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**Dileep Kumar NT**
Department of Entomology, University of Agricultural Sciences, GKVK, Bengaluru, Karnataka, India

**Manjunatha KL**
Department of Entomology, University of Agricultural Sciences, GKVK, Bengaluru, Karnataka, India

**Rakshitha TN**
Department of Entomology, University of Agricultural Sciences, GKVK, Bengaluru, Karnataka, India

**Basavaraj N Hadimani**
Division of Entomology, ICAR- Indian Agricultural Research Institute, New Delhi, India

**Pampareddy**
Department of Entomology, University of Agricultural Sciences, GKVK, Bengaluru, Karnataka, India

**Corresponding Author:**
**Dileep Kumar NT**
Department of Entomology, University of Agricultural Sciences, GKVK, Bengaluru, Karnataka, India

# A review: Phytoliths for insect pest management

**Dileep Kumar NT, Manjunatha KL, Rakshitha TN, Basavaraj N Hadimani and Pampareddy**

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**Abstract**
Phytoliths are inorganic, non-crystalline silica ($SiO_2$) structures that form through the polymerization of monosilicic acid (H4SiO4) absorbed from the soil. These phytoliths play a crucial role in enhancing plant growth and development, especially under challenging environmental conditions. They contribute mechanical support and rigidity to plant tissues, act as a defense mechanism against herbivores, pests, and fungal infections, and also improve water regulation, overall plant growth, photosynthesis efficiency and finally yield. Modern agriculture mainly depends on use of synthetic pesticides for the management of harmful insect pests. Pesticides are found as common contaminants in soil, air, water ecosystems and produce adverse effect on non-target organisms present in various ecosystems. They can harm plants and animals ranging from beneficial soil microorganisms and insects, non-target plants, fish, birds and other wildlife. Silicon is the second most abundant element in the earth crust and silicon soil amendment and foliar application has been shown to enhance plant defenses against insect pests. Silicon-mediated resistance to herbivorous insects and the mechanisms primarily involves formation of physical or mechanical barriers, and biochemical/molecular mechanisms, where silicon (Si) can enhance and prepare plant defense systems against insects. In addition, silicon also known to interact with other plant nutrients and induce the plant resistance against insect pests. A high Si level could influence the availability of other nutrients in plants, such as nitrogen, inducing insects to consume greater quantities of high-Si-treated plants. In addition, a high silica content in plant tissue reduces its digestibility and palatability, consequently slowing the insect growth rate. The role of phytoliths as mechanical barriers, and enhancers biochemical defense pathways against insect herbivores is elucidated in this review.

**Keywords:** Silicon, resistance, insect pests, mechanical barrier, induced resistance

## Introduction
Many groups of plants are known to deposit microscopic particles of silica within and between the cells and tissues in solid form creating amorphous structures known as Phytoliths or silica bodies. The term “phytolith” was proposed by Ruprecht (1866). It is composed of two Greek words ‘phyton’ meaning plant and ‘lithos’ meaning stone, typically a plant stone. It is also called by different name like opal phytolith, plant opal and opaline silica. The term opal has been used because of the colour of the particles in reflected light (Shakoor, 2014) [25].

Silicon is the second most abundant element in the crust of the earth after oxygen, with a mean content of 28.8% (weight) and an occurrence that ranges from 0.52 to 47% (weight). Soils containing Si consisting of mainly poorly soluble quartz and crystalline silicates. Si is an important element in plant nutrition and plants take up Si in the form of Silicic acid [Si (OH)4], and is generally found in soils at concentration ranging from 0.1 to 0.6 mM (Tubana and Heckman, 2015) [32].

## Silicon in Soil
Silicon is present in the soil solution in different forms and occurs primarily as monomeric ($H_4SiO_4$, the plant bioavailable form), oligomeric or polysilicic acid. The numerous chains of $H_4SiO_4$ up to ten silicon atoms in length are classified as the oligomeric or low molecular-weight silica, whereas the polysilicic acids with a higher degree of polymerization are the polymeric or the high-molecular weight-silica. The monosilicic acid form is relevant to plant absorption and nutrition, whereas the polysilicic acid influences soil aggregation. The fractions of dissolved silicic acid in the soil solution are adsorbed onto a variety of solid

phases in soils, including clay particles and Fe and Al hydroxides (Sommer *et al*., 2006) [27]. A minimal reduction in the concentration of silicon in the soil solution is attributed to the adsorption by secondary clay minerals (Siever and Woodford, 1973). However, the Fe and Al hydroxides have strong adsorption capacity, which can remove significant amounts of dissolved silicon from the soil solution (McKeague and Cline, 1963; Cornell and Schwertmann 1996) [4].

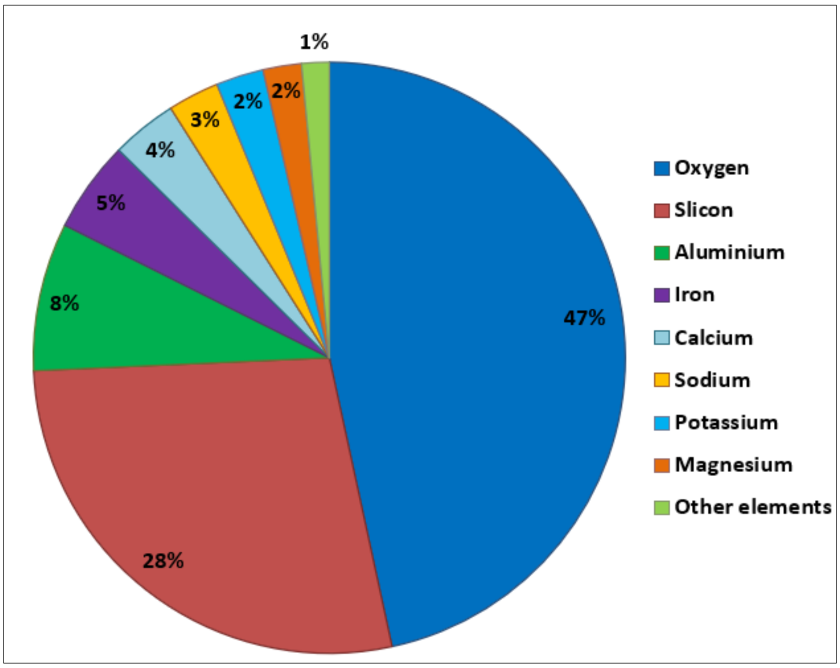


**Fig 1:** Composition of earth crust and percentage share of different elements to earth crust

**Silicon Cycle in Soil**

The solid, liquid, and adsorbed phases of silicon are the key components of the silicon cycle in soil. The liquid silicon phase consists of H4SiO4 and the polymerized and complexed silicic acid in soil solution, and the uncharged form ofH4SiO4 is the only form that is absorbed by plants and microorganisms. The absorbed silicon is later deposited as polymerized silica within the plant tissues or the cell structure of the microorganisms. These polymerized silica bodies return to the topsoil in the litter fall and the remains of microorganisms and eventually enter the highly soluble biogenic silica pool that contributes to the silicon in the soil solution. Silicon is also added to soils with applications of manure and compost, and the decomposition of silicon-rich manure can increase the level of available soil silicon. The natural waters used as irrigation may contain different forms of silicon, including ionic, molecular, and aggregate silicon. Silicon is also added to the soil in atmospheric deposition via windblown dust, ash and rain (Struyf *et al*., 2009) [29].

**Si in Plants**

Silicic acid, Si $(OH)_4$ is the bioavailable form of silicon in soil solution that is taken up by plant roots. Si is translocated through the xylem to the shoots where it condenses into polymerized silica gel. Concentration of Si in plants on the basis of dry weight varies between 0.1 - 10%.

A classification of plant species based on their ability to uptake Si and accumulate it in their tissues.

**1. Si accumulators**

Plants known as Si accumulators are characterized by active Si uptake that leads to a decrease of Si concentration in soil solution. The plants belong to this category are known to accumulate 10-15% Si on dry mass basis. Ex: Rice, Sugarcane and Bamboo

**2. Si intermediate**

Plants with an intermediate Si content perform passive Si uptake. The plants belong to this category are known to accumulate 1-3% Si on dry mass basis. Ex: Wheat (1-3% Si dry mass)

**3. Si excluders**

Plant species are rejective to Si and can able to accumulate less than 1% Si on dry mass basis. Ex: Tomato, Soybean and Cucumber

**Silicon deposition and formation of phytoliths in plants**

Si depositions as silica gel in plant in cell walls, cell lumens, trichomes, intracellular spaces, roots, leaves and reproductive organs. It is carried away towards various plant parts by transpiration stream through the vascular system. Upon transpiration, silicic acid gets concentrated in plant tissues as solid hydrated silica and it is precipitated as phytoliths. When plants die or decays, the phytoliths get incorporated into the soil. If soil conditions are right and if soil layers are buried, this phytoliths will also be preserved as fossils in rocks for many million years. (Nawaz *et al*., 2019) [18].

**Genetic background**

The gene responsible for Si uptake was first describes in rice plants. There are two types of genes namely, influx transporter gene and efflux transporter gene which are responsible for uptake and transport of Si from soil to various parts of the plant.

**Influx transporter gene (Lsi1)**

This gene assists the passive transport of Si across the plasma membrane to plant cells. The bio available form of Si, silicic acid present in the soil is taken up by roots with help of Lsi1 influx transporter genes.

**Efflux transporters gene (Lsi2)**

This gene is responsible for the transport of Si out of the plant root cells to the xylem. The process of transport of Si from plant roots cell to xylem is referred to as xylem loading, and it is under the influence of the Lsi2 efflux transporter gene.

Silica transportation in rice is mainly due to the presence of three low silica genes (LSi) i.e., LSi1, LSi2. LSi1 is a low silicon rice gene that belongs to aquaporin family, controlling the silicon accumulation in rice. LSi1 is primarily located in the basal zones of roots rather than at root tips. This gene is constitutively depressed in roots. LSi1 was localized on the plasma membrane of the distal side of both exodermises and endodermis cell where Casparian stripes are located. LSi2 is localized on the proximal side of the same cells. LSi1 shows influx transport activity for Si, while LSi2 shows efflux transport activity. LSi1 and LSi2 are responsible for transport of silica from root cells to the apoplast. Si in xylem sap is present in the form of monosilic acid and is unloaded by LSi6, a homolog of LSi1 in rice. LSi6 is a transporter involved in intravascular transfer i.e. transfer of silicon from the large vascular bundles to the panicles (Ma and Yamaji, 2011) [15].

**Role of phytoliths in plant resistance mechanisms**

The bio available Si absorbed by plants generally strengthens direct and indirect plant resistance to insect pests via the deposition of phytoliths, primarily in the epidermal cells of leaves, stems and roots. Two types of mechanisms counter insect pest attacks which includes physical or mechanical barriers and biochemical/molecular mechanisms in which Si can upregulate and prime plant defence pathways against insects.

**Si in plants enhance three type of defence mechanism against insect herbivore**

1. Physical defence.
2. Induced biochemical defence.
3. Nutritional defence.

**Silicon mediated physical defence to insect herbivores**

The bioavailable Si absorbed by plants generally strengthens direct and indirect plant resistance to insect pests via the deposition of SiO2 as biogenic opals (phytoliths), primarily in the epidermal cells of leaves, stems and roots. Silicon is deposited as a 2.5-µm-thick layer just beneath the cuticle layer (0.1 µm thick), forming a silicon-cuticle double layer in rice leaf blades. The abrasiveness of silicified leaves and other plant tissues associated with protection, storage, support and strengthening leads to the increased irreversible wear of mouthparts when insects are feeding, therefore deterring chewing insects. Si is involved in toughening plant tissues, acting indirectly by delaying insect penetration of host tissues and thus increasing the duration of insect exposure to natural enemies, adverse environmental conditions and chemical controls. A high silica content in plant tissue reduces its digestibility and palatability, consequently slowing the insect growth rate (Alhousari and Greger, 2018; Islama *et al*., 2020) [3, 7].

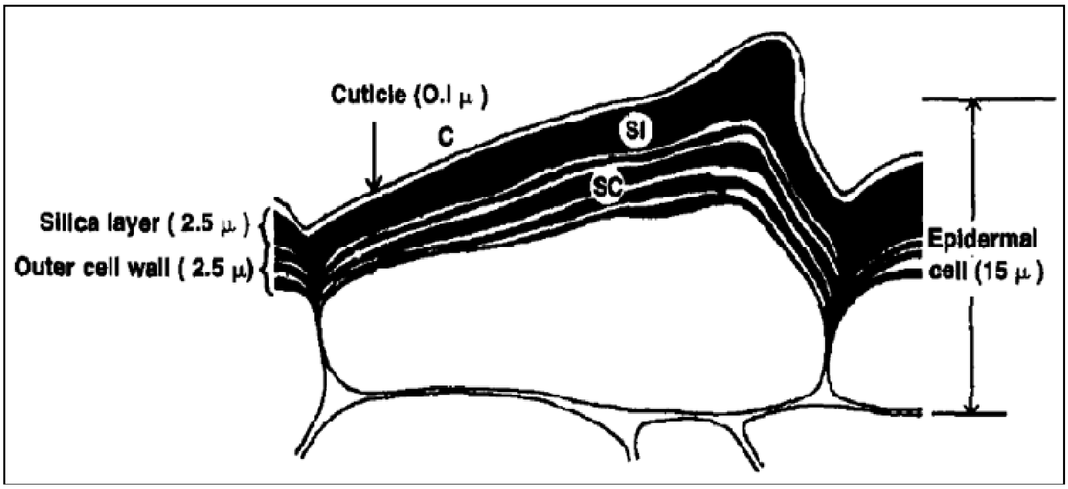


**Fig 2:** Cuticle Si Double layer in rice leaf blade (Source: Rao *et al.,* 2017)

The insect mid gut epithelium plays an important role in food digestion and conversion to nutrients by digestive enzymes, moreover, it is a site for insecticide detoxification. Si could damage the ultrastructure of the mid gut epithelium, mainly through detachment of epithelial cells from the basement membrane as observed in larvae of the leaf miner *Tuta absoluta* fed Si-treated leaves of tomato (Si excluder). This negatively affects the nutrient absorption and growth rate. It could also prevent insects from developing resistance to pesticides and could increase the efficacy of chemical controls combined with Si.

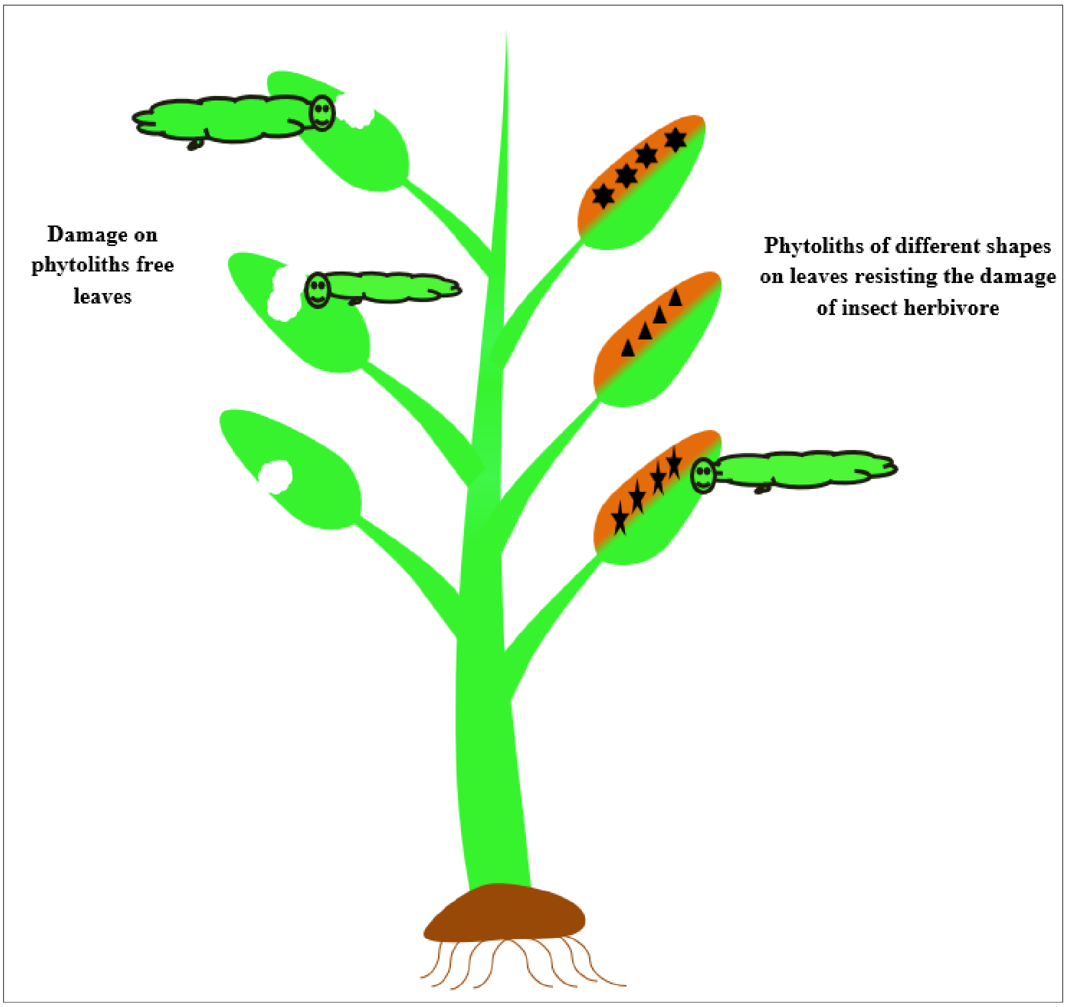


**Fig 3:** Silicon mediated defence against insect herbivore

### Induced biochemical defence

The use of plant resistance inducers is considered as an environmentally friendly strategy to efficiently decrease insect pest populations. In addition to acting as a mechanical barrier, Si can reduce pest damage by enhancing the induced chemical defences of plants following insect attack. Silicon acts as an abiotic elicitor of systemic stress signals, mediated by phytohormone pathways, leading to the efficient synthesis of defensive compounds. Plant defences are complex and can vary according to the feeding strategy of the insect pests (Islama *et al*., 2020) [7].

Each plant attacker has its own signal signature. The common phytohormones *viz*., salicylic acid (SA), jasmonic acid (JA) and ethylene play primary roles in orchestrating plant defence responses. JA is suggested to regulate defences against both cell-content-feeding and tissue-chewing insects. Defence against phloem-feeding insects is regulated by both SA and JA signals. Interestingly, evidence for the strong interaction between Si and JA against insects is accumulating, this being considered a possible mechanism by which Si enhances resistance to insect pests. Moreover, Si-induced resistance could also be expressed by priming the host plant to defend itself against insect pests attack. Priming is a process of sensitizing and preparing the plant's defence responses to be faster and stronger to future herbivorous insect threats (Leroy *et al*., 2019) [12].

### Nutritional defence

Silicon known to interact with other plant nutrients and induce the plant resistance against insect pests. A high Si level could influence the availability of other nutrients in plants, such as nitrogen, inducing insects to consume greater quantities of high-Si-treated plants. In addition, a high 12 silica content in plant tissue reduces its digestibility and palatability, consequently slowing the insect growth rate.

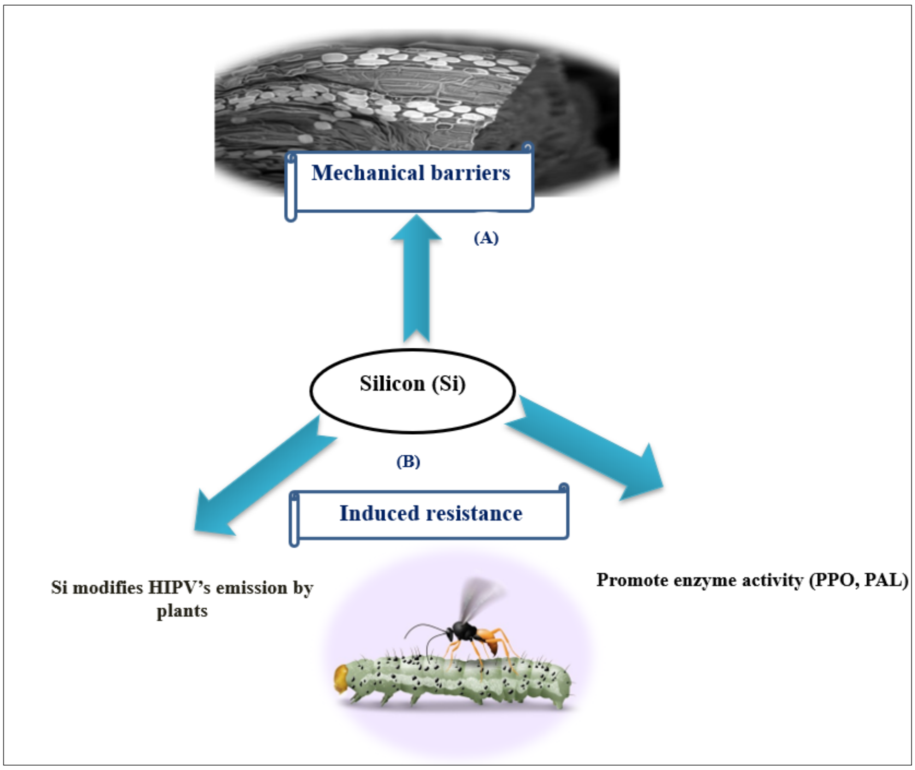


**Fig 4:** Silicon mediated defence against insect pests, A) Phytoliths formation acts as mechanical barriers for insect feeding B) Si application modifies the composition of herbivore induced volatiles released by plant, in turn volatiles are attractive to natural enemies of insect pest, and promotes activity of defense related enzymes (Alhousari and Greger, 2018) [3].

**Case history studies on silicon-mediated defence in plants against insect herbivores**

Rice, *Oryza sativa* L. is one of the most important staple crops in the world, providing a primary food source for more than half of the global population. The yellow stem borer (*Scirpophaga incertulas*) is an economically important pest of rice, causing significant damage to rice crop. Ranganathan *et al*., (2006) [23] found that application of silicon sources pyridine N-oxide (PNO), 4-morpholino pyridine N-oxide (MNO) and sodium meta silicate increases the plant growth characteristics (chlorophyll content and photosystem activity) and also induced the plant defense against the biotic stresses such as yellow stem borer and blast disease. The soil treatment with rice husk ash, a cheap renewable source of silicon and imidazole (a silicon solubilizer and carrier) were found to reduce the damage by yellow stem borer on rice. The application of orthosilicic acid @ 4ml/l as foliar spray four times during the cropping season was found to reduce the yellow stem borer incidence (1.51% dead heart and 3.33% white ear head) as compared to control treatment (5.0% dead heart and 11.44% white ear head) (Tripathy and Rath, 2017) [30]. Similarly, exogenous application of silicate fertilizers (diatomaceous earth) was found to enhance the resistance of rice plants to yellow stem borer (Panda *et al*., 2022) [19].

Sugarcane, *Saccharum officinarum* is a tall, perennial grass native to the tropical regions of Southeast Asia and New Guinea. It is cultivated primarily for its high sugar content, which is extracted from the stalks. This crop is prone to more than 200 insect pests; however, a dozen of insects causes severe damage. The *Silicon supplementation* on sugarcane was reported to enhance the defense against various abiotic and biotic stresses. Notably, silicon application imparts resistance against water stress, cold temperatures, arthropod invasion, and insect pests' infestations in sugarcane crops (Misra *et al*., 2023) [16]. On the same lines, Kvedaras and Keeping (2007) [10] revealed that sugarcane plants supplied with calcium silicate displayed the increased levels of resistance to attack by the borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae). Silicon treatment significantly decreased borer penetration, stalk damage and larval mass gain. Silicon appears to contribute to the suppression of *E. saccharina* directly through reduced larval growth and feeding damage to the crop, and indirectly by delaying stalk penetration, resulting most likely in increased exposure time of young larvae to natural enemies, adverse climatic factors, or control measures that target young larvae (Kvedaras and Keeping, 2007) [10]. The application of silicon at different dosage was found to enhance the available soil silicon, stalk silicon content and silicon deposition as phytoliths in epidermal tissue. The silicon deposition in soil and sugarcane plants negatively impact on stalk borer, *Chilo auricilius* (Priya *et al*., 2023) [20]. The early shoot borer, *Chilo infuscatellus* larvae fed on silica deposited plants lead to wear and tear of mandibles and in turn reduced the incidence on sugarcane (Priya and Kumar, 2023) [20]. Sugarcane top shoot borer *Scirpophaga excerptalis* Walker is one of the key insect pests of sugarcane. Rahardjo *et al*, (2021) [22] observed that supplying the organic silicate fertilizers was found to enhances the resistance against top shoot borer. Organic *Silica fertilizer* (compost) provides the same effect as inorganic *Silica fertilizer* in increasing the induction of sugarcane resistance to sugarcane top borer (*S. excerptalis*).

Maize is one of the important cereal crops grown in India. Fall armyworm, *Spodoptera frugiperda* is a new invasive species and has been occurring in serious proportions, causing significant damage to the maize crop, thus posing serious threat for maize production in the country. An experiment on the effect of silicon application to soil on growth and performance of fall armyworm reported that basal soil application of calcium silicate and foliar applications of silicic acid, gibberellic acid and potassium silicate was found to reduce the incidence of fall armyworm in maize (Srinivasan *et al*., 2023) [27]. Similarly, Haq *et al.* (2021) [6] recorded that foliar and soil application of silicon dioxide ($SiO_2$) and potassium silicate: ($K_2SiO_3$) was significantly induced the resistance of maize plants against fall armyworm. $SiO_2$ and $K_2SiO_3$ significantly was found to increase mortality percentage and developmental period and decrease larval and pupal biomass of fall armyworm. Similarly, both Si sources significantly reduced lipase activity of larvae, and fecundity of adults of fall armyworm. Under the field conditions, foliar and soil drenching applications of silicon dioxide to maize exhibited minimum FAW population density (Ghafar *et al*., 2023) [5].

Cotton (*Gossypium* spp.) stands as one of the most economically and agriculturally significant crops worldwide. As a key source of natural fiber, cotton supports an extensive global industry spanning textiles, apparel, and various consumer goods. The cotton crop is known to attacked by diverse array of insect pest species that target various stages of the cotton plant's growth cycle. The introduction of transgenic cotton led to secondary outbreak of miner pest species and causing significant loss in the yield of cotton. The whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) is a highly destructive and widespread sap-sucking pest that affects various economically significant greenhouse and field crops (Oliveira *et al*., 2001; Jones, 2003; Tay *et al*., 2017) [18, 9, 29]. The foliar application and soil drenching of silicon treatments ($SiO_2$ and $K_2SiO_3$) significantly reduced the oviposition preference of *B. tabaci*. Similarly, leaf discs harvested from plants treated with $SiO_2$ showed a significant decline in the number of oviposited eggs as compared to $K_2SiO_3$ treatments (Abbasi *et al*., 2020) [7]. Similarly. foliar application of silicon led to significantly higher silicon accumulation, reduced oviposition preference, and extended developmental periods for all nymph stages and the total life cycle of *B. tabaci*. Among the silicon sources tested, $SiO_2$ resulted in a notable decrease in egg deposition and a delay in the developmental period of *B. tabaci* with $K_2SiO_3$ showing somewhat less impact. Additionally, cotton plants treated with $SiO_2$ exhibited higher silicon levels in their leaves compared to those treated with $K_2SiO_3$ (Abbasi *et al*., 2022) [2].

Silicon (Si) is known to have a role in contributing to constitutive plant defence against insect pests, however, recent studies has illustrated involvement of silica in induced plant defences against insect herbivores. A study on the hypothesis that Si increases natural enemy attraction to pest-infested plants and improves biological control depicted that cucumber plants treated with potassium silicate significantly attracted adult of natural enemy, *Dicranolaius bellulus* to Si supplied plants upon which *Helicoverpa armigera* larvae had fed compared untreated plants. These results suggested that Si supplied to plants with a subsequent pest infestation increases the plants' attractiveness to natural enemies; an effect that was reflected in elevated biological control of *Helicoverpa armigera* in the field (Kvedaras *et al.*, 2010) [11].

Silicon (Si) build-up in plants can change their chemical makeup, which may enhance the attraction of natural enemies to insect herbivores on plants treated with Si. A case study on Si supplementation alters maize volatile compounds that mediate host location reported that Florida predatory stink bug, *Euthyrhynchus floridanus*, a generalist predator of fall armyworm would attracted more towards Si treated maize leaves than untreated plants. These results strongly suggested that Si supplementation to plants greatly enhances the biological control of fall armyworm (Zimba *et al*., 2022) [32].

Plant defenses can also work indirectly by producing herbivore-induced plant volatiles (HIPVs), which attract predators and parasitoids of the herbivores. These indirect defenses are generally mediated by the jasmonate pathway, however silica also found to involved in the alteration of HIPVs composition released by plants. A study on this hypothesis of Si supplementation alters the HIPVs and gas chromatography-mass spectrometry analyses showed lower production of α-bergamotene, β-sesquiohellandrene, hexanal 2-ethyl, and cedrol from +Si herbivore-infested plants compared with −Si infested plants. The variations in these biochemical compositions resulted in attraction of a greater number of *Trathala flavoorbitalis* parasitoid to Si supplemented rice plants which improved the biological control of rice leaf folder, *Cnaphalocrocis medinalis* on the crop (Liu *et al*., 2017) [13].

## Conclusion

Silicon plays a crucial role in enhancing plants' direct and indirect defenses against insect pests through two primary mechanisms: reinforcing physical barriers and triggering biochemical/molecular defense responses. Research across various plant species and insect feeding strategies shows that plants use both silicon-based resistance mechanisms together, integrating physical, chemical, and biochemical defenses to minimize insect damage. In addition, Silicon's influence on the emission of HIPVs might enhance the ability of natural enemies of pests to find their targets. Given the limited research so far and the vast array of potential plant-pest-natural enemy interactions, silicon's effect on tri-trophic relationships should be investigated across different plant models. When assessing volatile organic compound emissions from a plant, it's important to consider the effects of various types of insect herbivory.

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