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Nanosilica supplementation in tomato increases oviposition on stems and caterpillar mortality in the tomato pinworm

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Silicon-induced responses play a key role in plant defense against herbivory, though the underlying mechanisms remain underexplored. In this study, we examined how mesoporous silica nanoparticles (MSNs) affect tomato (*Solanum lycopersicum*) defense against an invasive and highly destructive lepidopteran herbivore, the tomato pinworm (TPW), *Phthorimaea absoluta*. In tomato plants supplemented with MSN, prior exposure to TPW oviposition shifted subsequent egg-laying from a preference for leaves to an even distribution between stems and leaves. This shift was not observed in nonsilicon-supplemented plants. Prolonged oviposition triggered pigmentation in the basal cells of type I glandular trichomes on the stems of silicon-supplemented plants. Chemical analysis by coupled gas chromatography-mass spectrometry revealed that the pigmented trichome was rich in soluble sugars (sucrose and L-arabinose) and waxes, dominated by the saturated hydrocarbon tetracosane. Bioassays with the crude extract of the pigmented trichome and a three-component sugar–wax blend replicated the oviposition and caterpillar response observed with the pigmented trichome, while individual components produced variable effects. While L-arabinose alone replicated the oviposition effects of the three-component sugar–wax blend, sucrose increased oviposition and caterpillar feeding and survival, while L-arabinose and tetracosane caused the highest caterpillar mortality. Additionally, these treatments altered caterpillar gut microbiota composition and influenced frass volatiles, which attracted the TPW natural enemies, *Nesidiocoris tenuis* (predator) and *Neochrysocharis formosa* (parasitoid). Our findings suggest that silicon supplementation increases tomato defense against TPW through oviposition-induced responses, which promotes recruitment of natural enemies.

silicon | plant defense | tritrophic interactions | oviposition | insect physiology

Plants have evolved a variety of defense strategies to protect themselves from biotic stressors like herbivores and pathogens, among which allelochemicals play a central role by influencing herbivore behavior, growth, and survival (1, 2). These chemical defenses are triggered by various stimuli, including direct interactions such as insect oviposition and feeding, as well as indirect cues through volatile-mediated communication between plants, enabling them to respond dynamically to threats (3, 4).

In the Solanaceae family, trichomes, specialized epidermal outgrowths, are crucial defense structures. They are classified into two types: nonglandular, which provide physical deterrence, and glandular, which secrete or store a range of bioactive metabolites for biochemical defense (5, 6). Tomato (*Solanum lycopersicum*) plants harbor eight distinct trichome types (I–VIII) classified based on their morphology and biochemical function. Among these, glandular trichomes (types I, II, IV, VI, and VII) are particularly important as they produce acyl sugars, volatile organic compounds (VOCs), and phenolic compounds, significantly impacting herbivory, particularly in neonate caterpillars (5–8). These bioactive compounds can deter feeding, reduce herbivore performance, and mediate complex interactions with natural enemies (9).

Although not an essential nutrient for plant growth, silicon plays a key role in enhancing plant resilience to both biotic and abiotic stressors (10, 11). Absorbed as soluble silicic acid [$Si(OH)_4$], silicon is transported through the xylem and incorporated into various tissues, including trichomes, via silicification (12, 13). In silica-accumulating plants such as rice, silicon strengthens cell walls, providing a physical barrier against herbivores (13, 14). In silica-deficient plants like tomatoes, silicon enhances biochemical defenses by promoting the production of phenolics, VOCs, secondary metabolites, and soluble sugars, which are vital for stress signaling and trichome-mediated defense (9, 15). Silicon also upregulates defense-related genes, increasing lignin biosynthesis and activating enzymes like peroxidase and polyphenol oxidase, further boosting resistance (16, 17).

Significance

Plants utilize physical and biochemical defenses to protect themselves from herbivores, yet the role of nonnutritional components like mesoporous silica nanoparticles (MSNs) in plant–herbivore interactions is not well understood. In this study, we explored silicon-mediated defenses in tomato plants against the tomato pinworm (TPW), a major agricultural pest. Supplementation with MSNs enhanced biochemical defenses in tomato trichomes, a key site of plant–herbivore interaction. TPW females are attracted to MSN-enriched trichomes for egg-laying on stems, but caterpillars that hatch and consume the trichomes experience high mortality, reducing pest survival and minimizing plant damage. Additionally, silicon supplementation indirectly strengthens plant defenses by altering volatile organic compound (VOC) emissions in caterpillar frass, which attract the TPW natural enemies *Nesidiocoris tenuis* (predator) and *Neochrysocharis formosa* (parasitoid). These results suggest that MSN supplementation could be an effective crop protection strategy, enhancing plant resilience and promoting the recruitment of natural enemies.

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In this study, we examined silicon-mediated plant defenses in a solanaceous crop, hypothesizing that soil amendment with mesoporous silica nanoparticles (MSNs) would alter the biochemical functions of trichomes in defending against insect herbivory. Using the tomato (*S. lycopersicum*) and its pest, the tomato pinworm (TPW) (*Phthorimaea absoluta*, TPW), as model systems, we explored how silicon supplementation influences plant defense mechanisms. TPW, a globally invasive pest, is responsible for significant economic losses in tomato production due to its rapid reproduction and resistance to conventional control measures (18, 19). Moreover, we explored how silicon supplementation influences tritrophic interactions involving tomatoes, TPW, and key natural enemies such as the predator *Nesidiocoris tenuis* and the parasitoid *Neochrysocharis formosa* (20, 21). These natural enemies play pivotal roles in suppressing TPW populations and are sensitive to changes in plant chemistry induced by silicon supplementation (20).

Results and Discussion

MSN Supplementation Combined with Prior Exposure to Oviposition Increases TPW Oviposition on Stems Relative to Leaves. Consistent with previous findings, 18-h oviposition assays showed that TPW females laid approximately three-fold more eggs on tomato leaves than stems, regardless of silicon (+Si) or nonsilicon (–Si) supplementation (χ^2 = 176.97, P < 0.0001, Fig. 1*A* and *SI Appendix*, *Methods*) (22–24). Similarly, after 48 h, oviposition on –Si plants followed the same trend (χ^2 = 23.27, P < 0.0001, Fig. 1*A*). However, in +Si plants, the difference in oviposition between leaves and stems decreased, with nearly twice as many eggs laid on +Si stems compared to –Si stems (χ^2 = 44.60, P < 0.0001, Fig. 1*A*). Despite these preferences, the total number of eggs laid per plant did not significantly differ between +Si and –Si plants (*SI Appendix*, Fig. S2*A*). Sequential oviposition bioassays validated the increased oviposition on +Si stems. In these experiments, initial oviposition on tomato plants

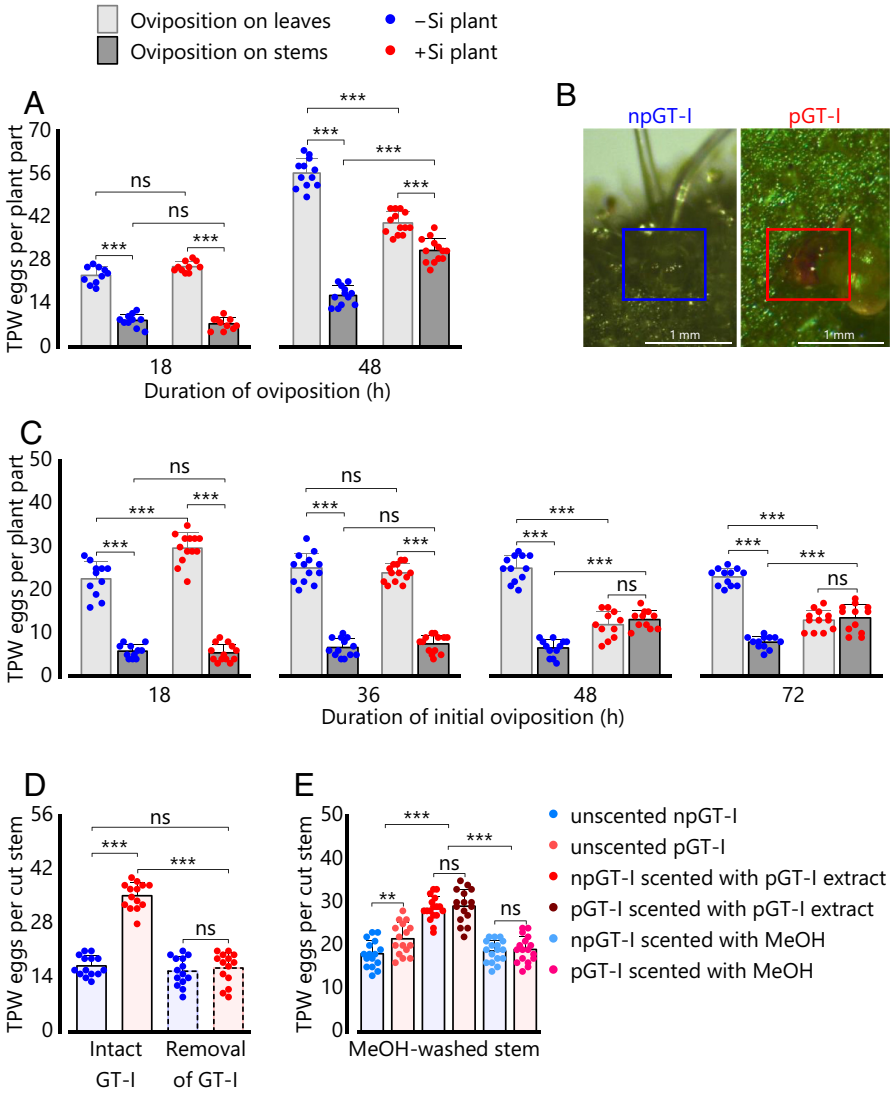

Fig. 1. Effects of mesoporous silica nanoparticles (MSN) supplementation and oviposition by TPW on tomato plants. (*A*) Oviposition patterns on leaves and stems of +Si and −Si plants after 18 h and 48 h of oviposition exposure. (*B*) Comparison of the basal cell of glandular trichome type I (GT-I) in response to oviposition, highlighting differences between nonpigmented GT-I (npGT-I) on −Si-iOVIP stems (blue box) and pigmented GT-I (pGT-I) on +Si-iOVIP stems (red box), where a distinct pigmented mass is observed. (Scale bar: 1 mm.) (*C*) Effect of initial oviposition duration (18, 36, 48, or 72 h) on subsequent oviposition preference. (*D*) Oviposition responses on cut stems with intact vs. removed GT-I trichomes. (*E*) Oviposition on methanol-washed cut stems scented with crude extracts from pGT-I and npGT-I trichomes. Bars represent mean ± SE (*B*: n = 10 to 13; *C*: n = 11 to 13; *D*: n = 14; *E*: n = 14 to 17). Dots indicate individual data points. Significant differences are denoted with $^{**}P$ < 0.01, $^{***}P$ < 0.001, and ns (not significant).

was designated as iOVIP. First, eggs were removed to eliminate potential density effects, then plants were re-exposed to moths for subsequent oviposition (*SI Appendix*, *Methods*). In the iOVIP plants preconditioned for 48 h or more, subsequent oviposition showed an even distribution of eggs between stems and leaves in +Si plants (χ^2 = 0.67, P = 0.41, Fig. 1*C*). In contrast, the leaves remained the preferred oviposition site in −Si plants (χ^2 = 228.92, P < 0.0001, Fig. 1*C*). This shift led to a twofold increase in egg-laying on +Si stems compared to −Si stems (χ^2 = 231.94, P < 0.0001, Fig. 1*C* and *SI Appendix*, *Methods*). Moreover, total egg deposition on iOVIP plants was significantly lower in +Si plants than in −Si plants (*SI Appendix*, Fig. S2*B*).

Additionally, we found that the stems of silicon-supplemented plants preconditioned through 48-h to 72-h initial oviposition (+Si-iOVIP) exhibited pigmentation in the basal cells of glandular trichome type I (GT-I) (hereafter referred to as the "pigmented mass"). This pigmentation was absent in nonsilicon plants (−Si-iOVIP) (Fig. 1*B*). Trichomes with this basal cell pigmentation are hereafter referred to as pigmented GT-I trichomes (pGT-I), while nonpigmented GT-I are designated as npGT-I.

To investigate the role of pGT-I in TPW oviposition on stems, two complementary experiments were conducted. First, oviposition responses were compared among intact pGT-I stems, pGT-I-removed stems, and these stems were washed with 65% methanol–water (PBS buffer solution) to eliminate potential stress-related secondary metabolites from surgical procedures. Oviposition on methanol-washed pGT-I stems decreased by ~53% compared to intact pGT-I stems (χ^2 = 158.18, P < 0.0001, Fig. 1*D*). Second, in dose–response assays, applying pGT-I extracts onto methanol-washed pGT-I and npGT-I stems restored oviposition levels to over 80% (χ^2 = 151.88, P < 0.0001, Fig. 1*E* and *SI Appendix*, Fig. S4*A*). These findings suggest that pGT-I trichomes may contain oviposition stimulants, that attract female moths to oviposit on stems. Furthermore, the partial recovery of oviposition on methanol-washed stems suggests that residual stimulants may persist despite trichome removal.

Sugars and Waxes in Pigmented Trichomes Stimulate TPW Oviposition. To identify oviposition stimulants in the pGT-I extract, chemical analysis by gas chromatography-mass spectrometry (GC-MS) revealed the presence of sugars based on their trimethylsilyl derivatives, with 8- and 9-fold higher levels of L-arabinose and sucrose in pGT-I (+Si-iOVIP) than npGT-I (−Si-iOVIP) stems (Fig. 2*A* and *SI Appendix*, Table S1). Since plant tissue surfaces contain waxes, *n*-hexane extracts from pGT-I and npGT-I were also analyzed by GC-MS and compared. Both the *n*-hexane extracts from pGT-I and npGT-I were rich in saturated hydrocarbons (C_{19}-C_{31}), but 4-fold more tetracosane (C_{24}) was detected in the pGT-I than npGT-I extracts (Fig. 2*B* and *SI Appendix*, Table S2). These findings suggest that potential TPW oviposition stimulants in pGT-I consist of a mixture of polar (sugars) and nonpolar (waxes) compounds.

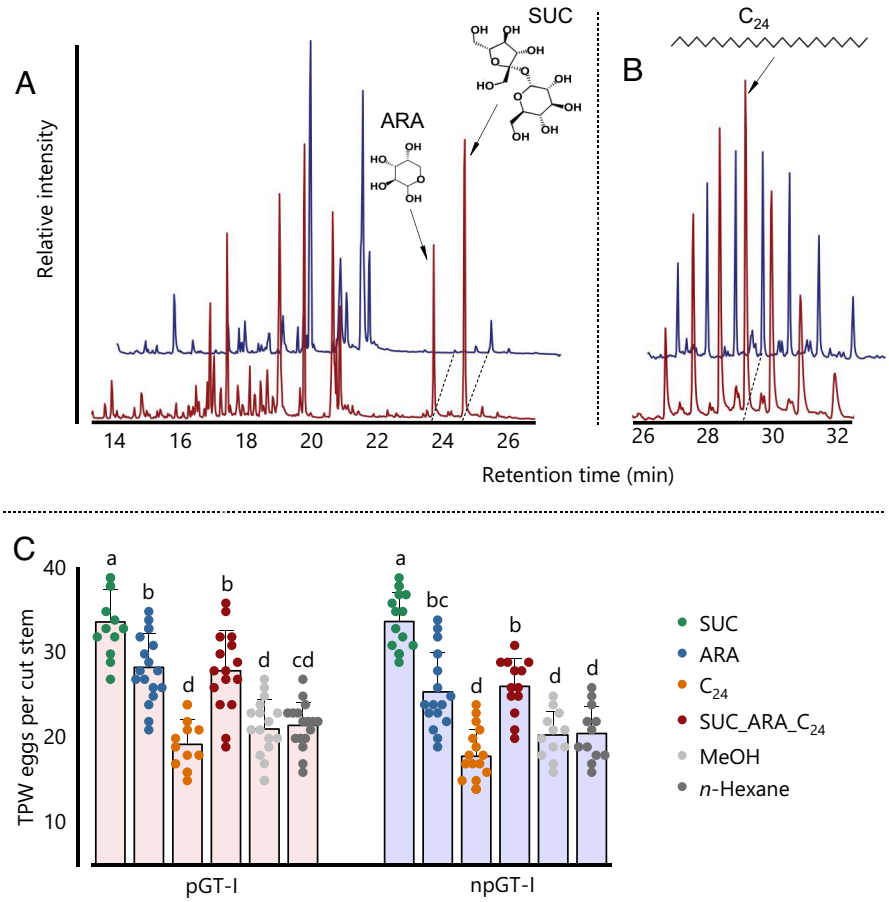

Fig. 2. Chemical composition and effects of sucrose, L-arabinose, tetracosane, and the blend of the three components on TPW oviposition. (*A*) GC-MS chromatograms of trimethylsilyl derivatives in glandular trichome type I (GT-I) extracts from +Si-iOVIP (pGT-I, red) and −Si-iOVIP (npGT-I, blue) tomato stems. Peaks corresponding to L-arabinose and sucrose are highlighted. (*B*) GC-MS chromatograms of hydrocarbons in pGT-I (red) and npGT-I (blue). The peak corresponding to tetracosane is highlighted. (*C*) Oviposition assays on methanol-washed tomato stems (pGT-I and npGT-I) scented with sucrose (SUC), L-arabinose (ARA), tetracosane (C_{24}), or their three-component blend (SUC_ARA_C_{24}). Controls included methanol and *n*-hexane treatments. Bars represent mean ± SE (n = 13 to 17) of TPW eggs per cut stem. Dots represent individual data points. Different letters indicate statistically significant differences between treatments (α = 0.05).

To assess the roles of these dominant compounds, exogenous applications of a three-component sugar–wax blend (sucrose, L-arabinose, and tetracosane) and individual components (at natural ratios) were compared on methanol-washed +Si-iOVIP (pGT-I) and –Si-iOVIP (npGT-I) cut tomato stems. Oviposition did not differ significantly between the two stem types ($\chi^2 = 1.86$, $P = 0.17$, Fig. 2*C*). Sucrose stimulated the highest and most significant TPW oviposition response (pGT-I: $\chi^2 = 7.77$, $P < 0.01$; npGT-I: $\chi^2 = 14.00$, $P < 0.001$), outperforming both L-arabinose and tetracosane. The three-component sugar–wax blend elicited a comparable oviposition response (93%) to that induced by the exogenous application of pGT-I crude extract ($\chi^2 = 1.40$, $P = 0.24$, Figs. 1*D* and 2*C*) and was not significantly different from L-arabinose (pGT-I: $\chi^2 = 0.05$, $P = 0.83$; npGT-I: $\chi^2 = 0.12$, $P = 0.73$), but it was ~20% lower than sucrose alone ($\chi^2 = 20.89$, $P < 0.0001$, Fig. 2*C*). In contrast, tetracosane elicited the weakest oviposition response, like control levels ($\chi^2 = 7.48$, $P = 0.19$), and on average ~55% less potent than sucrose alone ($\chi^2 = 134.07$, $P < 0.0001$, Fig. 2*C*). These findings demonstrate that the three-component sugar–wax blend and L-arabinose alone effectively mimic the oviposition response induced by the pGT-I extract, with sucrose acting as the primary stimulant and tetracosane exhibiting potentially deterrent properties in the mixture. Thus, silicon supplementation enhances the levels of sugars and waxes in trichomes.

Sugars and Waxes in Pigmented Trichomes Reduce TPW Caterpillar Feeding and Survival. While pGT-I stimulated oviposition in adult females, it also influenced neonate caterpillar feeding behavior and survival. Notably, 96.6% neonate caterpillars that hatched on stems of +Si plants fed on pGT-I, compared to only 1.8% which fed on –Si stems (Movie S1 and *SI Appendix*, Fig. *S4B*). Feeding on trichomes exhibited reduced subsequent leaf-feeding activity by 64 to 71% compared to caterpillars that exclusively fed on leaves of naive or iOVIP plants ($\chi^2 = 88.57$, $P < 0.0001$, Fig. 3*A*) and subsequently, up to 72.3% mortality ($\chi^2 = 150.15$, $P < 0.0001$, *SI Appendix*, Fig. S4*C*).

Tomato leaves treated with pGT-I extract significantly reduced TPW neonate caterpillar leaf-feeding by 58.9% compared to npGT-I extract ($\chi^2 = 76.48$, $P < 0.0001$, Fig. 3*B*), which mirrored caterpillar feeding response on pGT-I. On the other hand, caterpillar feeding responses to tomato leaves treated with the single compounds mirrored the pattern of the oviposition bioassays, with sucrose increasing the feeding response by 15.3%, while L-arabinose and tetracosane reduced feeding responses by 25.8 and 49.3%, respectively, relative to the npGT-I extract ($\chi^2 = 244.44$, $P < 0.0001$, Fig. 3*B*). By contrast, the three-component sugar–wax blend and the crude extract of pGT-I on average reduced caterpillar feeding by 55.3% relative to controls ($\chi^2 = 3.88$, $P = 0.14$, Fig. 3*B*).

The treatments differentially affected caterpillar mortality. Sucrose and the solvent controls caused the highest caterpillar survival rates, which were not significantly different ($\chi^2 = 0.10$, $P = 0.95$), followed by the extract of nonpigmented trichomes (Fig. 3*C*). On the other hand, the pGT-I extract, sugar–wax blend, L-arabinose, and tetracosane caused the highest mortality in caterpillars, which were not significantly different ($\chi^2 = 3.20$, $P = 0.36$, Fig. 3*C*), and caused ~49 to 68% more mortality relative to

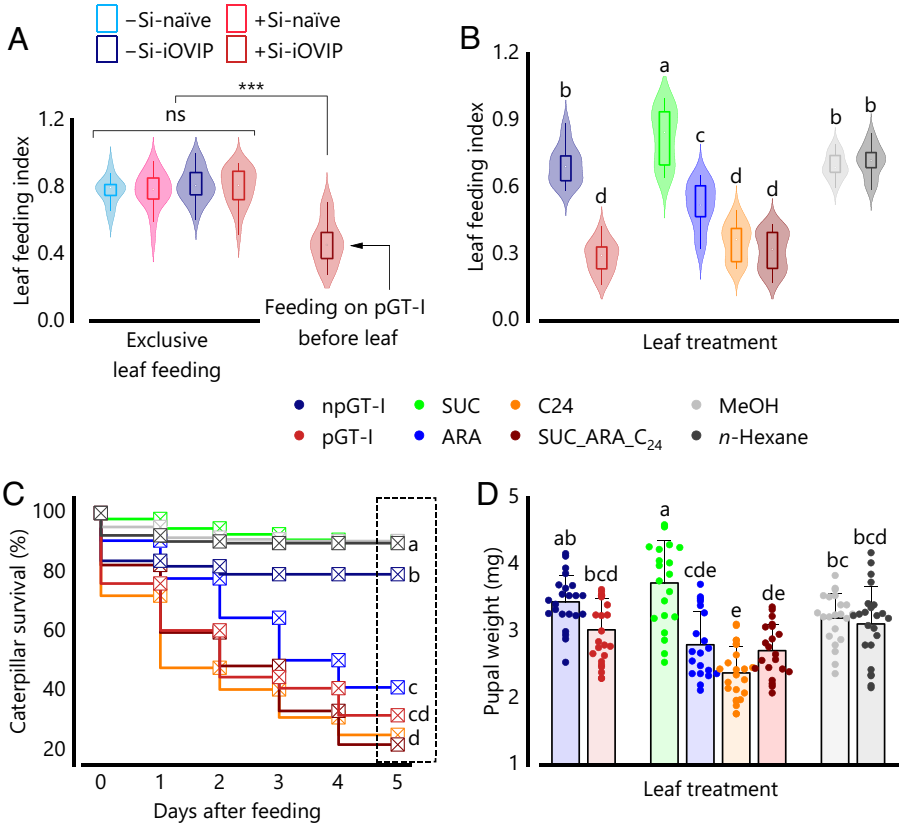

Fig. 3. Effects of ingestion of pigmented glandular trichomes type I (pGT-I), sucrose, L-arabinose, tetracosane, and their three-component blend on neonate caterpillar feeding and survival of TPW. (*A*) Leaf feeding index of TPW caterpillars exclusively feeding on leaves compared to caterpillars fed on pGT-I before leaf exposure. (*B*) Leaf feeding index of TPW caterpillars on leaves treated with extracts, individual compounds (SUC, ARA, C_{24}), the three-component blend (SUC_ARA_C_{24}), or control solutions [methanol (MeOH) or *n*-hexane]. (*C*) Caterpillar survival rates over five days following exposure to treated leaves, with cumulative mortality rates statistically compared at day five. (*D*) Pupal weights of TPW caterpillars after feeding on treated leaves. Bars and violin plots represent mean ± SE (*A*: $n = 18$ to 23; *B*: $n = 16$ to 21; *C*: $n = 11$ to 15; *D*: $n = 21$ to 25), with dots representing individual data points. Different letters indicate statistically significant differences among treatments ($\alpha = 0.05$).

sucrose (χ^2 = 197.85, P < 0.0001, Fig. 3*C*). Pupal weights also varied with treatment, with sucrose inducing the highest pupal weight (χ^2 = 98.60, P < 0.0001), whereas the three-component blend, L-arabinose, and tetracosane induced the lowest pupal weights, which were not significantly different (χ^2 = 11.94, P < 0.01, Fig. 3*D*), mirroring the pattern found for caterpillar survival rates.

These results suggest that mechanistically, the interaction between the contrasting physiological roles of the individual components in the three-component sugar–wax blend, most likely enhances plant defense and imposes metabolic costs on caterpillar biological traits (25–29). Additionally, they may impose different physiological costs in the insect's body including the gut microbiome.

Sugar–Wax Mixture and Individual Compounds Influence Caterpillar Gut Microbial Composition and Frass VOCs. Next, we compared the gut microbiome of caterpillars that consumed diets across the different treatments (synthetic sugar–wax blend and individual compounds) by analyzing microbial communities in their frass. The frass microbial profiles revealed treatment-specific clustering patterns (R = 0.85, P < 0.05, *SI Appendix*, Fig. S5*A*) and diversity (Chao1, ACE, and Shannon index, Fig. 4*A* and *SI Appendix*, Fig. S5 *B* and *C*), with the highest diversity recorded with L-arabinose treatment. The dominant bacterial phyla across all treatments were Firmicutes, Proteobacteria, Actinobacteria, and Cyanobacteria, with Firmicutes and Proteobacteria being the most abundant (Fig. 4*B*), consistent with their established roles in insect gut microbiota composition and function (30–32). L-Arabinose ingestion increased levels of bacterial genera including *Clostridium*, *Morganella*, *Paeniclostridium*, *Klebsiella*, *Escherichia*, *Bacillus*, and *Enterobacter*, while sucrose increased *Clostridium* and *Morganella* levels. In contrast, tetracosane selectively increased *Clostridium* levels, while reducing *Morganella*, *Paeniclostridium*, *Gluconobacter*, and *Peptacetobacter* levels (Fig. 4*C*). The three-component sugar–wax blend elevated *Gluconobacter* and *Lactococcus* levels while reducing *Paeniclostridium*, *Pantoea*, *Vibrio*, *Peptacetobacter*, *Enterobacter*, and *Clostridioides* levels. These results highlight the adaptive capacity of the gut microbiome to respond to dietary inputs by selectively enriching or suppressing bacterial taxa, thereby influencing caterpillar nutrient metabolism and stress resilience.

It appears that to enhance plant defense against herbivore attack, L-arabinose triggers a microbial stress response or compensatory mechanism, contributing to the proliferation of bacterial genera involved in carbohydrate metabolism, such as *Clostridium, Enterobacter*, *Escherichia,* and *Klebsiella* (33–35). The overgrowth of these bacteria in the gut of infected caterpillars has been associated with increased mortality (36, 37), suggesting that L-arabinose-mediated microbial shifts may disrupt nutrient assimilation and host–pathogen interactions, compromising caterpillar survival (33). However, this effect was not observed with the sugar–wax blend, suggesting that tetracosane may exert an inhibitory influence on microbial responses typically associated with L-arabinose metabolism. This disruption indicates that hydrocarbons like tetracosane, being nonnutritional, may interfere with bacterial metabolic pathways, altering gut microbial dynamics, leading to higher caterpillar mortality (32).

Next, the headspace of caterpillar frass was captured and analyzed, resulting in 47 identified VOCs across treatments (Fig. 4*D* and *SI Appendix*, Table S3). The frass from L-arabinose treatment emitted significantly higher levels of β-phellandrene, *n*-hexanol, and 3-octanol (P < 0.01, *SI Appendix*, Table S3). Sucrose treatment increased emissions of α-humulene and γ-terpinene, compounds linked to plant–herbivore signaling (21). Tetracosane treatment uniquely produced high levels of (*E*)-caryophyllene but had the lowest *n*-hexanol emissions (Fig. 4*D*). The three-component blend released elevated levels of δ-3-carene, β-phellandrene, and 3-octanol (P < 0.0001, Fig. 4*D* and *SI Appendix*, Table S3). These findings demonstrate that dietary composition affects gut microbial metabolic activity and alters the quality and quantity of frass VOC emissions.

Significant correlations emerged between VOCs and bacterial genera (Fig. 4*E*). For example, 3-octanol positively correlated with *Paeniclostridium* and *Gluconobacter*, while *n*-hexanol correlated with *Morganella* and *Paeniclostridium*. β-Phellandrene was positively associated with genera such as *Proteus* and *Enterobacter*. Conversely, α-humulene exhibited negative correlations with most bacterial genera, and (*E*)-caryophyllene showed a negative correlation with *Morganella* (Fig. 4*E*). These correlations illustrate the metabolic interplay between gut bacteria and VOC production, where specific bacterial taxa mediate the synthesis, modification, or suppression of certain volatiles. These interactions may result from bacterial specialization in metabolizing plant-derived substrates or competitive exclusion dynamics among gut microbiota (38). The observed VOC–bacterial relationships suggest that gut microbial activity directly influences the chemical composition of frass volatiles, potentially affecting larval interactions with their environment, including host plants, predators, and parasitoids.

Caterpillar Frass VOCs Indirectly Enhance Plant Defense by Attracting Natural Enemies. Finally, we investigated the influence of caterpillar frass VOCs on the responses of the TPW predator *N. tenuis* and parasitoid *N. formosa*. Predator nymphs and parasitoid female wasps responded distinctly to frass VOCs compared to charcoal-filtered air control (Fig. 4 *F* and *G*). Predators were selectively attracted to VOCs released from the three-component blend treatment (70.05%, P < 0.001). In contrast, parasitoids exhibited strong attraction to all the four different frass odors (P < 0.001), with sucrose and L-arabinose treatments inducing the highest responses (88.7 and 87.0%, respectively, P < 0.0001, Fig. 4 *F* and *G*). These findings suggest that predators and parasitoids rely on distinct VOC cues to locate their targets, reflecting differences in their foraging strategies and sensory preferences. The selective attraction of the predators to the three-component blend highlights the importance of specific sugar and hydrocarbon combinations in generating volatile cues essential for their detection. Conversely, the broad attraction of the parasitoid wasps across all treatments, particularly to sucrose and L-arabinose, underscores a reliance on sugar-derived volatiles as host-location signals (39).

Responses to individual synthetic compounds further elucidated these preferences. Predators showed significant attraction to β-phellandrene, δ-3-carene, 3-octanol, and α-humulene (P < 0.01) but weak responses to (*E*)-caryophyllene and *n*-hexanol (Fig. 4*H*). Parasitoids displayed strong attraction to 3-octanol and *n*-hexanol (P < 0.0001) but weak responses to (*E*)-caryophyllene, δ-3-carene, and α-humulene (Fig. 4*I*).

Predators exhibited significant attraction to a synthetic blend of β-phellandrene, δ-3-carene, 3-octanol, and α-humulene under filtered-air, sucrose-frass, and sugar–wax-frass VOCs conditions (P < 0.05, *SI Appendix*, Fig. S6*A*). Parasitoids, however, responded most strongly to the blend of 3-octanol and *n*-hexanol across all conditions (P < 0.0001, *SI Appendix*, Fig. S6*B*).

Silicon Supplementation Enhances Tomato Defenses Against TPW Through Biochemical Modifications and Natural Enemy Recruitment. Our results highlight three key findings. First, silicon supplementation modifies tomato plant biochemical defenses, resulting in the formation of a pigmented mass at the base of glandular trichomes. The pigmented mass, consisting of

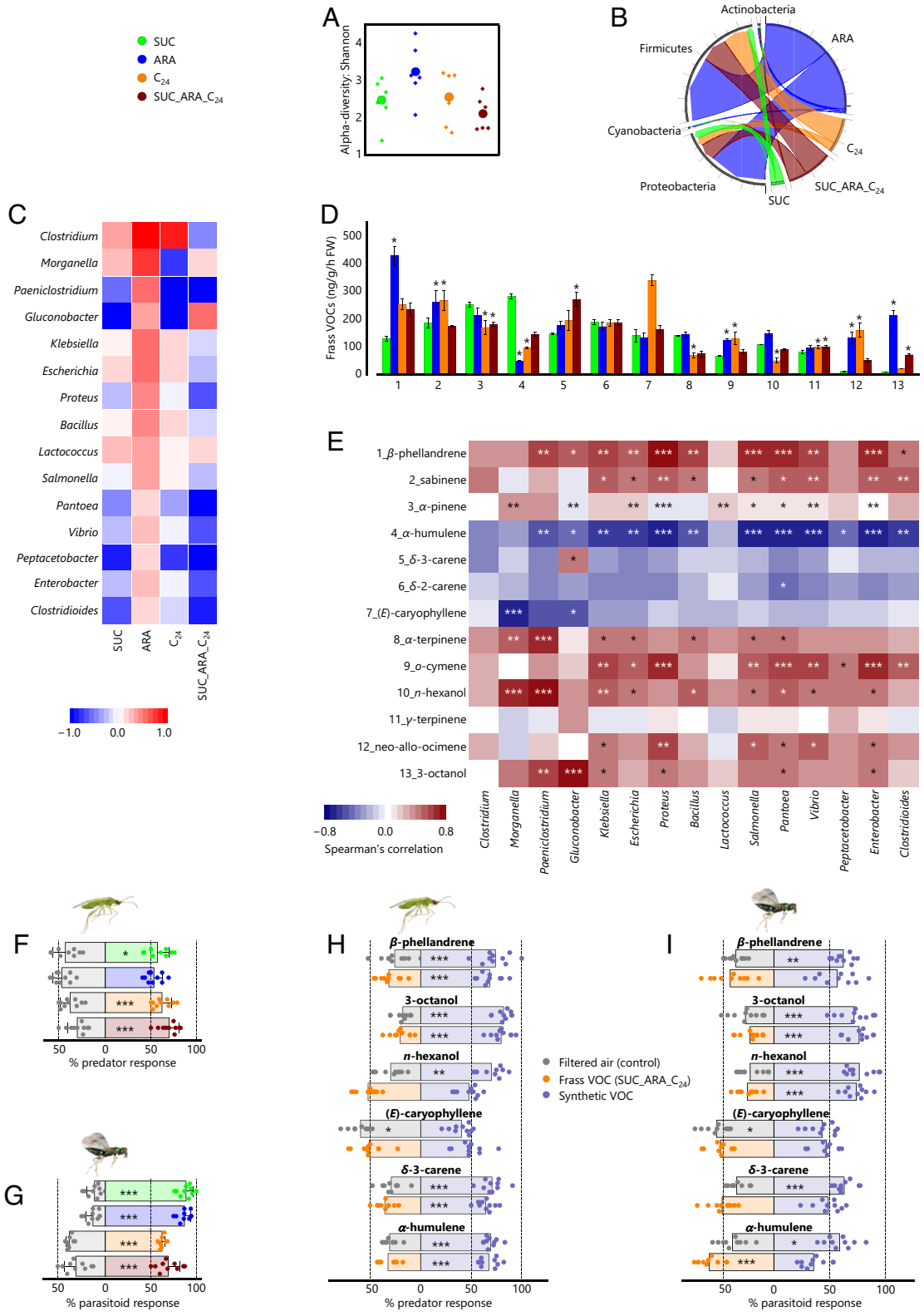

Fig. 4. (*A*) Shannon's alpha-diversity index of TPW caterpillar frass. (*B*) Chord diagram showing distribution of the major bacterial phyla (Actinobacteria, Firmicutes, Cyanobacteria, and Proteobacteria) across the treatments. (*C*) Heatmap illustrates the relative abundance of key bacterial genera across treatments. (*D*) VOCs detected in caterpillar frass ($n = 7$) via GC-MS, showing significant differences in key compounds across treatments, including β-phellandrene, sabinene, α-pinene, α-humulene, δ-3-carene, *n*-hexanol, and 3-octanol. Asterisks (*) indicate significant differences compared to the control (SUC). (*E*) Spearman's correlation heatmap showing associations between bacterial genera and frass VOCs. Positive correlations are shown in red, while negative correlations are shown in blue. (*F*) Olfactory responses of *Nesidiocoris tenuis* (predator) and (*G*) *Neochrysocharis formosa* (parasitoid) to frass VOCs compared to charcoal-filtered air. (*H*) Olfactory responses of *N. tenuis* and (*I*) *N. formosa* to synthetic standards of VOCs compared to charcoal-filtered air or SUC_ARA_C_{24}-frass VOC. Significant differences are indicated by asterisks: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

polar (sugars) and nonpolar (waxes) compounds, replicated its oviposition effect with a three-component synthetic sugar–wax blend and one of its components, L-arabinose alone, suggesting that herbivorous insect behaviors, such as TPW oviposition, may rely on detecting a phytochemical diversity derived from a balance between stimulants and deterrents (40, 41). This indicates that plants may defend against herbivore attacks by synthesizing additional phytochemicals (qualitative) or increasing levels of existing ones (quantitative), as observed in the current study. From an ecological perspective, producing higher levels of the same compounds may incur lower metabolic costs for the plant compared to synthesizing new ones, while also simplifying the detection of oviposition stimulants and deterrents in the pigmented mass by the herbivore. This plant defense strategy, investing in higher levels of existing phytochemicals, proved effective in the long term, as demonstrated in our caterpillar feeding assays. TPW ovipositing females may detect these plant defense chemicals through contact and olfactory chemoreceptors (25, 29, 42, 43), though further research is needed to clarify these mechanisms.

Second, diets laced with the pigmented mass, its dominant three-component sugar–wax blend, and individual components imposed differential physiological costs on TPW caterpillars. In caterpillars, gustatory perception is important to assess food quality for growth and survival (43). Thus, the fact that the pigmented mass, despite its higher phytochemical diversity than the three-component sugar–wax blend, affected caterpillar bionomics similarly suggests that the strong antagonistic effects of L-arabinose and tetracosane may override the stimulatory influence of sucrose and other sugars in the different treatments. Sucrose, a disaccharide of glucose and fructose, stimulates feeding of many insects, including Lepidoptera (25, 27). In contrast, arabinose, a pentose sugar, functions as an antifeedant for various insects and has been shown to reduce pupal weight in lepidopterans, consistent with our findings (27, 44). Overall, the commonality for plant defense against herbivore attack, whether female oviposition or caterpillar ingestion, is exposure to a diversity of plant chemicals instead of single compounds in the pigmented mass, with likely greater metabolic costs associated with increased mortality for herbivore caterpillars (40).

Third, our finding that frass-derived bacterial profiles associated with the different pigmented mass compounds exhibit distinct patterns aligns with previous studies reporting that plant secondary metabolites change herbivore gut microbiota (45, 46). This change may have ecological implications, including effects on both inter- and intraspecific interactions inside the gut (46) and on the herbivore's interaction with its environment, including natural enemies from the third trophic level (40). Consistent with these findings, we observed that altering the caterpillar gut microbiota with the sugar–wax blend and individual components indirectly enhanced plant defense through recruitment of the predator *N. tenuis* and parasitoid *N. formosa*, which were variably attracted to the resulting frass volatiles. Interestingly, the predator displayed selective responses, while the parasitoid showed nonselective responses to the different frass volatiles. This may benefit the parasitoid more than the predator because, from an evolutionary perspective, it has a stronger association and adaptation to induced plant defenses and herbivore frass-derived chemical signals as habitat selection and host-finding cues (47, 48). On the other hand, the predator is zoophytophagous and is more attracted to constitutive than induced plant volatiles (49, 50). Nonetheless, our results provide insights into the indirect role of gut microbiota in natural enemy recruitment for plant defense.

Taken together, these results suggest that silicon supplementation provides tomato plant with multiple defense mechanisms against herbivore attack, combining direct biochemical modifications with indirect ecological reinforcement through natural enemy recruitment. The formation of a pigmented mass at the base of glandular trichomes, enriched with key sugar and wax compounds, not only influences TPW oviposition behavior but also imposes significant physiological costs on caterpillar development, ultimately reducing pest survival. Additionally, the alteration of gut microbiota and its subsequent effects on frass volatiles influence the attraction of natural enemies, reinforcing the plant's defense network beyond direct chemical deterrence. However, to fully harness the potential of silicon-mediated defenses in sustainable pest management, field validation is crucial to determine its effectiveness in reducing crop damage and improving yield.

Materials and Methods

Plant and Insects. Tomato seeds (*cv.* Nova F1) were germinated in seed trays and transferred to a greenhouse (22 ± 3 °C day, 17 ± 3 °C night, 60 to 80% RH, 12-h light/dark). After 18 d, seedlings were transplanted into 13.5 × 16.0 cm pots containing a 5:2 sand-to-cattle manure compost substrate. Five MSN concentrations (0.2 to 1 g/kg substrate) were tested, with MSNs (≥99.9% purity, 50 to 80 nm, Chemazone Inc., Canada) mixed into the substrate preplanting (*SI Appendix*, *Methods*). Control plants (−Si) received no MSN. Stem diameter and chlorophyll concentration were measured at 6, 8, and 10 wk to determine optimal MSN application, identified as 0.4 g/kg (*SI Appendix*, Fig. S1).

The TPW (*Phthorimaea absoluta*), predator *N. tenuis*, and parasitoid *N. formosa* were obtained from the ICIPE insect mass rearing facility-Nairobi. TPW caterpillars were reared on 8-wk-old tomato plants. *N. tenuis* was maintained on tomato plants supplemented with *Ephestia kuehniella* eggs and pollen. *N. formosa* was fed honey solution and parasitized TPW caterpillars under controlled rearing conditions (25 ± 1 °C, 65 to 70% RH, 06:45 to 18:45 h photoperiod).

Oviposition Experiments. Time-dependent oviposition experiments were conducted to assess the impact of MSN supplementation on TPW oviposition behavior across two-time intervals (18 or 48 h; *SI Appendix*, *Methods*). These initial experiments revealed distinct time-dependent oviposition patterns (Fig. 1*A*), which informed subsequent sequential oviposition experiments aimed at evaluating the effects of initial oviposition (iOVIP) on subsequent egg-laying activity.

Eight-week-old tomato plants (+Si and −Si groups) were each exposed to five seven-day-old gravid TPW moths for initial oviposition durations of 18, 36, 48, or 72 h. Eggs were carefully removed post-iOVIP using a fine paintbrush to minimize density-related effects on subsequent oviposition. These plants (+Si-iOVIP and −Si-iOVIP) were then transferred individually into acrylic glass-mesh cages (50-cm-wide × 50-cm-long × 60-cm-high) and exposed to a fresh cohort of five seven-day-old gravid TPW moths for an additional 18-h oviposition phase under controlled environmental conditions (25 ± 1 °C, 65 to 70% relative humidity, 12-h light/dark cycle, with red light during the dark phase to simulate crepuscular activity).

Eggs deposited on leaves and stem-petioles were counted using a 45× magnification LED magnifier, with nine to twelve tomato plants serving as biological replicates per treatment group (*SI Appendix*, *Methods*).

GT-I Removal and Oviposition Experiments. Trichome density and distribution on tomato leaves and stems from −Si and +Si plants showed no significant differences (*SI Appendix*, Fig. S3). However, glandular trichome type I (GT-I), characterized by maroon-like basal cell pigmentation ("pigmented mass," pGT-I, Fig. 1*B*), was predominantly observed on stems of +Si after oviposition preconditioning. In contrast, GT-I trichomes on −Si plants lacked this pigmentation and are hereafter referred to as nonpigmented GT-I (npGT-I).

To investigate the role of pGT-I in influencing oviposition behavior on +Si-iOVIP stems, trichomes were carefully excised from 25 cm mid-stem segments of both −Si-iOVIP (npGT-I) and +Si-iOVIP (pGT-I) plants using a pair of fine forceps under a dissecting microscope (*SI Appendix*, *Methods*). The excised sites were rinsed with an aqueous charcoal suspension, followed by distilled water, and air-dried to eliminate residual exudates. Stems with intact trichomes served as controls.

For no-choice oviposition assays, the incised stem ends were wrapped in moist cotton and sealed with Parafilm to maintain hydration. The lower ends were placed in 50 mL Eppendorf tubes lined with moist cotton, providing structural support and moisture retention. These tubes were secured upright on a foam rack within a 30-cm-wide × 30-cm-long × 40-cm-high acrylic glass-mesh cage. Five seven-day-old gravid TPW moths were introduced into the cage for an 18-h oviposition period to compare egg-laying behavior of TPW, isolating the influence of pGT-I on the observed behavioral shifts. Environmental conditions were carefully controlled at 25 ± 1 °C, 65 to 70% relative humidity, and a 12-h light/dark cycle, with red light used during the dark phase to stimulate moth activity. Each treatment group included 14 cut tomato stems as biological replicates.

GT-I Extract Application for Oviposition Assays. Stem segments (~25 cm) were surface-sterilized and cleared of metabolites by immersion in 65% cold methanol-phosphate-buffered saline (PBS) for 8 h, followed by two PBS rinses and three rinses with ultrapure water (Type I). Segments were air-dried in a fume hood for 90 min.

GT-I extracts were prepared from mid-stem trichomes of +Si-iOVIP (pGT-I) and −Si-iOVIP (npGT-I) plants. Trichomes were homogenized in 100 μL of 80% methanol containing 0.1% formic acid using a FastPrep homogenizer (6 m/s, 90 s). The homogenate was centrifuged at 10,000 rpm for 10 min at 4 °C, and the resulting supernatant was air-dried (~90 min). The dried residue was reconstituted in 100 μL of ultrapure water. A dose–response pilot experiment was performed using pGT-I extract applied at three trichome densities (20, 80, and 160 trichomes per 100 μL) on +Si-iOVIP and −Si-iOVIP washed stems. The 80 pGT-I/100 μL dose yielded a response comparable to the 160 pGT-I/100 μL dose (*SI Appendix*, Fig. S4*A*) and was therefore selected for subsequent experiments. GT-I extracts were evenly applied to intact GT-I on methanol-washed receiver stem segments using a fine brush to ensure uniform distribution.

For no-choice oviposition assays, scented stems were placed in 30-cm-wide × 30-cm-long × 40-cm-high acrylic glass-mesh cages under controlled environmental conditions as described for previous GT-I removal experiments. Five seven-day-old gravid TPW moths were introduced per cage for an 18-h oviposition period to assess the influence of GT-I extract on oviposition behavior of TPW. Each treatment group included 14 to 17 stem segments as biological replicates.

Chemical Analysis of GT-I. Glandular trichome type I (GT-I) samples (~10 ± 0.04 μg, ~80 trichomes) were collected from the mid-stem region per plant, pooling ~20 trichomes from four plants per replicate. Samples were homogenized in 100 μL of 80% methanol with 0.1% formic acid using a FastPrep Tissue Homogenizer (6 m/s, 90 s), centrifuged (10,000 rpm, 10 min, 4 °C), and the supernatant oven-dried at 50 °C. The dried extract was derivatized with 75 μL BSTFA (60 °C, 15 min) and analyzed via GC-MS (Agilent 7890, HP-5MS column) using helium carrier gas (1.25 mL/min). The temperature program ramped from 35 °C (5 min hold) to 285 °C (10 °C/min) and was held for 20.4 min. Detector temperatures were set at 180 °C (quadrupole) and 230 °C (ion source), with mass spectra recorded at 70 eV across a 40 to 550 m/z range. Sugars were identified using authentic standards and NIST spectral libraries, quantified against a D-(−)-fructose calibration curve ($R^2 = 0.999$), and expressed as ng/g of trichome material. Five biological replicates were analyzed per group. All chemicals were at least 95% pure.

For hydrocarbon analysis, trichomes were washed thrice with 80% cold methanol (0.1% formic acid) and distilled water, homogenized in methanol-formic acid, and centrifuged (10,000 rpm, 10 min, 4 °C). The supernatant was air-dried under a fume hood and reconstituted in 100 μL *n*-hexane. A 1 μL aliquot was analyzed via GC-MS (Agilent 7890, HP-5MS column) with an oven temperature program ramping from 35 °C to 295 °C. Hydrocarbons were identified by comparing retention times and mass spectra with an alkane standard mixture (C_{10}–C_{40}, MilliporeSigma) and quantified using *n*-tricosane (MilliporeSigma) calibration curves. Results were expressed as ng/g of trichome tissue. Six biological replicates were analyzed per group.

Application of Individual and Blended Compounds for Oviposition Assays. Following the GT-I extract application protocol, sucrose (91 ng/μL, dissolved in ultrapure water, Sigma-Aldrich), L-arabinose (≥99% purity, 46 ng/μL, dissolved in ultrapure water, Sigma-Aldrich), and tetracosane (50 ng/μL, dissolved in *n*-hexane, MilliporeSigma) were applied individually and as a three-component blend. These compounds, identified as predominant metabolites in pigmented trichomes (*SI Appendix*, Tables S1 and S2), were selected based on their significant presence and potential influence on TPW oviposition behavior. The solutions were applied to methanol-washed GT-I on ~25-cm stem segments of −Si-iOVIP (with npGT-I). Methanol and *n*-hexane alone served as control treatments. The scented stem segments were exposed to five seven-day-old gravid TPW moths for an 18-h no-choice oviposition period. Egg counts were recorded, and each treatment was replicated across 13 to 17 segments.

Effect of Sucrose, L-Arabinose, and Tetracosane on TPW Caterpillar Feeding and Development. Neonate TPW caterpillars exhibited exclusive feeding on pigmented GT-I trichomes (pGT-I) (Movie S1 and *SI Appendix*, Fig. S4*B*). To assess the influence of key metabolites, three caterpillars per clip cage (Ø60 mm, BugDorm, UK) were transferred onto leaflets from naive and iOVIP plants using a fine paintbrush. Control leaflets lacked prior trichome exposure. After a 36-h feeding period, leaflets were flattened and imaged on millimeter grid paper (*SI Appendix*, *Methods*). Leaf area consumption was measured using ImageJ software (NIH), and a feeding index was calculated by normalizing the amount consumed per caterpillar cohort relative to the maximum consumption observed across treatments.

Natural trichome-equivalent concentrations of sucrose, L-arabinose, tetracosane, and their three-component blend were applied on to −Si-naive tomato leaves (~10 mL/leaf). Controls included methanol extracts of pGT-I and npGT-I, along with pure methanol and *n*-hexane. Treated leaves were air-dried (45 min) before feeding trials. Starved caterpillars (3 h) were placed onto treated leaflets under controlled conditions (25 ± 1 °C, 65 to 70% RH, 12-h light/dark cycle) with three caterpillars per cage. To ensure ingestion of the test compounds, caterpillars were transferred thrice during the initial 36 h to freshly treated leaves. Afterward, caterpillars were relocated daily to new leaflets until pupation.

Frass was collected daily and stored at −80 °C for subsequent analysis. Cumulative leaf damage was measured and analyzed using ImageJ software and feeding behavior was assessed to determine the impact of trichome feeding on subsequent leaf consumption. Daily mortality was recorded, and pupae were weighed individually within 12 h postemergence. The experiment included 16 to 23 cohorts of three caterpillars per treatment group.

16S rRNA Sequencing of Microbial Communities in TPW Caterpillar Frass. Frass samples were pooled by caterpillar cohort (1 g per sample), with six pooled replicates analyzed per treatment. DNA extraction was conducted using the DNeasy PowerSoil Kit (Qiagen) with extended bead-beating to optimize cell lysis. The 16S rRNA gene libraries were prepared using the 16S Barcoding Kit (SQK-16S024; Oxford Nanopore Technologies, Oxford, UK) and sequenced using ONT R9.4 flow cell (FLO-MIN106). The sequencing was conducted using the MinION Mk1C device (Oxford Nanopore Technologies) for 4 h, with real-time base calling performed by MinKNOW software (v. 21.11.6) and MinKNOW Core (v. 4.5.4).

Taxonomic classification was conducted using the Oxford Nanopore Technologies "What's In My Pot" (WIMP) workflow, enabling species identification and quantification. Microbial relationships were visualized using chord diagrams, while alpha diversity metrics (ACE, Chao1, and Shannon indices) were used to assess bacterial diversity. Principal Coordinate Analysis (PCoA) was employed to compare microbial community composition across treatments (*SI Appendix*, *Methods*).

Frass VOC Collection and Natural Enemy Responses. Headspace VOCs from frass samples were collected using a dynamic push–pull system over a 3-h period. Frass from neonate TPW caterpillars was pooled by cohort, with 3 g placed on filter paper in a 100-mL QuickFit glass tube. Charcoal-filtered air (260 mL/min) passed through the tube, and VOCs were trapped on solvent-cleaned Porapak Q 80/100-mesh adsorbents (MilliporeSigma). Each treatment group included seven biological replicates.

Trapped VOCs were eluted with 150 μL GC-MS grade dichloromethane (DCM, Sigma-Aldrich) and stored at −80 °C until analysis. Control tubes without frass were included to account for background contamination. VOC analysis was performed using GC-MS (Agilent 7890A, HP-5MSI column) with helium as the carrier gas (1.25 mL/min). The oven temperature was ramped from 35 °C to 290 °C at 10 °C/min. VOCs were identified using synthetic standards (when available) and the NIST spectral database and quantified as ng/g of frass material.

The behavioral responses of *N. tenuis* nymphs (predator) and parasitoid *N. formosa* female wasps (parasitoid) to crude caterpillar frass volatiles, individual synthetic compounds, and synthetic blends were evaluated using a Y-tube olfactometer (*SI Appendix, Methods*). The airflow was maintained at 120 mL/min under control conditions. VOC solutions were applied to filter paper, allowing the solvent to evaporate for ~60 secs before testing. Insects were acclimated to clean air for 45 min, and 15 to 25 individuals per condition were observed over 10 test days (*SI Appendix, Methods*). Responsiveness was defined as spending ≥30 secs in a VOC-treated arm during up to 10-min observation period.

Data Analysis. Data were organized using XLSTAT2025, analyzed in R-4.4.1, and visualized in OriginPro2025. Generalized Linear Models (GLMs) with likelihood ratio tests were used to examine relationships between categorical and continuous variables. Pairwise comparisons from GLMs were performed using estimated marginal means with Tukey-adjusted contrasts for equal variance assumptions. When variances were unequal, Games–Howell post hoc tests were applied. A significance level of $P < 0.05$ was used for all analyses.

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information. The sequences generated in this study have been deposited in and are publicly accessible via the GenBank database (www.ncbi.nlm.nih.gov/genbank) under the BioProject number PRJNA1214729 (https://www.ncbi.nlm.nih.gov/bioproject/1214729) (51).

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The authors declare no competing interest.

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