+</sup> and Na<sup>+</sup> transporters and of H<sup>+</sup>pumps that generate the driving force for transport. Although salt stress sensors remain elusive, some of the intermediary signaling components have been identified. Evidence suggests that a protein kinase complex is activated by a salt-stress-elicited signal. The protein kinase complex then phosphorylates and activates various ion transporters, such as the plasma membrane Na<sup>+</sup>/H<sup>+</sup> antiporter, thus Na<sup>+</sup> is discharged into the space outside plasma membrane and/or separated in vacuoles. H<sup>+</sup>-pumps mainly consist of PM- H<sup>+</sup>-ATPase and TP- H<sup>+</sup>-ATPase, as well as TP-H<sup>+</sup>-PPase. H<sup>+</sup>-ATPase and H<sup>+</sup>-PPase are integral membrane proteins, they hydrolyze ATP or pyrophosphoric acid, transfer H<sup>+</sup> across membranes, form membrane electro chemical proton potential gradient, and thus promote ion absorption and proton driving force of across membrane (Zhang and Liu 2002)<sup>[102]</sup>. Therefore, PM-H<sup>+</sup>-ATPase provides motive force for absorbing K<sup>+</sup> and excreting Na<sup>+</sup> through Na<sup>+</sup>/H<sup>+</sup> anti-transport protein. TP-H<sup>+</sup>-ATPase and TP-H<sup>+</sup>-PPase provide motive force for the compartment of salt ions in vacuole. H<sup>+</sup>-pumps also promote the secondary transport of nutrients, pH homeostasis, cell elongation, stomatal opening and so forth (Mansour *et al.* 2003)<sup>[56]</sup>. Because absorption, discharge and immobilization of K<sup>+</sup>, Na<sup>+</sup> and other ions are mainly influenced by membrane potential and proton gradient, plant salt tolerance can be significantly influenced by ion pump activities via acting on the membrane potential and proton gradient (Chinnusamy *et al.* 2005)<sup>[11]</sup>. Cultivation of Cape gooseberry (*Physalis peruviana*) *in vitro* revealed it as a non-tolerant plant to salt stress. The use of an exogenous silicon source is an alternative to ameliorate the stress generated, and in the case of this study, the silicon is effective to mitigate the damage to the photosynthetic pigments, number of stomata, and leaf blade thickness (Rezende *et al.* 2017)<sup>[74]</sup>.

#### Alleviation of low temperature stress

Many studies have found that Si can alleviate freezing stress and can enhance plant growth under freezing stress. Studies conducted in wheat cultivars showed that the major antioxidant enzyme activities and non-enzymatic antioxidants (i.e. glutathione and ascorbic acid) in the leaves of freezing-stressed plants were decreased, but were stimulated significantly by the exogenous Si. The possible mechanisms for Si enhanced freezing stress may be attributed to the higher antioxidant defence activity and lower lipid peroxidation through water retention in leaf tissues. Mechanisms of Silicon induced freezing tolerance have been proposed based on the biochemical and physiological changes related to freezing injury (Mc Kersie 1991)<sup>[58]</sup>.

#### Alleviation of Ultraviolet-B Radiation Stress

Rising solar UV-B levels resulting from anthropogenic thinning of the stratospheric ozone layer have increasingly attracted the attention of environmentalists and governments world-wide. UV-B stress has potential deleterious effects on agricultural production (Hideg *et al.* 2013)<sup>[38]</sup>. Under enhanced UV-B radiation, light-sensitive matters such as phenols and aromatic amino acids transfer the received

radiation energy to neighbouring oxygen molecules, as well as other UV-B-induced NADPH oxidation and/or peroxides, leading to increased reactive oxygen species (ROS) free radicals (Brosche and Strid 2003<sup>[4]</sup> and Zlatev *et al.* 2012<sup>[103]</sup>). Sequentially, this damages such macromolecules as DNA and proteins (e.g. PSII D1 protein) and consequently increases lipid peroxidation and membrane permeability, thus inhibiting plant growth (Alexiev *et al.* 2001<sup>[1]</sup> and Parihar *et al.* 2015<sup>[66]</sup>). The DNA is particularly sensitive to UV-B radiation which causes photo-transformations, resulting to the formation of pyrimidine dimers like cyclobutane pyrimidine dimers (CPDs) and pyrimidine (6-4) pyrimidinone dimers (6-4 PPs), thus hindering transcription and duplication of DNA (Kalbin *et al.* 2001)<sup>[43]</sup>. Of these, cyclobutane pyrimidine dimer (CPD), a characteristic photo product of ultraviolet irradiation, accounts for about 75 percent of UV-induced photoproducts and is the principal cause of UV-B-induced growth inhibition in plants and it is more frequently measured to detect UV-induced damage to DNA (Hidema *et al.* 2007)<sup>[39]</sup>. Plants respond differently depending on the level of UV-B irradiation by either stimulating protection mechanisms or activating repair mechanisms. The most common defence mechanism are the biosynthesis of UV-absorbing compounds, reactive oxygen scavenging compounds and enzymes, pathogenesis-related defence proteins and DNA repair mechanisms (Brosche and Strid 2003)<sup>[4]</sup>. The DNA is particularly sensitive to UV-B radiation and can readily be damaged by UV-B stress, resulting to the formation of photoproducts like cyclobutane pyrimidine dimers (CPDs). Silicon often has been extensively reported to improve plant tolerance of UV-B radiation by fortifying the cell wall and activating defence mechanisms. As an effective UV-B protectant, silicon provide protection against UV-B-induced CPD formation in three ways (i) repair mechanisms- damaged DNA is repaired by photolyase of cyclobutane pyrimidine dimers (CPD) (ii) avoidance mechanisms - epidermal screening of UV-B radiation by accumulation of UV-B absorbing compounds like phenolic compounds and (iii) antioxidation mechanism - formation of antioxidants like ascorbate (Epstein 1999<sup>[23]</sup> and Guntzer *et al.* 2012<sup>[33]</sup>). In dicotyledonous plants, exogenous Si significantly mitigated the membrane damage caused by UV-B radiation (Shen *et al.* 2010)<sup>[84, 85]</sup>.

#### Alleviation of nutrient deficiency stress

A probable underlying mechanism might involve the chelation of Fe bound in root apoplast by secreted phenolics, thus making it available for the reduction-based uptake by root cells and translocation to the upper plant parts. It has been proposed that soluble Si acts as a modulator of plant resistance to pathogens, including increased production of phenolics (e.g. lignin and phytoalexins) in response to fungal infection (Fautex *et al.* 2006)<sup>[26]</sup>. To date, Si-modulated changes in phenol metabolism have been reported in Al-exposed corn roots (Kidd *et al.* 2001)<sup>[47]</sup> as well as in the roots of cucumber subjected to high Mn concentrations (Dragisic *et al.* 2007)<sup>[20]</sup>. The shikimate pathway is typically described as a link coupling carbohydrate metabolism with the biosynthesis of aromatic compounds via the phenyl propanoid pathway (Herrmann and Weaver 1999)<sup>[37]</sup>. An increased synthesis of phenylpropanoids and terminal flavonoids in the symplast may then facilitate their secretion into the apoplast. Si can influence the carboxylate, shikimate and phenylpropanoid metabolism as well as the accumulation of riboflavin in cucumber roots. It is obvious that Si, either in

solid form of plant opal or by its mere presence as a soluble orthosilicic acid, cannot directly influence the metabolome of unstressed plants, but Si can act as an enhancer or positive modulator of cell responses to Fe deficiency. Many researches showed the results that the role of Si in alleviation of Fe deficiency (chlorosis) includes an increase of the apoplastic Fe pool in the roots, and an enhancement of Fe mobilization in the roots due to Si-mediated biosynthesis of Fe chelating compounds. In perspective, these findings may be of practical importance in the development of new sustainable measures for controlling Fe chlorosis in calcareous soils, which in general are low in available Si (Epstein 2009) [24].

#### Alleviation of biotic stresses

Biotic stress is defined as a stress that is caused in plants due to damage instigated by other living organisms, including fungi, bacteria, viruses, parasites, weeds, insects, and other native or cultivated plants (Newton *et al.* 2011) [63]. Besides abiotic stresses, biotic factors are another restraint to global agricultural potency. Pests and pathogens have become tolerant to the use of conventional methods to improve agricultural production. This has resulted in low yields of crops worldwide.

#### History related to role of Silicon with relation to Plant Pathology

Onodera (1917) [65], a Japanese plant nutrient chemist, the first researcher who suggested that Silicon was involved in rice resistance to blast. He published a milestone paper entitled 'Chemical studies on rice blast disease'. This was the first report on Silicon research published in a Scientific Journal of Agronomy. Kawashima (1927) first demonstrated that under controlled conditions application of Silicon to rice plants increased resistance to blast as well as increased Silicon content in rice. The amount of silicon applied to soil and the concentration of silicon in rice husks and straw had a linear relationship and both were inversely proportional with blast severity (Kawashima 1927) [45]. Inokari and Kubota (1930) [41], Ito and Hayashi (1931) [42] and Miyake and Ikeda (1932) [61] confirmed the beneficial effects of silicon application in conferring resistance against blast.

Silicon has significantly contributed to the reduction in intensity of various economically important diseases in monocotyledon and dicotyledon species (Belanger *et al.* 1995 [3], Datnoff *et al.* 1997 [14], Datnoff *et al.* 2007 [17], Kiirika *et al.* 2013 [48], Resende *et al.* 2009 [73] and Silva *et al.* 2010 [88]). Datnoff *et al.* (2001) [15] reported a significant reduction in severity of brown spot disease. However, the beneficial effects of Silicon have been primarily reported for resistance against fungal plant pathogens (Cherif *et al.* 1994 [10], Rodrigues *et al.* 2003 [76], Tesfagiorgis and Annegarn 2013 [93] and Tesfagiorgis *et al.* 2014 [94]). In pathosystems involving plant pathogenic bacteria, the effects of Silicon have not been widely studied. Although the effect of Silicon on plant disease control is still poorly understood, plant resistance to disease is considered to be either due to accumulation of absorbed Silicon in the epidermal tissue or expression of pathogenesis-induced host defence responses. Accumulated monosilicic acid polymerizes into polysilicic acid and then transforms to amorphous silica, which forms a thickened Si-cellulose membrane (Hayasaka *et al.* 2008) [35]. By this means, a double cuticular Silicon layer protects and mechanically strengthens plants. Silicon also might form complexes with organic

compounds in the cell walls of epidermal cells, therefore increasing their resistance to degradation by enzymes. Research also points to the role of Silicon in plant as being active since phenolic compounds, phytoalexins, glucanases, peroxidase and PR-1 transcripts were all found to be associated with limited colonization by a number of fungal plant pathogen (Rodrigues *et al.* 2003) [76]. Recently, a number of pathogenicity or stress-related genes were found to be either up- or down- regulated by Silicon at both the physiological and molecular level suggest that Silicon might be mediating defence reactions to plant diseases, Brunings *et al.* 2009 [5] and Chain *et al.* 2009 [7].

#### Alleviation of bacterial diseases

Silicon-induced resistance has been suggested as a potential mechanism for controlling bacterial diseases. Silicon in roots plays a role in the signalling network and can induce resistance systemically in other organs (Fawe *et al.* 2001 [28] and Silva *et al.* 2010 [88]). Silicon's role in the induced resistance may be due to its effect in strengthening cell wall structures, increasing lignification or activating specific mechanisms, such as phytoalexins production and pathogenesis related (PR) proteins synthesis (Cherif *et al.* 1994 [10], Fawe *et al.* 2001 [28], Menzies *et al.* 1991 [59] and Silva *et al.* 2010 [88]). Silicon application in bacterial disease control was suggested by Conceicao *et al.* (2014) [12] when they sprayed potassium silicate alone or in combination with the yeast *Rhodotorula aurantiaca* LMA1 which increased the activity of polyphenol oxidase and ascorbate peroxidase in melon leaves, respectively. Moreover, the silicon-induced basal resistance was demonstrated when Si (1.0 g SiO<sub>2</sub> /L of substrate) reduced the area under the disease progress curves of tomato bacterial wilt for the King Kong 2 and Hawaii 7998 genotypes, respectively, by 34 percent and 81 percent (Diogo and Wydra 2007) [19]. According to these authors, this resistance is expressed at the cell wall level and in pit membranes that are preferred by the pathogen for movement within the plant. Ghareeb *et al.* (2011) [31] research supported the idea that Si induces basal defence but their work also suggested that it induces a priming effect because changes in the expression of defence genes were mainly observed after challenging the Si-treated plants with *Ralstonia solanacearum*.

#### Alleviation of fungal stresses

The accumulation of silica induces resistance by (i) playing a mechanical role as a barrier for the invading pathogen either by reducing the rate of progress of the disease or by restricting the lesion size and production of spores for secondary infection (Seebold *et al.* 2001) [83] and (ii) by inducing host resistance by enhancing the levels of preformed inhibitors like phenolics or by mediating the synthesis of post infectionally formed antifungal phytoalexins or by activating oxidative enzymes (Fautex *et al.* 2005) [25]. Silicon nutrition suppressed the leaf and neck blast, brown spot, sheath blight, leaf scald, grain discoloration, stem rot and bacterial leaf blight infection in rice (Datnoff and Rodrigues 2005 [16], Gangopadhyay and Chattopadhyay 1975 [30] and Winslow 1992 [100]). Silicon application at 1000 kg/ha through calcium silicate reduced neck blast by 30.5 percent and brown spot by 15.0 percent over the control (Datnoff and Rodrigues 2005) [16]. It was found to suppress ring spot in sugarcane, root rot and powdery mildews in cucumber (Menzies *et al.* 1991) [59].

## Mechanisms involved in silicon-mediated disease resistance against fungi

### (A) Physical Mechanisms

The beneficial effects of Silicon on plant growth are attributed to improve overall mechanical strength and an outer protective layer (Epstein 1999 <sup>[23]</sup> and Sun *et al.* 2010 <sup>[89]</sup>). Silicon accumulates in the cell wall of plants and form Silicon-cellulose network which acts as a mechanical barrier against pathogen (Takahashi *et al.* 1977) <sup>[90]</sup>. Successful infection requires plant pathogens to enter the host plant by penetrating physical barriers including wax, cuticles, and cell walls (Lazniewska *et al.* 2012 <sup>[49]</sup>, Nawrath 2006 <sup>[62]</sup> and Schmelzer 2002 <sup>[82]</sup>). Silicon-enhanced resistance is associated with the density of silicified long and short epidermal cells, the thick layer of silica under the cuticle, the double cuticular layer, the thickened Silicon cellulose membrane, formation of papilla, and complexes formed with organic compounds in epidermal cell walls that strengthen plants mechanically. The physical barriers inhibit pathogen penetration and make plant cells less susceptible to enzymatic degradation caused by fungal pathogen invasion, Datnoff *et al.* 2007<sup>[17]</sup>, Fautex *et al.* 2005 <sup>[25]</sup>, Inanaga *et al.* 1995 <sup>[40]</sup> and Van *et al.* 2013 <sup>[98]</sup>. Most Silicon is cross-linked with hemicellulose in cell walls, which improves mechanical properties and regeneration, Guerriero *et al.* 2016 <sup>[32]</sup>, He *et al.* 2015 <sup>[36]</sup>.

### (B) Biochemical Mechanisms

Silicon-enhanced biochemical resistance is associated with (i) increasing the activity of defence-related enzymes, such as polyphenoloxidase, glucanase, peroxidase, and phenylalanine ammonia-lyase (PAL), (ii) inducing antimicrobial compounds production, such as phenolic, flavonoids, phytoalexins and pathogenesis-related (PR) proteins in plants and (iii) regulating systemic signals, such as salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) Datnoff *et al.* 2007 <sup>[17]</sup>, Fautex *et al.* 2005 <sup>[25]</sup>, Van *et al.* 2013 <sup>[98]</sup>. It also reduces the rate of progress of the disease by restricting the lesion size and production of spores for secondary infection. It may be due to the formation of papillae, deposition of callose and H<sub>2</sub>O<sub>2</sub>, up-regulation of phenyl propanoid pathway and by stimulating systemic stress signals like salicylic acid, jasmonic acid and ethylene (Shetty *et al.* 2012) <sup>[86]</sup>.

### (C) Molecular Mechanisms

Silicon is involved in the metabolic processes of plant-pathogen interaction, activating defence genes of host plants via a series of physiological and biochemical reactions and signal transductions, as well as inducing the resistance response in plants to prevent plant diseases (Fautex *et al.* 2005, Vivancos *et al.* 2015) <sup>[25, 99]</sup>. Silicon may act in the primary response and modulate the activity of post-elicitation intracellular signaling systems which regulate the expression of defence genes related to structural modifications of cell walls, hypersensitivity responses, hormone synthesis, antimicrobial compound synthesis, and PR proteins (Fautex *et al.* 2005) <sup>[25]</sup>. Transcriptomic and proteomic studies have been conducted to illustrate the defence responses of Silicon in various pathosystems (Chain *et al.* 2009, Fautex *et al.* 2006, Ghareeb *et al.* 2011, Majeed *et al.* 2010, Nwugo and Huerta 2011) <sup>[64, 7, 26, 31, 35]</sup>.

### Alleviation of Nematode Infection

Plant-parasitic nematodes represent an important limiting factor in sugarcane agriculture (Cadet and Spaul 2005) <sup>[6]</sup>. However, due to the irregular efficacy of conventional

nematicides and the disappearance of many registered products, alternative control methods are needed. A control method based on nutrient-induced resistance, particularly one where organic amendments are added to the soil, would be ideal for sugarcane cultivation as growers could fertilise their crops, protect against nematodes and provide additional organic matter with the inclusion of organic products available from many sugar mills. The work reported here investigated the effect of applying sugarcane by-products (bagasse, filtercake, fly ash) and a by-product from the paper industry (thume) on uptake of Si by the sugarcane plant and whether this uptake of Si has an effect on the nematodes associated with sugarcane. It is presumed that the mechanism of Si-induced resistance in the plant is based on the hardening of the plant tissues (Keeping *et al.* 2009) <sup>[46]</sup> and/or the triggering of physiological defences Fautex *et al.* 2005 <sup>[25]</sup>, Fautex *et al.* 2006 <sup>[27]</sup>. However, the distribution of Silicon in sugarcane roots has not received much attention. To our knowledge only one such publication exists by Parry Kelso (1977) <sup>[67]</sup> which showed that Silicon aggregates in the sett and shoots & roots of sugarcane in the inner tangential wall of the endodermis. In most other plants of Gramineae family, Si has been found mostly in the endodermal root cell walls and also in the epidermal layer, Sangster 1978 <sup>[78]</sup>, Sangster and Hodson 1992 <sup>[79]</sup>. Endodermal cells are as deep as 50 µm in the root tissues. Assuming that cell walls of the endodermis, cortex and epidermis were harder from Si deposition, the long and flexible stylets of the two ecto parasitic genera found in the rhizosphere of higher Si plants, the *Criconematid* spp. and *Xiphinema* spp., average stylet length, 106 and 150 µm, respectively (Tarjan and Luc 1963)<sup>[92]</sup>, gave them the option of accessing the deeper, softer cell layer, by pushing their stylet between the external cells, to feed even behind the endodermal layer. Consequently, their multiplication will not be affected by the presence of Si and might even be favoured by the lack of competition from the disadvantaged genera (*Helicotylenchus* and *Pratylenchus* spp.). In contrast, the other three ectoparasitic genera, with a stylet length of 26 µm for *Helicotylenchus* spp., 28 µm for *Scutellonema* spp. and 30µm for *Paratrichodorus* spp. Siddiqi (2000) <sup>[87]</sup>, could not access the deeper layers and would probably experience difficulties in perforating the external cell walls for feeding. The endoparasitic nematodes (*Meloidogyne* and *Pratylenchus* spp.) also have short stylets. However, *Meloidogyne* sp. does not perforate the epidermal cells for feeding. This genus enters the roots between the cells of the growing point and initiates the formation of giant cells, upon which it feeds, in the vicinity of the central cylinder (Wyss *et al.* 1992) <sup>[101]</sup>. It is assumed that Si is not accumulated in this region of the plant. The other endoparasite, the migratory *Pratylenchus* sp., which enters the root several times and which moves and feeds in the cortex will encounter problems with the hardening of the cortical cell walls. According to above hypothesis, their multiplication should be reduced in the Si-rich plants, as was observed by Fortuner (1976) <sup>[29]</sup>.

### Silicon reduces insect attack and pest incidence on plants

Literature indicates that a higher silicon content in the soil and growth medium reduced the incidence of several crop pests (Liang *et al.* 2006) <sup>[51]</sup>. In rice, it was reported that the application of Silicon sources for pest management can save the cost of expensive fungicides and insecticides (Datnoff *et al.* 1997) <sup>[14]</sup>. It has been observed that sucking pests and leaf eating caterpillars have a low preference for the silicified tissues than low silica containing succulent parts. Silicon

decreases the food intake, growth longevity, fecundity and population growth of xylem feeding by White Backed Plant Hopper, *Sogatella frucifera* (Salim and Saxena, 1992) <sup>[77]</sup>. Soluble silicon reduces reproduction capacity of phloem feeding aphids *Myzus persicae* in potato and wheat and white fly (*Bemisia tabaci*) in cucumber plants. The hardness of cane of sugarcane plants is due to a higher silica content which reduces the shoot borer attack (Rao, 1967) <sup>[72]</sup>. The attack of stem maggot, plant hopper, green leaf hopper and leaf folder on rice plants were reduced with silicon nutrition. Low silicon concentration in rice tissues is associated with increased susceptibility to insect pest and fungal diseases (Sawant *et al.* 1994) <sup>[81]</sup>. Whitefly (*Bemisia tabaci*) is important pest of cotton, wheat, cucumber and sugarcane which reduces their yield but soil or foliar application of silicon as calcium silicate increases the mortality of the nymphs of whitefly (Correa *et al.* 2005) <sup>[13]</sup>. Chang *et al.* (2002) <sup>[8]</sup> revealed that silicon fertilizer can shorten the leaf lesion caused by bacterial leaf blight up to 5-22 percent. Reduction in size of lesions was directly proportional to the reduction in the soluble sugar in the leaves due to the presence of silicon. The possible control measures of this disease is by using pesticides to control the vector, application of organic amendments, balanced application of NPK fertilizers and micronutrients in addition to rouging out infected plants at the early stage of infection. The current recommendations in management of the disease are through eco-friendly methods such as balanced application of nutrients, use of organic amendments and use of biocontrol agents. The above methods are proposed after experiencing the ill effects from indiscriminate use of chemical pesticides that resulted in environmental pollution and threat to food safety. Resistance of crops to plant diseases was attributed to many factors among which silica appears to play a major role. Of late, control of the pest problems in agriculture with natural substrates has been given much emphasis. Lignite Fly Ash (LFA) is one of the cheapest sources of silica and it is a by-product from the combustion of pulverized coal /lignite in thermal power plants of India. As the LFA contains significantly larger amount of silica (available silica – 430 ppm and water soluble silica – 35 ppm) and other elements, it has been suggested by many workers as an amendment or source of silica especially useful in disease management (Ramabadran and Karpagavalli 1995) <sup>[71]</sup>. In addition to reduction of the disease incidence, LFA application in crops like cholam, maize and sugarcane (Ragupathy 1989) <sup>[70]</sup> and rice (Karpagavalli, 1999) <sup>[44]</sup> also increased crop yield. Karpagavalli (1999) <sup>[44]</sup> stated that foliar application of silicon stimulated the photosynthetic capacity, marked by suppressed reducing sugars, starch phosphorylase and phosphate in the plants. The plants inoculated with virus showed 272 higher ortho-dihydroxy (OD) and total phenols compared with the healthy ones. The mean OD and total phenol contents of healthy and inoculated plants were 1.37; 2.75 and 2.29; 3.77 mg/g, respectively. Increase in phenolic content in plants due to pathogenic attack has been reported by Karpagavalli (1999) <sup>[44]</sup> and Thind *et al.* (1977) <sup>[96]</sup>. This study indicated that LFA is suited as a dust pesticide not only to tackle the white fly problem in papaya but also to reduce the incidence of papaya leaf curl disease. Further study with LFA application in papaya in relation to the silicification of leaf cells, nitrogen uptake and nitrogen metabolism will give a clearer understanding of the actual mechanism.

## Conclusion

Modern agricultural practices do not replenish the soil's

Silicon lost after harvesting. When Silicon is not returned to the soil through crop residue a net loss or reduction in soil Silicon levels occur. Si phytoliths are proving to be a valuable source of Silicon in the soil. The combination of the available Silicon coming from phytoliths and exogenous applications of Silicon from new sources will have a significant impact on crop yields around the world.

Silicon has numerous functions on plant physiology, and its most significant effects are focused on cell wall. The presence of silicon in the cell wall increases their strength, resistance to salinity, drought tolerance and photosynthetic activity. It supports root and foliage growth and leads to prevention of oxidative stress by antioxidant enzymes. Exogenous application of silicon was effective in mitigating several responses of biotic and abiotic stress damages by improving the plant water uptake and transport. The other important role of silicon in reducing the adverse effects of stress may be by improving soil conditions. Therefore, silicon could be used as a growth regulator to improve plant growth and resistance under stress conditions. There is need for applied research to evaluate water use efficiency and drought tolerance and resistance to disease and insects on more crops. Although Silicon is not considered to be an essential nutrient for plant but beneficial to many plants. In plants such as rice, Si fertilization even increases growth and yield in addition to reducing disease severity. As we learn more about the importance of silicon in plant physiology, we may find more ways to use this important element in plant health and disease resistance.

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