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RESEARCH ARTICLE

Silica-mediated resistance in cauliflower against diamondback moth (*Plutella xylostella*)

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Abstract

Diamondback moth (DBM) (*Plutella xylostella* L.) is a destructive pest of cruciferous crops with a high propensity to develop resistance against synthetic insecticides, necessitating eco-friendly management strategies. The present study investigated the insecticidal potential of natural silica against *P. xylostella* and silica-mediated resistance in cauliflower under greenhouse conditions through pot culture experiments with three treatments, viz., natural silica, azadirachtin 1 % emulsifiable concentrate (EC) (neemazal) and an untreated control. Foliar application of natural silica significantly reduced larval survival, recording 68.57 % mortality at 5 days after treatment (DAT), which was statistically comparable to neemazal (77.14 %). Natural silica-treated larvae showed reduced body size, cuticular abrasion, desiccation and eventual death. Biophysical studies using scanning electron microscopy (SEM) confirmed silica deposition in leaf tissues, reinforcing cell walls and inducing mandibular wear in larvae, thereby restricting feeding. Biochemical assays revealed that silica-treated plants exhibited elevated activities of defense enzymes such as polyphenol oxidase (PPO), peroxidase (PO) and phenylalanine ammonia lyase (PAL), recording 0.19, 0.38 and 0.95 ΔOD min^{-1} g^{-1}, respectively, along with higher phenolic content (0.71 g 100 g^{-1} fresh weight), indicating induction of systemic resistance. Safety assessment through a contact filter paper assay revealed minimal effects of silica on honey bee, *Apis cerana indica* (8.57 % mortality at 48 hr), lower than neemazal (14.29 %). These results demonstrate that natural silica can serve as a promising alternative to synthetic pesticides in controlling *P. xylostella* and can function as a defensive component in integrated pest management by reinforcing induced defenses and enhancing plant resistance.

Keywords: cauliflower; defense enzymes; diamondback moth; mandible wear; resistance; silica

Introduction

Silicon (Si), recognized as a quasi-essential nutrient, contributes to enhancing the defense mechanisms of plants (1, 2). Application of Si has proven to be an effective, sustainable and environmentally benign approach by reducing reliance on conventional insecticides for chewing insect pests, viz., *Cnaphalocrocis medinalis*, *Spodoptera frugiperda*, *Chilo infuscatelus* and *Scirpophaga incertulas* (3–5). In plants, Si accumulates predominantly as silicon dioxide (SiO_2), which remains immobile after deposition and reinforces tissues by forming a mechanical barrier on the plant surface, thereby providing resistance against both biotic and abiotic stresses (6, 7). Due to deposition, abrasiveness in leaves increases, thereby reducing their nutritional quality for herbivores and causing mandibular wear to their mouthparts, which ultimately decreases feeding efficiency and retards growth rates (8). However, the positive effects of Si in mitigating abiotic and biotic stresses are not always apparent, as the degree of its accumulation differs considerably among plant species and cultivars (9–11). Application of Si to plants enhances the accumulation of defensive metabolites such as phenols and phytoalexins. In addition, it upregulates defense-related enzymes, including polyphenol oxidase (PPO), peroxidase (PO) and phenylalanine ammonia lyase (PAL), which collectively strengthen resistance against biotic stress (12). Much of Si's contribution to induced plant defenses occurs through activation of jasmonic acid signaling, the primary regulatory pathway governing herbivore-induced volatiles that increase attractiveness to natural enemies (13).

Cauliflower (*Brassica oleracea* var. *botrytis*) is an economically important cruciferous vegetable crop, both in India and globally. The crop is susceptible to infestation by several insect pests throughout its growth stages, from sowing to harvest. Key pests include the diamondback moth (DBM) (*P. xylostella*), tobacco caterpillar (*Spodoptera litura*), cabbage leaf webber (*Crocidolomia binotalis*), aphids (*Lipaphis erysimi*, *Brevicoryne brassicae*), painted bug (*Bagrada cruciferarum*) and flea beetle (*Phyllotreta cruciferae*) (14). Among these, the DBM is considered the most destructive pest of cauliflower worldwide, capable of causing yield losses ranging from 42 to 97 % (15). A major challenge in its management is the insect's rapid development of resistance to multiple classes of chemical insecticides (16), which complicates control strategies. This has driven the search for alternative strategies, with growing emphasis on eco-friendly and sustainable pest management options due to the detrimental effects of chemical insecticides on non-target organisms. The present study addresses this need by evaluating the insecticidal efficacy of silica against *P. xylostella*, along with its role in inducing biophysical and biochemical resistance in cauliflower. Furthermore, the safety of silica was assessed against the key beneficial organism, the honey bee (*Apis cerana indica*), to ensure its environmental safety.

Materials and Methods

Insect culture maintenance

Diamondback moth cultures were maintained under controlled laboratory conditions at the Department of Agricultural Entomology, Tamil Nadu Agricultural University (TNAU), Coimbatore. Adult moths were reared in net cages (30 × 30 × 30 cm) at 25 ± 2 °C, 60–65 % relative humidity and a 16:8 hr light: dark photoperiod. Mustard seedlings raised in small pots were provided as oviposition substrates, while adults were supplied with a 10 % honey solution as a food source. The eggs laid on mustard were allowed to hatch and larvae were reared on fresh cauliflower leaves until pupation. Pupae were collected and transferred to separate cages to ensure continuous culture for adult emergence. Late second instar larvae of uniform size were used for all the experiments.

Pot culture experiment

The experiment was conducted using potted cauliflower plants maintained in the glasshouse of the Department of Agricultural Entomology, TNAU, Coimbatore. Pot culture experiments were performed to evaluate the efficacy of silica against *P. xylostella* larvae under greenhouse conditions. The trial was arranged in a completely randomized block design (CRBD) comprising three treatments, viz., natural silica at 25 g L^{-1}, azadirachtin 1 % emulsifiable concentrate (EC) (neemazal) at 2 ml L^{-1} and an untreated control, with seven replications each. Twenty-five-day-old cauliflower seedlings were transplanted into earthen pots filled with a potting mixture of red soil, sand, farmyard manure and vermicompost in a 2:1:1:1 ratio. Foliar sprays were applied when the plants were 50 days old, using a hand compression sprayer until incipient runoff, ensuring thorough coverage of both leaf surfaces. After drying, late second instar larvae from laboratory culture were released gently with a hair brush at the rate of 10 larvae per potted plant. Each pot, along with the plant, was enclosed in an insect-proof nylon net cage to prevent larval escape and to provide adequate ventilation. Observations on larval mortality were recorded at 1, 3 and 5 days after treatment (DAT).

Silica-mediated mechanisms of resistance

The study was designed using a CRBD with three treatments replicated seven times to ensure the reliability and statistical validity of the results. The treatments were imposed on potted cauliflower plants and then subjected to biophysical and biochemical studies of resistance.

Biophysical mechanism

Deposition of silica in cell walls

Fully expanded fourth leaves were collected from cauliflower plants treated with natural silica and untreated controls. Leaf samples were surface-cleaned, cut into approximately 2 cm fragments and fixed in a solution of glacial acetic acid, formaldehyde, 95 % ethanol and distilled water (5:5:50:40) according to a previously described method (17). For scanning electron microscopy (SEM) analysis, samples were pre-fixed in 2.5 % glutaraldehyde (0.1 M phosphate buffer, pH 7.2) at 4 °C for 24 hr, post-fixed in 2 % osmium tetroxide for 4 hr, dehydrated through a graded ethanol series and critical-point dried. Dried samples were mounted on aluminum stubs, sputter-coated with gold (EMITECH SC7620, 3 min) and examined under a scanning electron microscope (FEI Quanta 250) at high vacuum (3.99×10^{-4} Pa) to visualize Si deposition in leaf tissues.

Mandibular abrasion

Five days after larval release, *P. xylostella* larvae were collected from all treatments and preserved in a fixative solution (70 % ethanol: 30 % glacial acetic acid). Mandible preparation was carried (18), with minor modifications. Preserved larvae were boiled in 5 % sodium hydroxide (NaOH) for 4 hr until transparent, after which mandibles were dissected under a stereo zoom microscope. Detached mandibles were mounted on glass slides in glycerol to prevent dehydration and examined under a stereo zoom microscope (LEICA M205C) for abrasive wear, particularly in the incisive region.

Biochemical mechanism

Biochemical analyses were conducted to evaluate the influence of silica in activating the key defensive enzymes, including PPO, PO and PAL, along with the secondary metabolite, total phenol. The fourth fully expanded healthy leaves were collected from each treatment plant in the morning for the estimation of defensive compounds.

Polyphenol oxidase

Polyphenol oxidase activity was assayed with minor modifications following a standardized protocol (19). Fresh leaf tissue (0.5 g) was homogenized in 5 mL of 0.1 M sodium phosphate buffer (pH 6.5) and centrifuged at 3,000 rpm for 15 min at 4 °C. The supernatant served as the enzyme source. The reaction mixture contained 2 mL of 0.1 M phosphate buffer, 0.5 mL of enzyme extract and 0.3 mL of 0.1 M catechol, with buffer alone as blank. Absorbance was measured at 495 nm at 30 sec intervals for 3 min using a UV-VIS spectrophotometer (Model: Cary 100) and PPO activity was expressed as $\Delta A495\ min^{-1}\ g^{-1}$ fresh weight.

Peroxidase

Peroxidase activity was estimated with minor modifications following a standardized protocol (20). Enzyme extract was prepared as described for PPO. The reaction mixture contained 2.5 mL of 0.1 M sodium phosphate buffer (pH 6.5), 0.1 mL of 0.05 M pyrogallol, 0.2 mL of 0.2 M hydrogen peroxide (H_2O_2) and 0.2 mL of enzyme extract. Absorbance was recorded at 430 nm at 30 sec intervals for 3 min using distilled water as a blank. Activity was expressed as $\Delta A430\ min^{-1}\ g^{-1}$ fresh weight.

Phenylalanine ammonia lyase

Phenylalanine ammonia lyase activity was assayed according to a standardized method (21), with slight modifications. Fresh leaf tissue (0.5 g) was homogenized in 5 mL of 0.1 M sodium borate buffer (pH 8.8) containing polyvinyl pyrrolidone and centrifuged at 12,000 rpm for 20 min. The reaction mixture consisted of 0.5

mL of 0.2 M sodium borate buffer (pH 8.7), 0.5 mL of enzyme extract and 1 mL of 0.1 M L-phenylalanine, incubated at 40 °C for 30 min. The reaction was terminated with 0.5 mL of 1 M trichloroacetic acid and absorbance was recorded at 290 nm. Phenylalanine ammonia lyase activity was expressed as ΔA290 min^{-1} g^{-1} fresh weight.

Total phenolics

Total phenolic content in cauliflower leaves was determined using Folin-Ciocalteu reagent (22). Fresh leaf tissue (250 mg) was homogenized in 10 mL of 80 % ethanol and centrifuged at 10,000 rpm for 20 min; the residue was re-extracted and the pooled supernatants were adjusted to 15 mL. An aliquot (0.1 mL) was mixed with distilled water, Folin-Ciocalteu reagent and sodium carbonate and absorbance was recorded at 650 nm. Phenolic content was calculated from a pyrocatechol standard curve and expressed as g pyrocatechol equivalents 100 g^{-1} sample.

Safety assessment on honey bees

The experiment was carried out following the Organisation for Economic Co-operation and Development (OECD, 1998) guidelines, with slight modifications (23). The dry film method was used to assess the safety of different treatments on the honey bee, *Apis cerana indica*, with seven replicates per treatment. Test solutions were applied onto filter paper discs, shade-dried and placed inside perforated plastic containers. Fifteen adult bees were released into each container and allowed to contact the treated surfaces for 1 hr. After exposure, bees were transferred to perforated nylon bags (20 × 30 cm) and provided with 40 % sucrose solution. Mortality was recorded at 12, 24 and 48 hr post-exposure.

Statistical analysis

Data were analyzed using a CRBD. Before statistical analysis, per cent mortality data were subjected to arc-sine transformation and were then analyzed using R statistical software (version 4.2.2). Mean comparisons were performed using the least significant difference (LSD) test at a 5 % significance level (p<0.05).

Results and Discussion

Entomotoxic effect of silica

Pot experiments under greenhouse conditions evaluated foliar applications of natural silica (25 g L^{-1}) and azadirachtin 1 % EC (2 mL L^{-1}) against *P. xylostella*, alongside an untreated control, in a CRBD. Foliar application of Si consistently suppressed *P. xylostella*, inducing an initial larval mortality of 11.43±3.78 % at 1 DAT (Fig. 1). Although the larval mortality gradually rose to 28.57±9.00 % at 3 DAT, which was significantly lower than neemazal (42.86±9.51 %), a further progressive increase was observed, with Si treatment achieving 68.57±12.15 % larval mortality by 5 DAT, statistically comparable to neemazal (77.14±11.13 %). Importantly, no significant difference was noticed between Si and neemazal treatments after 5 days of treatment, indicating that Si is equally effective in reducing larval survival. Earlier studies support this trend, with high mortality of *P. xylostella* observed on Si-treated cabbage leaves (24) and the effect was attributed to increased leaf firmness (25). Similar defensive roles of Si have been observed in other pests, such as reduced survival and delayed development of *C. medinalis* (26) and reduced survival of *Bemisia tabaci* in soybean (27), although no impact was noted on *Chilo partellus* in maize (28), suggesting species-specific responses.

Silicon-treated larvae exhibited distinct morphological changes, including reduced body length, suppressed feeding activity, extremely dry cuticle and cuticular abrasion leading to desiccation and eventual death. The disruption of the water barrier caused progressive moisture loss, resulting in high mortality. Neemazal also significantly affected *P. xylostella*, as evidenced by larvae exhibiting body shrinkage, discoloration and eventual death. Neemazal prolonged larval development and reduced pupal weight at higher concentrations (15–20 ppm) due to reduced food consumption (29). Neem-derived formulations additionally interfere with oviposition while exerting direct insecticidal action, reducing egg laying in treated plots (30, 31). However, unlike neem, which acts through anti-feedant and reproductive interference, silica imposes biophysical stress on insects, making its action more mechanical and less prone to resistance development.

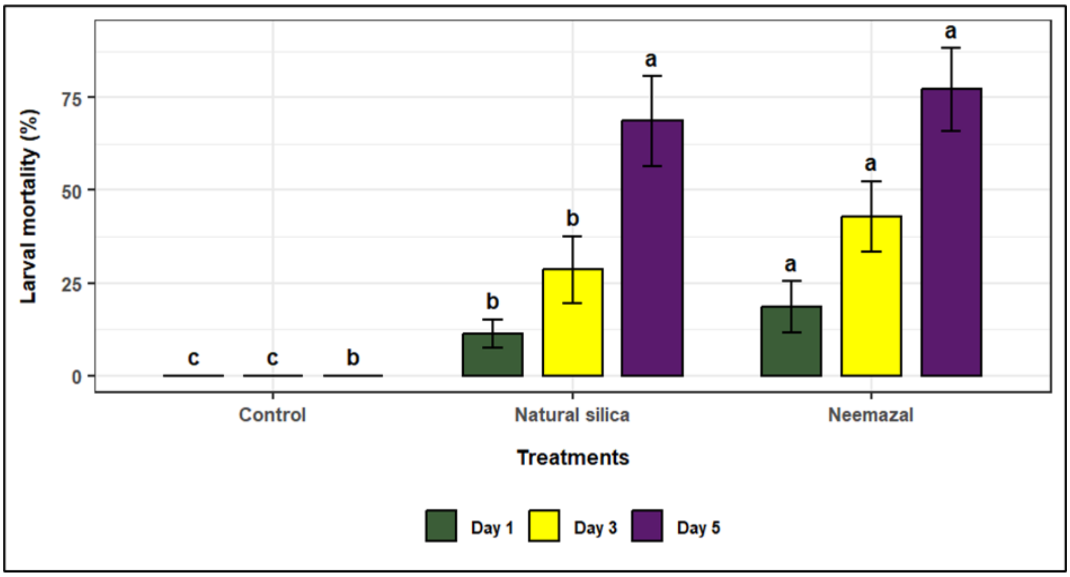

Fig. 1. Cumulative larval mortality (%) of *Plutella xylostella* after 1, 3 and 5 DAT under pot culture experiments. Bars represent the mean ± SD of seven replicates. Different letters above the bars indicate significant differences among treatments according to ANOVA followed by LSD test (p<0.05).

Overall, the findings establish silica as a promising, eco-friendly and sustainable pest management tool. Its comparable efficacy to neemazal, coupled with unique physical disruption of pest survival, underscores its potential as a long-term alternative to chemical insecticides for the effective management of *P. xylostella* in cauliflower.

Biophysical mechanism of resistance

Deposition of silica in cell walls

Silica triggers defense mechanisms in plants by reinforcing the surface tissues, thereby increasing hardness and resistance to abrasion and ultimately creating a physical barrier against pest attack (32). In the present study, SEM confirmed the deposition of Si in cauliflower leaves following foliar application (Fig. 2), which facilitated the formation of mechanical barriers by strengthening the leaf surface, particularly the epidermal cell walls, by increasing their abrasiveness and rigidity. Silicon, deposited as biogenic opals (phytoliths) within the epidermal tissues of leaves, stems and roots, reinforces plant defense mechanisms by enhancing both direct and indirect resistance against insect pests (33). For instance, accumulation of silica in the internode and root band of sugarcane improved the resistance to *Eldana saccharina,* by impeding larval penetration into the stalk (34).

In the current study, Si accumulation in leaf tissues is likely an indirect defense mechanism, reducing herbivore accessibility and palatability, thereby negatively impacting larval survival and development. Moreover, Si-enriched trichomes imposed mechanical constraints on insects, limiting their mobility, colonization and feeding behavior while potentially affecting oviposition preference (35). Collectively, these observations highlight that Si-mediated structural reinforcement of plant tissues constitutes a key component of enhanced pest resistance, both by direct physical barriers. Additionally, it may influence herbivore behavior, consistent with the results obtained in the present study.

Mandibular abrasion

Chewing insects are deterred from feeding on silicified leaves and other plant tissues, due to enhanced irreversible mandibular wear in their mouthparts (8, 36). In the current study, foliar application of Si induced mandibular wear, particularly in the incisor region of the DBM larvae, as observed under a stereo zoom microscope (Fig. 3), indicating a direct mechanical interference with feeding. These findings align with earlier reports, wherein the mandibles of fall army worm larvae showed significant wear in the incisors when fed with silica-treated maize and the degree of wear correlated with the concentration of silica deposited in the leaf tissue (37). The observed reduction in larval growth and feeding efficiency in DBM larvae may be attributed to mandibular wear induced by Si application, as previously demonstrated in a study that reported that such mandibular damage resulted in decreased body weight in insect larvae (34).

Conversely, SEM analysis revealed no structural damage to the mandibular incisors of *Tuta absoluta* following feeding on Si-treated tomato leaves (38). However, in the case of sap feeders, accumulation of Si in plant tissues interferes with insect feeding behaviour by inducing frequent stylet withdrawals, thereby limiting nutrient uptake, which in turn impairs growth and reproduction and, in severe cases, can lead to mortality of nymphal instars (5). Overall, Si application to plants functions as an effective defense inducer, restricting the insect's growth and performance while contributing to sustainable pest management.

Biochemical mechanism of resistance

Biochemical analyses revealed significant differences among treatments in the activity of defense-related enzymes and total phenolic content in cauliflower leaves. Silicon-treated plants exhibited a significant enhancement in the activities of plant defense enzymes recording the highest levels of PAL (0.95), PPO (0.19) and PO (0.38), all expressed as ΔOD min^{-1} g^{-1} fresh weight (Table 1). Similar trends were reported in wheat, where Si

Table 1. Efficacy of different treatments on biochemical parameters of cauliflower

Treatments	Total phenols (g/100g)	Activity of plant defensive enzymes (changes in OD value/min/g of fresh leaf tissue)		
		Phenyl alanine ammonia lyase	Polyphenol oxidase	Peroxidase
Natural silica	0.71^{a}	0.95^{a}	0.19^{a}	0.38^{a}
Neemazal	0.62^{b}	0.70^{b}	0.12^{b}	0.23^{b}
Control	0.45^{c}	0.48^{c}	0.07^{c}	0.18^{b}
SEd	0.04	0.04	0.02	0.03
CD (p = 0.05)	0.08	0.08	0.05	0.06

In a column, means followed by common letter(s) are not significantly different according to LSD.

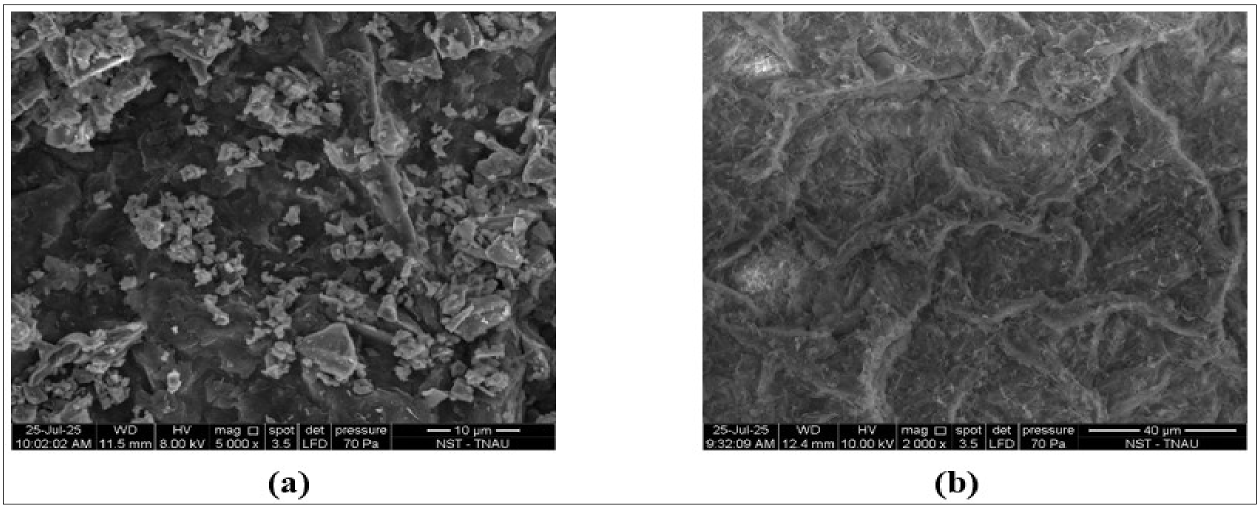

Fig. 2. Deposition of silica in cell walls of cauliflower leaves: (a) natural Si-treated leaf, (b) no deposition in the untreated control.

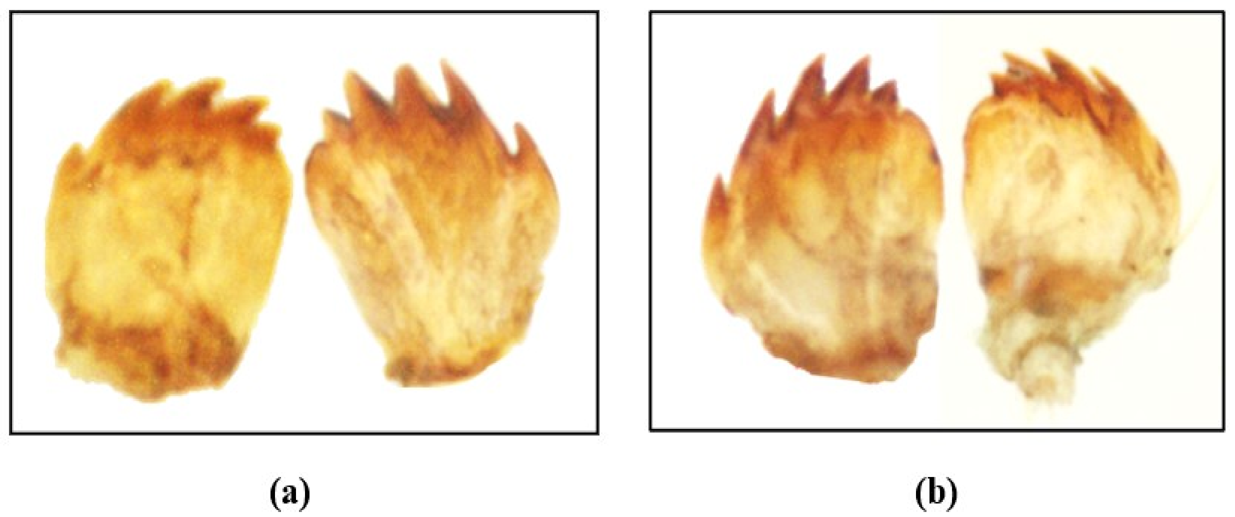

Fig. 3. Mandible wear in *Plutella xylostella* larvae: (a) treated with natural silica, (b) untreated control.

application induced defense mechanisms by upregulating PO, PAL and PPO activities (39). Such induction of biochemical defense substantiated the role of Si as a plant resistance inducer, which is widely recognized as a sustainable and eco-friendly approach for managing insect pest populations. By triggering induced chemical defenses, Si strengthens plants against herbivore attack, thereby reducing insect damage (36).

Foliar application of Si significantly enhanced PPO activity in cauliflower leaves, which was consistent with earlier reports. Notably, PAL activity was significantly higher in Si-treated plants, representing a 35.7 % increase over neemazal and 97.9 % increase over the untreated control, underscoring the role of Si in strengthening plant defense. Such elevation in PAL and PPO activity is functionally important, as these enzymes catalyse the oxidation of phenols into quinones. This biochemical transformation reduces tissue palatability and ultimately deters insect feeding and development, as previously demonstrated in brown plant hopper and rice interactions (33). In general, PO plays a pivotal role in plant defense by facilitating lignification, suberization, quinone formation and the generation of reactive oxygen species, all of which contribute to antimicrobial activity (40). In the present study, the activity of PO in cauliflower leaves was markedly enhanced under Si application, suggesting that it stimulated PO activity to reinforce plant defense mechanisms against oxidative stress and pest attack (1). It is worth noting that the interaction of PO with phenolic compounds leads to the formation of toxic quinones, which decrease tissue digestibility and thereby ultimately hinder insect feeding, development and reproductive potential (41).

In addition, Si application has been shown to stimulate the accumulation of secondary metabolites like phenols and flavonoids in leaves, thereby enhancing plant resilience and improving defense against insect pests (12). In the present study, Si amendment significantly increased the phenolic content in cauliflower leaves, recording 0.71 g pyrocatechol equivalents 100 g^{-1} leaves, which is consistent with the findings of another study (39). Previous studies have also demonstrated that silica, along with lignin, phenolics and phytoalexins, can modulate the synthesis and accumulation of allelochemicals (42, 43) and such effects collectively impaired herbivore feeding, growth and development (12). Furthermore, the induction of systemic stress responses through phytohormone signalling pathways is known to trigger the production of defensive compounds, thereby contributing to enhanced resistance (44). However, some studies reported a decline in phenolic content with Si supplementation, indicating a potential defensive trade-off (27, 45), highlighting the complexity of Si-phenol interactions, which appear to vary with plant species, growth stage and environmental conditions.

Neemazal also stimulated defense enzyme activity and phenolic accumulation, but its effects were comparatively moderate. These findings are consistent with other study (46), which reported increased PAL and PO levels in barley following the application of aqueous neem leaf extract. Similarly, neem extract treatments have been shown to significantly enhance PAL activity, likely through the stimulation of salicylic acid synthesis, which subsequently activates induced systemic resistance (47). While neemazal provided both direct insecticidal action and partial defense induction (48), the consistently superior biochemical response observed under Si treatment suggested that silica offers a more sustainable and long-lasting mode of plant protection. Overall, these findings supported the premise that Si application not only strengthens plant structure but also enhances biochemical defense pathways, making it a promising eco-friendly alternative to conventional pesticides for managing *P. xylostella* in cauliflower.

Safety to honey bees, *Apis cerana indica*

The safety of treatments on non-target organisms, particularly honey bees, is a crucial consideration despite their pest control potential. In the present study, honey bee mortality was monitored at 12, 24 and 48 hr post-exposure. No mortality was observed up to 24 hr, whereas, after 48 hr, marginal mortality was recorded in honey bees exposed to Si treatment (8.57 %), followed by neemazal (14.29 %), while no mortality was observed in the untreated control (Fig. 4). These results indicate that Si application exerted minimal adverse effects on honey bees under laboratory conditions. The adverse effect of insecticidal agents on non-target organisms is influenced by factors such as application rate, exposure route and the specific insect species (49). These findings corroborate earlier reports, wherein honey bee mortality remained below 25 % when exposed to diatomaceous earth (SiO_2) under controlled conditions (50). Similarly, investigations into azadirachtin demonstrated minimal toxicity to *Apis cerana, A. mellifera* and *A. dorsata* (51, 52), while another study reported that even high

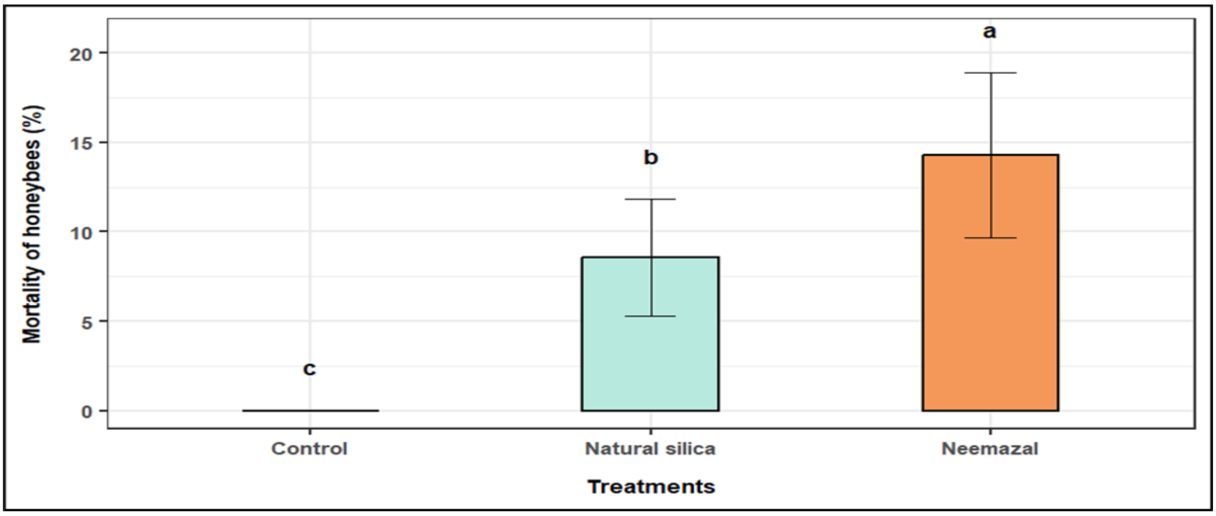

Fig. 4. Mortality (%) of honey bee, *Apis cerana indica,* to different treatments. Bars represent the mean ± SD of seven replicates.

concentrations of commercial neem formulations did not adversely affect *A. mellifera* (53). Overall, these results indicate that both treatments pose minimal risk to honey bees, with Si exhibiting significantly lower contact toxicity than neemazal, reinforcing its potential as a safer and eco-friendly alternative for pest management.

Conclusion

Developing novel strategies for managing *P. xylostella* is crucial due to its high resistance potential; moreover, such alternatives often pose lower risks to humans and non-target organisms compared to conventional insecticides. Although synthetic insecticides often provide short-term efficacy, their long-term use causes detrimental effects on non-target beneficial organisms and high resistance potential among pest populations. Foliar application of Si effectively suppressed *P. xylostella* by causing cuticular damage and desiccation and also by inducing both biophysical and biochemical defense mechanisms in cauliflower. SEM confirmed Si deposition in leaf tissues, which reinforced epidermal cell walls, formed a mechanical barrier to herbivory. In addition to structural defenses, Si significantly enhanced the activities of PAL, PPO and PO enzymes and increased phenolic content, thereby strengthening induced resistance pathways. Importantly, Si treatments were safe to honey bees, exhibiting lower toxicity than neemazal, which underscores its environmental compatibility. Collectively, these findings establish Si as a promising, eco-friendly and sustainable alternative to conventional insecticides, with the added advantage of a mechanical mode of action that reduces the likelihood of resistance development in *P. xylostella*. Future research should focus on field trials and optimized application strategies to validate its efficacy under diverse agroecosystem conditions.

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Authors' contributions

JJ drafted the manuscript. MS contributed to the conceptualization, writing and editing of the research paper. MM, PJ, SKR and DJSS were involved in manuscript editing. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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