PLANT SCIENCE TODAY
Vol 13(4): 1-16
https://doi.org/10.14719/pst.14025

eISSN 2348-1900
OPEN ACCESS

Review Article | [Agriculture]
2026, Volume 13, Issue 4, pp. 1-16

Silicon: A bio stimulant for plant defence against herbivores

Manisha Gautam[1], Samriti Sharma[1*], Prashant Chechi[2], Natasha Sharma Awasthi[2] & Priya Kamboj[3]

[1]Department of Biotechnology, University Institute of Biotechnology, Chandigarh University, Mohali 140 413, Punjab, India
[2]University Centre for Research and Development (UCRD), Chandigarh University, Mohali 140 413, Punjab, India
[3]Department of Applied Sciences, School of Engineering and Technology, Chandigarh Group of Colleges University, Mohali 140 307, Punjab, India

***Correspondence:** Samriti Sharma, 1992samritisharma@gmail.com

Abstract

Herbivorous performance mainly depends on the defensive and nutritional traits of the plants they consume. Herbivory can inhibit plant growth and yield, or may affect plant responses at morphological, physiological, biochemical and molecular levels. Plants have developed complex anatomical, physiological and biochemical protectors to recognise the herbivorous attacker and activate the appropriate defensive reactions. Plant defence mechanisms are divided into two categories: direct or indirect strategies. Direct defence involves physical barriers (e.g., trichomes), toxic chemicals (e.g., alkaloids) and antinutritional factors (e.g., protease inhibitors), whereas indirect defence involves the release of volatile compounds, which lure the herbivore's natural predators and thus reduce herbivore populations. Silicon (Si)-rich plants activate various defence responses and phytochemicals which alleviate different biotic and abiotic stresses, mainly against vertebrate and invertebrate herbivores. Silicon may form a discrete structure or deposit in the cell wall, which confers physical resistance to herbivory. Silicon may interact with the defence phytochemical pathways of herbivores and can enhance the production of secondary metabolites for defence. This review presents a comprehensive overview of the complex interactions between plants and herbivores and the relationship between Si-mediated defence responses and phytohormonal regulation of plant immunity and outlines potential future research areas for developing more sustainable pest management strategies.

Keywords: defence mechanism; herbivores; phytohormones; silicon-mediated plant defence

Received: 07 February 2026. **Accepted:** 11 July 2026. **Published:** Version 1.0: 03 October 2026; Version 2.0: 13 October 2026.

Cite this article: Manisha G, Samriti S, Prashant C, Natasha SA, Priya K. Silicon: A bio stimulant for plant defence against herbivores. Plant Science Today. 2026; 13(4): 1-16. https://doi.org/10.14719/pst.14025

1. Introduction

Over the previous 400 million years, plants and insects have engaged in an ongoing co-evolutionary arms race, resulting in shaping a diverse array of plant structural, biochemical and molecular defence systems alongside intricate insect adaptation mechanisms (1). Although mutualistic interactions, such as pollination, exist, herbivory exerts one of the most powerful selective pressures, driving the evolution of complex plant defence strategies. To mitigate the effects of insect herbivory, plants have evolved complex multilayered defensive mechanisms, which encompass both constitutive structural barriers such as trichomes, thorns and fortified epidermal tissues in addition to inducible biochemical responses that involve phenolic compounds, alkaloids, terpenoids and proteins associated with defence (2, 3). All these responses are regulated by intricate signalling networks that are activated upon recognition of herbivore-associated molecular patterns (HAMPs), which lead to the activation of phytohormonal pathways, alterations in transcriptional profiles and metabolic processes (4). Significantly, plant defence is not constrained to direct toxicity; some indirect strategies, mainly the emission of volatile organic compounds (VOCs) not only influence phytophagous insects such as aphids and chewing feeders but also attract pollinators and natural enemies, thereby enhancing indirect plant defence and ecological balance (5) (Fig. 1). The effectiveness of these defence mechanisms mostly depends on three factors: the plant genotype, herbivore feeding behaviour and surrounding environmental factors.

The coexistence of abiotic stresses, including drought, salinity and extreme temperatures, further complicates plant defensive responses by affecting nutrient allocation, metabolic processes and defence signalling pathways (6). Various recent studies have shown that these reactions are regulated through phytohormonal crosstalk and epigenetic processes, including DNA methylation, non-coding RNAs and histone changes (7, 8). Even with all the significant progress made in discovering plant immune responses, major agricultural losses continue to be caused on a global scale by insect herbivores. From this paradigm, Si is considered a necessary element for sustainable crop protection resilience in the integrative defence

models. Though formerly, Si was considered nonessential, currently a vast quantity of growing evidence shows that Si can enhance a plant's resistance to different biotic and abiotic stresses significantly (9). Silicon (Si) mediated plant defence employs a wide range of strategies. Structurally, Si reduces the nutritional value of tissues and makes it harder for herbivores to feed by strengthening their cell wall through deposition. Biochemically, Si regulates antioxidant systems, accumulates secondary metabolites and modulates defence enzyme activity and, therefore, influences the defence responses. At the molecular level, it also regulates important phytohormonal signalling pathways, most specifically those controlled by jasmonic acid (JA), salicylic acid (SA) and ethylene (ET) (10, 11). Emerging research further elucidates Si capacity to potentiate indirect defence mechanisms through VOC modulation and reconfiguration of multitrophic ecological networks among plants, herbivores and natural enemies (12, 13). At the same time, there are many beneficial effects that determine considerable heterogeneity across plant taxa and environmental milieus. It indicates that Si-mediated defence operates as a highly nuanced and context-dependent system.

Regardless of the increasing interest in the biological role related to Si, multiple necessary knowledge gaps still exist to be address. The primary focus of most of the research conducted to date is on Si's contribution to abiotic stress tolerance, whereas Si's involvement in plant-herbivore interactions, mainly with respect to signalling integration, epigenetic regulation and ecological outcomes, is still uncovered. Additionally, due to the isolated examination of structural, biochemical and molecular responses, there is fragmentation in the interpretations of Si-mediated defence. Development of reliable predictive models for crop protection is considered challenging as well as complex due to conflicting data regarding Si-phytohormone interactions and variable outcomes that have been observed across the various insect feeding groups (14). Hence, an assessment of Si-mediated defence is required to bridge molecular mechanisms with ecological function and to establish sustainable crop protection strategies.

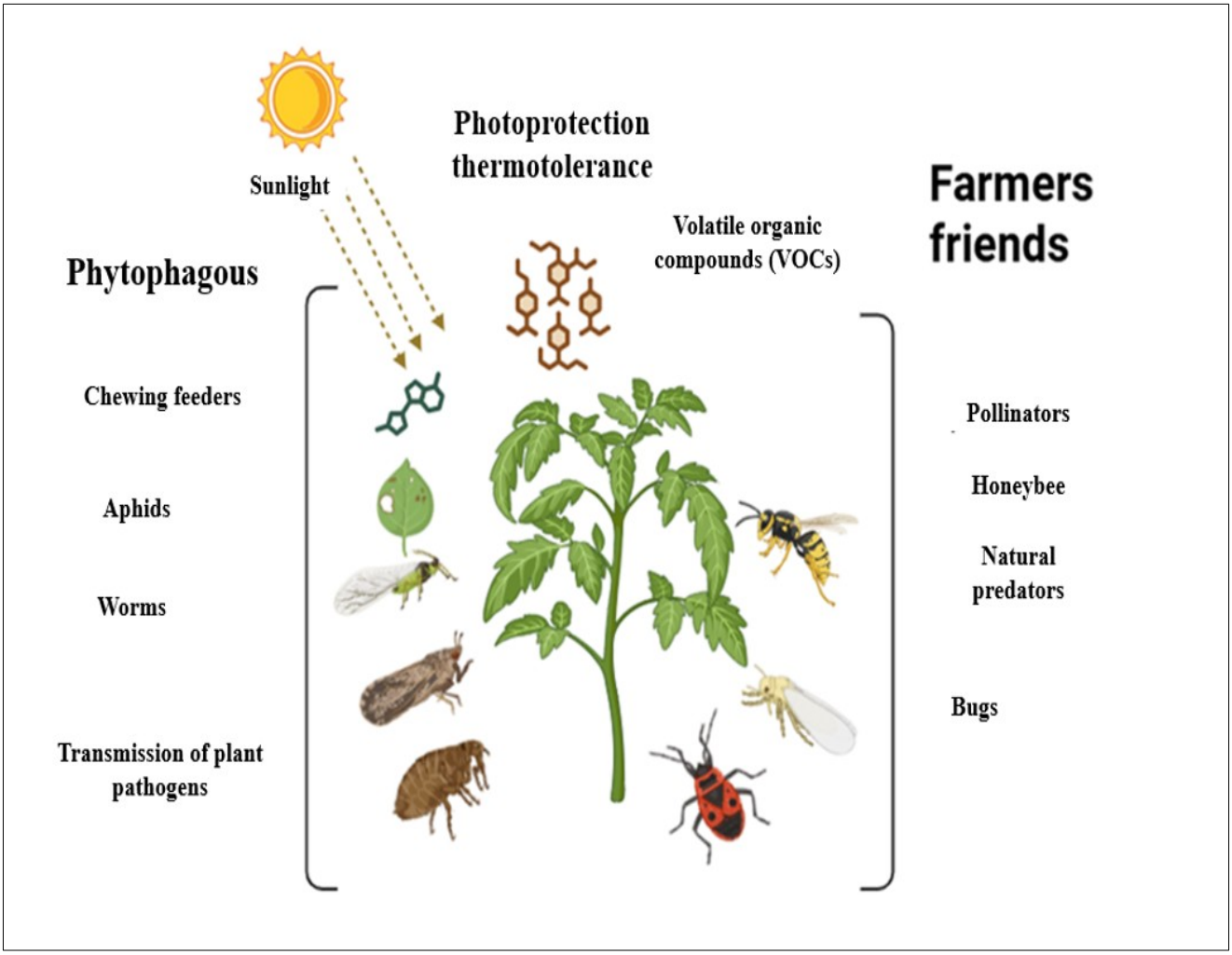

Fig. 1. Dual ecological role of plant-emitted volatile organic compounds (VOCs) in mediating interactions between plants, herbivorous insects and beneficial organisms.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

Plant-herbivore interactions

Molecular signalling, structural features and ecological interactions are part of the integrated defence system that plants utilise to deal with herbivore attacks. Herbivores are recognised through HAMPs, triggering intracellular cascades including calcium (Ca^{2+}) mobilisation, reactive oxygen species (ROS) production and phytohormone signalling via JA, SA and ET whenever herbivores feed on plants. These coordinated responses are responsible for distributing the defensive mechanisms in overall plant tissues (15, 16). Conventionally, plant defence strategies have been classified into two mechanisms, that is, direct or indirect mechanisms. However, recent studies showed that instead of differences, both defence mechanism responses are closely interconnected by signalling pathways (17). Direct defences include both physical structures (barriers) and biochemical compounds that restrict the herbivore infestation and their feeding activity effectively. Structural adaptations, including trichomes and cuticle reinforcement, lead towards reduced herbivore feeding activity, while the secondary metabolite function is to inhibit the herbivore's growth and survival (18, 19). Although these defensive mechanisms provide effective and immediate protection for the plants, they also demand substantial metabolic expenditure and often fail to protect the plants against specialist herbivores equipped with detoxification capabilities (20–22). In contrast, indirect defences operate through ecological interactions (pathways) and primarily involve the emission of VOCs that attract natural enemies such as predators and parasiticides, which reduces the pressure of the herbivores on the plants (23, 24).

Despite metabolic efficiency and evolutionary edge within a community setting, indirect strategies have demonstrated their high effectiveness and variability in degrees of success because of the environment, food web structures and the presence of predators (25, 26). This means that despite providing a dependable but costly form of defence, direct defence offers an ecological flexibility at the cost of unpredictability. Some of the mechanisms employed by plants when they are attacked by herbivores are shown in Fig. 2. Recent studies showed that the effectiveness of plant defences mostly remains dependent on the context of its surroundings. Environmental variables such as nutrient availability, rise in atmospheric carbon dioxide (CO_2) levels and deviations in climate can significantly modify the interaction between plants and herbivores, as well as reduce the effectiveness of VOC-mediated signalling (27). Silicon has increasingly been recognised as a key modulator, bridging structural and biochemical defence responses in plants. The accumulation of Si enhances tissue rigidity, thereby reducing herbivore feeding efficiency and physical damage to plant tissues (28–31) and Si also affects the activity of defence-related enzymes and signalling pathways that are involved in plant stress responses. Meta-analytical studies further demonstrate that Si supplementation can significantly suppress herbivore performance; however, the magnitude of this effect varies according to herbivore feeding guilds and plant genotypes (32). Besides, different evidence suggests that Si may either potentiate or attenuate JA-mediated defence responses under various stress conditions, emphasising potential trade-offs between constitutive structural defences and inducible biochemical mechanisms (33, 34). Environmental factors, such as higher atmospheric CO_2 levels, can reduce the accumulation of Si in plants, which may weaken its protective role (35). This variation suggests that Si-based resistance is not constant but instead depends on the interaction between plant genotype, environmental conditions and herbivore behaviour (Tables 1 and 2).

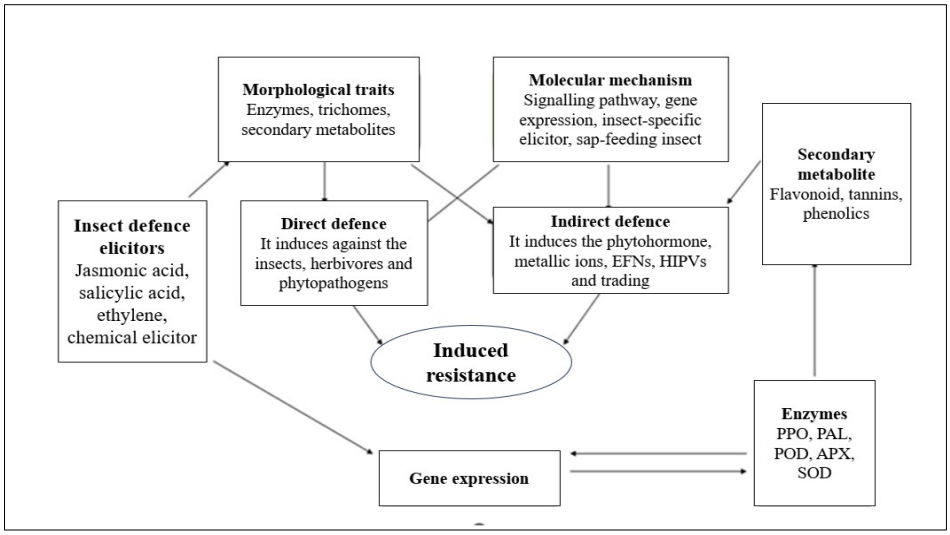

Fig. 2. Direct and indirect mechanisms involved in plant defence.

EFNs: extrafloral nectaries; HIPVs: herbivore-induced plant volatiles; PPO: polyphenol oxidases; PAL: phenylalanine ammonia-lyase; POD: peroxidase; APX: ascorbate peroxidase; SOD: superoxide dismutase.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

Table 1. Major phytopathogens and arthropod pests associated with plant damage, highlighting their effects on plant physiology, defence responses and overall crop productivity

Phytopathogens	Arthropods	Plant-herbivore interaction	Reference
Glucoronates oxydans and *Acetobacter acetic*	*Drosophila melanogaster* and *Drosophila suzukii*	The coexistence of the insect vectors promotes the emergence of phytopathogens in the wounded grape plants.	(36)
Fusarium spp.	*Xyleborus affinis*	The fungi and insects induce damage to the plant host.	(37)
Yeast-like symbionts (YLSs)	*Nilaparvata lugens*	The microbes provide essential amino acids and sterol precursors to assist in recycling nitrogen.	(37)
Pseudomonas syringae	*Tetranychus urticae*	The association of the bacteria with the insect compromised the insect's attack on the plants.	(38)
Stemphylium sp.	*Nezara viridula* and its egg parasitoid (*Trissolcus basalis*)	*Trissolcus basalis* utilises oviposition-induced plant volatiles.	(38)
Fusarium	Insects	*Fusarium* and insects involved in symbiosis association in plant disease epidemiology.	(39)
Gut bacteria (*Citrobacter* spp.)	*Bactrocera dorsalis*	These bacteria in the gut of insects give them the potential to feed and reproduce on the affected plants.	(40)
Nematodes and protozoa	Fleas, lice, flies, mites and ticks	These involve crop and animal pests that affect the growth of crop plants.	(41)
Phytophthora infestans, Xanthomonas campestris and *Puccinia graminis*	Arthropod pests	The phytopathogens and the insect pests destroy crops including bananas and wheat.	(42)
Botrytis cinerea, *Fusarium oxysporum* and *Alternaria alternate*	*Chrysodeixis chalcites*	The insect species and the phytopathogens attack and reduce the production of *Magonia pubescens.*	(43)
Xanthomonas citri, Ralstonia solanacearum, Alternaria alternata, Aspergillus niger, Botrytis cinerea, Colletotrichum graminicola, Fusarium oxysporum, Fusarium verticillioides, Pythium ultimum, Verticillium dahliae, Verticillium longisporum and *Urocystis agropyri*	*Aphis gossypii, Diaphorina citri, Schizaphis graminum, Tricoplusia in, Plutella xylostella, Spodoptera frugiperda* and *Leptinotarsa decemlineata*	They are pathogenic organisms and insect pests attacking plants.	(43)
Geminiviridae, Closteroviridae, Nanoviridae, Rhabdoviridae and *Potyviridae*	*Aphididae* and *Bemisia tabaci*	The association between the insect and the virus improves pathogen transmission thereby encouraging the destruction of plants.	(44)

Despite this, existing research treats molecular signalling, Si-based defence and ecological interactions as separate problems, which makes it hard to draw connections between them. The influence of indirect Si defences, particularly those driven from VOC's in complex food webs, is still not well understood. Very few studies are available till now which show Si as an indirect defence against herbivores. This requires a more joined-up approach which links Si uptake and deposition that shows changes at the hormonal and ecological levels. Without this, it's difficult to assess the role of Si in crop protection strategies that hold up in practice.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

Table 2. Plant secreted compounds against herbivores

Compounds	Mechanism	Reference
1.HIPVs	Plant release special scents when eaten by herbivores. These scents attract insects that attack the herbivore.	(45)
2.Trade-offs	The plant balances the energy between defences. Excessive indirect defence can reduce the growth or reproduction of plants.	(45)
3.EFNs	Plant feed or house protective insects. Ants and predators guard the plant and reduce the damage.	(46)
4.Priming	When the neighbour plant detects warning scents or signals. It helps the nearby plants prepare defence fast.	(47)

HIPVs: herbivore-induced plant volatiles; EFNs: extrafloral nectaries.

Silicon uptake, transport and defence mechanisms against herbivores

The mechanisms linked to Si are intricate examples of how plants protect themselves from predators by using a combination of structural, biochemical and molecular regulatory methods. Through specialised transporter proteins like Lsi1, Lsi2 and Lsi6, plants take up Si in the form of monosilicic acid (Fig. 3). Especially important in species noted for high Si levels, such as rice (*Oryza sativa* L.), wheat (*Triticum turgidum* L.), barley (*Hordeum vulgare* L.), maize (*Zea mays* L.) and horsetail (*Equisetum* spp.) (48). Silicon moves in the transpiration stream and converts into amorphous silica ($SiO_2 \cdot nH_2O$), therefore forming phytoliths in both the epidermal and sub-epidermal layers. Although much study has concentrated on the physiological mechanisms of Si absorption and deposition, the regulation of Si build-up during plant stress caused by environmental changes and herbivore interactions is still mostly unknown (49). By increasing tissue firmness, abrasiveness and general mechanical strength, Si improves plant resilience structurally and so lowers herbivorous organism feeding efficiency via mechanisms such as mandible wear and decreased digestibility. Meta-analytical studies have shown that adding Si can reduce feeding of herbivores by 30–35 % in different plant systems. This supports the idea that Si has a strong ability to protect plants (50). Still, the degree of this impact varies across several herbivore feeding guilds: chewers are much more affected than sap-sucking insects like aphids, which often avoid silicified plant tissues. This difference highlights a fundamental limitation of structural defences and suggests a close relationship between Si's protective effectiveness and herbivore feeding behaviours (51).

In addition to its structural functions, Si controls important defensive biochemical processes. Plants given Si frequently shows higher activity of defence enzymes, like peroxidase, polyphenol oxidase and phenylalanine ammonia-lyase (PAL), as well as higher levels of secondary metabolites, including phenolics and flavonoids. Still, Si's biochemical reactions aren't always consistent. Some research suggests decreased herbivory without noticeable changes in these metabolites, implying that structural and biochemical defences might operate either independently or synergistically depending on plant species and environmental conditions (52). This inconsistency requires uniform experimental designs to separate the relative contributions of structural and biochemical defences. Silicon, at the molecular level, interacts with phytohormone signalling cascades, most notably JA, SA, abscisic acid (ABA) and ET, controlling plant defence. Studies indicate that Si can enhance JA-dependent defence against herbivores via upregulation of defence genes, whereas under abiotic stress, it may suppress JA and SA pathways (53, 54). For example, Si has been shown to prime JA-related signalling pathways in rice, thereby enhancing herbivore resistance (55), whereas Si treatment has also been reported to reduce JA accumulation under abiotic-stress conditions (56). Further, environmental factors such as elevated CO_2 can reduce Si accumulation in plant tissues, dampening its defensive impact despite ongoing defence signalling (57, 58). These findings suggest that Si acts as a regulator of hormonal balance rather than as a simple defence activator.

In addition, based on current scientific evidence, Si is an essential component for controlling defence activities in plants (Table 3). Silicon changes the signals of plants known as Herbivore-induced plant volatiles (HIPVs), making such signals more attractive to predators and parasitoids and thus enhancing indirect defence mechanisms. Silicon acts as an inhibitor to immune responses in insects and makes plants more susceptible to predators. In this respect, it must be stressed that indirect defence mechanisms regulated through Si are highly dependent on certain environmental conditions (13).

Silicon–hormone crosstalk in herbivore defence

Silicon modulation of phytohormones represents a modulatory process, rather than a direct activator of plant defence response-mechanisms. Initially, it was thought that JA was the key component responsible for triggering an inducible defence response against herbivory (77). However, it is now evident that the function of Si is mainly the priming of inducible JA defences while simultaneously inhibiting wasteful constitutive activation. For example, rice experiments have shown increased resistance to the chewing herbivores (*Mythimna loreyi*) due to coordinated alterations in defence-associated and core metabolic processes, suggesting that resistance is achieved through combined changes in the structure and metabolism of the plant (78). It should be noted that

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

Si-mediated defence against various insects depends greatly on the type of herbivore and its feeding habits. When it comes to chewing herbivores, Si induces a response through enhancing the effectiveness of JA and inhibiting insect larvae growth (78). Conversely, defence against sap-feeding herbivores appears mostly associated with physical inhibition of herbivory and modification of feeding behaviour, without a significant role played by the JA pathway. Thus, the limitations of JA-mediated models are apparent.

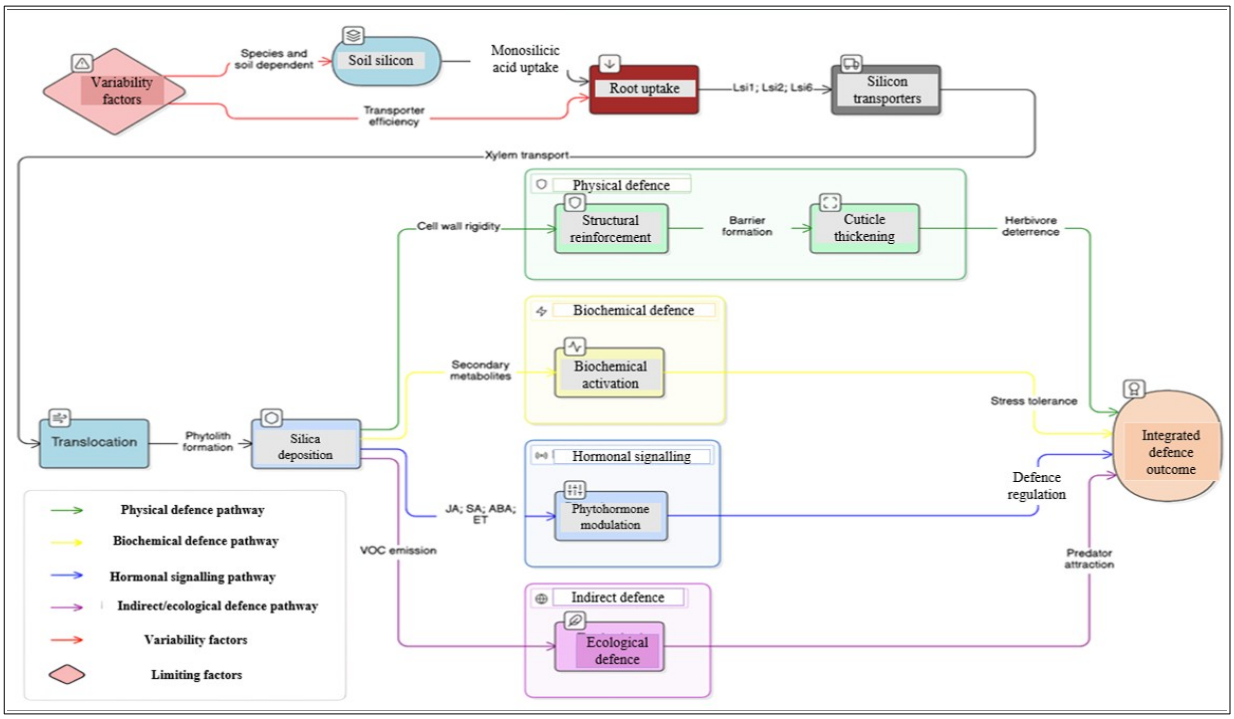

Fig. 3. Integrated model of silicon-regulated defence signalling.

Table 3. Silicon-augmented anti-herbivore defence mechanisms in crop plants

Sl. No.	Insect/pest	Silicon application on host plants/artificial diet	Reference
1.	*Sogatella furcifera*	*Oryza sativa* L.	(59)
2.	*Aphidius colemani*	*Triticum aestivum* L.	(59)
3.	*Bemisia tabaci*	*Cucumis sativus* L.	(60)
4.	*Busseola fusca*	*Zea mays* L.	(61)
5.	*Cnaphalocrocis medinalis*	*Oryza sativa* L.	(62)
6.	*Cnaphalocrocis medinalis*	*Oryza sativa* L.	(62)
7.	*Spodoptera frugiperda*	*Zea mays* L.	(63)
8.	*Dermolepida albohirtum*	*Saccharum officinarum* L.	(64)
9.	*Sitobion avenae*	*Triticum aestivum* L.	(65)
10.	*Anthracnose*	*Solanum lycopersicum* L.	(66)
11.	Early blight *(Alternaria solani)*	*Solanum lycopersicum* L.	(67)
12.	*Fusarium oxysporum f. sp. cucumerinum*	*Cucumis sativus* L.	(68)
13.	Bacterial blight *(Xanthomonas oryzae pv. Oryza)*	*Oryza sativa* L.	(69)
14.	*Ralstonia solanacearum*	*Capsicum annuum* L.	(70)
15.	Brown plant hopper *(Nilaparvata lugens (Stål)*	*Oryza sativa* L.	(71)
16.	Fall armyworm *Spodoptera frugiperda* (Smith)	*Triticum aestivum* L.	(72)
17.	Spider mites	*Fragaria × ananassa* (Duchesne ex Weston) Duchesne ex	(73)
18.	Leaf blight (*Phomopsis obscurans*)	*Fragaria × ananassa*	(74)
19.	Bird cherry-oat aphid (*Rhopalosiphum padi*)	*Triticum aestivum* L.	(75)
20.	Whitefly (*Bemisia tabaci*)	*Solanum melongena* L.	(76)

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

In addition to the modulatory effect of Si, there are also complicated interactions between the JA, SA and ET hormone networks. The antagonism between JA and SA is modulated by Si (79), but it has been shown that Si-induced hormone-based defence mechanisms can be compromised by external factors such as elevated concentrations of CO_2 in the atmosphere (80). Furthermore, Si potentiates indirect defence through modulation of VOC emission, thereby amplifying natural enemy attraction and integrating hormonal signalling with ecological defence processes (81). Table 4 illustrates Si interacts with phytohormones such as JA, SA, ET and ABA to regulate plant defence and stress responses. These interactions enhance hormonal crosstalk, antioxidant activity and stress tolerance under biotic and abiotic stress conditions. It should be stressed, for instance, that Si-based defence involves unique temporal characteristics. Recent studies have found that about 72 hr are needed to deposit Si in plants and integrate it into signal networks, thus implying that defence reactions depend on adaptive responses rather than direct action. This time component was not considered in previous frameworks of defence reactions, thus limiting the transferability of experimental data to agricultural practice. Despite all these new perspectives, no unified theory explaining all aspects of Si defence from Si absorption and deposition kinetics to interactions between hormones and responses to herbivores has yet been proposed. According to recent research, Si may act as a systemic regulator of structural, hormonal and metabolic plant defence reactions.

Silicon-induced stress tolerance and hormonal signalling

The effects of Si on plant defences occur mainly through changing hormonal signal transduction pathways, as opposed to directly inducing plant resistance. In the case of herbivore attacks, plant defence reactions are mostly controlled via JA signal transduction pathways. Salicylic acid and ET, on the other hand, have considerable significance within hormone crosstalk and stress signal integration. Although there has been less information, because most of the study focused on individual mechanisms rather than combining them on molecular, physiological and ecological perspectives. Moreover, there is a difference in Si interaction with different plants, which causes variability in its performance as a plant stimulator. Another problem arises from the absence of field-based tests under multi-factorial stressful situations.

During herbivore attack, it is the control of defence reactions that is performed by JA signal transduction pathways, whereas SA and ET are important in hormone crosstalk and stress perception. The stress-induced hormonal state of a plant normally consists of high JA levels with an inhibited SA signal transduction pathway, but Si can significantly alter this hormone balance, depending on the environment (82). Comparative studies have shown that Si-treated plants generally have lower concentrations of JA and SA during the onset of abiotic stress conditions to reduce their metabolic stress. However, in instances of insect or pathogen attack, Si has been found capable of inducing JA defence mechanisms, along with an induction in the transcription of genes involved. For example, the JA defence priming process by Si in rice plants results in better protection against insects, while in the absence of Si, plant cells respond inadequately to the defence signal, which implies that Si can function as a modulator but not an activator. The involvement of ET serves as an example. On the other hand, certain research findings indicate that extended stress periods may cause the downregulation of JA signalling mechanisms. These complex control mechanisms include Si's ability to inhibit ET synthesis during physical and abiotic stresses but stimulate its synthesis when pathogenic attack occurs. This is another example of stress-specific hormonal regulation. Like many other hormones, Si exerts a profound influence on ABA. It promotes quick resistance against initial stressors, whereas it inhibits chronic stress, helping maintain physiological balance (82).

Additional studies also provide new insights. Increased levels of CO_2 in the atmosphere have been found to impair the effectiveness of Si defence strategies and disturb hormone regulation. Furthermore, the Si effect on indirect defence is evident from its ability to influence VOC synthesis through hormonal signalling pathways, hence linking the JA signalling with multitrophic ecological relationships. Although some studies revealed role of Si in the amplification of the JA signalling pathway, other investigations indicate its antagonistic effects on the same pathway when tested under similar conditions. This points out the fact that the role played by Si in terms of plants' responses is heavily dependent on plant genotypes, type of stress and the environment as well. In this way, Si could be considered as a complex modulator of hormonal interactions in plants, not just a regulator of plant defence processes (82).

Table 4. Silicon interaction with phytohormones under stress conditions

Hormone	Role in defence	Effect of silicon	Critical interpretation
Jasmonic acid (JA)	Herbivore defence	Enhanced or regulated	Silicon may prime JA response rather than directly induce it.
Salicylic acid (SA)	Pathogen defence	Modulated or reduced under stress	Prevents excessive defence cost.
Ethylene (ET)	Stress and defence signalling	Context-dependent regulation	Role varies with stress type.
Abscisic acid (ABA)	Abiotic stress response	Early increase, later reduction	Suggests role in stress optimisation.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

Cell signalling in silicon-mediated plant defence against herbivory

Silicon plays a key role in the regulation of defence responses at the plant-herbivore interface by modulation of primary cellular signalling events associated with HAMP-triggered immunity (HTI), as well as initiation of defences. Upon herbivory, such organisms release HAMPs, which are detected by pattern recognition receptors (PRRs) and activate cellular events that include the production of ROS, Ca^{2+} mobilisation and phytohormone signal transduction pathways. Results from comparative analyses show that plants supplied with Si undergo faster and stronger early signalling events, like higher ROS levels and gene expression of defence-related proteins, compared to Si-deficient plants; hence, Si can be considered an eliciting agent rather than a direct activator of plant defences. On the other hand, plants initiate effector-triggered immunity (ETI) in response to effectors found in the saliva, egg deposition and faeces of herbivores.

Although ETI is well characterised in plant–pathogen interactions, its specific role in plant–insect dynamics remains less well defined. Recent research suggests that herbivore effectors may manipulate host signalling pathways to dampen defence responses; however, the extent to which Si directly modulates effector recognition or downstream signalling remains unresolved. Some findings suggest that Si accumulation within the apoplastic space may restrict effector translocation or receptor availability, consequently enhancing resistance indirectly (83), whereas alternative investigations contend that Si's mechanism operates predominantly at the level of downstream signalling cascades rather than at the initial perception phase. Additionally, recent findings suggest that Si predominantly enhances the amplification, rather than the initiation, of defence signalling. Silicon-treated plants exhibiting elevated defence gene transcription and increased signalling intermediate activity following herbivore feeding, with marginal alterations detected under non-stressed conditions. This substantiates a Si-mediated priming model, whereby defence cascades are potentiated exclusively upon herbivory. Alternatively, several studies have found moderate impacts of Si on early signalling events, especially under heterogeneous conditions, indicating the contextual and taxonomic nature of Si-induced responses.

The most crucial knowledge gap in the existing scientific literature lies in the relationship between the apoplastic bioaccumulation of Si and intracellular signalling pathways. Although the impact of Si accumulation on plant resistance by providing structural strengthening is relatively well understood. The signalling factors responsible for the regulation of Si bioaccumulation, its impact on PRRs, Ca^{2+} signalling and ROS homeostasis are poorly studied. In addition, how Si regulates plant responses to biotic stress at the community level and how it influences plant defence through the modulation of VOCs is still not clear.

Integrated hormonal and redox signalling in herbivore defence

The mechanism of plant defence against herbivores involves the complicated regulation of interactions of hormone and redox signalling, where JAs, SAs, ETS, Ca^{2+} and ROS are not separate signalling pathways but interdependent regulators. Even though the involvement of JAs in the activation of defence responses against chewing herbivores is well understood, the role of the crosstalk between JAs and SAs/Ets cannot be ignored (76, 78). In particular, JAs promote the biosynthesis of secondary metabolites and VOCs; nevertheless, the excessive activity of this signalling pathway is associated with a high metabolic load that should be counteracted by antagonistic signalling pathways of SAs (84). Silicon is involved in activating defence signalling pathways, which in turn leads to the production of ROS (Fig. 4). On the other hand, SA-mediated pathways are more often utilised in defence against sap-feeding insects, although the interaction between SA and JA leads to ecological conflicts when different herbivores are involved. Recent research shows that modulation of the balance between JA and SA induced by herbivory has an important role dependent on the environment, which is complicated for prediction under natural conditions. In addition, ET interferes with regulation as it acts in synergy with JA, as well as suppresses SA-induced defence mechanisms and acts either as a promoting or inhibiting hormone depending on the system in which it works (85, 86). The initial signalling events triggered by herbivore attack include Ca^{2+} signalling and ROS accumulation as early responses. Entry of Ca^{2+} ions into the cell initiates activity of calcium-dependent protein kinases (CDPKs), followed by transcriptional processes, whereas ROS acts as a second messenger and cytotoxic element (87). Nonetheless, current research has shown that the role played by ROS signalling is tightly coupled with that of hormones such as JA and ET (88). However, comparative studies revealed Si can control the signalling network by regulating the amount of ROS and controlling the signalling in response to JA, which improves signalling. This strategy not only improves the plant's defence system but also reduces its metabolic load (89). Nowadays, no information is available which shows coordination in the signalling by Ca^{2+}-ROS-hormones under the influence of Si and biotic/abiotic stresses.

Approaches to enhance plant immunity against herbivores

Contemporary strategies for boosting plant immunity from herbivore pests rely more on the application of molecular technologies, such as genetic engineering, but their effectiveness is not always reliable; major concerns are sustainability, selectivity and environmental adjustment. The cultivation of *Bacillus thuringiensis* (BT)-transgenic crops reduces pink bollworm populations, but quick adaptation is limitation of gene-based defence methods (90). Consequently, the emergence of CRISPR/Cas9

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

technology for genome modification at the loci responsible for plant susceptibility to insects, that is, MLO, DMR6 and important regulatory factors of the JA signalling pathway, provides an improvement in defensive ability with no effect on growth (91, 92); yet, the majority of these studies have focused on defending plants from pathogens. The RNA interference (RNAi) enhanced specificity is provided by silencing particular genes in pests. Field applications are hindered due to problems like the instability of dsRNA and uptake among insect species, hence limiting the effectiveness of RNAi in the field (93). Improvements of dsRNA synthesis using chloroplasts are improving stability and target selection, although safety and scalability are the main problems (94). Metabolic engineering, on the other hand, uses a wider range of techniques such as the number of secondary metabolites and VOCs that repel the pest and attract predators is increased. However, these methods usually have growth-defence conflicts (95). In comparison, RNAi is characterised by high specificity but low field robustness; metabolic engineering provides comprehensive protection but reduces plant health. Molecular technologies are independently developed from Si-based defence methods, providing additional resistance through physical reinforcement and regulation of signalling pathways while keeping the plant's genome intact. One of the critical knowledge gaps includes a lack of integrative solutions which combine molecular engineering and Si technology. Initial results show the impact of Si on hormonal signalling and its impact on plant defences, which could enhance the stability and longevity of resistance. However, integrative solutions are yet to be tested in the field. Genome editing plays a crucial role in developing sustainable and long-term pest management strategies, thereby opening a significant area for research.

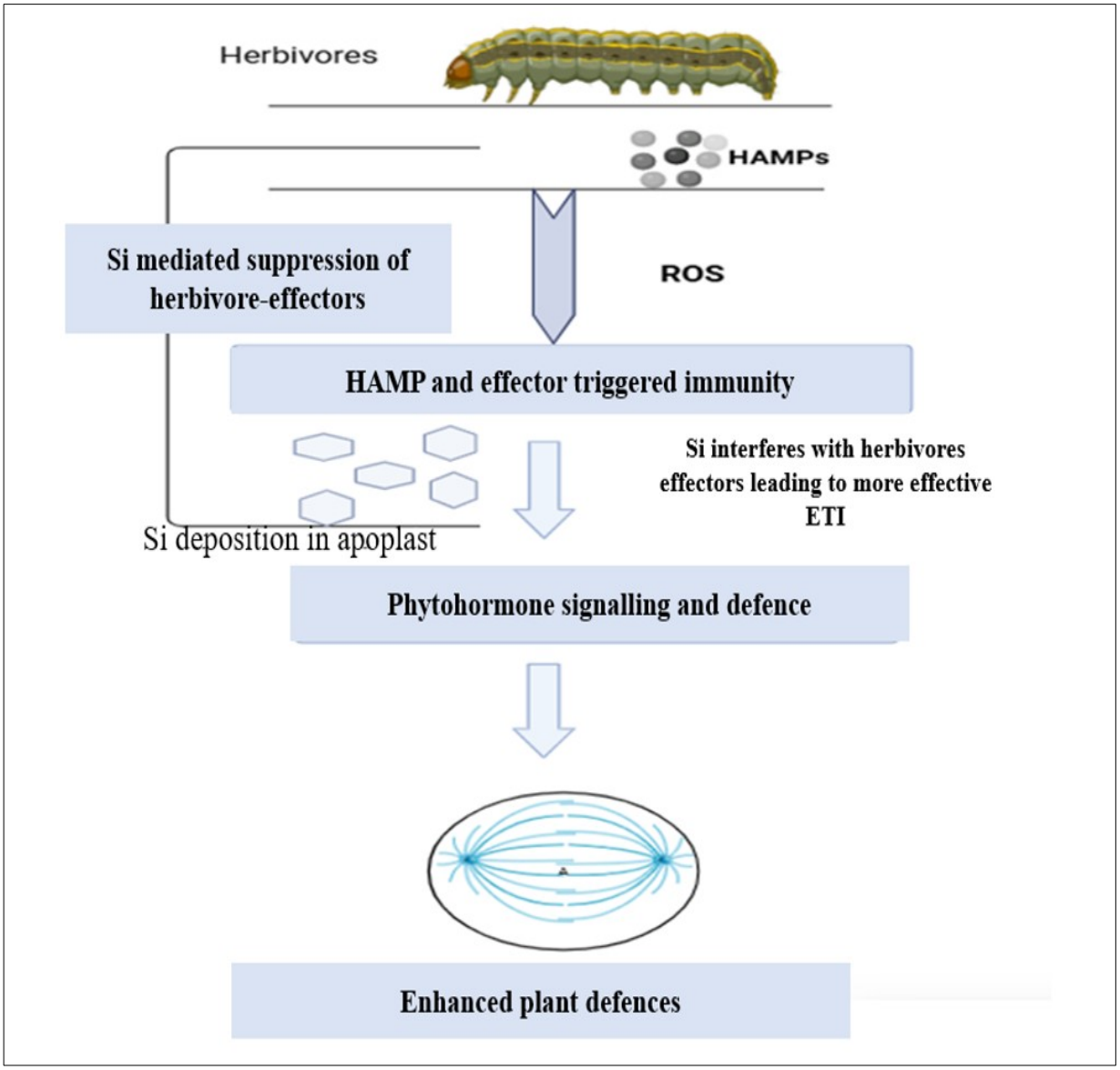

Fig. 4. Cell signalling during silicon-mediated enhanced plant defence against herbivory.

HAMPs: herbivore-associated molecular patterns; ROS: reactive oxygen species; Si: silicon; ETI: effector-triggered immunity.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

Challenges and research gaps in plant defence against herbivores

Even with many improvements, the prediction of plant defence mechanisms against herbivores still poses challenges when applied in natural conditions because of the complicated interaction among the JA, SA and ET signalling pathways, which exhibit different behaviour in response to stress combinations (96). Molecularly, the regulation of defence responses involves transcription factors, microRNA and epigenetics, but interaction with hormonal and biochemical pathways needs further exploration (97). Moreover, species-specific and herbivore-specific responses present another level of complexity not considered in most studies. Monolithic strategies like BT plants and chemicals have proven themselves to be inefficient on account of their ineffectiveness against pests that become resistant to them, such as the pink bollworm (97). Ecological solutions like biological control provide increased sustainability but suffer from decreased predictability and create a crucial compromise between efficiency and stability. Technologies such as CRISPR/Cas9 and RNAi are highly precise, but they bring up the issues of off-target and non-target effects. The most important is to observe the critical gap in the literature arises because there is an inadequate synergy between the molecular defence mechanism and Si-related resistance. This phenomenon can be attributed to the ability of Si to trigger both structural and signalling-based defence systems. However, synergy between genetically modified defence and ecologically driven defence remains to be thoroughly examined. Therefore, future research will have to focus more on molecule-based, ecology-based and Si-based defence strategies (Fig. 5).

Application in agriculture

Growing concern regarding sustainability in agriculture has led to research concerning the development of alternative methods of crop protection that will aid in decreasing reliance on chemical pesticides but will not affect crop production amidst changing climatic conditions (Table 5). The traditional method of pest control using excessive chemicals and genetically modified crops such as BT cotton has been found to be ineffective due to the possibility of developing resistance against pests as well as other environmental risks. Hence, the application of a Si-based defence mechanism for sustainability and climate change-resistant agriculture has become an important area of study due to its wide range of applications. Some of the latest findings obtained through recent agricultural experiments reveal that Si's function in improving defence is not restricted merely to increasing the physical strength of plant cell structures but also extends to regulating defence signalling at a molecular level. Molecular studies have identified that Si regulates defence pathways of the plants, for instance, JA, SA, ET and ABA. The presence of Si in plants under herbivory stress has been found to cause some transcriptional changes, resulting in the upregulation of defence genes and the antioxidant system. Moreover, another study, based on analysis of transcriptomic and metabolomic data, has suggested that Si may be used to prime the plant defence system to become more resilient to environmental stresses in future. Despite many discoveries, some important aspects regarding the regulation of defence signalling by Si are yet to be explored.

The use of modern genome editing techniques, including the CRISPR/Cas9 system and RNAi technology, seems to be highly promising for the development of crop varieties which possess high Si acquisition efficiency and increased stress tolerance. Modern studies have indicated that gene editing may increase the ability of plants to defend themselves from insects without resorting to chemicals. Nevertheless, there are still some difficulties related to off-target effects, ecological risk factors, legislation and the environmental impact of the novel gene-based methods. Apart from that, precision farming in association with climate-smart agriculture is gradually becoming popular, along with Si farming. Advanced technologies such as remote sensing, aerial crop assessment using drones, automatic watering and fertiliser sensors ensure effective management of Si in practice. This approach will help achieve efficient use of Si fertiliser according to the crop growth stage, soil condition and stress caused by the environment. The advent of nanosilicon technology has paved new ways for increasing nutrient absorption and decreasing fertiliser loss (97).

Climate change adds another dimension to the importance of Si-based defence in agriculture. Increased temperature, CO_2 concentration, drought, salinity and climatic fluctuations will simultaneously increase the susceptibility of the plant to biotic and abiotic stresses. Under conditions of stress with the presence of multiple variables, the Si-based defence mechanism may be significant in protecting the crops through strengthening the plant's physical barriers, managing oxidative stress, enhancing photosynthesis and ensuring that the signalling pathway for the plant defence response is appropriate. An important aspect in agricultural science involves the application of Si in ecological or integrated pest management (IPM) strategies. The incorporation of Si has been shown to enhance indirect defence through modification of HIPVs that attract predators and parasitoids towards herbivores. In this case, Si can interact with biological control mechanisms and symbiosis between plants and microorganisms to ensure environment friendly pest management. This aspect is particularly important in contemporary agriculture, where sustainable pest management is sought in place of chemical pesticides. Hence, for further studies in the field of agriculture to be successful, the importance of multidisciplinary studies must be taken into account when dealing with molecular biology, ecology, agronomy and climatology in order to fully comprehend the complex regulatory systems controlling the Si defence mechanism. Further research must also concentrate more on performing larger-scale

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

studies, mastering Si fertilisation, developing plant species capable of withstanding climatic variations and making sure that it is ecologically safe. All these developments may result in new crop protection measures, increasing food security throughout the world without harming the ecosystem (97).

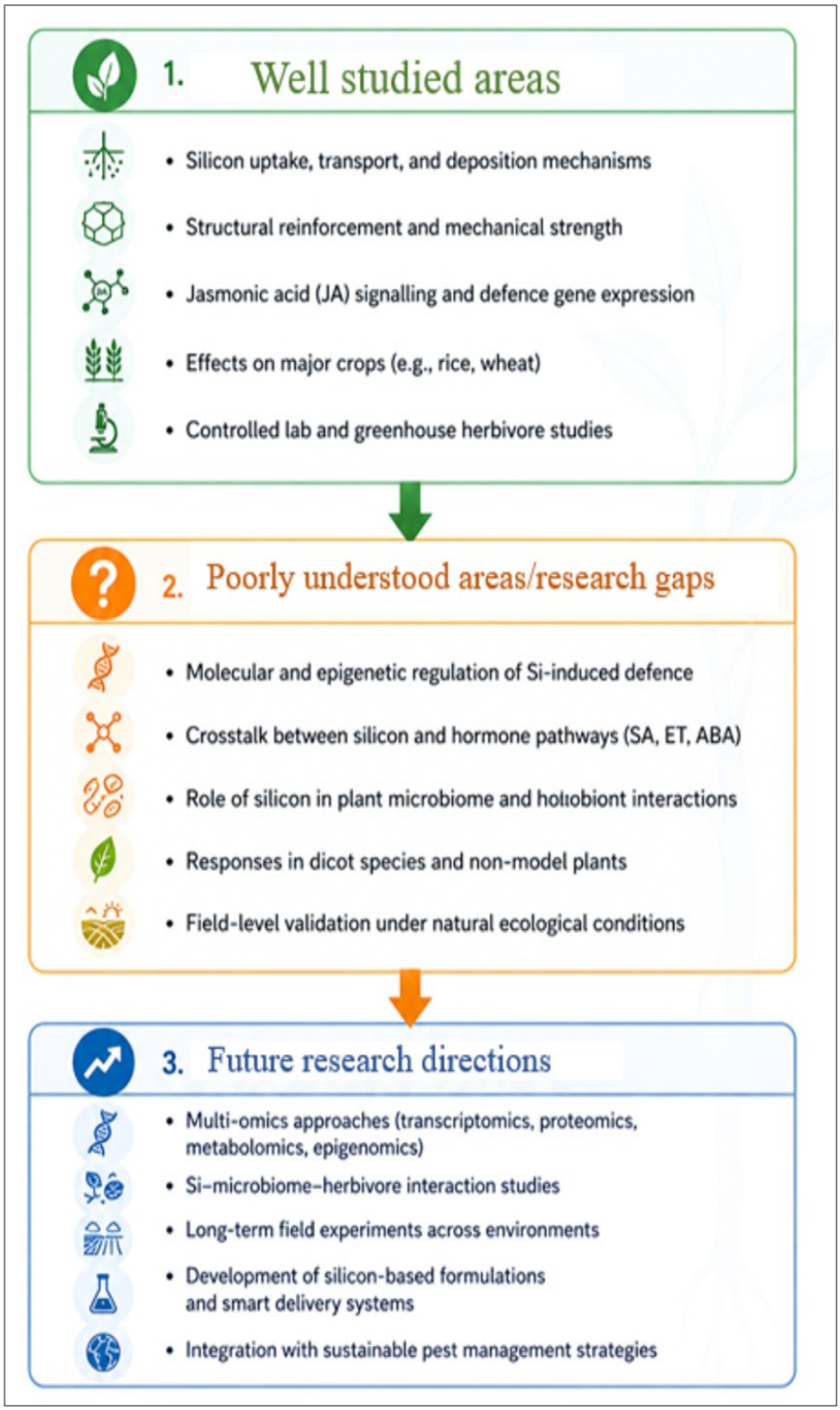

Fig. 5. Addressing these gaps will advance our understanding of silicon-mediated plant defence and enable innovative, sustainable agricultural solutions.

SA: salicylic acid; ET: ethylene; ABA: abscisic acid; Si: silicon.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

Table 5. Major advances, challenges and future perspectives in silicon-mediated sustainable agriculture

Research area	Major advances	Current limitations	Future perspectives	Agricultural significance
Silicon-mediated structural defence	Enhanced cell wall fortification, phytolith formation, reduced herbivore feeding efficiency and increased tissue abrasiveness	Variable effectiveness across herbivore feeding guilds and plant species	Development of crop-specific Si management strategies and optimisation of Si uptake efficiency	Reduces crop damage and pesticide dependence
Molecular signalling pathways	Regulation of JA, SA, ET and ABA signalling pathways; activation of defence-related genes; antioxidant regulation	Incomplete understanding of hormonal crosstalk and defence priming mechanisms	Integrative transcriptomic, proteomic and metabolomic investigations under combined stress conditions	Improves stress resilience and defence regulation
Silicon transporter biology	Identification of Lsi1, Lsi2 and Lsi6 transporters involved in Si uptake and translocation	Limited understanding of transporter regulation under environmental stress	Genetic manipulation of Si transport systems to improve uptake and defence responses	Enhances nutrient-use efficiency and crop protection
Genetic engineering and biotechnology	Application of CRISPR/Cas9, RNA interference (RNAi) and molecular breeding for crop improvement	Off-target effects, ecological concerns, regulatory constraints and public acceptance issues	Engineering climate-resilient and insect-resistant crop varieties with improved Si utilisation	Supports sustainable and precision agriculture
Nano-silicon applications	Improved nutrient delivery, enhanced stress tolerance, increased bioavailability and reduced oxidative damage	Insufficient long-term ecological and toxicological assessments	Development of environmentally safe nano-Si formulations for field application	Increases productivity under environmental stress
Climate-smart agriculture	Silicon-mediated tolerance against drought, salinity, heat stress and elevated CO_2 conditions	Inconsistent Si accumulation and defence responses under changing climates	Multifactorial field studies under realistic climate-change scenarios	Improves crop resilience and food security
Ecological and indirect defence mechanisms	Enhanced emission of HIPVs and improved attraction of predators and parasitoids	Strong dependence on environmental conditions and ecological variability	Integration with biological control and agroecological pest management systems	Promotes sustainable pest suppression
Field-level implementation	Increasing use of Si fertilisation and integrated pest management (IPM) approaches	Scarcity of long-term and large-scale field validation studies	Standardisation of Si dosage, formulation and application methods across crop systems	Facilitates large-scale agricultural adoption
Integrated multidisciplinary research	Growing integration of molecular biology, ecology, agronomy and climate science	Fragmentation among structural, biochemical and ecological studies	Development of predictive and systems-level models for Si-mediated defence	Enables holistic and sustainable crop protection strategies
Precision agriculture and smart farming	Use of remote sensing, drone monitoring, automated irrigation and sensor-based nutrient management	High implementation cost and limited accessibility in developing agricultural systems	Integration of AI-driven nutrient delivery and precision Si fertilisation systems	Optimises resource use and reduces fertiliser wastage

JA: jasmonic acid; SA: salicylic acid; ET: ethylene; ABA: abscisic acid; AI: artificial intelligence; Si: silicon.

2. Conclusion

The plant defence mechanisms against herbivores are a complicated interaction that uses physical, chemical and other forms of defence. Physical defence reduces pest attacks, while ecological defence uses biological mechanisms, such as the emission of volatiles to attract predators of pests. Both interactions are highly dependent on the environment because of the influence of nutrients, the environment and genetic composition. The silicon (Si) has shown its importance in defence interactions by offering support and regulating the signalling process involved in defence reactions. Though there is evidence to show the importance of Si in the defence mechanism, very little information is available regarding the involvement of Si in interaction with jasmonic acid (JA), salicylic acid (SA) and ethylene (ET). The approaches being used today to enhance the resistance of plants through contemporary approaches are genome editing via the CRISPR-Cas9 approach, RNA interference (RNAi) and metabolic engineering. Even though the approaches mentioned above have

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

been proven to be very efficient in enhancing resistance, their wide application has faced a lot of challenges emanating from issues of instability, ecology and lack of transferability of laboratory results without incorporating other techniques. In the future, there will be a need to integrate Si defences with modern molecular and ecological techniques. This will be done by combining Si defence mechanisms with genome editing, omics and agronomics for better resistance mechanisms without any conflict between growth and resistance.

Authors' contributions

MG wrote the rough draft of the manuscript. PC, NSA and PK edited the rough draft. SS performed the final editing of the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

References

1. Mahanta DK, Bhoi TK, Komal J, Samal I, Nikhil RM, Paschapur AU, et al. Insect-pathogen crosstalk and the cellular-molecular mechanisms of insect immunity: Uncovering the underlying signaling pathways and immune regulatory function of non-coding RNAs. Front Immunol. 2023;14:1169152. https://doi.org/10.3389/fimmu.2023.1169152
2. Rani UP, Jyothsna Y. Biochemical and enzymatic changes in rice plants as a mechanism of defense. Acta Physiol Plant. 2010;32:695–701. https://doi.org/10.1007/s11738-009-0449-2
3. Majhi PK, Samal I, Bhoi TK, Pattnaik P, Pradhan C, Gupta A, et al. Climate-smart agriculture: An integrated approach to address climate change and food security. In: Climate Change and Insect Biodiversity. CRC Press; 2023. p. 221–45. https://doi.org/10.1201/9781003382089-14
4. Hossain MA, Hossain MS, Akter M. Challenges faced by plant growth-promoting bacteria in field-level applications and suggestions to overcome the barriers. Physiol Mol Plant Pathol. 2023;126:102029. https://doi.org/10.1016/j.pmpp.2023.102029
5. Doughari J. An overview of plant immunity. J Plant Pathol Microbiol. 2015;6(11):10–4172. https://doi.org/10.4172/2157-7471.1000322
6. Mahanta DK, Jangra S, Priti, Ghosh A, Sharma PK, Iquebal MA, et al. Groundnut bud necrosis virus modulates the expression of innate immune, endocytosis and cuticle development-associated genes to circulate and propagate in its vector, *Thrips palmi*. Front Microbiol. 2022;13:773238. https://doi.org/10.3389/fmicb.2022.773238
7. Singh P, Singh A, Choudhary KK. Revisiting the role of phenylpropanoids in plant defence against UV-B stress. Plant Stress. 2023;7:100143. https://doi.org/10.1016/j.stress.2023.100143
8. Kloth KJ, Abreu IN, Delhomme N, Petrik I, Villard C, Strom C, et al. PECTIN ACETYLESTERASE9 affects the transcriptome and metabolome and delays aphid feeding. Plant Physiol. 2019;181(4):1704–20. https://doi.org/10.1104/pp.19.00635
9. Gong Z, Xiong L, Shi H, Yang S, Herrera-Estrella LR, Xu G, et al. Plant abiotic stress response and nutrient use efficiency. Sci China Life Sci. 2020;63(5):635–74. https://doi.org/10.1007/s11427-020-1683-x
10. Zhang H, Zhu J, Gong Z, Zhu JK. Abiotic stress responses in plants. Nat Rev Genet. 2022;23(2):104–19. https://doi.org/10.1038/s41576-021-00413-0
11. Kutty NN, Mishra M. Dynamic distress calls: Volatile info chemicals induce and regulate defence responses during herbivory. Front Plant Sci. 2023;14:1135000. https://doi.org/10.3389/fpls.2023.1135000
12. Hall CR, Waterman JM, Vandegeer RK, Hartley SE, Johnson SN. The role of silicon in antiherbivore phytohormonal signalling. Front Plant Sci. 2019;10:1132. https://doi.org/10.3389/fpls.2019.01132
13. Liu J, Chen X, Zhang Y, Wang L. Silicon alters VOC-mediated indirect defence in plants. Trends Plant Sci. 2025;30(2):145–58.
14. Coskun D, Deshmukh R, Sonah H, Menzies JG, Reynolds OL, Ma JF, et al. The controversies of silicon's role in plant biology. New Phytol. 2019;221(1):67–85. https://doi.org/10.1111/nph.15343
15. Malik G, Chaturvedi R, Hooda S. Role of herbivore-associated molecular patterns (HAMPs) in modulating plant defences. In: Plant-Pest Interactions: From Molecular Mechanisms to Chemical Ecology. Singapore: Springer; 2021. p. 1–29. https://doi.org/10.1007/978-981-15-2467-7_1
16. Divekar PA, Rani V, Majumder S, Karkute SG, Molla KA, Pandey KK, et al. Protease inhibitors: An induced plant defence mechanism against herbivores. J Plant Growth Regul. 2023;42(10):6057–73. https://doi.org/10.1007/s00344-022-10767-2
17. Markus Lange B, Turner GW. Terpenoid biosynthesis in trichomes-current status and future opportunities. Plant Biotechnol J. 2013;11(1):2–22. https://doi.org/10.1111/j.1467-7652.2012.00737.x
18. Jha Y, Mohamed HI. Plant secondary metabolites as a tool to investigate biotic stress tolerance in plants: A review. Gesunde Pflanzen. 2022;74(4):771–90. https://doi.org/10.1007/s10343-022-00669-4
19. Walker TW, Alexander JM, Allard PM, Baines O, Baldy V, Bardgett RD, et al. Functional traits 2.0: The power of the metabolome for ecology. J Ecol. 2022;110(1):4–20. https://doi.org/10.1111/1365-2745.13826
20. Divekar PA, Narayana S, Divekar BA, Kumar R, Gadratagi BG, Ray A, et al. Plant secondary metabolites as defence tools against herbivores for sustainable crop protection. Int J Mol Sci. 2022;23(5):2690. https://doi.org/10.3390/ijms23052690
21. Xiao L, Zhang J, Huang W, Carrillo J, Siemann E, Ding J. Tallow tree allocates contrasting secondary chemicals in response to varying environments along elevational gradients. J Plant Ecol. 2020;13(3):295–303. https://doi.org/10.1093/jpe/rtaa014

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.

22. Chauhan P, Sharma N, Tapwal A, Kumar A, Verma GS, Meena M, et al. Soil microbiome: Diversity, benefits and interactions with plants. Sustainability. 2023;15(19):14643. https://doi.org/10.3390/su151914643

23. Hu L, Zhang K, Wu Z, Xu J, Erb M. Plant volatiles as regulators of plant defence and herbivore immunity: Molecular mechanisms and unanswered questions. Curr Opin Insect Sci. 2021;44:82–8. https://doi.org/10.1016/j.cois.2021.03.010

24. Meents AK, Mithofer A. Plant-plant communication: Is there a role for volatile damage-associated molecular patterns. Front Plant Sci. 2020;11:583275. https://doi.org/10.3389/fpls.2020.583275

25. Moura RF, Del-Claro K. Plants with extrafloral nectaries share indirect defences and shape the local arboreal ant community. Oecologia. 2023;201(1):73–82. https://doi.org/10.1007/s00442-022-05286-6

26. Singh S, Prasad SM. Environmental modulation of plant-herbivore interactions under changing climate conditions. Plant Ecol. 2024;225:145–60.

27. Kumar A, Choudhary A, Kaur H, Singh K, Guha S, Choudhary DR, et al. Exploring the role of silicon in enhancing sustainable plant growth, defence system, environmental stress mitigation and management. Discov Appl Sci. 2025;7(5):406. https://doi.org/10.1007/s42452-025-06866-w

28. Guar A, Yung J. Lsi6 transporter in barley leaves. J Plant Physiol. 2020;247:106743.

29. Li L, Zhong W. StLsi1 transporter in potato roots and leaves. J Agric Food Chem. 2022;70(3):743–52.

30. Johnson SN, Waterman JM, Hartley SE, Cooke J, Ryalls JMW, Lagisz M, et al. Plant silicon defences suppress herbivore performance, but the mode of feeding is key. Ecol Lett. 2024;27(10):e14519. https://doi.org/10.1111/ele.14519

31. Debona D, Rodrigues FA, Datnoff LE. Silicon's role in abiotic and biotic plant stresses. Annu Rev Phytopathol. 2017;55:85–107. https://doi.org/10.1146/annurev-phyto-080516-035312

32. Khan I, Awan SA, Ikram R, Rizwan M, Akhtar N. Silicon-mediated regulation of plant stress responses under elevated CO_2 conditions. Environ Exp Bot. 2024;217:105950.

33. Contreras E, Rodriguez-Herva JJ, Diaz I, Lopez-Solanilla E, Martinez M. Previous interaction with phytopathogenic bacteria alters the response of *Arabidopsis* against *Tetranychus urticae* herbivory. J Plant Interact. 2023;18(1):2144651. https://doi.org/10.1080/17429145.2022.2144651

34. Berasategui A, Jagdale S, Salem H. *Fusarium* phytopathogens as insect mutualists. PLoS Pathog. 2023;19(7):e1011497. https://doi.org/10.1371/journal.ppat.1011497

35. Zhang Y, Zhang S, Xu L. The pivotal roles of gut microbiota in insect plant interactions for sustainable pest management. NPJ Biofilms Microbiomes. 2023;9(1):66. https://doi.org/10.1038/s41522-023-00435-y

36. Castro HLB, Braga FR, de Freitas Soares FE. Potential of plant cysteine proteases against crop pests and animal parasites. J Nat Pestic Res. 2023;6:100049. https://doi.org/10.1016/j.napere.2023.100049

37. Tamborindeguy C, Hata FT, Molina RDO, Nunes WMDC. A new perspective on the co-transmission of plant pathogens by hemipterans. Microorganisms. 2023;11(1):156. https://doi.org/10.3390/microorganisms11010156

38. Gomis-Cebolla J, Berry C. *Bacillus thuringiensis* as a biofertilizer in crops and its implications in the control of phytopathogens and insect pests. Pest Manag Sci. 2023;79(9):2992–3001. https://doi.org/10.1002/ps.7560

39. Moraes AR, Sabina SR, Exposito DG, Gimenez C, Espinel G, Sousa GF, et al. Evaluation of *Magonia pubescens* A. St.-Hil. roots extract against phytopathogens: Searching for eco-friendly crop protection products. Appl Sci. 2023;13(11):6736. https://doi.org/10.3390/app13116736

40. Salim M, Saxena RC. Iron, silica and aluminium stresses and varietal resistance in rice: Effects on whitebacked planthopper. Crop Sci. 1992;32(1):212–19. https://doi.org/10.2135/cropsci1992.0011183X003200010044x

41. Moraes JC, Goussain MM, Basagli MA, Carvalho GA, Ecole CC, Sampaio MV. Silicon influence on the tritrophic interaction: Wheat plants, the greenbug *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae) and its natural enemies, *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae) and *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae). Neotrop Entomol. 2004;33:619–24. https://doi.org/10.1590/S1519-566X2004000500012

42. Karaca MM, Alınç T, Cusumano A, Mirabile G, Torta L, Guarino S, et al. Insect oviposition in herbaceous plants attracts egg parasitoids despite fungal phytopathogen infection. Biol Control. 2024;188:105384. https://doi.org/10.1016/j.biocontrol.2023.105384

43. Castillo-Esparza JF, Mora-Velasco KA, Rosas-Saito GH, Rodriguez-Haas B, Sanchez-Rangel D, Ibarra-Juarez LA, et al. Microorganisms associated with the ambrosial beetle *Xyleborus affinis* have plant growth-promotion activity in *Arabidopsis* seedlings and antifungal activity against the phytopathogenic fungus *Fusarium* sp. INECOL_BM-06. Microb Ecol. 2023;85(4):1396–1411. https://doi.org/10.1007/s00248-022-01998-7

44. Ma JF, Yamaji N. A cooperative system of silicon transport in plants. Trends Plant Sci. 2015;20(7):435–42. https://doi.org/10.1016/j.tplants.2015.04.007

45. Hall CR, Johnson SN, Hartley SE, Frew A. Silicon reduces herbivore performance: A meta-analysis. Funct Ecol. 2024;38(5):1123–35.

46. Reynolds OL, Keeping MG, Meyer JH. Silicon augments plant resistance to herbivory: A review. Trends Plant Sci. 2009;14(12):654–60.

47. Wang J, Wang X, Zhao J. Silicon supplementation improves resistance of beans to *Pseudocercospora griseola*. Plant Pathol Control. 2017;12(2):155–62.

48. Zargar M, Singh A, Khan S. Influence of silicon amendment on soil microbial communities. Microb Ecol. 2019;78(2):401–12.

49. Ye M, Song Y, Long J, Wang R, Baerson SR, Pan Z, et al. Priming of jasmonate-mediated antiherbivore defence responses in rice by silicon. Plant Physiol. 2013;162(1):363–73.

50. Kim YH, Khan AL, Waqas M, Lee IJ. Silicon regulates antioxidant activities and osmotic stress tolerance in plants. Front Plant Sci. 2014;5:209.

51. Hao Z, Zhang X, Li Y, Wang J. Elevated CO_2 reduces silicon-based defence in plants. Environ Exp Bot. 2024;216:105621.

52. Correa RS, Moraes JC, Auad AM, Carvalho GA. Silicon and acibenzolar-S-methyl as resistance inducers in cucumber, against the whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) biotype B. Neotrop Entomol. 2005;34:429–33. https://doi.org/10.1590/S1519-566X2005000300011

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.
https://doi.org/10.14719/pst.14025

53. Juma G, Ahuya PO, Ongamo G, Le Ru B, Magoma G, Silvain JF, et al. Influence of plant silicon in *Busseola fusca* (Lepidoptera: Noctuidae) larvae-Poaceae interactions. Bull Entomol Res. 2015;105(2):253–58. https://doi.org/10.1017/S000748531500005X

54. Han Y, Li P, Gong S, Yang L, Wen L, Hou M. Defence responses in rice induced by silicon amendment against infestation by the leaf folder *Cnaphalocrocis medinalis*. PLoS One. 2016;11(4):e0153918. https://doi.org/10.1371/journal.pone.0153918

55. Alvarenga R, Moraes JC, Auad AM, Coelho M, Nascimento AM. Induction of resistance of corn plants to *Spodoptera frugiperda* (JE Smith, 1797) (Lepidoptera: Noctuidae) by application of silicon and gibberellic acid. Bull Entomol Res. 2017;107(4):527–33. https://doi.org/10.1017/S0007485316001176

56. Frew A, Powell JR, Hiltpold I, Allsopp PG, Sallam N, Johnson SN. Host plant colonisation by arbuscular mycorrhizal fungi stimulates immune function, whereas high root silicon concentrations diminish growth in a soil-dwelling herbivore. Soil Biol Biochem. 2017;112:117–26. https://doi.org/10.1016/j.soilbio.2017.05.008

57. De-la-Cruz IM, Nunez-Farfan J. Inter-annual variation in the abundance of specialist herbivores determines plant resistance in *Datura stramonium*. Ecol Evol. 2023;13(12):e10794. https://doi.org/10.1002/ece3.10794

58. Somapala K, Weerahewa D, Thrikawala S. Silicon-rich rice hull-amended soil enhances anthracnose resistance in tomato. Procedia Food Sci. 2016;6:190–93. https://doi.org/10.1016/j.profoo.2016.02.046

59. Gulzar N, Ali S, Shah MA, Kamili AN. Silicon supplementation improves early blight resistance in *Lycopersicon esculentum* Mill by modulating the expression of defence-related genes and antioxidant enzymes. 3 Biotech. 2021;11(5):232. https://doi.org/10.1007/s13205-021-02789-6

60. Sun H, Duan Y, Mitani-Ueno N, Che J, Jia J, Liu J, et al. Tomato roots have a functional silicon influx transporter but not a functional silicon efflux transporter. Plant Cell Environ. 2020;43(3):732–44. https://doi.org/10.1111/pce.13679

61. Song A, Xue G, Cui P, Fan F, Liu H, Yin C, et al. The role of silicon in enhancing resistance to bacterial blight of hydroponic- and soil-cultured rice. Sci Rep. 2016;6(1):24640. https://doi.org/10.1038/srep24640

62. Alves AO, Santos MMB, Souza LJN, Souza EB, Mariano RLR. Use of silicon for reducing the severity of bacterial wilt of sweet pepper. J Plant Pathol. 2015;97(3):419–29.

63. Tenguri P, Chander S, Ellur RK, Yele Y, Sundaran AP, Madhu NT, et al. Effect of silicon application to the rice plants on feeding behaviour of the brown planthopper, *Nilaparvata lugens* (Stål) under elevated CO_2. Silicon. 2023;15(13):5811–20. https://doi.org/10.1007/s12633-023-02480-w

64. Haq IU, Zhang K, Ali S, Majid M, Ashraf HJ, Khurshid A, et al. Effectiveness of silicon on immature stages of the fall armyworm [*Spodoptera frugiperda* (JE Smith)]. J King Saud Univ Sci. 2022;34(6):102152. https://doi.org/10.1016/j.jksus.2022.102152

65. Liu B, Davies K, Hall A. Silicon builds resilience in strawberry plants against both strawberry powdery mildew, *Podosphaera aphanis* and two-spotted spider mites, *Tetranychus urticae*. PLoS One. 2020;15(12):e0241151. https://doi.org/10.1371/journal.pone.0241151

66. Abd-El-Kareem F, Elshahawy IE, Abd-Elgawad MM. Management of strawberry leaf blight disease caused by *Phomopsis obscurans* using silicate salts under field conditions. Bull Natl Res Cent. 2019;43(1):1–6. https://doi.org/10.1186/s42269-018-0041-2

67. De Oliveira RS, Penaflor MFG, Gonçalves FG, Sampaio MV, Korndorfer AP, Silva WD, et al. Silicon-induced changes in plant volatiles reduce the attractiveness of wheat to the bird cherry-oat aphid *Rhopalosiphum padi* and attract the parasitoid *Lysiphlebus testaceipes*. PLoS One. 2020;15(4):e0231005. https://doi.org/10.1371/journal.pone.0231005

68. Li D, Li HY, Zhang JR, Wu YJ, Zhao SX, Liu SS, et al. Plant resistance against whitefly and its engineering. Front Plant Sci. 2023;14:1232735. https://doi.org/10.3389/fpls.2023.1232735

69. Lin Y, Sun Z, Li Z, Xue R, Cui W, Sun S, et al. Deficiency in silicon transporter Lsi1 compromises inducibility of anti-herbivore defence in rice plants. Front Plant Sci. 2019;10:652. https://doi.org/10.3389/fpls.2019.00652

70. Han Y, Lei W, Wen L, Hou M. Silicon-mediated resistance in a susceptible rice variety to the rice leaf folder, *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae). PLoS One. 2015;10(4):e0120557. https://doi.org/10.1371/journal.pone.0120557

71. Frew A, Weston LA, Reynolds OL, Gurr GM. The role of silicon in plant biology: A paradigm shift in research approach. Ann Bot. 2018;121(7):1265–73. https://doi.org/10.1093/aob/mcy009

72. Osibe DA, Hojo Y, Shinya T, Mitani-Ueno N, Galis I. Comprehensive analysis of silicon impact on defence and metabolic responses in rice exposed to herbivory stress. Front Plant Sci. 2024;15:1399562. https://doi.org/10.3389/fpls.2024.1399562

73. Islam T, Brown MS, Koppenhofer AM. Harnessing plant silicon defences for biological control. Trends Plant Sci. 2025;30(8):846–56. https://doi.org/10.1016/j.tplants.2025.03.004

74. Chen Y, Wang Z, Gao T, Huang Y, Li T, Jiang X, et al. Deep learning and targeted metabolomics-based monitoring of chewing insects in tea plants and screening defence compounds. Plant Cell Environ. 2024;47(2):698–713. https://doi.org/10.1111/pce.14749

75. Sarkar AK, Sadhukhan S. Impact of salinity on growth and development of plants with the central focus on glycophytes: An overview. Bull Env Pharmacology Life Sci. 2023;12:235–66.

76. Zhou S, Lou YR, Tzin V, Jander G. Alteration of plant primary metabolism in response to insect herbivory. Plant Physiol. 2023;191(2):1071–85.

77. Dubois M, Van den Broeck L, Inze D. The pivotal role of ethylene in plant growth and stress responses. Plant Physiol. 2018;176(1):33–48.

78. Ravi B, Foyer CH, Pandey GK. The integration of reactive oxygen species (ROS) and calcium signalling in abiotic stress responses. Plant Cell Environ. 2023;46(7):1985–2006. https://doi.org/10.1111/pce.14596

79. Rai KK. Revisiting the critical role of ROS and RNS in plant defence. J Plant Growth Regul. 2023;42(10):6202–27. https://doi.org/10.1007/s00344-022-10804-0

80. Janicka M, Reda M, Mroczko E, Wdowikowska A, Kabała K. Jasmonic acid effect on *Cucumis sativus* L. growth is related to inhibition of plasma membrane proton pump and the

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.

uptake and assimilation of nitrates. Cells. 2023;12(18):2263. https://doi.org/10.3390/cells12182263

81. Singh AA, Ghosh A, Agrawal M, Agrawal SB. Secondary metabolites responses of plants exposed to ozone: An update. Environ Sci Pollut Res Int. 2023;30(38):88281–312. https://doi.org/10.1007/s11356-023-28634-2

82. Waszczak C, Carmody M, Kangasjarvi J. Reactive oxygen species in plant signalling. Annu Rev Plant Biol. 2018;69:209–36. https://doi.org/10.1146/annurev-arplant-042817-040322

83. Tabashnik BE, Carriere Y. Global patterns of resistance to Bt crops. Nat Biotechnol. 2017;35:926–35. https://doi.org/10.1038/nbt.3974

84. Borrelli VMG, Brambilla V, Rogowsky P, Marocco A, Lanubile A. The enhancement of plant disease resistance using CRISPR/Cas9 technology. Front Plant Sci. 2018;9:1245. https://doi.org/10.3389/fpls.2018.01245

85. Nekrasov V, Wang C, Win J, Lanz C, Weigel D, Kamoun S. Rapid generation of disease-resistant plants by genome editing. Sci Rep. 2017;7(1):482. https://doi.org/10.1038/s41598-017-00578-x

86. Zhu KY, Palli SR. Mechanisms, applications and challenges of insect RNA interference. Annu Rev Entomol. 2020;65:293–311. https://doi.org/10.1146/annurev-ento-011019-025224

87. Bulle M, Sheri V, Aileni M, Zhang B. Chloroplast genome engineering: A plausible approach to combat chili thrips and other agronomic insect pests of crops. Plants. 2023;12(19):3448. https://doi.org/10.3390/plants12193448

88. Pichersky E, Noel JP, Dudareva N. Biosynthesis of plant volatiles: Nature's diversity and ingenuity. Crit Rev Plant Sci. 2013;311(5762):808–11. https://doi.org/10.1126/science.1118510

89. Hilfiker O, Groux R, Bruessow F, Kiefer K, Zeier J, Reymond P. Insect eggs induce a systemic acquired resistance in *Arabidopsis*. Plant J. 2014;80(6):1085–94. https://doi.org/10.1111/tpj.12707

90. Erb M, Reymond P. Molecular interactions between plants and insect herbivores. Annu Rev Plant Biol. 2019;70:527–57. https://doi.org/10.1146/annurev-arplant-050718-095910

91. Baldrich P, San Segundo B. MicroRNAs in rice innate immunity. Plant Physiol. 2016;171(2):697–712. https://doi.org/10.1186/s12284-016-0078-5

92. Kost C. Herbivore-induced indirect plant defences of Lima bean (*Phaseolus lunatus*, Fabaceae). Campinas: Universidade Estadual de Campinas; 2006.

93. Sharma S, Sehgal J, Pundir RK, Kumar V, Jain M. Exploration of essential oil of *Rubus ellipticus* and *Rubus fruticosus* against fungal and bacterial infection. Proc Natl Acad Sci India Sect B Biol Sci. 2026. https://doi.org/10.1007/s40011-026-01766-4

94. Sharma S, Chahal A, Chandel A, Walia A. *In vitro* bioactivity and antimicrobial efficacy of modified solvents evaporation assisted *R. ellipticus*. Proc Natl Acad Sci India Sect B Biol Sci. 2025;95:695–707. https://doi.org/10.1007/s40011-025-01719-3

95. Sharma S, Roy R, Prasad H, Kumar B, Kumar A, Kumari N, et al. Phytochemical analysis and antifungal activity of *Mentha* against *Phytophthora infestans*. S Afr J Bot. 2024;172:501–14. https://doi.org/10.1016/j.sajb.2024.07.037

96. Jasrotia P, Sharma S, Nagpal M, Kamboj D, Kashyap PL, Kumar S, et al. Comparative transcriptome analysis of wheat in response to corn leaf aphid, *Rhopalosiphum maidis* F. infestation. Front Plant Sci. 2022;13:989365. https://doi.org/10.3389/fpls.2022.989365

97. Sharma S, Chauhan A, Dobbal S, Kumar R. Biology of plants coping stresses: Epigenetic modifications and genetic engineering. South African Journal of Botany. 2022;144:270–83. https://doi.org/10.1016/j.sajb.2021.08.031

Additional information

Peer review: Publisher thanks the Sectional Editor and anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information: Available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy.

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting.

Copyright: © The Author(s). This is an open-access article distributed under the Creative Commons Attribution License CC BY 4.0.

Publisher information: Plant Science Today is published by Horizon e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.

© The Author(s) 2026. Creative Commons CC BY 4.0. Published by Horizon e-Publishing Group.