



BEHAVIOURAL RESPONSES OF THE SOLITARY ENDOPARASITOID *COTESIA VESTALIS* (HALIDAY) TO DAMAGED CABBAGE

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ABSTRACT

Cotesia vestalis (Haliday) is the key biological control agent of *Plutella xylostella* L, the diamond back moth. This study investigated the influence of induced chemical defenses in cabbage (*Brassica oleracea*) on the olfactory responses of *C. vestalis* females. Herbivores trigger plants to release more volatile organic compounds (VOCs), attracting natural enemies. This study hypothesized that *C. vestalis* would be more attracted to specific volatiles emitted from differently herbivore-damaged cabbage compared to undamaged plants. Y-olfactometer experiments revealed that *C. vestalis* females were significantly more attracted to volatiles emitted by *P. xylostella*-damaged cabbage. This preference was also observed for plants damaged by *Crociodolomia* spp. Gas chromatography analysis confirmed qualitative and quantitative differences in volatile profiles between damaged and undamaged cabbage. Findings suggest that induced plant volatiles play a critical role in attracting *C. vestalis* to host plants, highlighting the potential for using plant-mediated attraction to enhance biological control strategies.

Key words: *Cotesia vestalis*, *Plutella xylostella*, parasitoids, herbivorous, plant volatiles, Brassica, Y-olfactometer, screen cage, bioassays, plant mediated attraction, IPM, olfactory responses

Plants have evolved sophisticated chemical defenses, continuously producing defensive compounds regardless of herbivore attack (Parsons, 2021). When attacked, plants release volatile organic compounds (VOCs) that attract natural enemies like parasitic wasps and predators (Dicke, 1999). These VOC emissions can vary depending on the attacking herbivore species, allowing plants to tailor their defenses (Dicke, 1999; Bruinsma and Dicke, 2008). VOCs released by plants serve as a chemical signal that attracts parasitoids to the location of their host insects (Saini et al., 2019; Takabayashi and Shiojiri, 2019; Blažytė-Čereškienė et al., 2022). By attracting herbivore enemies, these plant-induced volatiles offer protection against herbivory (Shiojiri et al., 2010; Dicke, 1999). While individual compounds can attract natural enemies, blends of numerous compounds are often used in nature (Takabayashi et al., 2006). The combination of

relatively common VOCs in a particular way creates a specific blend that acts as a signal for target acquisition by parasitoids (Blažytė-Čereškienė et al., 2022). The structure of these blends can be complex and specific, varying qualitatively and quantitatively depending on the plant and herbivore species (Pierre et al., 2011).

The intricate olfactory system of insects governs behaviour critical for their survival and reproduction. This system plays a pivotal role in enabling insects to detect food sources, avoid unsuitable hosts, select suitable oviposition sites, locate mates, and even evade natural enemies (Cao et al., 2020; Wang et al., 2022). *Cotesia vestalis*, a specialist solitary endoparasitoid of the diamond back moth (DBM) *Plutella xylostella*, is a major global pest of cruciferous plants (Shi et al., 2008). While studies have shown that *C. vestalis* is attracted to volatiles emitted from infested host plants

(Furlong et al., 2013), the influence of damage types on the parasitoid's olfactory response remains largely unexplored. This study investigates the olfactory responses of *C. vestalis* females to volatiles emitted from cabbage plants (*Brassica oleracea*) that have been subjected to four different damage types. It was hypothesized that *C. vestalis* will exhibit a greater attraction to specific volatiles emitted from plants damaged by herbivores compared to undamaged plants. The findings of this study will contribute to a better understanding of the role of plant volatiles in mediating the interactions between herbivores, plants, and parasitoids, with potential implications for enhancing biological control strategies.

MATERIALS AND METHODS

Cabbage plants (*Brassica oleracea* L.) were cultivated in a greenhouse for 4-5 weeks to the 6-leaf stage. Seedlings were grown in pots with soil, watered twice daily, and fertilized less than three times at two-week intervals. Adults and larvae of *Plutella xylostella* were collected from small farms near Kuala Lumpur, Malaysia. Mass rearing occurred on potted cabbage plants in a controlled environment ($27 \pm 2^\circ\text{C}$, $60 \pm 5\%$ RH, 16 hr photoperiod) using small netting cages (Abuzid et al., 2014a). Adults were fed a 20% honey and newly hatched larvae received fresh cabbage plants. Field-collected larvae (both parasitized and non-parasitized) were used to establish a stock colony of the parasitoid wasp *C. vestalis* (Kermani et al., 2014). Briefly larvae were housed with cabbage leaves in cages and monitored for parasitoid cocoon formation. Emerged wasps were fed a honey solution. Larvae of cabbage leaf webber *Crocidolomia pavonana* were collected from fields near Serdang, Malaysia. Rearing followed the methods used for DBM (Abuzid et al., 2014a). The aphid *Lipaphis erysimi* Kaltendbach (Homoptera: Aphididae) was collected from Chinese mustard plants and reared on the same plant species in screened cages under controlled conditions ($27 \pm 2^\circ\text{C}$, $60 \pm 5\%$ RH).

Y-Tube olfactometer assay was used to test the response of female *C. vestalis* to volatile compounds from cabbage plants (Girling et al., 2011). Briefly, females were released into the Y-tube and allowed to choose between airflow-carrying volatiles from undamaged plants or plants infested with DBM larvae, *C. pavonana* larvae, aphids, or mechanically damaged. The effect of cabbage plant volatiles on *C. vestalis* was evaluated in a screen cage experiment at a UKM University greenhouse. Cabbage plants at the 6-leaf

stage were damaged mechanically or infested with DBM larvae, *C. pavonana* larvae, or aphids (details on damage levels provided in [reference for damage levels]). Damaged and undamaged plants were placed in screen cages, and mated *C. vestalis* females were released. The number of wasps found on each plant was counted at various time points (1, 2, 3, 6, and 24 hr) to assess their preference. Volatile compounds from undamaged and damaged cabbage plants were collected using headspace solid-phase microextraction (HS-SPME) following established protocols (Risticvic et al., 2010). Briefly, plants were enclosed in jars for one hour, and volatiles were absorbed into an SPME fibre. Collected volatiles were analyzed using gas chromatography-mass spectrometry (GC-MS) with a DB-5 msec column (Saad et al., 2014). Compounds were identified by comparison of the mass spectra with those available in the library of the GC-MS system of the National Institute of Standards and Technology (NIST). Data were pooled and transformed ($x + 0.5$) to normalize and handle zero values. Parametric tests, including one-way ANOVA and paired t-tests, were used to compare VOC profiles across damage types, as well as to analyze data from the Y-tube and screen cage experiments to determine significant differences in *C. vestalis* behaviour. All analyses were conducted in Minitab version 16.

RESULTS AND DISCUSSION

Cotesia vestalis females exhibited differential olfactory responses to volatile organic compounds (VOCs) emitted by cabbage damaged by various herbivores. In a Y-tube olfactometer assay, naive parasitoids were significantly attracted to VOCs from cabbage plants damaged by their specialist host DBM larvae, compared to undamaged plants. Similarly, *C. vestalis* females showed a preference for VOCs from plants damaged by *Crocidolomia pavonana* larvae, another chewing herbivore. Conversely, no significant attraction was observed towards plants damaged by aphids or mechanically damaged plants (Fig. 1). These findings align with previous studies demonstrating

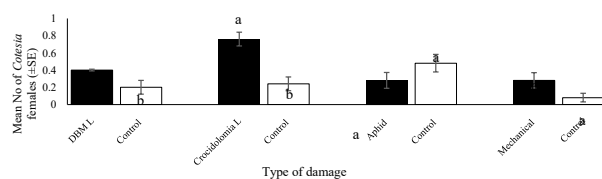


Fig. 1. *Cotesia vestalis* females attracted to VOCs from undamaged (control) (*Brassica oleracea*) and DBM, crocidolomia, aphids, and mechanical damaged cabbage plants tested in Y-olfactometer

that herbivore-induced plant volatiles (HIPVs) play a crucial role in parasitoid host location (Geervliet et al., 1994). The qualitative and quantitative differences in VOC profiles triggered by herbivore feeding likely provide crucial information for *C. vestalis* to distinguish between host and non-host infested plants, as well as undamaged ones (Paré and Tumlinson, 1999). Yang et al. (2016) identified specific plant volatiles like trans-2-hexenal, benzaldehyde, β -caryophyllene, and cis-3-hexenol as attractive to *C. vestalis*. This research aligns with the broader understanding that a diverse array of plant volatiles plays a crucial role in insect foraging behaviour (Debnath et al., 2023; Franco et al., 2021). Plant volatiles are essential for egg-laying female insects to locate and identify suitable host plants, highlighting the critical role these chemical signals play in host plant specialization (Lin et al., 2024).

Screen cage experiments corroborated the olfactometer results, with *C. vestalis* females spending significantly more time on DBM-damaged plants compared to other treatments (Table 1, Fig. 2). This suggests that while VOCs play a significant role in the initial host location, other cues like contact pheromones from DBM larvae might further guide the parasitoid's behaviour within proximity to the host (Abuzid et al., 2014a; Abuzid et al., 2014b). GC-MS analysis revealed distinct volatile profiles for each damage type. Notably,

DBM and *Crocidolomia*-damaged plants displayed higher quantities of specific hydrocarbons and fatty acids. These findings further highlight the distinct VOC profiles elicited by different types of damage. Notably, DBM infestation led to a significant increase in hexacosane, while mechanical damage significantly increased hexacosane and triacontane. Interestingly, aphid infestation resulted in a decrease in oxalic acid and heptadecane, suggesting that the type of damage influences the specific VOCs produced. These specific compounds, previously implicated in host recognition by parasitoids (O'Hara et al., 1996; Kumazaki et al., 2000), likely contribute to the attraction of *C. vestalis*. Interestingly, *C. vestalis* responded similarly to VOCs from DBM and *Crocidolomia* larvae in the olfactometer assay, but showed a preference for DBM-damaged plants in the screen cage experiment. This discrepancy suggests that additional cues, potentially from host body odours, frass, or ozone, might be crucial for final host discrimination during close-range encounters (Blande, 2021; Turlings et al., 1991). Ayelo et al. (2021) introduces an interesting complexity, suggesting that high doses of HIPVs can sometimes act as repellents in addition to their attractive properties.

In various cases, the defense compounds are released through different pathways. Present findings on the significant increase in VOC emissions after herbivore damage align with prior research (Heil et al. 2008; Allmann and Baldwin, 2010). These studies demonstrate that intact leaves release minimal amounts of green leaf volatiles (GLVs), but mechanical damage or herbivore feeding significantly triggers the release of these compounds, making them the initial surge in VOCs following herbivore attack. Shiojiri (2000) demonstrated that in *C. vestalis* females' specific attraction to DBM-infested cabbage plants, a synthetic blend of four key HIPVs (*Z*)-3-hexenyl acetate, α -pinene, sabinene, and n-heptanal played a key role and it has been successfully used to attract these parasitoids (Shiojiri, 2010; Ozawa et al., 2018). This highlights the potential for utilizing HIPVs for the development of environmentally friendly pest management strategies. GC-MS analysis revealed distinct VOC fingerprints in cabbage responding to diverse damage (insect feeding, mechanical injury). While total VOC quantity remained similar, specific compounds varied. Undamaged plants boasted a rich VOC profile, while those damaged by different herbivores or mechanically emitted unique blends (Table 2). These results align with earlier work (Alborn et al., 1997). Notably, defensive glucosinolates (GSLs), known for their sulphur content (Tripathi

Table 1. Two-way ANOVA for mean numbers of *Cotesia vestalis* females found on *Brassica oleracea* (screen-cage bioassay)

| Source | df | Sum of squares | F-value | P-value |
|-------------------|----|----------------|---------|---------|
| Time | 4 | 52.81 | 11.03 | 0.001 |
| Treatments | 4 | 300.93 | 15.72 | 0.000 |
| Time x Treatments | 4 | 79.16 | 4.13 | 0.005 |
| Error | 65 | 311.10 | | |

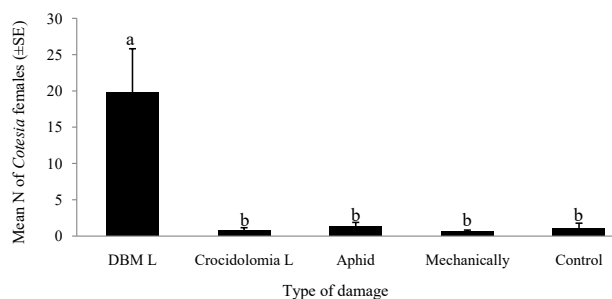


Fig. 2. Mean (\pm SE) of total numbers of *Cotesia vestalis* females found on cabbage (*Brassica oleracea*) damaged and control plants after 24 hr under free choice in Screen Cage bioassay, using two-way ANOVA

Table 2. GC-MS analysis of changes in some key volatile compounds in *B. oleracea* in response to DBM, crocidolomia, aphids, and mechanical damage (*) p-values are significant

| Compound | RT (min) | Control (DBM) | DBM | Control (Crocidolomia) | Crocidolomia | Control (Aphid) | Aphid | Control (Mechanically) | Mechanically |
|------------------------------|----------|---------------|-------------|------------------------|--------------|-----------------|----------|------------------------|--------------|
| Squalene | 56.5 | 0.58±0.2 | 0.38±0.038 | 0.58±0.2 | 0 | 0.58±0.2 | 0.37±0.3 | 0.58±0.2 | 0.2±0.2 |
| Hexadecanoic acid | 34.8 | 0 | 1.04 | 0 | 2.184 | 0 | 7.5±4 | 0 | 0 |
| Oxalic acid | 29 | 0.56±0.012 | 0.03±0.005* | 0.56±0.012 | 0.12±0.1 | 0.56±0.012 | 0* | 0.56±0.012 | 0.05±0.01* |
| 1,2-Benzenedicarboxylic acid | 46.5 | 2.5±0.67 | 2.2±2.2 | 2.5±0.67 | 2.47±1.2 | 2.5±0.67 | 4.56±1.9 | 2.5±0.67 | 2.2±2.2 |
| Hexacosane | 59 | 0.05±0.05 | 5.60±0.09* | 0.05±0.05 | 5.43±2.09 | 0.05±0.05 | 2.1±1.3 | 0.05±0.05 | 9.0±1.1* |
| Heptadecane | 35 | 0.13±0.02 | 0.21±0.01 | 0.13±0.02 | 0.423±0.23 | 0.13±0.02 | 0* | 0.13±0.02 | 0.07±0.07 |
| Dodecane | 44 | 0.14±0.02 | 0.02±0.02 | 0.14±0.02 | 3.68±2.9 | 0.14±0.02 | 0* | 1.0.02 | 0* |
| Heptacosane | 40 | 1.46±0.88 | 0 | 1.46±0.88 | 5.37±2.04 | 1.46±0.88 | 1.12±1.1 | 1.46±0.88 | 0 |
| Triacotane | 41.1 | 1.25±0.53 | 12.95±4.5 | 1.25±0.53 | 0.43±0.43 | 1.25±0.53 | 6.85±1.4 | 1.25±0.53 | 10.6±1.7* |
| Tetrapentacontane (alkane) | 39.6 | 2.69±2.06 | 0 | 2.69±2.06 | 0.06±0.03 | 2.69±2.06 | 0 | 3.2.06 | 0 |
| Neopentane | 7.9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1.0.003* |
| (3Z)-hex-3-en-1-ylacetate | 9.8 | 0.32±0.3 | 0.87±0.8 | 0 | 0 | 0 | 0.32±0.3 | 0.32±0.3 | 0.32±0.3 |

and Mishra, 2007) were not detected, possibly due to sampling limitations (Olsen and Sørensen, 1981). The findings of this study highlight the complexity of plant stress responses and the crucial role of VOCs in mediating interactions with herbivores and natural enemies, potentially attracting or repelling parasitoids (Caarls et al., 2021; Conboy et al., 2020).

In conclusion, this study demonstrates that *C. vestalis* females effectively utilize herbivore-induced plant volatiles for host location. The specific composition of VOCs emitted by damaged plants, particularly the presence of specific hydrocarbons and fatty acids, plays a significant role in attracting parasitoids. While VOCs provide initial cues for host location, additional contact cues from the host itself might be crucial for final host discrimination.

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AUTHOR CONTRIBUTION STATEMENT

AI: Designed and conducted the experiments; analyzed the data; and wrote the manuscript. M S, KN and SK: Participated in study design and data analysis. SM and MR: Participated in volatile analysis and identification. HM Y: Participated in plant cultivation and insect collecting and rearing. IA G and RM: Provided supervision and finalized the manuscript. All authors approved the final manuscript for publication.

CONFLICT OF INTEREST

No conflict of interest.

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