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ORIGINAL PAPER

The orientation and oviposition choices of *Plutella xylostella* and its parasitoid *Diadegma semiclausum* on a range of *Brassica* plants

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Abstract

Plants emit volatile organic compounds (VOCs) that mediate interactions with organisms in the surrounding community, such as herbivorous insects and their natural enemies. Understanding on plant attractiveness for insects can help to design intercropping systems, such as trap crops. Here we present the results of laboratory tests designed to compare the attractiveness of cabbage (*Brassica oleracea*), broccoli (*Brassica oleracea* var. *italica*), turnip (*Brassica rapa* var. *rapa*), and yellow rocket (*Barbarea stricta*) to *Plutella xylostella* and its natural enemy, the parasitoid wasp, *Diadegma semiclausum*. Plants were selected based on the results of a cabbage intercropping field experiment and a screening of VOC emissions of a variety of landrace *Brassica* plants both intact and damaged by *P. xylostella*. *Plutella xylostella* selected turnip and *B. stricta* over cabbage and broccoli in oviposition tests. Reproductive success of *Diadegma semiclausum* in oviposition tests was higher on host larvae feeding on turnip plants compared to cabbage and broccoli, while *B. stricta* was not tested. According to principal component analyses, volatile blends emitted by turnip and *B. stricta* differed from each other as well as from other plants, while volatile blends emitted by cabbage and broccoli were more similar, both when intact and when damaged by *P. xylostella*.

Keywords *Plutella xylostella* · *Diadegma semiclausum* · *Brassica* · Volatile organic compounds · HIPV · Oviposition · Volatile-mediated interactions

Introduction

Herbivore-induced plant volatiles (HIPVs) are thought to mediate tritrophic interactions in both natural environments and agroecosystems (Aartsma et al. 2017). To enhance pest control in agroecosystems, orientation of pests and beneficial insects may be manipulated through careful selection and arrangement of crop plant varieties. In trap crop systems, pests are lured to crop areas that are more attractive than the main crop (Shelton and Badenes-Pérez 2006; Hokkanen 1991). HIPVs are attractive to herbivores' natural enemies, such as parasitoid wasps (Ohara et al. 2003). In an optimal system, the trap crop would be attractive to both pests and their natural enemies.

Brassicaceous plants are fed upon by many specialized herbivores, which are often associated with their distinct secondary metabolites, particularly glucosinolates and their breakdown products (Hopkins et al. 2009). One of the most destructive agricultural pests is the Diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae), which has a cosmopolitan distribution and has developed resistance to a wide range of pesticides (Banazeer et al. 2022) leading to an increased need for pest control methods based on biological control. *Diadegma semiclausum* (Hymenoptera: Ichneumonidae) is a solitary larval endoparasitoid and specialized in the parasitism of *P. xylostella* (Pourian et al. 2015). It is widely used in biological control programs in Europe and Asia (Furlong et al. 2013). The olfaction-mediated foraging behavior of *D. semiclausum* has been subject to a few studies (Bukovinszky et al. 2005), but understanding *D.*

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semiclausum foraging behavior more comprehensively would aid development of intercropping strategies to enhance its effectiveness in biological control. Bukovinszky et al. (2005) have shown that odors of host-damaged mustard and Brussels sprout plants were more attractive to *D. semiclausum* than undamaged conspecifics, but interestingly, undamaged mustard was more attractive than damaged Brussels sprout or feral cabbage. This indicates that the plant species can have a significant role in the olfaction-guided orientation of *D. semiclausum*. Naïve female *D. semiclausum* has been shown to avoid methyl salicylate (MeSa) as a part of a damaged *Arabidopsis thaliana* odor blend (Snoeren et al. 2010), but in field experiments it has been shown to be attractive (Orre et al. 2013). Parasitoid learning of host-related cues might be a reason for this observation (Orre et al. 2010).

Oviposition choices of *P. xylostella* are guided by chemical cues released by plants, such as airborne volatile organic compounds (VOCs) (Yan et al. 2023) and non-volatile or semivolatile compounds on leaf surfaces (Li and Blande 2015). Visual, structural cues, and plant architectural traits (Ang et al. 2014), including the quantity and quality of the leaf wax layer (Zhu et al. 2022), trichomes, and surface structures, also have important roles to play in the selection of oviposition sites. In a laboratory study by Li and Blande (2015), evidence was provided that semivolatile sesquiterpenes may be used by *P. xylostella* as oviposition stimulants. This observation suggests that sesquiterpenes may represent a potential tool for manipulating orientation by *P. xylostella* in an applied agricultural setting, but this phenomenon is not well understood.

The plant species selected for this study were determined following an initial screening of the VOC profiles of five brassicaceous plant landraces. In addition, the VOC profiles of plants used in an earlier documented intercropping field experiment (Ruhanen et al. 2023) were screened. The plants used for this study were selected to vary in their emission of sesquiterpenes and included cabbage (*Brassica oleracea* var. *capitata*), broccoli (*Brassica oleracea* var. *italica*), *Barbarea stricta*, and turnip (*Brassica rapa* var. *rapa*). All selected plants were used in at least one year of the aforementioned field trial (Ruhanen et al. 2023), with cabbage representing the main crop and the other selected plants trialed as trap crops.

Landrace plants are traditional varieties adapted to local circumstances and not as intensively bred as new commercial varieties and hybrids (Casañas et al. 2017; Villa et al. 2005). Breeding typically aims for a good taste with reduced production of bitter secondary metabolites (Chodur et al. 2018; Shang et al. 2014), which might also change composition of defense-related metabolites, such as HIPVs (Rowen and Kaplan 2016). Landraces offer an interesting opportunity to study varieties that might have more defense-related chemical properties than modern varieties (Chen et al. 2015; Tamiru et al. 2011). Here, we studied the potential for landrace and wild varieties of brassicaceous plants to be used as trap crops in cultivation of conventional cabbage.

The aims of the study were to determine a preferred host plant for *P. xylostella* oviposition under laboratory conditions, and if *D. semiclausum* differentially orientated toward *P. xylostella* feeding on the selected plant varieties. To achieve this, VOC emissions were measured from both intact and *P. xylostella*-damaged individuals of eight brassicaceous plants (one F1 hybrid, six landraces and one wild). Based on the VOC profiles and particularly, the sesquiterpene emissions, turnip, white cabbage, broccoli, and *B. stricta* were selected for further laboratory bioassays. Oviposition choices of *P. xylostella* and *D. semiclausum* were studied in cage experiments and olfaction-based orientation of insects toward plant odors was studied in Y-tube tests.

We hypothesized that (1) *P. xylostella* larvae feeding would induce VOC emissions in all brassicaceous plant species tested, but that the quality and quantity of induced emission would differ among species; (2) VOC emissions of plants would differentially affect the orientation of moths and parasitoids in Y-tube tests; (3) high sesquiterpene-emitting plants would be subject to more oviposition by *P. xylostella* than lower- or non-emitting plants; and (4) *D. semiclausum* differentiate between *P. xylostella* hosts feeding on different plant varieties.

Methods

Plant and insect material

Screening of VOCs was conducted for eight different Brassicaceae species or varieties, including one cultivated F1 hybrid, six landraces, and one wild species. The cultivated variety was white cabbage (*Brassica oleracea* var. *capitata* cv. Lennox F1), seeds of which were purchased from Puutarhaliike Helle Oy, Finland. The six landrace species were cauliflower (*Brassica oleracea* var. *botrytis* cv. Early Snowball x), red cabbage (*Brassica oleracea* var. *rubra* cv. Kalibos), kale (*Brassica napus* var. *pabularia* cv. Red Russian), which were purchased from Exotic garden, Finland, and broccoli (*Brassica oleracea* var. *italica* cv. Green Calabrese), swede (*Brassica napus* var. *napobrassica* cv. Sulikka), and turnip (*Brassica rapa* var. *rapa* cv. Eno), which were purchased from Maatiainen—The Finnish Landrace Association, Finland. The wild variety, *Barbarea stricta* (small-flowered yellow rocket), was collected from a wild population in Kuopio, Finland.

Plant seeds were sown individually in 0.8-L plastic pots containing a mix of peat, soil, and sand (3:1:1). The plants for the VOC measurements and bioassays with *P.*

xylostella were grown in controlled environment chambers (Weiss Technik, Lindenstruth, Germany) under LED lamps (NS1 and G2, Valoya, Finland) with an artificial light–dark cycle (16L:8D), day and night temperatures of 21 °C and 16 °C, respectively, and day and night relative humidity of 60.0% and 80.0%, respectively. The plants were watered every other day and fertilized twice per week (0.2% solution, N:P:K, 19:4:20 (Kekkilä Oyj, Finland)). The plants for tests with *D. semiclausum* were grown in a plant growth room under LED lamps (AC100, Sunritek, China) with similar growth conditions as described above.

The diamondback moth, *Plutella xylostella*, was reared in a laboratory on broccoli plants (*Brassica oleracea* var. *italica*) with an artificial light–dark cycle (16L: 8D) at 23 ± 0.5 °C. A population of the parasitoid, *Diadegma semiclausum*, was reared from specimens collected from an unsprayed *Brassica* field at the Maaninka research station of the Natural Resources Institute Finland, in Kuopio, Finland (27°19'E, 63°8'N) two years prior to the experiment. The *D. semiclausum* colony was supplemented with additional individuals collected each year in Kuopio, Finland. Parasitoids were reared on broccoli plants infested with first to third instar *P. xylostella* larvae. Adult moths and wasps were provided with approximately 30% honey solution diluted in water and soaked into cotton wool as a food source.

Collection of volatile organic compounds

Volatile organic compounds were collected with dynamic headspace sampling. Samples were collected from five intact plants and five *P. xylostella*-damaged plants per species five weeks after seeds were sown. Herbivore damage was made by placing 20 third instar *P. xylostella* larvae per plant for 24 h prior to VOC collections and larvae were removed just before sampling. For sampling, plants were enclosed in plastic bags (polyethylene terephthalate; overall dimensions 35 × 43 cm; Look® Isopussi Eskimo oy, Finland) that had been heated for 1 h at 120 °C prior to experiments in order to remove contaminants. Each bag was used once. Air filtered through activated charcoal was pumped into bags at 300 mL min^{-1} until they had been fully flushed. Volatiles were collected in Stainless steel tubes filled with 200-mg Tenax TA 60/80 adsorbent (Markes International Ltd., UK) for 30 min with a flux of 220 ml min^{-1} using a vacuum pump (KNF, Germany). Plants were illuminated with lamps (Shuttle Plus, LIVAL, Sipoo, Finland; PAR, approximately 350 µmol m^{-2} s^{-1}) during the flushing and collections. For each sampling round, five plants and a blank (empty bag) sample were made using a similar method.

Analysis of volatile organic compounds

The samples were analyzed by gas chromatography–mass spectrometry (Hewlett-Packard GC type 6890, Germany; MSD 5973, UK). Trapped compounds were desorbed with an automated thermal desorption unit (PerkinElmer ATD400 Automatic Thermal Desorption System, Wellesley, USA) at 250 °C for 10 min and cryofocused at − 30 °C. The compounds were then transferred in a split mode 1:20 to an HP5MS capillary column (0.25 µm × 60 m × 0.25 µm, Agilent Technologies, USA). The carrier gas was helium. The oven temperature was held at 40 °C for 2 min and then programmed to ramp by 5 °C min^{-1} to 210 °C and then by 20 °C min^{-1} to 250 °C under a constant flow of 1.2 mL min^{-1}. Mass spectra were acquired by scanning from 33 to 400 m/z. Compound identification was made by comparison with the injection of 33 analytical standards (Sigma-Aldrich, USA). For the unknown compounds, we calculated the retention indices RI, through the injection of alkanes C8–C20 and compared their mass spectra to those in the NIST and Wiley libraries. Compound quantification was based on using the total ion chromatograms (TIC) and the responses of analytical standards. Volatile organic compound emission rates (E) were calculated by considering the compound amounts in the inlet and outlet air as follows: $E = (F^*(C2 - C1))/m$, where E is the emission rate expressed in ng g^{-1} h^{-1}, F is the flow rate into the bag (L min^{-1}), C1 is the mass of volatile compound in the incoming air (ng) (which is considered to be 0 due to the incoming air being filtered and any compounds recorded in the blank samples being subtracted from the plant emissions), C2 is the mass in the outgoing air (ng), and m is the dry biomass of plants (g) obtained after 3 days of drying in an oven at 60 °C.

Y-tube tests with *P. xylostella* and *D. semiclausum*

Y-tube and oviposition tests were conducted in the laboratory following measurement of VOC emissions of potential trap crop plants (SI Fig. 1, Fig. 2, and Table 1). Turnip was selected to be studied with white cabbage, broccoli (*B. oleracea* var. italica cv. Green Calabrese), and *B. stricta* based on its high emission of sesquiterpenes and attractiveness for *P. xylostella* oviposition. Five-week-old plants were used.

Olfactometry tests were conducted for *P. xylostella* with intact plants. The odor pairs tested were cabbage–broccoli, cabbage–turnip, cabbage–*B. stricta*, and broccoli–*B. stricta*. For *D. semiclausum*, tests were conducted with plant pairs of cabbage–broccoli, cabbage–turnip, and turnip–broccoli when both of the plants were either intact or herbivore damaged. Herbivore damage was elicited by placing 20 third instar *P. xylostella* larvae on plants for 24 h prior to the experiment and larvae were removed just before the test. Five plant pairs were used for each odor choice combination with 10–12 *P. xylostella* and 10 *D. semiclausum* females assayed per pair, giving a total of 50 to 54 *P. xylostella* or *D. semiclausum* tested for each odor pair combination. Prior to the experiment, the responsiveness of *P. xylostella* and *D. semiclausum* females to plant odors was tested by assaying a pair of intact white cabbage plants versus an empty glass chamber, similar to the other treatments.

This olfactory experiment was conducted with a Y-tube olfactometer of the following dimensions: main arm 10.5 cm, other arms 10 cm, inner diameter 1.6 cm, and angle between the two arms ~90°. The Y-tube was placed in a light green plastic container and was illuminated from above with a lamp (LIVAL Shuttle Plus Finland, Max 24 W/230 V). Potted plants were placed in 5-L glass chambers with two inlets and a metallic lid and the pot and surface of the soil were covered with aluminum foil. Purified air (AADCO 474–30 Ultra-High Purity Zero Air Generator (ZAG)) was pumped into and through the chambers containing the odor sources and then into one of the Y-tube arms.

The air flow arriving at a Y-tube arm was set to 300 ml/min with a maximum difference of 10 ml/min per test between arms. The air flow rates were determined for each plant combination with a mini-Buck calibrator (M-5, A.P. Buck Inc,, Orlando, Florida, USA). Before starting a new test pair, glass chambers and Y-tubes were cleaned with 70% ethanol, dried, and then heated to 120 °C for 1 h. The Y-tube was rotated 180° after each insect was assayed and replaced after every 10 insects. The olfactometer treatments were alternated between left and right olfactometer arms after every five insects to prevent locational bias. Plants were placed into the glass chambers for 5 min prior to Y-tube tests starting to enable the system to stabilize. Maximum two-day-old female *P. xylostella* adults and *D. semiclausum* were introduced individually into the main arm of the Y-tube via two cm long pieces of plastic tube with a fabric mesh covering one end. The tubes fit to the main arm of the Y-tube and the mesh cover allows air to flow through the system. Insects that did not move into either of the arms were recorded as non-decisive. Each insect was tested once. *Plutella xylostella* females used in Y-tube tests were separated from males at the larval stage and reared in a separate cage so that they had not mated prior to the test. *Diadegma semiclausum* and *P. xylostella* females for use in oviposition tests were kept together with males since hatching, until to the experiments, giving ample opportunity for mating prior to experiments, but that was not further verified.

Oviposition tests for *P. xylostella* and *D. semiclausum*

Oviposition choice assays were conducted for *P. xylostella* in square-based 33 × 33 × 60 cm polycarbonate cages with meshed fabric sides. Four-week o-d cabbage, broccoli, turnip, and *B. stricta* plants were placed 2 cm from corners of the cage in a randomized order. A group of cabbage-broccoli-*B. stricta* and pairs of cabbage–broccoli, cabbage–turnip, and cabbage–*B. stricta* were also tested. Twenty adult *P. xylostella* were collected in plastic jars and released at the center point of each cage. After 48 h, the number of eggs deposited on each plant was counted. A total of 15–20 cage replicates were established for each tested plant combination.

To estimate reproductive success of *D. semiclausum*, oviposition tests were conducted in square-based 100 × 100 × 150 cm transparent plastic chambers with meshed fabric short sides. Cages were placed in climatic chambers (Weiss Technik, Lindenstruth, Germany), under fluorescent lamps with the same program used for growing plants. The plants tested were five-week-old cabbage, broccoli, and turnip, which were placed in the cage in random order in an equilateral triangle formation with 35 cm between each plant. A bottle cap filled with approximately 30% honey solution soaked in cotton wool was placed at the middle point of the triangle to feed the wasps. Plants used in each replicate were selected so that the leaf area estimated by eye was as equal as possible. Two hours prior to releasing parasitoids, thirty second instar *P. xylostella* larvae were placed on the three youngest leaves in the middle of each plant with a fine paintbrush. One two-day-old male and one female *D. semiclausum* adults were released into the test cage for 24 h. After the oviposition period, parasitoids were removed and plants with larvae were placed individually in 33 × 33 × 60 cm polycarbonate cages for larvae rearing in the climate chambers. Plants were watered every 2 to 3 days and fertilized two times per week. Resulting *P. xylostella* and *D. semiclausum* pupae were carefully removed from the rearing cages after about 12 days and placed in glass Petri dishes in a climate chamber to hatch. The number of pupae of both species was recorded. Percentages of larvae parasitized and not parasitized by *D. semiclausum* and the *P. xylostella* mortality at the larval stage were calculated from the 30 larvae placed on each plant prior to oviposition.

Statistical analysis

Statistical analyses were performed using SPSS 25 software (IBM Corp. Armonk, USA). The normality of oviposition and VOC data were tested using the Shapiro–Wilk test and homogeneity of variances was tested using the Levene's test. Square root transformation was performed for the *P. xylostella* oviposition test data with three plant species and log + 1 transformation was performed for the test with four plant species.

The *P. xylostella* oviposition test data comparing oviposition choices with three or four plant species was analyzed by one-way ANOVA with Tukey's post hoc test. Pairwise oviposition tests were analyzed with a Mann–Whitney *U* test because assumptions of One-Way ANOVA were not met. *D. semiclausum* oviposition test data were analyzed with Kruskal–Wallis test and the Bonferroni post hoc test.

Results of Y-tube bioassays were analyzed with a generalized linear mixed model (GLMM) with a binomial distribution and logit link function, without fixed effects, using the lme4 package (Bates et al. 2015) in R version 4.3.2 (R Core Team 2023) and R Studio (Posit Team 2023). Insects nested within each plant pair were included in the model as random effects to avoid pseudoreplication (insects tested with the same plant pair). The Wald test was used to extract the *P* value of the intercept.

VOC -data were analyzed as individual compounds in a VOC blend with the Mann–Whitney test to test for differences between intact and *P. xylostella*-damaged plants.

A Principal Component Analysis (PCA) was performed on the VOC data with SIMCA 17.0.2 (Umetrics, Umeå, Sweden) to visualize differences between VOC blends emitted by different *Brassica* plants and to determine which VOCs are important for the separation of the different odor sources. The loadings of the PCA model were identified to determine which compounds contributed most to the variation among the odor sources.

Results

Orientation of *P. xylostella* in Y-tube tests

Plutella xylostella females oriented toward the volatiles of intact cabbage significantly more often than clean air ($Z = 4.685$, $P < 0.0001$) (Fig. 1). *Plutella xylostella* olfactory orientation was tested with intact plants only and a near significant orientation toward volatiles from turnip over cabbage ($Z = 1.953$, $P = 0.0508$) was observed. Orientation of *P. xylostella* did not significantly differ between any of the odors in the other tests conducted: cabbage vs *B. stricta* ($Z = 1.343$, $P = 0.1790$), broccoli vs cabbage ($Z = 0.565$, $P = 0.5720$), or *B. stricta* vs turnip ($Z = 0.565$, $P = 0.5720$) (Fig. 1).

Orientation of *D. semiclausum* in Y-tube tests

Diadegma semiclausum females oriented toward the volatiles of intact cabbage significantly more often than clean air ($Z = 3.183$, $P = 0.0015$) (Fig. 2). Olfactory orientation of *D. semiclausum* was tested for pairs of intact plants and pairs of host-damaged plants. *Diadegma semiclausum* females oriented toward volatiles from intact turnip significantly more than intact cabbage ($Z = 2.108$, $P = 0.0351$) and more toward volatiles from intact broccoli than intact cabbage ($Z = 1.486$, $P = 0.0137$) but they did not significantly differentiate between intact broccoli and turnip ($Z = 0.152$, $P = 0.879$). In addition, they significantly oriented toward volatiles emitted by host-damaged turnip ($Z = 2.788$, $P = 0.0053$) and host-damaged broccoli ($Z = 2.031$, $P = 0.0423$) over volatiles from host-damaged cabbage. However, they did not differ in their orientation toward volatile blends of host-damaged broccoli and host-damaged turnip ($Z = 0.410$, $P = 0.6820$).

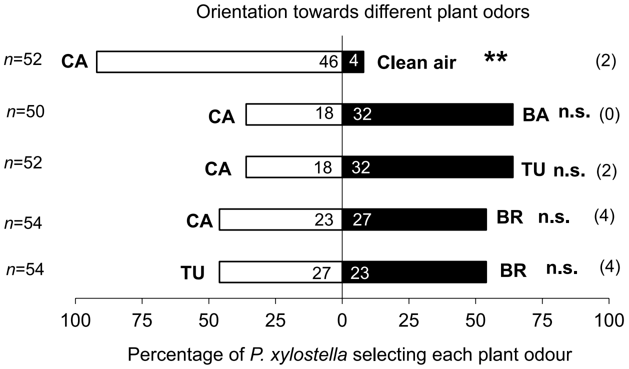

Fig. 1 Orientation of *P. xylostella* females to odor pairs presented in a Y-tube olfactometer (% of moths making a selection). The odors presented were intact white cabbage (*Brassica oleracea* var. *capitata*) (CA), yellow rocket, (*Barbarea stricta*) (BA), turnip (*Brassica rapa* var. *rapa*) (TU), and broccoli (*Brassica oleracea* var. *italica*) (BR). Fifty to fifty-four moths were tested per combination; the number on the bar indicates the number of moths that selected that odor source. The number in parentheses is the number of individuals not making a selection. Asterisks indicate a significant difference tested with GLMM). $^{*}P < 0.05$ and $^{**}P < 0.001$

Oviposition bioassays for *P. xylostella*

Plutella xylostella oviposition choices differed significantly between cabbage, broccoli and *B. stricta* (One-Way ANOVA: $F_{2,42} = 30.159$, $P < 0.001$) (Fig. 3a), and cabbage, broccoli, *B. stricta*, and turnip (One-Way ANOVA: $F_{3,76} = 13.479$, $P < 0.001$) (Fig. 3b). *Plutella xylostella* laid nine times more eggs on *B. stricta* than cabbage or broccoli (Fig. 3a). When turnip was also included in the oviposition test, significantly more eggs were laid on turnip and *B. stricta* than cabbage or broccoli (Fig. 3b). There were no significant differences in the number of eggs laid on turnip and *B. stricta* or between cabbage and broccoli. The largest number of eggs was deposited on turnip plants, which had 3.5 times more eggs deposited on them than cabbage plants, which had the least eggs of the tested plants.

Oviposition tests were also conducted for plant pairs of cabbage–-turnip, cabbage–broccoli, cabbage–*B. stricta*, and *B. stricta*–turnip (Fig. 4). The differences in oviposition choices of *P. xylostella* were similar to when all four plants were tested simultaneously. *Plutella xylostella* laid significantly more eggs on turnip than cabbage (Fig. 4a) and on *B. stricta* than cabbage (Fig. 4b) (Mann–Whitney: $U = 12$, $z = -5.246$, $P < 0.001$ and $U = 10$, $z = -4.256$, $P < 0.001$,

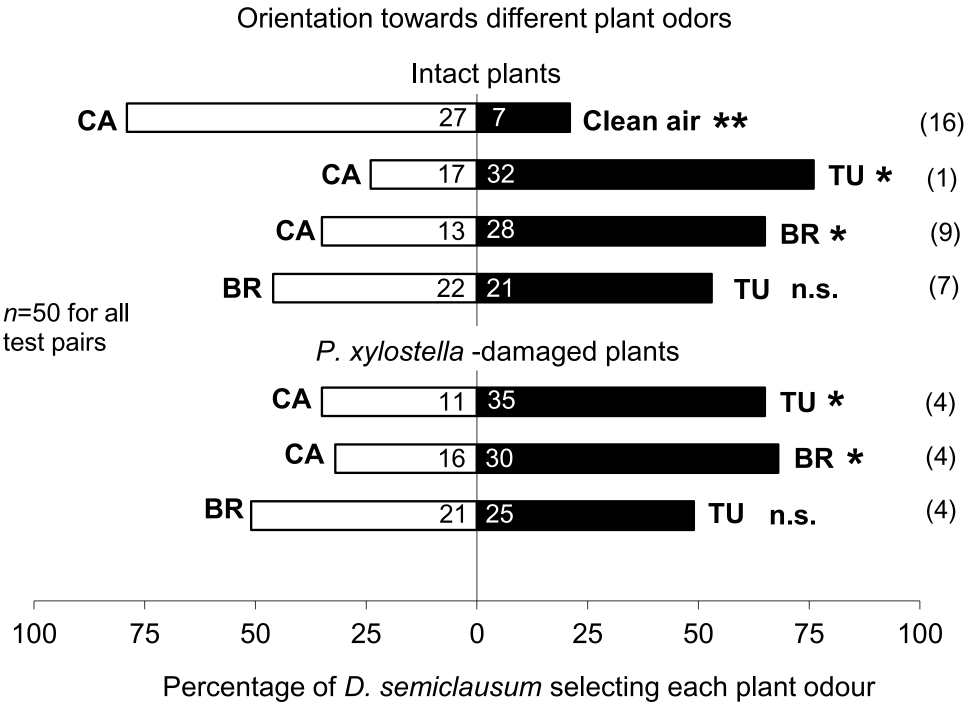

Fig. 2 Orientation of *Diadegma semiclausum* females to odor pairs presented in a Y-tube olfactometer (% of parasitoids making a selection). The odors presented were intact white cabbage (*Brassica oleracea* var. *capitata*) (CA), turnip (*Brassica rapa* var. *rapa*) (TU), and broccoli (*Brassica oleacera* var. *italica*) (BR). Fifty parasitoids were tested per combination; the number on the bar indicates the number of parasitoids that selected that odor source. The number in parentheses is the number of individuals not making a selection. Asterisks indicate a significant difference tested with GLMM. $*P<0.05$ and $**P<0.001$

respectively) and there were no significant differences in the number of eggs laid between cabbage and broccoli (Fig. 4c) ($U=165.5$, $z=-0.934$, $P=0.355$) and *B. stricta* and turnip (Fig. 4c) ($U=197$, $z=-0.591$, $P=0.554$).

Oviposition bioassays for *D. semiclausum*

Plant species affected the reproductive success of *D. semiclausum*, which was observed as significant differences in the percentage of *P. xylostella* larvae parasitized (Kruskal–Wallis: $H_2=7.730$, $P=0.021$) and non-parasitized ($H_2=7.774$, $P=0.021$) on each plant (Fig. 5). According to Bonferroni-corrected post hoc tests, wasps parasitized significantly more *P. xylostella* larvae placed on turnip plants than cabbage plants. Correspondingly, the number of non-parasitized *P. xylostella* larvae was significantly higher for larvae placed on cabbage plants compared to turnip plants but there was no statistically significant difference between cabbage and broccoli. Plant species did not affect mortality of unparasitized *P. xylostella* larvae ($H_2=0.411$, $P=0.814$).

VOC profiles of plants

The VOC emissions of individual compounds emitted by intact and herbivore-damaged cabbage, broccoli, *B. stricta*, and turnip are shown in Supplementary file (SI Table 1), as well as for cauliflower, red cabbage, kale, another broccoli variety, and swede which information was used to select additional trap crop, turnip to the study. Turnip had highest emission of (*E,E*)-α-farnesene as intact and herbivore-damaged (SI Table 1). Turnip and *B. stricta* induced emission of Methyl salicylate (MeSa) after herbivore damage in this study (SI Table 1).

Principal component analyses for intact and herbivore-damaged cabbage, broccoli, turnip, and *B. stricta* are presented in Figs. 6 and 7, respectively. The separation between species was pronounced for both intact and damaged plants that had been subjected to 24 h of *P. xylostella* feeding. For intact plants, the first and second PC explained altogether 58.9% of the variation of the dataset and for damaged plants the first and second PC explained altogether 50.8% of the variation of the dataset. The volatile profiles of intact turnip and cabbage separated from each other and from broccoli and *B. stricta*, which had more similar VOC profile PCA loadings. High emissions of 12 monoterpenoids and 3-methyl-2-pentanone contributed the most to the separation of the VOC blend of cabbage from the other plants. The VOC blend of turnip was characterized by high emissions of five N- or S-containing compounds, caryophyllene, (*E*)-(*E*)-α-Farnesene, three green leaf volatiles (GLV), 6-methyl-5-hepten-2-one, anisole, and benzaldehyde (Fig. 6). However, when the plants were damaged, volatile profiles of cabbage and broccoli overlapped, while turnip and *B. stricta* clustered more separately. The VOC blend of damaged *B. stricta* was characterized by high emissions of ocimenes, caryophyllene, (*E*)-DMNT, and three GLVs.

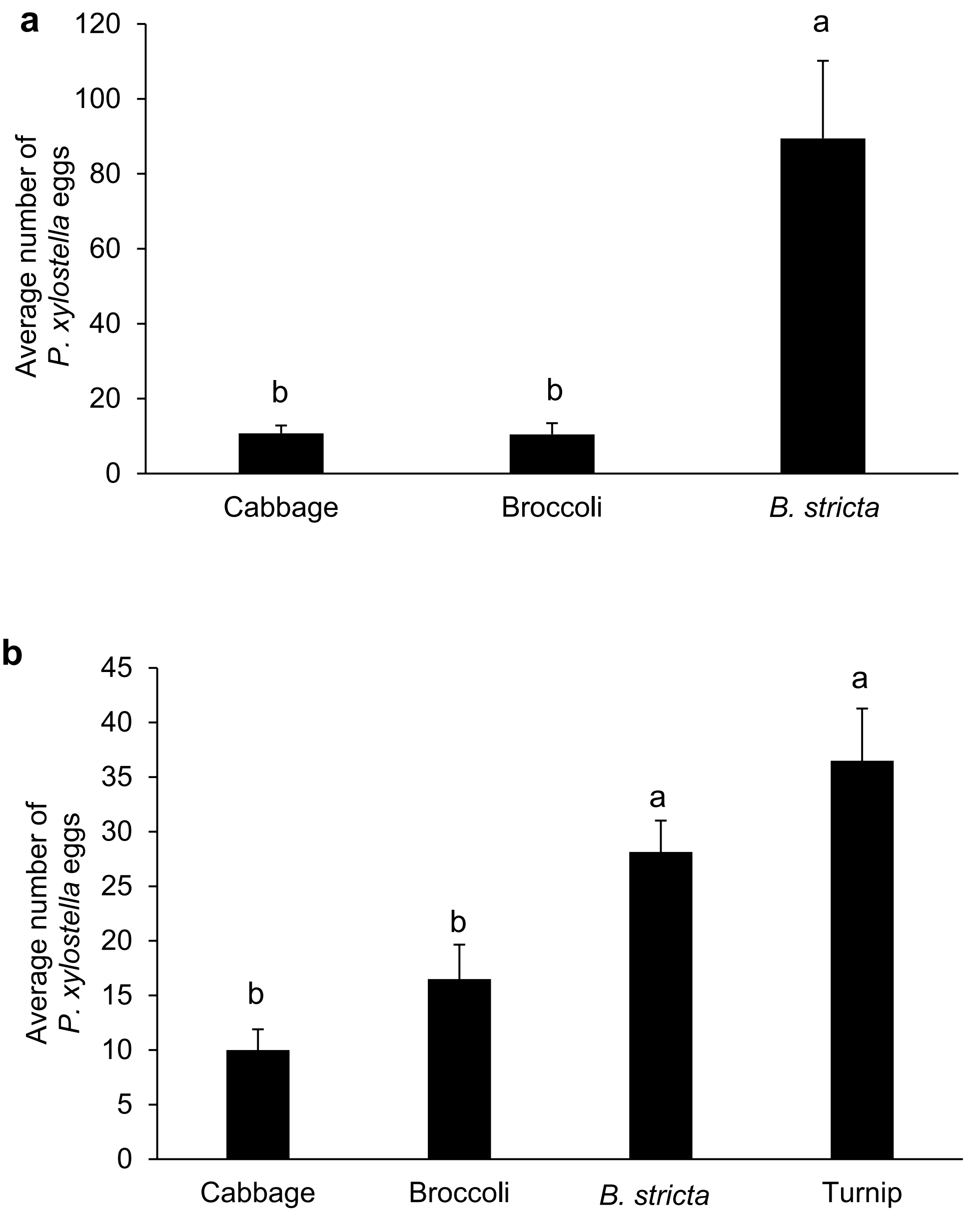

Fig. 3 Average numbers (±S.E.) of *P. xylostella* eggs laid on cabbage, broccoli, *B. stricta* and turnip in oviposition test. $N = 20$. Different letters above the bars reveal differences between plants ($P < 0.05$, Tukey's post hoc test)

Discussion

In order to identify potential trap crop plants for the farming of white cabbage, we investigated the oviposition choices of *P. xylostella* when presented with four different brassicaceous plant varieties. The selected plants included cabbage, broccoli, turnip, and *B. stricta*. The orientation of virgin *P. xylostella* females to the odors of intact plants of these varieties was also tested. In addition, three of these plants, cabbage, broccoli, and turnip, were assessed for their differential levels of attractiveness to a natural enemy of *P. xylostella*, the parasitoid wasp *D. semiclausum*.

In oviposition tests, *P. xylostella* deposited similar numbers of eggs on turnip and *B. stricta*, which were both subject to greater oviposition than broccoli and cabbage. This is in line with other studies that have shown *Barbarea* species to be highly attractive for *P. xylostella* oviposition and promoted their use as trap crops (Badenes-Pérez et al. 2011; 2014; 2017). The similar attractiveness of turnip and *B. stricta* is noteworthy, because there is little information on this plant pair combination in the literature. The explicit role of VOCs in oviposition selection could not be separated from other leaf characteristics that have been shown to affect oviposition choice, such as color, surface waxes (Zhu et al. 2022), and their surface chemistry and trichome density (Agerbirk et al. 2003). It is notable that leaves of *B. stricta*, cabbage, and broccoli were glabrous, while leaves of turnip were pubescent (Ruhanen, personal observation) which may have affected *P. xylostella* oviposition choice.

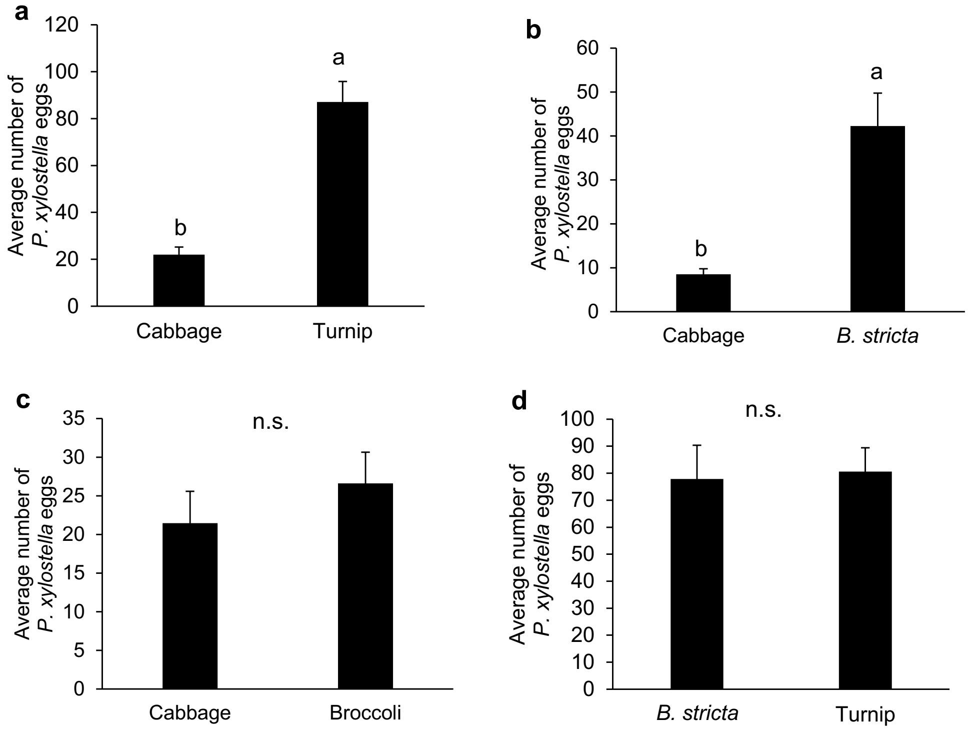

Fig. 4 Average numbers (±S.E.) of *P. xylostella* eggs laid on cabbage, broccoli, yellow rocket, and turnip in oviposition test. $N=20$. Different letters above the bars reveal differences between plants ($P<0.05$, Mann–Whitney test)

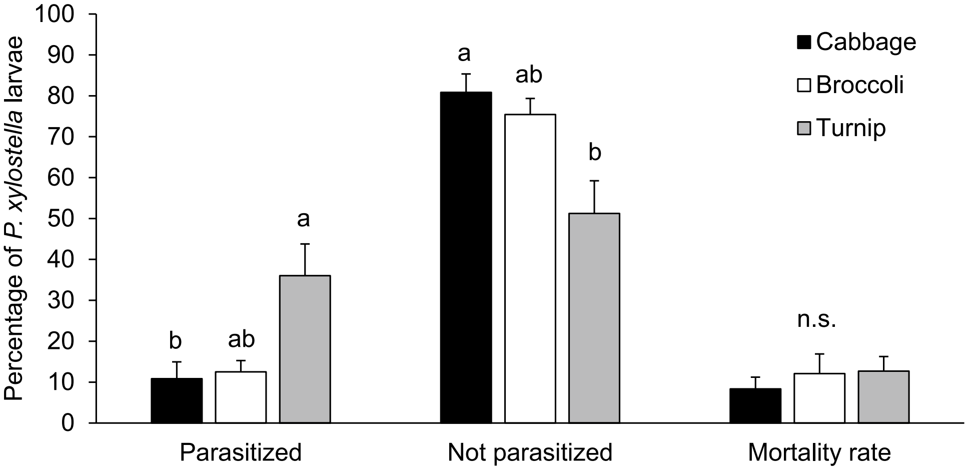

Fig. 5 Average numbers (±S.E.) of *P. xylostella* larvae parasitized or not parasitized by *D. semiclausum*, and the *P. xylostella* mortality at the larval stage. For each replicate, 30 second instar larvae were placed on cabbage, broccoli, and turnip plants and percentages are calculated based on this number. The 'Parasitized' bars indicate the percentage of larvae that yielded a *D. semiclausum* adult or pupa. The 'not parasitized' bars indicate larvae that developed into *P. xylostella* adults or pupae $N=16$. Different letters above the bars reveal differences between the plant species ($P<0.05$, Bonferroni test, after Kruskal–Wallis test)

Intact non-volatile indole glucosinolates are important *P. xylostella* oviposition determinants (Sun et al. 2009). Glucosinolates are present in the leaf surface waxes of *Barbarea* species, which is not the case for some other Brassicaceous plants, such as *B. napus* and *Nasturtium officinale* (Badenes-Pérez et al. 2011). This phylloplane chemistry can explain the high level of *P. xylostella* oviposition on *Barbarea* even though some *Barbarea* strains contain triterpenoid saponins which prevent feeding by larvae (Badenes-Pérez et al. 2011). In this study, the glucosinolate content of plants was not measured, but could potentially have explained the attractiveness of turnip and *B. stricta* in the oviposition tests. Turnip emitted the highest amounts of glucosinolate breakdown products, including two isothiocyanates that are attractive to *P. xylostella* (Renwick et al. 2006; Yan et al. 2023) as

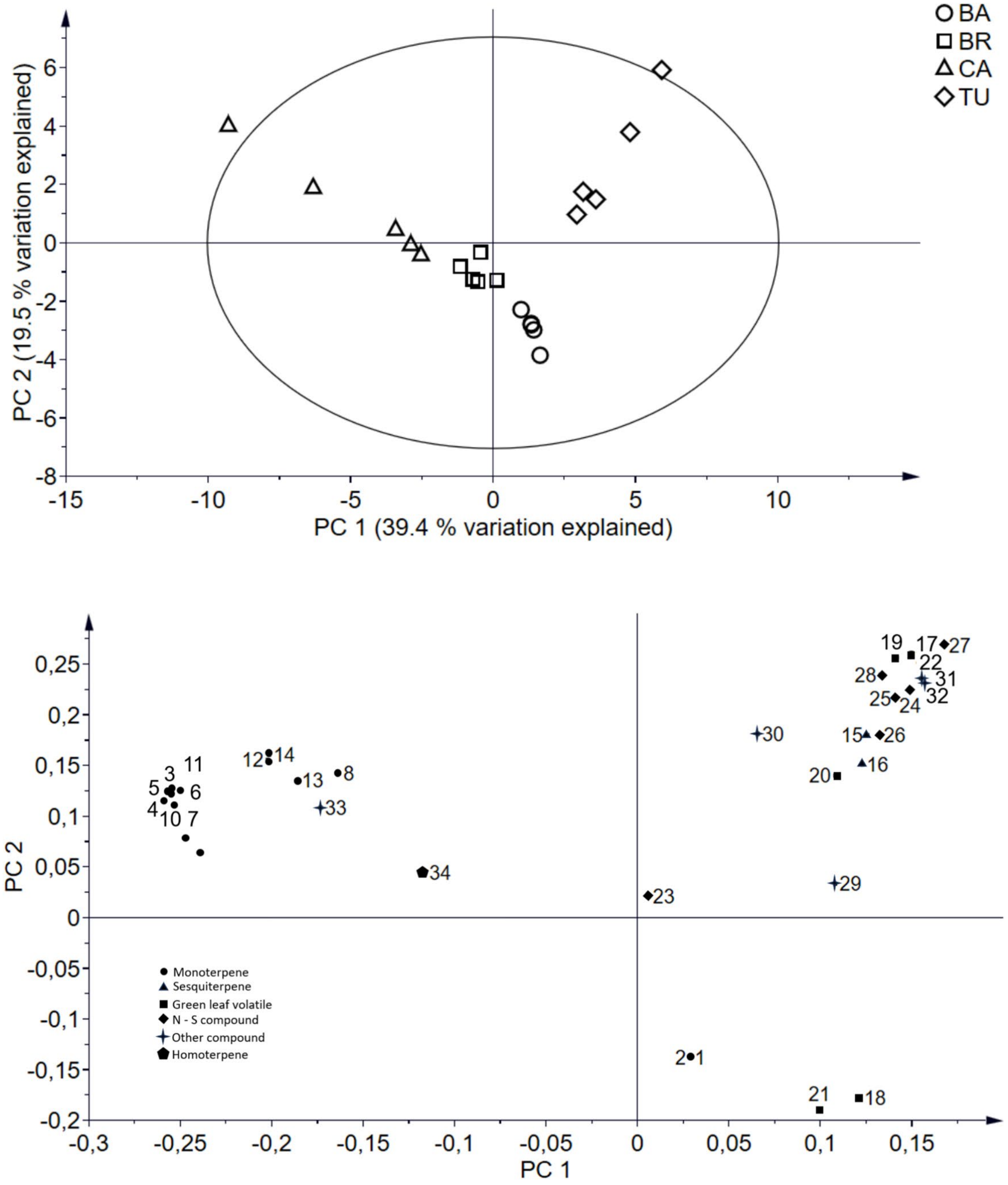

Fig. 6 Principal Component Analysis (PCA) of the VOC blends of intact cabbage (CA), broccoli (BR), turnip (TU), and *B. stricta* (BA). Top panel: score plot of the samples. The ellipse defines the Hotelling's T2 confidence region (95%). Bottom panel: loading plot of the two components of the PCA, showing the contribution of each of the compounds toward the model

well as other N-and S-containing compounds including 2-methyl-butanenitrile. Isothiocyanates are enzymatically produced from glucosinolates when plant tissue is damaged by herbivore feeding (Jeschke et al. 2016). This defense-related process potentially structures interactions with other organisms, such as *P. xylostella* and its natural enemies. In future, it would be important to conduct studies focusing on both measurements in order to get a more comprehensive understanding of interactions between brassicaceous plants, their herbivores, and natural enemies.

Brassica variety affected the orientation of female *D. semiclausum* in Y-tube tests when both intact and herbivore-damaged plants were assayed. Odors of broccoli and turnip were similarly attractive to *D. semiclausum*, but in oviposition tests the reproductive success of *D. semiclausum* was

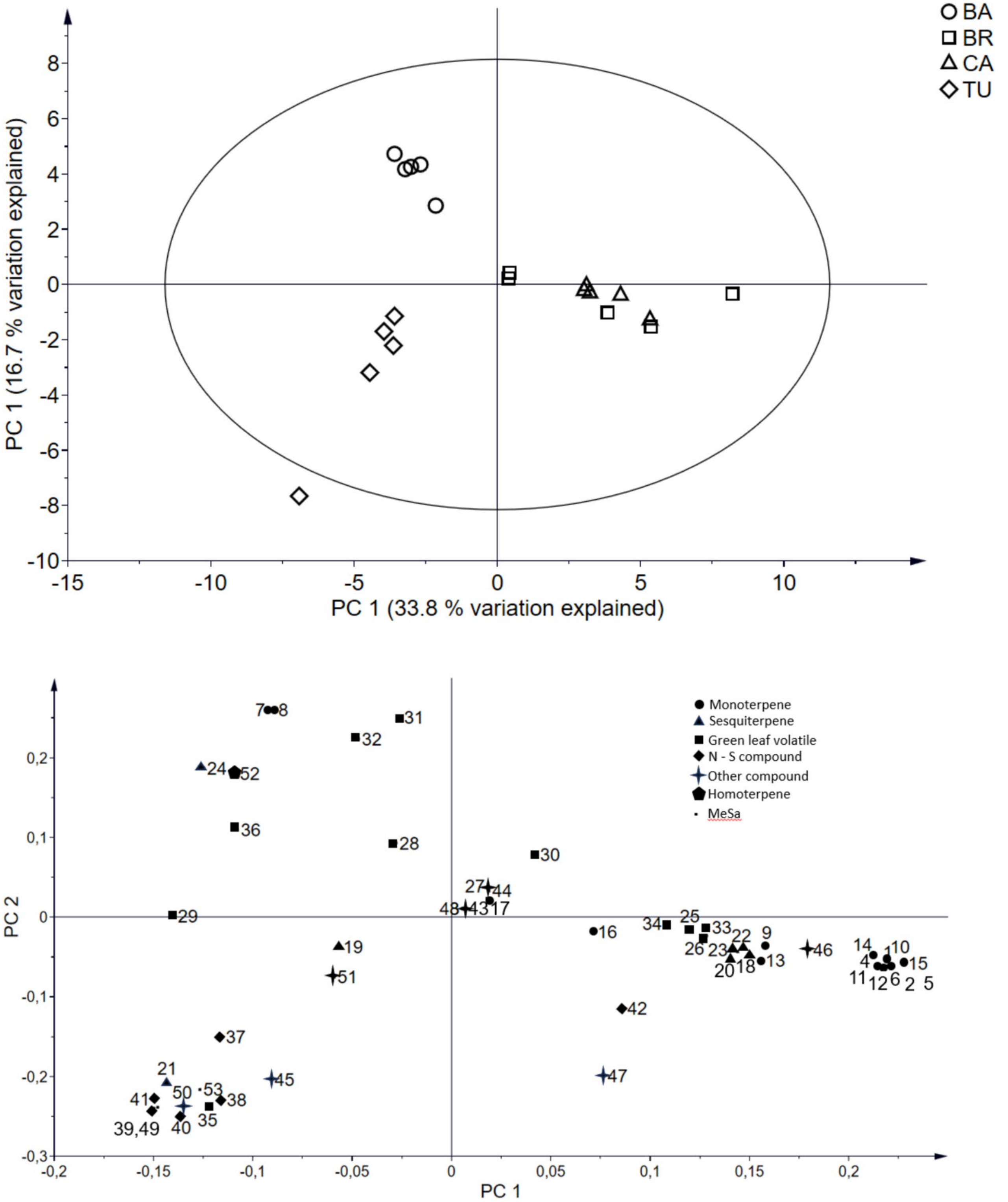

Fig. 7 Principal Component Analysis (PCA) of the VOC blends of *P. xylostella*-damaged cabbage (CA), broccoli (BR), turnip (TU), and *B. stricta* (BA). Top panel: score plot of the samples. The ellipse defines the Hotelling's T2 confidence region (95%). Bottom panel: loading plot of the two components of the PCA, showing the contribution of each of the compounds toward the model

higher for *P. xylostella* larvae that were feeding on turnip. Parasitoid females also orientated toward odors of broccoli over odors of cabbage in Y-tube tests, but the reproductive success of *D. semiclausum* on host larvae feeding on broccoli and cabbage did not differ in the oviposition tests. Here, reproductive success was calculated as the percentage of *D. semiclausum* developed from the total number of *P. xylostella* larvae placed on each plant. Early instars of *P. xylostella* mine leaves, so the ability of *D. semiclausum* to parasitize *P. xylostella* may have been affected by the different leaf characteristics. Cabbage leaves are slightly thicker than broccoli and turnip leaves, which may reduce the ability of the parasitoid to attack the small leaf-mining instars of *P. xylostella* larvae. Consequently, this may have reduced the reproductive success of *D. semiclausum* on *P. xylostella* feeding on cabbage. Differences in the host plant quality might also have affected the survival of larvae (Ghosh et al. 2023). Host plant species can affect the development time and body size of *P. xylostella* (Jaleel et al. 2017); hence, we recommend that the survival and development of *P. xylostella* larvae feeding on each studied plant is assessed in further studies.

Here, we studied in the laboratory the same plant species that had been used in a field trial where cabbage was a main crop and turnip, broccoli, and *Barbarea* were trap crop candidates (Ruhanen et al. 2023). In the laboratory, broccoli was not more attractive to *P. xylostella* than cabbage, either in oviposition or Y-tube tests, which does not further support its use as a conventional trap crop. However, in a field trial run with the same plants used in this study, there was evidence that broccoli can represent a beneficial perimeter crop plant when combined with *B. stricta* as a second component of the perimeter crop and faba bean as an intercrop (Ruhanen et al. 2023). Laboratory tests can help to understand plant–insect interactions important in biological control applications in agricultural fields. However, it is still challenging to correlate findings from the laboratory with the situation at the ecosystem level (Furlong et al. 2018). One reason might be that interactions of *P. xylostella* and its host plants are complicated and effects of herbivory on oviposition choice can differ between the plant species (Silva and Furlong 2012) and can also depend on the time after herbivore damage (Ang et al. 2016). Associative learning of natural enemies, like *D. semiclausum,* makes it more difficult to predict parasitoid foraging decisions at field conditions based on laboratory findings (Furlong et al. 2018). The higher reproductive success of *D. semiclausum* from *P. xylostella* on turnip plants in our laboratory test does not reflect the result of our field experiment where the abundance of *D. semiclausum* was the highest in plots with cabbage only (Ruhanen et al. 2023). *Barbarea stricta* was as attractive as turnip for oviposition of *P. xylostella*, but it was not included in oviposition tests conducted for *D. semiclausum* due to a low number of *P. xylostella* being found on *B. stricta* in field observations (Ruhanen et al. 2023). However, flowering *Barbarea vulgaris* has been found to increase the presence of *Diadegma insulare* in a field experiment (Badenes-Pérez et al. 2017). Since *Barbarea* plants are recommended as trap crops for *P. xylostella*, it would be important to study their attractiveness to parasitoids in laboratory conditions.

Sesquiterpene emissions of plants were targeted in this study, because (*E*,*E*)-α-farnesene, β-elemene, and α-selinene have been implicated as an oviposition stimulant of *P. xylostella* in studies demonstrating passive plant–plant interactions in broccoli and cabbage (Li and Blande 2015; Girón-Calva et al. 2016). It has also been shown to elicit electroantennography responses in *P. xylostella* when presented as a mixture of (*E,E*) and (*E,R*)-α-farnesene (Houjun et al. 2018). Turnip had the highest emission of (*E,E*)-α-farnesene, in both intact and herbivore-damaged plants, which may explain its attractiveness to *P. xylostella*. Green leaf volatiles are also attractive to *P. xylostella* (Reddy and Guerrero 2000; Yan et al. 2023). Here, we tested unmated females in Y-tube experiments, but it has been shown that mated females respond more strongly to plant volatiles (Reddy and Guerrero 2000). Olfactory orientation of mated *P. xylostella* females would possibly have better reflected host-seeking behavior of moths looking for oviposition sites. Sesquiterpenes might have more importance in attracting *P. xylostella* for plants with relatively low glucosinolate content, like cabbage and less importance for plants with higher glucosinolate content, like *B. stricta* and turnip. However, it should be noted that turnip also had the highest sesquiterpene emission in this study, so the role of sesquiterpenes as *P. xylostella* oviposition stimulants is worth further investigation. Sesquiterpenes might also be cues for natural enemies. Kroes et al. (2017) connected biosynthesis and emission of (*E,E*)-α-farnesene of *Arabidopsis* to choice of *D. semiclausum* for host-infested and host- and aphid-infested plants. More mechanistic studies on effects of semivolatile sesquiterpenes in plant–insect interactions would be needed in the laboratory to elucidate their role.

Conclusion

The results presented indicate that both turnip and *B. stricta* are more attractive than cabbage to *P. xylostella* oviposition, but we could not separate effects of plant chemistry from other traits, such as plant architecture. *Diadegma semiclausum* had greater reproductive success on turnip than cabbage and more *D. semiclausum* females oriented toward odors of turnip than cabbage. This observation suggests that these plant species both have potential for use as trap crops of *P. xylostella* in the farming of cabbage. However, it is important to note that the properties of each as a viable trap crop also depends on their interactions with other pest insects and natural enemies.

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Author contributions JB, MK, and HR designed the study. SB and HR conducted the GC–MS analysis and analyzed the data. JP conducted Y-tube tests for *D. semiclausum.* HR conducted oviposition tests and Y-tube tests for *P. xylostella.* HR wrote the original draft of the manuscript and all authors contributed to revising and editing the draft. All authors approved the final version of the manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on request.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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