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Antennal detection of host plant volatiles as a function of sex and physiological state in the cabbage stem flea beetle, *Psylliodes chrysocephala*

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Background: Due to different requirements, olfactory guided behavior can vary between insect sexes and as a function of the physiological state. These variations result in an evolutionary strategy driven by selective pressure, to enhance insect sensitivity to specific resources according to their sex and physiological state. Compared to males, females may be highly sensitive to volatile organic compounds (VOCs) from host plants for foraging or oviposition. In addition, age and mating status also influence insect sensitivity to certain VOCs depending on related specific needs. Modulation of olfactory sensitivity can occur at the peripheral and central levels and often results in behavioral plasticity. The cabbage stem flea beetle (CSFB) is a serious pest of winter oilseed rape crops (WOSR, *Brassica napus*) and the time of crop colonization coincides with shifts in CSFB sex ratio and physiology. This study investigated the peripheral responses to several VOCs emitted by Brassicaceae as a function of the physiological status (pre- or post-estivation and sexually immature or mature) of both male and female CSFB using electroantennographic (EAG) recordings. The vapor phase concentration of the Pasteur pipette headspace was considered to investigate the sensitivity of the CSFB antenna to different VOCs. VOCs for EAG recordings were selected based on a literature review of the VOCs emitted by several host plants of the CSFB.

Results: All tested VOCs were detected by the CSFB antenna in a dose-dependent manner, independently of the sex and the physiological status. The volatility of a few VOCs was then considered to compare sensitivity between VOCs and showed a specifically high sensitivity of the CSFB antenna for 3-carene.

Conclusion: Even though no differences in peripheral detection of VOCs depending on the physiological state or the sex were found in this study, differences in the sensitivity to different VOCs were revealed, opening new perspectives to decipher their effect on CSFB behavior and their ecological implications. Behavioral responses of the CSFB to the tested VOCs need now to be tested to assess behavioral plasticity.

KEYWORDS

cabbage stem flea beetle, electroantennography recording, plant volatiles, plasticity of antennal sensitivity, vapor phase concentration

1 Introduction

Olfaction is a highly developed sense for insects and olfactory cues play a major role in insect behavior (Bruce and Pickett, 2011; Conchou et al., 2019). Indeed, olfactory cues are involved in locating the right host plants and avoiding unsuitable ones (Bruce et al., 2005; Bruce and Pickett, 2011), and in finding mating partners (Anton et al., 2007; Gadenne et al., 2016). Olfactory-guided behavior can be sex-, age- and mating-dependent (Anton et al., 2007; Gadenne et al., 2016; Williams et al., 2022, and references therein). Such plasticity appears crucial to be studied in case of insect pests against which odorant-based management strategies are to be developed (Anton and Cortesero, 2022). Olfactory plasticity can originate from sensitivity variations at the peripheral or central level of the insect nervous system (Anton et al., 2007; Gadenne et al., 2016).

In many herbivorous insect species, plant-emitted VOCs can induce sex-specific olfactory-guided behaviors, because only females search for oviposition sites. In the turnip moth, *Agrotis segetum*, differences in antennal responses to the sex pheromone, but also to several plant-emitted volatiles have been described between sexes (Hansson et al., 1989). For Hymenoptera like the solitary bee *Eucera berlandi* or the social bee *Apis mellifera*, female behavior is mostly driven by foraging, while males are mostly looking for mates (Alcock et al., 1978; Streinzer et al., 2013). Accordingly, in *E. berlandi* differences in the peripheral olfactory system were found between males and females in size, sensillar equipment and the total number of receptor neurons (Streinzer et al., 2013). Similarly, in the cabbage root fly *Delia radicum*, female antennae responded with higher sensitivity to several host plant-emitted VOCs than male antennae, which indicates some level of plasticity at the peripheral level in this species (Menacer et al., 2023). On the other hand, in the white clover seed weevil, *Apion fulvipes*, no differences in the peripheral olfactory system were revealed between males and females, in spite of females being attracted to host plant VOCs, whereas males are not, suggesting that, in this case, olfactory plasticity occurs at the central nervous level (Andersson et al., 2012a; Nyabuga et al., 2015; Raffa et al., 2016). In addition, age and mating status also influence insect sensitivity to certain VOCs. In the grapevine moth *Lobesia botrana* the central processing of host plant VOCs depends on the sex and mating status of the moth, correlating with different behavioral responses to host plant volatiles (Masante-Roca et al., 2002; Masante-Roca et al., 2007), while in *Manduca sexta* the central nervous system matures with moth age (Huetteroth and Schachtner, 2005) and in *Agrotis ipsilon* age-dependent sex-pheromone responsiveness is modulated in the central nervous system by juvenile hormone (Gadenne and Anton, 2000). However, mating-dependent olfactory plasticity can also be modulated at the peripheral level, as shown in *Spodoptera littoralis*, where it explains why virgin individuals are more sensitive to plant VOCs and sex pheromone than mated individuals (Kromann et al., 2015; Martel et al., 2009). Investigations of age- and sex-dependent insect responses to plant volatiles are, however, still relatively scarce, and

therefore further studies are needed to better understand plant-insect interactions.

The cabbage stem flea beetle *Psylliodes chrysocephala* L. (Coleoptera: Chrysomelidae; CSFB) is a serious pest of winter oilseed rape crops (*Brassica napus*, WOSR) (Bonnemaïson and Jourdeuil, 1954; Ortega-Ramos et al., 2022). It is an oligophagous species that can feed and reproduce on a range of host plants from the Brassicaceae family (Bonnemaïson and Jourdeuil, 1954). Plants belonging to this family are characterized by the presence of glucosinolates and their breakdown products, isothiocyanates (ITCs), which are secondary metabolites restricted to the order Brassicales (Blažević et al., 2020; Liu et al., 2020). Glucosinolate profiles of Brassicaceae plants are known to be involved in CSFB selection and preference of its host plants (Bartlet and Williams, 1991; Döring and Ulber, 2020). Glucosinolates are precursors to isothiocyanates which are volatile compounds known to affect CSFB behavior (Bartlet et al., 1992; Liu et al., 2018; Nguyen et al., 2020; Tóth et al., 2007; Rüde et al., 2025), and induce antennal response (Blight et al., 1989). Mixtures of 3-butenyl, 4-pentenyl and phenylethyl ITC as well as allyl ITC attract adult CSFB in the field (Bartlet et al., 1992; Tóth et al., 2007). These results suggest the role of specific compounds such as glucosinolates and their breakdown products, in the localization and then the selection of host plants. However, Brassicaceae plants can emit a large variety of diverse VOCs, such as terpenes, alcohols, ketones (Tollsten and Bergstrom, 1988; Pierre et al., 2011; Kergunteuil et al., 2015); and their effect on CSFB antennal detection and behavioral response is hardly known. So far only one green leaf volatile, indole-3-carbinol has been found to be attractive for females in pre-estivation stage in olfactometry trials but not for males (Rüde et al., 2025). CSFB colonize young WOSR seedlings in late summer-early autumn, and the colonizing population is composed of mature males and immature females that just ended estivation (Bonnemaïson and Jourdeuil, 1954; Sivcev et al., 2016; Vig, 2003). Females acquire their sexual maturity soon after colonization and intense feeding on WOSR plants (Bonnemaïson and Jourdeuil, 1954; Tixeront et al., 2023). Therefore, WOSR crop colonization is concomitant with a physiological shift in the CSFB population, which may induce changes in the detection and response to host plant VOCs. Differences in the antennal structure of male and female CSFB have been reported, as well as different behavioral responses to ITCs between females and males in pre estivation stage, suggesting a sexual dimorphism in olfactory sensitivity (Bartlet et al., 1994; Rüde et al., 2025). However, CSFB olfactory sensitivity in relation to physiological state has not been investigated. This study aims to examine which Brassicaceae VOCs, specifics and ubiquitous, are detected physiologically by CSFB and to determine whether antennal responses vary depending on the insect's physiological status, which is a first mechanistic step toward a better understanding of the CSFB host plant interaction. We assessed antennal responses of male and female CSFB to various Brassicaceae-emitted VOCs, considering sex and physiological status (pre- vs. post-estivation, and sexually immature vs. mature) using electroantennographic recordings. The aims of this study were i) to identify key VOCs emitted by CSFB host plants that may

influence CSFB in the localization process and subsequent preference for these plants. VOCs were selected by reviewing studies deciphering the VOCs emitted by Brassicaceae; ii) to investigate the peripheral responses of different populations of males and females using electroantennographic recordings. The real concentration of several VOCs in the headspace of the stimulation device was also estimated to compare the sensitivity of CSFB antennae between different VOCs.

2 Materials and methods

2.1 Insects

CSFB individuals used in the experiments were collected in Brittany every year and reared under controlled conditions (pre-estivation individuals: 21 ± 1 °C, 16L:8D, $70 \pm 10\%$ RH, and post-estivation individuals: 18 ± 1 °C, 8L:16D, $70 \pm 10\%$ RH). A first set of electroantennography assay, aiming to compare antennal detection between sexes, was performed on both male and female CSFB in pre-estivation and thus sexually immature (Bonnemaïson and Jourdheuil, 1954; Ortega-Ramos et al., 2022). A second set of electroantennography assay, aiming to discriminate antennal detection between the different physiological states, was performed on the following population: sexually immature pre-estivation males; sexually mature post-estivation males; sexually immature pre-estivation females; sexually immature post-estivation females; sexually mature post-estivation females. Female maturity was checked after the experiments by dissecting the ovaries and assessing their development according to Bonnemaïson and Jourdheuil (1954), and male maturity was assumed as soon as estivation ended. All populations were fed with fresh leaves of commercial Chinese cabbage *ad libitum*, and the transition from one physiological status to another was estimated according to feeding intensity that is much higher after estivation. The individuals used for the experiments were of maximum one generation.

2.2 Choice of VOCs according to the CSFB ecology

A literature review focusing only on brassicaceous plants at the vegetative stage and known to be host plants for adults and larvae of the CSFB was carried out. The literature review focused on entire, intact and undamaged plants (*i.e.*, not macerated organs, nor infested plants) from 4 to 9 or more fully expanded leaves [BBCH scale: 4-9 (Lancashire et al., 1991)] to identify the Brassicaceae volatilome under natural conditions. Plants were chosen for their ecological relevance to the CSFB (based on Bonnemaïson and Jourdheuil, 1954; Ortega-Ramos et al., 2022). VOC emissions of the following Brassicaceae were then reviewed: *Brassica napus*, *B. oleracea*, *B. rapa* ssp. *pekinensis*, *B. rapa* ssp. *oleifera*, *B. rapa* ssp. *rapa*, *B. nigra*, *Sinapis alba* and *Raphanus sativus* (Supplementary Table 1). Considering different adsorbent phases used for VOC sampling, known for their different VOC affinities (Bicchi and

Maffei, 2012; Schieweck et al., 2018; Sovová et al., 2019), allowed to combine information for different types of VOCs and to provide a broader view of the Brassicaceae volatilome. Among the 90 VOCs described in the literature, 13 were retained for the first set of experiments, as they were either commonly emitted by the brassicaceous plants studied or specific to some of the species included in the review. Then, for the second set of experiments six VOCs representative of various chemical families among the 13 previously tested were retained. We made the hypothesis that either common VOCs emitted by Brassicaceae, or specific VOCs of the species considered might be involved in the CSFB preference for its host plants (Supplementary Table 2).

2.3 Electroantennography recordings

2.3.1 Insect preparation

Whole individuals were used for EAG recordings, with CSFB slipped into a plastic disposable pipette tip with the upper thorax, the head and antennae protruding, secured with dental wax. Glass capillaries filled with Beadle Ephrussi Ringer were used as electrodes (Ephrussi and Beadle, 1936). The reference electrode was inserted between the head and the thorax, and the recording electrode was connected to the tip of the antenna, where the first flagellar segment had been previously cut to establish a good connection. The electrodes were connected to an amplifier (axoclamp 2B, Molecular Devices, San Jose, CA, USA), and an IDAC-4 device to digitize signals (Syntech, Kirchzarten, Germany). EAG Pro software (Syntech, Kirchzarten, Germany) was used to record the antennal responses.

2.3.2 Stimulation procedure

All chemical compounds were purchased from Sigma Aldrich (Saint-Quentin-Fallavier, France) and solutions were prepared at six different doses ranging in decadic steps from 0.001 to $100 \mu\text{g}\cdot\mu\text{l}^{-1}$, diluted in mineral oil. Ten microliters of solution were applied on a filter paper inserted in a Pasteur pipette for stimulation. A humidified air stream ($300 \text{ ml}\cdot\text{min}^{-1}$), filtered through a charcoal filter, was continuously delivered to the insect antenna through a glass tube (diameter: 7 mm, length: 15 cm). Stimuli were applied onto a piece of filter paper inserted into a Pasteur Pipette and the pipette was introduced into the glass tube through a hole in the sidewall. A stimulus controller (CS 55, Syntech, Kirchzarten, Germany) was used to apply a 500 ms air pulse through the stimulation pipette. Inter-stimulus intervals lasted at least 30 s. For each stimulus, increasing doses in decadic steps (0.01 to $1000 \mu\text{g}$) were applied to obtain dose-responses curves. Mineral oil was applied before and after each stimulus. An external positive control (eucalyptol) was applied before and after each stimulus series to ensure that the recordings remain stable over the entire recording period and to evaluate if data needed to be normalized. The mean response to mineral oil obtained was subtracted from each amplitude value in response to a stimulus, to compensate for air flow or contaminant responses. For each stimulus, at least 10 individuals of each sex were tested.

2.3.3 VOC concentrations reaching the insect antennae

Solutions used for EAG recording being highly diluted, we assumed that the number of molecules in the vapor phase in the headspace of the Pasteur pipette followed the Henry's law for ideal diluted solutions, considering the molar concentration in the gaseous and liquid phases (Cometto-Muniz, 2003). Assuming that equilibrium has been reached between the VOC liquid concentration and its vapor phase, the VOC concentration in the headspace of the Pasteur pipette was calculated according to Equation 1 (Cometto-Muniz, 2003).

$$[C]_{\text{vap}} = a[C]_{\text{liq}}^{\beta} \quad (1)$$

where parameters a and β were estimated from the literature for VOCs diluted in mineral oil, $[C]_{\text{liq}}$ is the VOC concentration in the liquid phase (% v/v) and $[C]_{\text{vap}}$ the vapor concentration (ppmv) (Cometto-Muniz, 2003). The vapor concentration in the headspace of the pipette was calculated for the VOCs for which a and β have been previously estimated: α -pinene, linalool, 3-carene and (R)-limonene (Cometto-Muniz, 2003). The approximate concentration reaching the insect antenna was then estimated using the following hypothesis: 1) the interaction between the VOCs and the glass tube is negligible, 2) the stimulus is not diluted in the air flow as the setup is equipped with a flow compensator; therefore, the concentration in the headspace of the Pasteur pipette is approximately the concentration reaching the insect antenna, resulting in the following Equation 2:

$$[C]_{\text{vap}} = [C]_{\text{sent}} \quad (2)$$

2.4 Statistical analyses

All statistical analyses were performed with the R software v. 4.1.3 (R Core Team, 2022). Presence-absence of the VOCs identified in the literature review in the different plant profiles was analyzed multivariately using a Principal Component Analysis (PCA) on data transformed with the Hellinger transformation (Legendre and Gallagher, 2001) [R package *vegan* (Oksanen et al., 2020)]. For each VOC of the first set of experiments comparing males and females from pre-estivation, the EAG amplitude responses were analyzed using Wald tests applied to Linear Mixed Models (LMMs) in which the sex, the VOC dose and their interaction were considered [R packages *lme4* (Bates et al., 2015) and *car* (Fox and Weisberg, 2019)]. Then, the same procedure was followed for each VOC of the second set of experiments comparing multiple CSFB populations (males, females, pre and post estivation and sexually mature and immature individuals). The EAG response amplitudes were analyzed using Wald tests applied to a Linear Mixed Model (LMM) in which the combination of sex and physiological status, the VOC dose and the interaction between these two variables were considered [R packages *lme4* (Bates et al., 2015) and *car* (Fox and Weisberg, 2019)]. The CSFB individual was included as a random factor in all models. EAG responses were transformed to ensure

model fitting as follows: $\ln(x + 1.1 \cdot |\min(x)|)$. Pairwise comparisons of estimated marginal means (EMMeans) were performed using the *emmeans* R package (Lenth, 2022) and p-values were adjusted using the False Discovery Rate (FDR) method (Benjamini and Hochberg, 1995). Finally, the EAG amplitude response was compared between (R)-limonene, linalool, α -pinene and 3-carene using a Wald test applied on a LMM, in which the sex, the VOC concentration, the VOC identity, and the triple interaction was considered. The CSFB individual was included as a random factor in the model, and EAG responses were transformed as described previously. Pairwise comparisons of EMMeans were then performed with p-values adjusted using the FDR method.

3 Results

3.1 Brassicaceae emit ubiquitous and specific VOCs

Our literature review allowed the identification of 90 VOCs emitted by *B. rapa* ssp. *oleifera*, *B. rapa* ssp. *rapa*, *B. rapa* ssp. *pekinensis*, *B. juncea*, *B. nigra*, *B. oleracea*, *B. napus*, *S. alba* and *R. sativus*. These VOCs mainly consisted in monoterpenes (16), alcohols (16), alkanes (12), aldehydes (9), ketones (9), isothiocyanates (6), esters (6), sesquiterpenes (5), sulfides (3), alkenes (2), and other VOCs (Supplementary Table 3). The PCA summarizes the VOC variability between the different plants and allows the identification of similarities and dissimilarities between plant VOC profiles (Supplementary Figure 1). For example, some ubiquitous VOCs such as (Z)-3-hexenyl acetate, α -pinene and benzaldehyde were emitted by all Brassicaceae reviewed, while others like 3-carene were only emitted by one host plant (Supplementary Figure 1, Supplementary Table 3). The literature review allowed the selection of 13 VOCs to be tested in EAG recordings. Among the most ubiquitous VOCs, the following were selected: (Z)-3-hexenyl acetate, benzaldehyde, (Z)-3-hexen-1-ol, α -pinene, limonene, β -myrcene, β -ocimene, α -farnesene, β -caryophyllene (Supplementary Table 3, Supplementary Figure 1). In addition, VOCs more specific of particular species or subspecies were selected, such as linalool (*B. napus*), 3-carene (*B. rapa* ssp. *pekinensis*) and allyl ITC (*B. rapa* ssp. *pekinensis*, *B. juncea* and *B. nigra*) (Supplementary Table 3, Supplementary Figure 1).

3.2 CSFB detect all VOCs tested

All VOCs tested in EAG were detected by the CSFB antennae in a dose-dependent manner. Detection thresholds varied between different VOCs. Indeed, some VOCs, such as allyl ITC, (Z)-3-hexenyl acetate and 3-carene induced an EAG response at 0.01 μg , while VOCs such as (E)- β -farnesene, benzaldehyde, or β -ocimene induced EAG responses at higher doses (100, 100 and 1000 μg respectively) (Figures 1, 2). No statistical differences were found in the EAG responses between sexes (Table 1; Supplementary Figure 2) and physiological states (Table 2; Supplementary Figure 3).

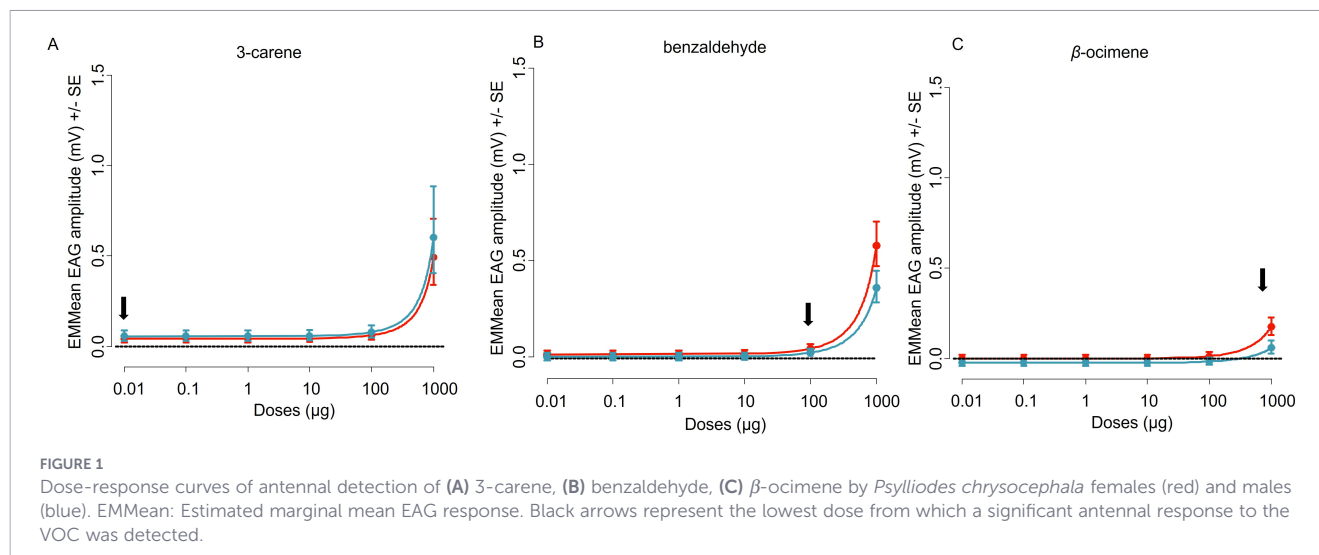


FIGURE 1

Dose-response curves of antennal detection of (A) 3-carene, (B) benzaldehyde, (C) β -ocimene by *Psylliodes chrysocephala* females (red) and males (blue). EMMean: Estimated marginal mean EAG response. Black arrows represent the lowest dose from which a significant antennal response to the VOC was detected.

3.3 CSFB antennal responses depend on the VOC identity

The vapor phase concentration and therefore the concentration sent to the insect antenna in the pipette headspace of α -pinene, 3-carene, linalool and (*R*)-limonene was calculated. This concentration depended on the VOC identity (Supplementary Figure 4, Supplementary Table 3). At the doses tested, α -pinene was the most volatile of the four VOCs. At a dose of 0.01 μ g applied on the filter paper, the concentration of α -pinene in the pipette headspace was five times higher than the concentration of 3-carene (respectively 0.025 ppmv and 0.005 ppmv), other VOCs being intermediate. This difference decreased with the concentration, and at the highest dose applied on the filter paper (1000 μ g) the concentration of α -pinene in the pipette headspace was only 1.5 times higher than that of 3-carene (respectively 714.150 ppmv and 479 ppmv).

Indeed, the volatility curves tended to converge at higher doses as the slope for α -pinene was smaller than for the other VOCs (Supplementary Figure 4).

Finally, EAG amplitude responses were compared between (*R*)-limonene, linalool, α -pinene and 3-carene depending on the concentration sent to the antenna. CSFB antennae detected differentially the VOCs depending on their identity and in a concentration-dependent manner (effect of the interaction: $\chi^2 = 14.65$, $df = 3$, $p = 0.002$), while the sex of the individual had no effect on the detection ($\chi^2 = 0.04$, $df = 1$, $p = 0.847$) (Figure 3). Whatever the sex, 3-carene elicited the strongest EAG responses, followed by (*R*)-limonene, linalool and α -pinene (Figure 3). 3-carene and (*R*)-limonene induced the strongest EAG responses for CSFB females compared to α -pinene and linalool (Supplementary Figure 5A) and 3-carene induced the strongest EAG responses for males compared to the three other VOCs (Supplementary Figure 5B).

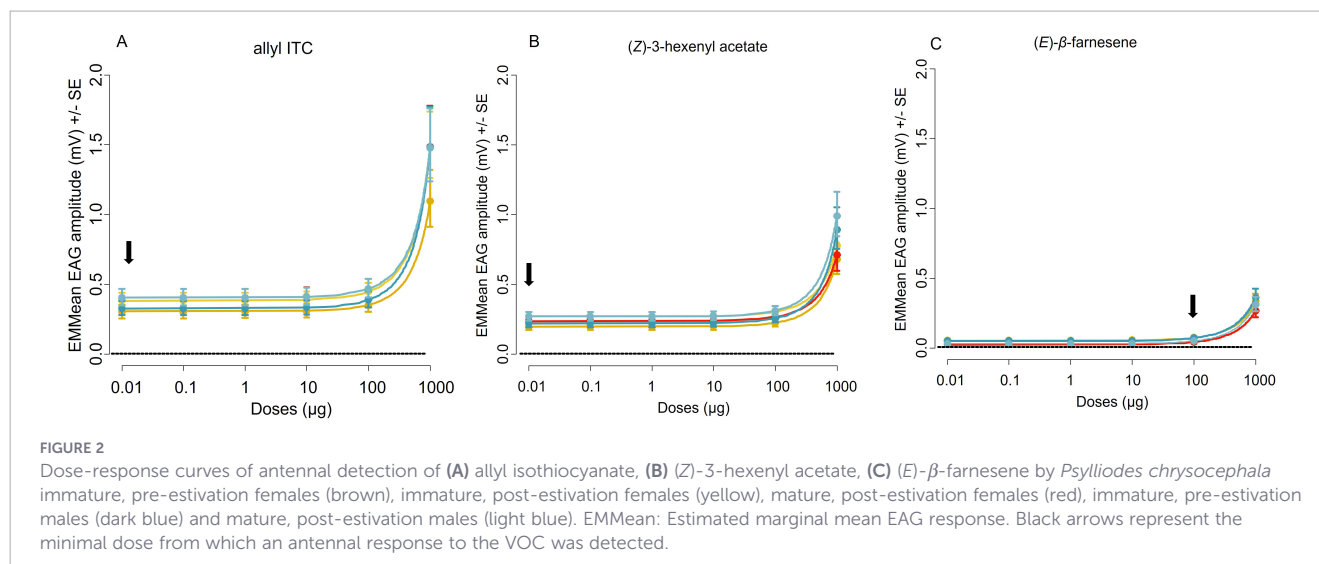


FIGURE 2

Dose-response curves of antennal detection of (A) allyl isothiocyanate, (B) (*Z*)-3-hexenyl acetate, (C) (*E*)- β -farnesene by *Psylliodes chrysocephala* immature, pre-estivation females (brown), immature, post-estivation females (yellow), mature, post-estivation females (red), immature, pre-estivation males (dark blue) and mature, post-estivation males (light blue). EMMean: Estimated marginal mean EAG response. Black arrows represent the minimal dose from which an antennal response to the VOC was detected.

TABLE 1 Statistical results of Wald tests used to assess the effect of the VOC dose, the sex of the individual and their interaction on the antennal response of *Psylliodes chrysocephala* for the different VOCs tested (1st set of experiment).

Compound	Class	Results								
		Dose			Sex			Dose: Sex		
		χ^2	df	p	χ^2	df	p	χ^2	df	p
benzaldehyde	aldehyde	126.96	1	< 0.001	0.78	1	0.377	1.69	1	0.193
(Z)-3-hexenyl acetate	acetic acid	143.69	1	< 0.001	0.99	1	0.320	0.09	1	0.763
(Z)-3-hexen-1-ol	alcohol	51.95	1	< 0.001	1.02	1	0.313	2.23	1	0.135
linalool	alcohol	102.74	1	< 0.001	0.03	1	0.871	0.66	1	0.418
methyl salicylate	ester	83.23	1	< 0.001	0.005	1	0.941	3.60	1	0.058
3-carene	monoterpene	54.78	1	< 0.001	0.20	1	0.654	0.01	1	0.904
α -pinene	monoterpene	121.29	1	< 0.001	0.04	1	0.849	0.78	1	0.376
(R)-limonene	monoterpene	92.66	1	< 0.001	0.46	1	0.500	0.001	1	0.974
β -myrcene	monoterpene	109.17	1	< 0.001	2.54	1	0.111	0.058	1	0.809
β -ocimene	monoterpene	32.07	1	< 0.001	1.39	1	0.239	2.48	1	0.115
α -farnesene	sesquiterpene	93.50	1	< 0.001	0.24	1	0.627	0.14	1	0.710
β -caryophyllene	sesquiterpene	49.21	1	< 0.001	0.65	1	0.423	0.05	1	0.819
allyl isothiocyanate	isothiocyanate	93.30	1	< 0.001	0.08	1	0.778	1.79	1	0.181

Bold letters indicate significant differences.

4 Discussion

4.1 The CSFB detects all VOCs tested independently of sex and physiological state

EAG recordings revealed that all VOCs tested were detected by CSFB antennae in a dose-dependent manner, with no effect of the sex or the physiological status of the individuals. These results reveal a low plasticity in the antennal responses of the CSFB concerning sex and maturity. Sexual dimorphism has been revealed in the CSFB behavior from pre-estivation individuals, with females being attracted to different ITCs and a green leaf volatile whereas males were not (Rüde et al., 2025). Our findings, combined with previous ones indicate that these behavioral differences potentially

stem from different integration in the central nervous system rather than different antennal sensitivity. Depending on the insect species both sensitivity changes at the peripheral and more frequently at the central level have been observed (Anton et al., 2007; Anton and Cortesero, 2022; Gadenne et al., 2016). Plasticity can occur according to the ecological needs of the insect and sensitivity can be modulated according to the type of odor encountered by the insect. For instance, the central processing of plant VOCs is age-independent for *Agrotis ipsilon*, whereas the sensitivity for the sexual pheromone depends on the age and is modulated at the antennal lobe level (Greiner, 2002). Therefore, these results suggest that investigating the ecological implications of the VOCs detected by the CSFB on its behavior appears crucial to better deciphering its host plant interactions. In the present study all the tested VOCs were detected, which was expected as these VOCs were chosen to be

TABLE 2 Results of Wald tests assessing the effect of the VOC dose, the combination of sex and physiological status, and their interaction on the antennal response of *Psylliodes chrysocephala* to the different volatile organic compounds tested (2nd set of experiment).

Compound	Chemical class	Results								
		Dose			sex-physiological status			Dose*sex-physiological status		
		χ^2	df	p	χ^2	df	p	χ^2	df	p
benzaldehyde	aldehyde	264.07	1	< 0.001	5.93	4	0.204	0.60	4	0.963
(Z)-3-hexenyl acetate	ester	240.57	1	< 0.001	5.39	4	0.249	2.88	4	0.577
methyl salicylate	ester	226.39	1	< 0.001	1.95	4	0.744	1.35	4	0.853
β -myrcene	monoterpene	334.66	1	< 0.001	4.51	4	0.341	1.11	4	0.893
(E)- β -farnesene	sesquiterpene	237.13	1	< 0.001	3.39	4	0.495	0.91	5	0.922
allyl ITC	isothiocyanate	281.56	1	< 0.001	2.95	4	0.566	1.11	4	0.893

Bold letters indicate significant effects.

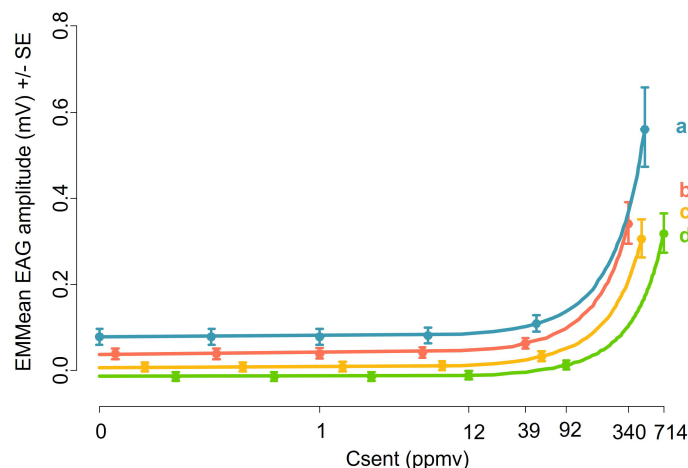


FIGURE 3

Dose-response curves of antennal detection by *Psylliodes chrysocephala* individuals (females and males combined), depending on the calculated concentration of volatile organic compounds (VOCs) sent to the antenna: α -pinene (green), 3-carene (blue), (*R*)-limonene (red) and linalool (yellow). Different letters indicate significant differences between the slope of the VOCs detection. EMMean: Estimated mean EAG response.

ecologically relevant to this species, and the doses sent to the antennae were at their maximum much higher than amounts that could be emitted naturally (Kergunteuil et al., 2015; Tollsten and Bergstrom, 1988).

Our results provide information on detection thresholds for the tested VOCs, allowing behavioral effects to be further tested with multiple doses above detection thresholds. Indeed, behavioral evaluations often focus on single or few VOC doses, thus hiding dose- or concentration-dependent behaviors which have nevertheless been shown for different insect species like flies (Knaden et al., 2012; Semmelhack and Wang, 2009), aphids (Dardouri et al., 2019) and mosquitoes (Huff and Pitts, 2020; Seenivasagan et al., 2014; Verhulst et al., 2016). Therefore, the spatial distribution of ORs and the actual VOC concentration at the antennae should be considered for further evaluation of antennal sensitivity in the CSFB.

4.2 The CSFB antennal sensitivity depends on the VOC tested

In this study, the concentration in the headspace of the Pasteur pipette and reaching the insect antennae was calculated for four VOCs. This showed that the dose applied on the filter paper does not reflect the concentration volatilized in the pipette headspace and reaching the insect antennae. Indeed, α -pinene was more volatile at lower doses than the three other VOCs studied. EAG recordings revealed variable sensitivities of CSFB antennae depending on the applied VOC and the highest sensitivity was found for 3-carene among the four VOCs compared. Such calculations confirm that as evaporation rates differ between VOCs, comparisons of the doses applied to filter papers are often tenuous (Andersson et al., 2012b; Cometto-Muniz, 2003). Indeed, the VOC chemical structure, its affinity for the solvent, and the dose tested influence the amount of stimulus delivered to the insect antennae (Andersson et al., 2012b; Brockerhoff and Grant, 1999; Cometto-Muniz, 2003;

Gorur-Shandilya et al., 2019). Therefore, considering the actual amount of stimulus reaching the insect antennae may probably be of more interest in investigations testing the effect of VOCs on insect behaviors, comparing from which doses the different VOCs are detected, or comparing studies using different solvents. However, the quantity of stimulus reaching the insect antennae also depends on the odor delivery system and the VOC affinity for the filter paper and the glass tube, which were not considered in the present study but could affect the final concentration (Andersson et al., 2012b; Gorur-Shandilya et al., 2019). Additionally, differences in CSFB antennal sensitivity to VOCs may depend on the location of both the recording electrode and the olfactory receptor neurons (ORNs) receiving the tested signal in the insect antenna. For instance, in Tephritidae species it has been shown that EAD amplitude varies with the recording position on the antenna (Ramiaranjatovo et al., 2023), and for *Drosophila melanogaster* methyl salicylate induces a cellular response in the proximal part of the antenna (Jacob, 2018) revealing that different ORNs could be distributed spatially differentially along the antenna (Ramiaranjatovo et al., 2023; Jacob, 2018). In our experiment, electrodes were placed at the tip of the CSFB antennae; ORNs located further from the tip may show weaker responses to the same VOC concentration and sensitivity. Therefore, the spatial distribution of ORNs and the actual VOC concentration at the antennae should be considered for further evaluation of antennal sensitivity in the CSFB.

The present study focused on assessing the CSFB antennal detection towards various chemical families of VOCs emitted by Brassicaceae plants, rather than focusing solely on ITCs, which are specific compounds emitted by Brassicaceae and known to attract CSFB individuals (Bartlett et al., 1992; Tóth et al., 2007; Rude et al., 2025). All VOCs tested, including more ubiquitous compounds, were detected by the CSFB antennae with varying sensitivity depending on the VOC identity and the actual concentration reaching the antennae. These results indicate that it would be

relevant to investigate the behavior of the CSFB towards both, specific and ubiquitous compounds in order to better understand its interactions with different species of its host plant range in future studies. Altogether our results highlight varying antennal sensitivity to the VOCs tested with no effect of sex and maturity. Further experimentations are required to elucidate which behavioral implications are linked to the varying sensitivity to the VOCs tested. Investigating whether the behavioral responses of the CSFB to the VOCs tested here depend on the sex and physiological status of the individuals is needed for further applied research (Anton and Cortesero, 2022). Indeed, antennal sensitivity alone does not determine the behavioral effects of the tested VOC and cannot be used alone to draw conclusions on their ecological implication in the CSFB host plant interaction. In addition, WOSR crop colonization is concomitant to a physiological shift in the CSFB population, and deciphering if this physiological shift originates from plasticity in behavioral responses to host plant odors would help to design alternative crop protection methods based on plant-derived odorants.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical approval was not required for the studies involving humans because the manuscript presents research on animals that do not require ethical approval for their study. The studies were conducted in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study. The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

MT: Investigation, Data curation, Validation, Conceptualization, Methodology, Writing – review & editing, Visualization, Resources, Formal analysis, Writing – original draft. FD: Conceptualization, Methodology, Funding acquisition, Supervision, Writing – review & editing, Project administration. AC: Supervision, Conceptualization, Funding acquisition, Writing – review & editing, Project administration,

Validation, Methodology. MH: Methodology, Supervision, Writing – review & editing, Conceptualization, Project administration, Validation. SA: Validation, Methodology, Investigation, Data curation, Conceptualization, Writing – review & editing, Supervision, Visualization.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2026.1799538/full#supplementary-material>

References

- Alcock, J., Barrows, E. M., Gordh, G., Hubbard, L. J., Kirkendall, L., Pyle, D. W., et al. (1978). The ecology and evolution of male reproductive behaviour in the bees and wasps. *Zool. J. Linn. Soc* 64, 293–326. doi: 10.1111/j.1096-3642.1978.tb01075.x
- Andersson, M. N., Larsson, M. C., Svensson, G. P., Birgersson, G., Rundlöf, M., Lundin, O., et al. (2012a). Characterization of olfactory sensory neurons in the white clover seed weevil, *Apion fulvipes* (Coleoptera: Apionidae). *J. Insect Physiol.* 58, 1325–1333. doi: 10.1016/j.jinsphys.2012.07.006
- Andersson, M. N., Schlyter, F., Hill, S. R., and Dekker, T. (2012b). What reaches the antenna? How to calibrate odor flux and ligand-receptor affinities. *Chem. Sens.* 37, 403–420. doi: 10.1093/chemse/bjs009

- Anton, S., and Cortesero, A.-M. (2022). Plasticity in chemical host plant recognition in herbivorous insects and its implication for pest control. *Biology* 11, 1842. doi: 10.3390/biology11121842
- Anton, S., Dufour, M., and Gadenne, C. (2007). Plasticity of olfactory-guided behaviour and its neurobiological basis: lessons from moths and locusts. *Entomol. Exp. Applicata* 123, 1–11. doi: 10.1111/j.1570-7458.2007.00516.x
- Bartlett, E., Isidoro, N., and Williams, I. H. (1994). Antennal glands in *Psylliodes chrysocephala*, and their possible role in reproductive behaviour. *Physiol. Entomol.* 19, 241–250. doi: 10.1111/j.1365-3032.1994.tb01048.x
- Bartlett, E., and Williams, I. H. (1991). Factors restricting the feeding of the cabbage stem flea beetle (*Psylliodes chrysocephala*). *Entomol. Exp. Applicata* 60, 233–238. doi: 10.1111/j.1570-7458.1991.tb01543.x
- Bartlett, E., Williams, I. H., and Blight, M. M. (1992). “Response of the oilseed rape pests, *Ceutorhynchus assimilis* and *Psylliodes chrysocephala*, to a mixture of isothiocyanates”, in: *Proceedings of the 8th international symposium on insect-plant relationships*, (Dordrecht: Springer Netherlands). 103–104.
- Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. doi: 10.18637/jss.v067.i01
- Benjamini, Y., and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc.* 57, 289–300. doi: 10.1111/j.2517-6161.1995.tb02031.x
- Bicchi, C., and Maffei, M. (2012). “The plant volatilome: Methods of analysis,” in *High-throughput phenotyping in plants: Methods and protocols, Methods in Molecular Biology*, (Totowa: Humana Press), 289–310. doi: 10.1007/978-1-61779-995-2_15
- Blažević, I., Montaut, S., Burčul, F., Olsen, C. E., Burrow, M., Rollin, P., et al. (2020). Glucosinolate structural diversity, identification, chemical synthesis and metabolism in plants. *Phytochemistry* 169, 112100. doi: 10.1016/j.phytochem.2019.112100
- Blight, M. M., Pickett, J. A., Wadhams, L. J., and Woodcock, C. M. (1989). Antennal responses of *Ceutorhynchus assimilis* and *Psylliodes chrysocephala* to volatiles from oilseed rape. *Aspects. Appl. Biol.* 23, 329–334.
- Bonnemaizon, L., and Jourdeuil, P. (1954). *L'altise d'hiver du colza*. (Ann Épiphyties). 4, 345–324.
- Brockerhoff, E. G., and Grant, G. G. (1999). Correction for differences in volatility among olfactory stimuli and effect on EAG responses of *Dioryctria abietivorella* to plant volatiles. *J. Chem. Ecol.* 25, 1353–1366. doi: 10.1023/A:1020930910416
- Bruce, T. J. A., and Pickett, J. A. (2011). Perception of plant volatile blends by herbivorous insects – Finding the right mix. *Phytochemistry* 72, 1605–1611. doi: 10.1016/j.phytochem.2011.04.011
- Bruce, T. J. A., Wadhams, L. J., and Woodcock, C. M. (2005). Insect host location: a volatile situation. *Trends Plant Sci.* 10, 269–274. doi: 10.1016/j.tplants.2005.04.003
- Cometto-Muniz, J. E. (2003). Quantification of chemical vapors in chemosensory research. *Chem. Sens.* 28, 467–477. doi: 10.1093/chemse/28.6.467
- Conchou, L., Lucas, P., Meslin, C., Proffit, M., Staudt, M., and Renou, M. (2019). Insect odorscapes: From plant volatiles to natural olfactory scenes. *Front. Physiol.* 10. doi: 10.3389/fphys.2019.00972
- Dardouri, T., Gomez, L., Schoeny, A., Costagliola, G., and Gautier, H. (2019). Behavioural response of green peach aphid *Myzus persicae* (Sulzer) to volatiles from different rosemary (*Rosmarinus officinalis* L.) clones. *Agr. For. Entomol.* 21, 336–345. doi: 10.1111/afe.12336
- Döring, A., and Ulber, B. (2020). Performance of cabbage stem flea beetle larvae (*Psylliodes chrysocephala*) in brassicaceous plants and the effect of glucosinolate profiles. *Entomol. Exp. Applicata* 168, 200–208. doi: 10.1111/eea.12891
- Ephrussi, B., and Beadle, G. W. (1936). A technique of transplantation for *Drosophila*. *Am. Nat.* 70, 218–225. doi: 10.1086/280658
- Fox, J., and Weisberg, S. (2019). *An R companion to applied regression* (CRAN R), 3rd ed.
- Gadenne, C., and Anton, S. (2000). Central processing of sex pheromone stimuli is differentially regulated by juvenile hormone in a male moth. *J. Insect Physiol.* 46, 1195–1206. doi: 10.1016/S0022-1910(00)00040-8
- Gadenne, C., Barrozo, R. B., and Anton, S. (2016). Plasticity in insect olfaction: To smell or not to smell? *Annu. Rev. Entomol.* 61, 317–333. doi: 10.1146/annurev-ento-010715-023523
- Gorur-Shandilya, S., Martelli, C., Demir, M., and Emonet, T. (2019). Controlling and measuring dynamic odorant stimuli in the laboratory. *J. Exp. Biol.* 222 (23), jeb.207787. doi: 10.1242/jeb.207787
- Greiner, B. (2002). Central processing of plant volatiles in *Agrotis ipsilon* males is age-independent in contrast to sex pheromone processing. *Chem. Sens.* 27, 45–48. doi: 10.1093/chemse/27.1.45
- Hansson, B. S., Pers, J. N. C. V. D., and Löfqvist, J. (1989). Comparison of male and female olfactory cell response to pheromone compounds and plant volatiles in the turnip moth, *Agrotis segetum*. *Physiol. Entomol.* 14, 147–155. doi: 10.1111/j.1365-3032.1989.tb00946.x
- Huetteroth, W., and Schachtner, J. (2005). Standard three-dimensional glomeruli of the *Manduca sexta* antennal lobe: a tool to study both developmental and adult neuronal plasticity. *Cell Tissue Res.* 319, 513–524. doi: 10.1007/s00441-004-1016-1
- Huff, R. M., and Pitts, R. J. (2020). Carboxylic acid responses by a conserved odorant receptor in culicine vector mosquitoes. *Insect Mol. Biol.* 29, 523–530. doi: 10.1111/imb.12661
- Jacob, V. E. I. M. (2018). Current source density analysis of electroantennogram recordings: a tool for mapping the olfactory response in an insect antenna. *Front. Cell. Neurosci.* 12. doi: 10.3389/fncel.2018.00287
- Kergunteuil, A., Dugravot, S., Danner, H., Van Dam, N., and Cortesero, A. M. (2015). Characterizing volatiles and attractiveness of five brassicaceous plants with potential for a ‘push-pull’ strategy toward the cabbage root fly, *Delia radicum*. *J. Chem. Ecol.* 41 (4), 330–339. doi: 10.1007/s10886-015-0575-9
- Knaden, M., Strutz, A., Ahsan, J., Sachse, S., and Hansson, B. S. (2012). Spatial representation of odorant valence in an insect brain. *Cell Rep.* 1, 392–399. doi: 10.1016/j.celrep.2012.03.002
- Kromann, S. H., Saveer, A. M., Binyameen, M., Bengtsson, M., Birgersson, G., Hansson, B. S., et al. (2015). Concurrent modulation of neuronal and behavioural olfactory responses to sex and host plant cues in a male moth. *Proc. R. Soc. B.* 282, 20141884. doi: 10.1098/rspb.2014.1884
- Lancashire, P. D., Bleiholder, H., Boom, T. V. D., Langelüddeke, P., Stauss, R., Weber, E., et al. (1991). A uniform decimal code for growth stages of crops and weeds. *Ann. Appl. Biol.* 119, 561–601. doi: 10.1111/j.1744-7348.1991.tb04895.x
- Legendre, P., and Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia* 129 (2), 271–280.
- Lenth, R. V. (2022). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. (R package version 1.7. 3.).
- Liu, Y., Rossi, M., Liang, X., Zhang, H., Zou, L., and Ong, C. N. (2020). An Integrated Metabolomics Study of Glucosinolate Metabolism in Different Brassicaceae Genera. *Metabolites* 10, 313. doi: 10.3390/metabo10080313
- Liu, Y., Zhang, H., Umashankar, S., Liang, X., Lee, H., Swarup, S., et al. (2018). Characterization of plant volatiles reveals distinct metabolic profiles and pathways among 12 Brassicaceae vegetables. *Metabolites* 8, 94. doi: 10.3390/metabo8040094
- Martel, V., Anderson, P., Hansson, B. S., and Schlyter, F. (2009). Peripheral modulation of olfaction by physiological state in the Egyptian leaf worm *Spodoptera littoralis* (Lepidoptera: Noctuidae). *J. Insect Physiol.* 55, 793–797. doi: 10.1016/j.jinsphys.2009.04.012
- Masante-Roca, I., Anton, S., Delbac, L., Dufour, M., and Gadenne, C. (2007). Attraction of the grapevine moth to host and non-host plant parts in the wind tunnel: effects of plant phenology, sex, and mating status. *Entomol. Exp. Applicata* 122, 239–245. doi: 10.1111/j.1570-7458.2006.00510.x
- Masante-Roca, I., Gadenne, C., and Anton, S. (2002). Plant odour processing in the antennal lobe of male and female grapevine moths, *Lobesia botrana* (Lepidoptera: Tortricidae). *J. Insect Physiol.* 48, 1111–1121. doi: 10.1016/S0022-1910(02)00204-4
- Menacer, K., Hervé, M. R., Marie Cortesero, A., Aujames, T., and Anton, S. (2023). Sex- and maturity-dependent antennal detection of host plant volatiles in the cabbage root fly, *Delia radicum*. *J. Insect Physiol.* 146, 104500. doi: 10.1016/j.jinsphys.2023.104500
- Nguyen, V. P. T., Stewart, J., Lopez, M., Ioannou, I., and Allais, F. (2020). Glucosinolates: Natural occurrence, biosynthesis, accessibility, structures, and biological activities. *Molecules* 25, 4537. doi: 10.3390/molecules25194537
- Nyabuga, F. N., Carrasco, D., Ranaker, L., Andersson, M. N., Birgersson, G., Larsson, M. C., et al. (2015). Field abundance patterns and odor-mediated host choice by clover seed weevils, *Apion fulvipes* and *Apion trifolii* (Coleoptera: Apionidae). *J. Econ. Entomol.* 108, 492–503. doi: 10.1093/jeet/ou099
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2020). *vegan: community ecology package*. 1–295. doi: 10.32614/cran.package.vegan
- Ortega-Ramos, P. A., Coston, D. J., Seimandi-Corda, G., Mauchline, A. L., and Cook, S. M. (2022). Integrated pest management strategies for cabbage stem flea beetle (*Psylliodes chrysocephala*) in oilseed rape. *Glob. Change Biol. Bioenergy* 14, 267–286. doi: 10.1111/gcbb.12918
- Pierre, P. S., Jansen, J. J., Hordijk, C. A., Van Dam, N. M., Cortesero, A.-M., and Dugravot, S. (2011). Differences in volatile profiles of turnip plants subjected to single and dual herbivory above- and belowground. *J. Chem. Ecol.* 37, 368. doi: 10.1007/s10886-011-9934-3
- Raffa, K. F., Andersson, M. N., and Schlyter, F. (2016). “Host selection by bark beetles,” in *Advances in Insect Physiology* (Academic Press: Elsevier), 1–74. doi: 10.1016/b.s.aip.2016.02.001
- Ramiranjatovo, G., Reynaud, B., and Jacob, V. (2023). Triple electroantennography captures the range and spatial arrangement of olfactory sensory neuron response on an insect antenna. *J. Neurosci. Methods* 390, 109842. doi: 10.1016/j.jneumeth.2023.109842
- R Core Team (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing (Vienna, Austria).
- Rüde, D., Ulber, B., Cook, S. M., and Rostás, M. (2025). Attraction of cabbage stem flea beetle (*Psylliodes chrysocephala*) to host plant odors. *Pest Manage. Sci.* 81, 7440–7447. doi: 10.1002/ps.8697

- Schieweck, A., Gunschera, J., Varol, D., and Salthammer, T. (2018). Analytical procedure for the determination of very volatile organic compounds (C3–C6) in indoor air. *Anal. Bioanal. Chem.* 410, 3171–3183. doi: 10.1007/s00216-018-1004-z
- Seenivasagan, T., Guha, L., Parashar, B. D., Agrawal, O. P., and Sukumaran, D. (2014). Olfaction in Asian tiger mosquito *Aedes albopictus*: flight orientation response to certain saturated carboxylic acids in human skin emanations. *Parasitol. Res.* 113, 1927–1932. doi: 10.1007/s00436-014-3840-x
- Semmelhack, J. L., and Wang, J. W. (2009). Select *Drosophila* glomeruli mediate innate olfactory attraction and aversion. *Nature* 459, 218–223. doi: 10.1038/nature07983
- Sivcev, L., Graora, D., Sivcev, I., Tomic, V., and Dudic, B. (2016). Phenology of cabbage stem flea beetle (*Psylliodes chrysocephala* L.) in oilseed rape. *Pestic. fitomed.* 31, 139–144. doi: 10.2298/PIF1604139S
- Sovová, K., Spesyvyi, A., Bursová, M., Pásztor, P., Kubišta, J., Shestivska, V., et al. (2019). Time-integrated thermal desorption for quantitative SIFT-MS analyses of atmospheric monoterpenes. *Anal. Bioanal. Chem.* 411, 2997–3007. doi: 10.1007/s00216-019-01782-6
- Streinzer, M., Kelber, C., Pfabigan, S., Kleineidam, C. J., and Spaethe, J. (2013). Sexual dimorphism in the olfactory system of a solitary and a eusocial bee species. *J. Comp. Neurol.* 521, 2742–2755. doi: 10.1002/cne.23312
- Tixeront, M., Dupuy, F., Cortesero, A. M., and Hervé, M. R. (2023). Understanding crop colonization of oilseed rape crops by the cabbage stem flea beetle (*Psylliodes chrysocephala* L. (Coleoptera: Chrysomelidae)). *Pest Manage. Sci.* 80 (5), 2260–2266. doi: 10.1002/ps.7424
- Tollsten, L., and Bergstrom, G. (1988). Headspace volatiles of whole plants and macerated plants parts of Brassica and Sinapis. *Phytochemistry* 27, 2073–2077. doi: 10.1016/0031-9422(88)80099-2
- Tóth, M., Csonka, É., Bakcsa, F., Benedek, P., Szarukán, I., Gomboc, S., et al. (2007). Species spectrum of flea beetles (*Phyllotreta* spp. Coleoptera, Chrysomelidae) attracted to allyl isothiocyanate-baited traps. *Z. Naturforsch.* 62, 772–778. doi: 10.1515/znc-2007-9-1022
- Verhulst, N. O., Weldegergis, B. T., Menger, D., and Takken, W. (2016). Attractiveness of volatiles from different body parts to the malaria mosquito *Anopheles coluzzii* is affected by deodorant compounds. *Sci. Rep.* 6, 27141. doi: 10.1038/srep27141
- Vig, K. (2003). Data on the biology of cabbage stem flea beetle, *Psylliodes chrysocephalus* (Linnaeus 1758) (Coleoptera Chrysomelidae, Alticinae). *Commun. Agric. Appl. Biol. Sci.* 68, 231–237.
- Williams, A. T., Verhulst, E. C., and Haverkamp, A. (2022). A unique sense of smell: development and evolution of a sexually dimorphic antennal lobe – a review. *Entomol. Exp. Applicata* 170, 303–318. doi: 10.1111/eea.13145