

Research papers

Emission of oilseed rape volatiles after pollen beetle infestation; behavioural and electrophysiological responses in the parasitoid *Phradis morionellus*

Martin Jönsson and Peter Anderson

Department of Crop Science, Swedish University of Agricultural Sciences, Box 44, SE-230 53 Alnarp, Sweden

Summary. The pollen beetle, *Meligethes aeneus*, is an important pest of oilseed rape, *Brassica napus*. Larvae of this species feed only in the buds and flowers of Brassicaceae. One important natural enemy of this beetle is the parasitoid *Phradis morionellus* that attacks larvae in buds and flowers and also feeds on the flowers. The preferences for odours of non-infested and infested rape were tested for both starved and fed parasitoids in Y-tube olfactometer experiments. The volatile blend released from pollen beetle-infested and non-infested flowering rape and from pollen beetle larvae was identified and quantified. Gas chromatography-electroantennodetection analyses were performed with female *P. morionellus*. Parasitoids in both treatment groups preferred infested rape, but the proportion of responding female *P. morionellus* was significantly lower for the group that was starved. Six of the 20 volatiles identified were released at higher rates from infested rape than from non-infested. None of these compounds was found in pollen beetle larvae headspace. *P. morionellus* antennae detected both major and minor components in the volatile blend. The volatiles released at a significantly higher rate from infested rape and detected by *P. morionellus* antennae were (Z)-3-hexenylacetate, (Z)-3-hexenol, 3-butenyl isothiocyanate and (E,E)- α -farnesene.

Key words. Tritrophic interactions – induced defence – plant volatiles – semiochemicals – *Meligethes aeneus* – *Phradis morionellus* – *Brassica napus*

Introduction

Changes in release of plant odours caused by herbivory can be important cues for natural enemies in search for hosts (Dicke *et al.* 2003; Turlings & Wäckers 2004). The plant odours are often easier to detect than those derived from the host organism itself and are therefore explored by host-seeking parasitoids (Vet *et al.* 1995). Several studies support the idea that herbivore-induced signals attracting parasitoids can be a part of the plant's indirect defence against herbivorous insects, *i.e.* increasing plant fitness (van Loon *et al.* 2000;

Fritzsche-Hoballah & Turlings 2001). Adult parasitoids also visit plants for nectar feeding (Jervis *et al.* 1993) and odours are known to be important in food location (Wäckers 2004). Preferences for host and food-associated odours can shift depending on hunger state (Wäckers 1994; Lewis *et al.* 1998).

Pollen beetles, *Meligethes spp.* (Coleoptera: Nitidulidae) occur throughout Europe. The predominant species in most areas, including southern Sweden, is *M. aeneus* Fabr. (Alford *et al.* 2003). This species reproduces solely on cruciferous plants and is an important pest of oilseed rape, *Brassica napus* L. (Brassicaceae). The adult beetles arrive in the oilseed rape fields in early spring and oviposit in the buds. Both adults and larvae feed in and on the buds and flowers of the oilseed rape (Williams & Free 1978; Nilsson 1988). The parasitoid *Phradis morionellus* Thomson (Hymenoptera: Ichneumonidae) is one of the most important natural enemies of pollen beetles in central and northern Europe (Nilsson & Andreasson 1987; Billqvist & Ekbohm 2001; Büchi 2002). This species is a univoltine larval parasitoid, specialized on *Meligethes spp.* (Osborne 1960; Nilsson 2003) that attacks pollen beetle larvae both inside oilseed rape buds and in open flowers (Jönsson 2005). *P. morionellus* and other ichneumonid pollen beetle parasitoids have been shown to distinguish between volatile blends from different developmental stages of oilseed rape (Jönsson *et al.* 2005).

An increased release of volatiles from crucifers infested by insects has been described in several species, such as cabbage (Agelopoulos & Keller 1994; Geervliet *et al.* 1997) and Brussels sprouts (Mattiacci *et al.* 1994; 2001). Odours released during larval feeding on oilseed rape leaves can attract parasitoids (Potting *et al.* 1999). The difference in volatile blends released from infested and non-infested oilseed rape has not been studied previously.

We investigated if female *P. morionellus* can discriminate between odours of pollen beetle infested and non-infested oilseed rape plants, and if the discrimination is affected by feeding status of the parasitoids. Furthermore we describe the volatiles released from oilseed rape infested by pollen beetles in comparison with volatiles of non-infested rape. The ability of female *P. morionellus* to detect these volatiles was tested in gas chromatography-electroantennodetection (GC-EAD) experiments.

Material and methods

Insects

Adult pollen beetles used to infest the plants were collected in winter and spring oilseed rape fields at the University farm near Malmö in southern Sweden. Parasitoids of both sexes were collected in spring rape fields in the same area and placed in ventilated plastic boxes (24 cm × 18 cm × 7 cm) containing wet paper. The parasitoids used in behavioural experiments were collected in the afternoon and stored indoors until tested the next day. Only female parasitoids were used in experiments. Those used in electrophysiological experiments were provided with water and honey and stored in a refrigerator (8 °C) for up to one week if not used on the day of collection. After experiments, the parasitoids were placed individually in test tubes with 70% ethanol for taxonomic identification of species, according to Horstmann (1971).

Plants

Spring-sown oilseed rape plants of a double-low variety (Maskot, Svalöf Weibull) were individually grown from seeds in 3-litre pots. The soil was fertilized at the time of planting with a 3- to 4-month formulation of Osmocote® (Bayer Home & Garden, Lomma, Sweden) controlled-release NPK-fertilizer. The pots were kept in a greenhouse chamber at 20 °C during daytime (9 am - 19 pm) and 15 °C during night-time at 70 ± 10 % r.h. In addition to natural light, artificial light (Philips, SGR 050-400, T400W) was provided between 6 am - 10 pm. Plants were infested at the bud stage by keeping them in fine mesh cages together with 50-100 pollen beetles for two days. Control plants were kept in cages without beetles. The plants used were in the mid-flowering stages 64-67 according to the BBCH scale (Lancashire *et al.* 1991). The infested plants had 1-5 visible pollen beetle larvae per plant.

Bioassay

Two-choice tests were made indoors at 22 °C ± 2 between 10 am and 16 pm. A Y-shaped glass olfactometer with 220 mm long arms and a 15 mm inner diameter was used. The Y-tube was fixed on a piece of cardboard (39 cm × 39 cm), positioned with side arms slightly upwards (15° angle). The Y-tube was placed inside a box of white fabric (40 cm × 40 cm × 50 cm) with light sources behind. Pieces of 2 cm long black tubing were placed around each arm at the Y-junction. These shading tubes made the insects slow down or stop before choosing an arm, thereby decreasing the number of random choices. The odour sources consisted of two non-infested plants enclosed in one cooking bag and two infested plants in another cooking bag. These two pairs of plants in their pots were placed behind the Y-tube set up. The plants and the rear of the box were symmetrically illuminated with two fluorescent lamps (27 W) and two reflector lamps (75 W, Osram, Concentra® Spot Natura). A regular aquarium pump was used to push air through a flow-meter (BA-4AR, Kytölä) to a gas-wash bottle (250 ml) containing activated charcoal and into the bottom of each bag at a rate of 0.4 l/min. The air above the plants of each bag was pulled out via flow meters into the pumps (Micro pump NMP 30 KNDC, 12 V, KNF) and pushed into each arm of the Y-tube at a rate of 0.3 l/min (approximately 3 cm/s in each arm). The tubes were of Teflon (5 mm i.d.). After each session, the tubing and the Y-tube were rinsed with ethanol. The Y-tube was heated to 350 °C between experimental days. Pumps and flow meters contaminated with plant volatiles were allowed to pump clean air for several hours between experimental days. Positions of plants and pumps were shifted between experimental sessions to compensate for possible side and pump effects. To test the effects of physiological state, the parasitoids were provided with either only humidified paper or with humidified paper and honey from the time of collection until tested. Parasitoids were released individually in the central arm

and allowed to walk up and choose one arm. Parasitoids that walked 7 cm up into one of the arms were considered to have made a choice. Parasitoids not making a choice within five minutes were counted as non-responding. The differently pre-treated parasitoids were tested alternately throughout each experimental day.

Collection of volatiles from plants and larvae

Volatiles were collected indoors at 22 °C ± 2 for 24 hrs, artificial light was provided in addition to natural light between 6 am and 10 pm (Osram powerstar, HQI-T, 400W). A volatile collection method similar to that of Turlings *et al.* (1998) was used. Collections were made from ten non-infested and ten infested individual plants. The central shoot and the two uppermost side shoots were enclosed in polyethylene terephthalate cooking bags (35 cm × 43 cm, Toppits, Melitta). The bags were sealed around the stems with steel wire. Part of the outlet flow of a laboratory pump (N 811, 220 V, KNF, Neuberger, Germany) was used to push air through Teflon tubing (5 mm i.d.) into the bottom of the bags at a rate of 0.4 l/min via a charcoal filter and a flow meter (BA-4AR, Kytölä). With the same pump, air was pulled out from the top of the bag via an adsorbent at a rate of 0.3 l/min. Air flows were set by adjusting the amount of air entering and leaving the system through a split of the tubing between the pump and the flow meters. Consequently air from outside was continuously introduced into the system. The adsorbent (50 mg Super Q, Alltech, Deerfield, IL, USA) was fixed inside a glass tube (50 mm × 5 mm o.d.) by two stoppers made of Teflon tubing and glass wool. Filters were extracted with 300 µl of redistilled hexane into a 1.5 ml vial and 200 ng heptyl acetate (10 µl of 20 ng/µl hexane) was added as an internal standard. The vials were kept at -20 °C until analysed. Between collections, the adsorbents were rinsed with 2 ml of dichloromethane, 2 ml of pentane and finally 0.5 ml of redistilled hexane. Three collections were made with empty bags to check for contamination. In order to get more concentrated extracts for combined gas chromatography and mass spectrometry (GC-MS) and GC-EAD analyses, four collections were made from groups of four infested plants enclosed in a cooking bag (45 cm × 55 cm) using the same method as described above. The four samples were pooled and concentrated by evaporation under nitrogen to 25% of the initial volume.

To identify volatiles of larval origin collections were made from larvae without plant material present. A system consisting of four gas-wash bottles (250 ml) connected with Teflon tubing were used to collect volatiles released from pollen beetle larvae during 24 hrs. Using the laboratory pump, air was pulled through one bottle containing water and through a second bottle containing activated charcoal. After the charcoal bottle the air stream was split into two, one passing through a bottle with 200 larvae and another through an empty bottle for blank collection. Adsorbents of the same type as described above were connected to the outlets. After the adsorbents, the airstreams passed through two flow meters (0.2 l/min) connected to the pump. Adsorbents and samples were treated as described for collection of plant volatiles.

Chemical analysis

Major plant volatiles were quantified on a Hewlett Packard (HP 6890) gas chromatograph (GC) with flame ionisation detector (FID). A SolGel-Wax column was used (SGE, 30 m × 0.25 mm i.d., 0.25 µm stationary phase) with hydrogen as carrier gas at a velocity of 50 cm/s, injector temperature 220 °C and detector temperature 250 °C. Splitless injection (2 µl) was made at an oven temperature of 40 °C held for 2 min and then increased by 7 °C/min up to 220 °C. The quantity of components was determined in relation to the internal standard by comparing area units. Initial identification was based on GC-MS on a HP-5890 with a SolGel-Wax column (described above) connected to a HP-5970 mass detector, using the same temperature conditions as described above, but with helium as carrier gas. Ionisation potential was 70 eV and the scan range 30-400 amu. The mass spectra obtained

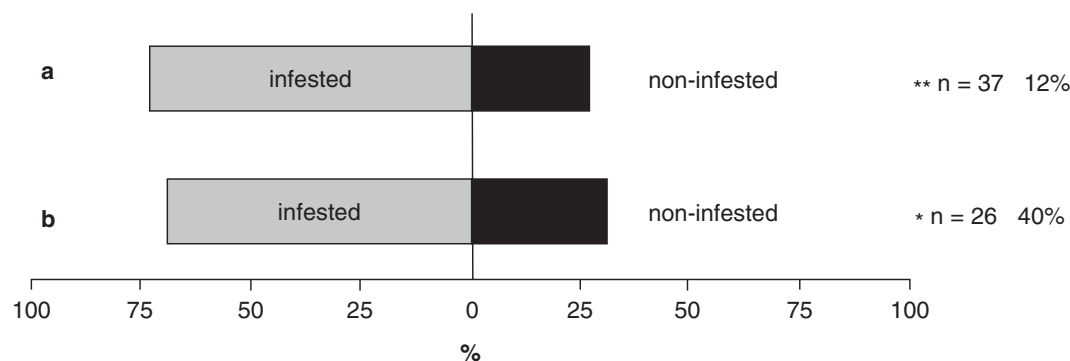


Fig. 1 Response of *Phradis morionellus* in Y-tube experiments to odours from non-infested oilseed rape and infested oilseed rape. a) Females supplied with water and honey; b) females only supplied with water. On the right are statistically significant differences (* $P < 0.05$; ** $P < 0.01$, G-test), number of females making a choice and the percentage of all parasitoids tested not making a choice given.

were compared with the Wiley/NIST mass spectral database (1990) and with spectra obtained from standards. The identities were confirmed by comparison of retention times with standards on the GC-FID described and also on a HP-5890 GC-FID with an apolar column, DB-5 (J&W Scientifics, 30 m \times 0.32 μ m i.d., 0.25 μ m stationary phase). Similar temperature conditions as described above were used.

GC-EAD recordings

GC-EAD recordings with female parasitoid antennae were performed on the same system and using a similar method to Jönsson & Anderson (1999). A SolGel-Wax column (described above) was installed in a HP-6890 gas chromatograph equipped with a column four-way cross, for make-up gas (nitrogen) and 1:1 split for EAD and FID. The head of the parasitoid was cut off and the posterior of the head was placed in the grounded glass electrode containing Beadle-Ephrussi ringer solution (Bjostad 1998). The two tips of the antennae were introduced into the recording electrode connected to a high impedance DC amplifier (Syntech, The Netherlands). The mounted antennae were placed in the air stream carrying the compounds eluting from the GC. Six successful GC-EAD experiments with the same sample of volatiles were evaluated. Compounds eliciting responses in three or more of these runs were regarded as active. To confirm the electrophysiological activity of the identified compounds, GC-EAD experiments were performed with the same standard compounds as used in the chemical identification (30 ng/ μ l, injection volume 2 μ l).

Statistical analysis

Preferences in the dual choice Y-tube experiments were analysed by goodness of fit tests (G-tests) against an expected ratio of 50:50. To test for differences in responses between different pre-treatments, the heterogeneity G (G_H) was calculated (Sokal & Rohlf 1995). Mann-Whitney U-tests were made with the computer programme Minitab to test for differences between the amounts of volatiles collected from non-infested and infested plants.

Results

Bioassay

Both females supplied with honey and water and those given only water preferred infested rape over non-infested

rape (Figure 1). There was no difference in preference between the two treatments ($G_H = 0.108$; $df = 1$; $p = 0.75$). However, the proportion of non-responding females was clearly higher among the females only given water compared to those supplied with both water and honey ($G_H = 9.68$; $df = 1$; $p = 0.002$).

Plant volatiles

Approximately 50% more in total amounts of volatiles were released from infested plants compared to non-infested. In Table 1, compounds with a mean amount collected of 50 ng or more in any of the two treatments are presented. One compound, 3-butenyl isothiocyanate, was included although found in lower amounts. Compounds found in blank collections were excluded. The compounds released at higher rates from infested plants than non-infested plants were (Z)-3-hexenylacetate, (Z)-3-hexenol, 3-butenyl isothiocyanate and the sesquiterpenes. Two geometrical isomers of α -farnesene were found. The most abundant isomer was identified as (E,E)- α -farnesene, while the identity of the minor α -farnesene isomer was not established. Nonanal and decanal were the dominant compounds in the blank collections. None of the compounds in Table 1 were identified in the volatiles collected from pollen beetle larvae. Instead a number of aliphatic hydrocarbons and fatty acids were found in these collections.

GC-EAD

Twelve compounds elicited responses from parasitoid antennae in three or more of the six GC-EAD experiments with a natural blend of oilseed rape volatiles (Table 2 and Figure 2). Ten of these volatiles were identified and their electrophysiological activity was confirmed in at least three GC-EAD experiments with standards. Responses were found to four different classes of oilseed rape volatiles: lipoxygenase derived volatiles, terpenoids, aromatic flower volatiles, and isothiocyanates.

Table 1. Volatiles collected during 24 hrs from the upper part of non-infested and pollen beetle-infested oilseed rape in flowering stage. Mean values from 10 replicates are presented. Mann-Whitney U-test was used for the statistical calculations, n.s.=not significant, *= $p < 0.05$, **= $p < 0.01$, ***= $p < 0.001$.

Compound ^a	ng collected \pm s.e.m		Statistics
	Non-infested	Infested	
α -Thujene	77 \pm 16	59 \pm 11	n.s.
Sabinene	145 \pm 22	193 \pm 30	n.s.
Myrcene	247 \pm 36	158 \pm 15	n.s.
Limonene	172 \pm 23	181 \pm 28	n.s.
1,8-Cineole	104 \pm 9	142 \pm 19	n.s.
(<i>E</i>)- β -Ocimene	56 \pm 7	50 \pm 4	n.s.
Hexyl acetate	199 \pm 64	105 \pm 20	n.s.
(<i>E</i>)-4,8-Dimethyl-1,3,7-nonatriene	40 \pm 7	61 \pm 9	n.s.
(<i>Z</i>)-3-Hexenyl acetate	43 \pm 5	304 \pm 101	***
Unidentified 1	145 \pm 20	139 \pm 36	n.s.
1-Hexanol	43 \pm 12	72 \pm 25	n.s.
(<i>Z</i>)-3-Hexenol	25 \pm 3	202 \pm 73	***
3-Butenyl isothiocyanate	6 \pm 3	21 \pm 5	*
Benzaldehyde	219 \pm 21	183 \pm 27	n.s.
β -Elemene	39 \pm 9	148 \pm 25	**
Phenyl-acetaldehyde	30 \pm 6	58 \pm 19	n.s.
α -Farnesene (isomer not determined)	156 \pm 18	308 \pm 53	*
Unidentified 2	17 \pm 5	97 \pm 21	*
(<i>E,E</i>)- α -Farnesene	670 \pm 93	1424 \pm 316	*
(<i>E,E</i>)-4,8,12-Trimethyl-1,3,7,11-tridecatetraene	63 \pm 15	77 \pm 17	n.s.
Unidentified 3	66 \pm 6	74 \pm 12	n.s.
2-Phenyl-ethanol	60 \pm 6	74 \pm 13	n.s.
Indole	227 \pm 45	99 \pm 18	*

^aCompounds are arranged in order of increasing retention times on a polar GC-column.

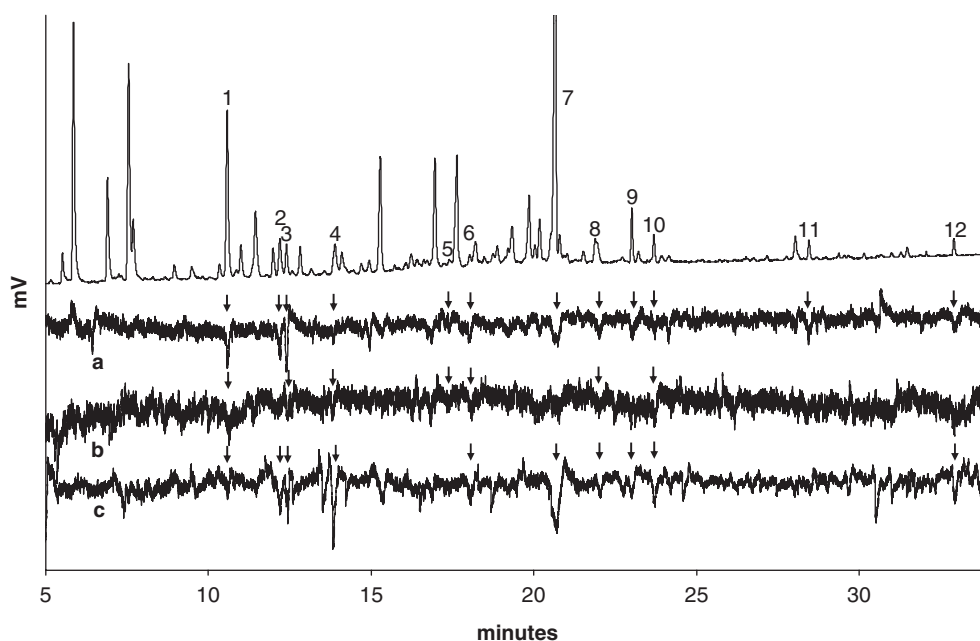


Fig. 2 Simultaneously recorded gas chromatography-electroantennodetection analysis of volatiles collected from pollen beetle-infested oilseed rape. The upper trace represents FID response and the lower trace represents antennal responses (EAD) of female *Phradis morionellus* in three of the six evaluated experiments. Activity was found in three or more of the six experiments to: 1) (*Z*)-3-hexenylacetate. 2) (*Z*)-3-Hexenol. 3) Nonanal (contamination). 4) 3-Butenyl isothiocyanate. 5) Methyl benzoate. 6) Phenyl-acetaldehyde. 7) (*E,E*)- α -Farnesene. 8) (*E,E*)-4,8,12-Trimethyl-1,3,7,11-tridecatetraene. 9) Unidentified 3. 10) 2-Phenyl-ethanol. 11) Unidentified 4. 12) Indole. Arrows indicates peaks recognized as responses to the active compounds.

Table 2. Responses recorded in gas chromatography-electroantennodetection (GC-EAD) experiments with female *Phradis morionellus*. Six experiments with different pairs of antennae with the same blend of volatiles collected from pollen beetle-infested oilseed rape were evaluated.

Number	Compound	Number of responses
1	(Z)-3-Hexenylacetate	4
2	(Z)-3-Hexenol	5
3	Nonanal	5
4	3-Butenyl isothiocyanate	4
5	Methylbenzoate	3
6	Phenyl-acetaldehyde	4
7	(E,E)- α -Farnesene	4
8	(E,E)-4,8,12-Trimethyl-1,3,7,11-tridecatetraene	4
9	Unidentified 3	3
10	2-Phenyl-ethanol	4
11	Unidentified 4	3
12	Indole	5

Discussion

Female *P. morionellus* were more attracted to odours from infested plants when compared with uninfested plants. This indicates that *P. morionellus* use plant odours to find their hosts, as has been found in other parasitic wasps (Vet *et al.* 1995). There was no difference in the response between females that had been supplied with food or not. The proportion of non-responding females in the Y-tube experiments was higher among the parasitoids that were not given honey and it is clear that sugar intake is essential for the condition of these parasitoids. Nectar feeding is known to be important for other Ichneumonids and can be performed in oilseed rape flowers (Idris & Grafius 1995). It is also known that other parasitoids respond differently to odours associated with hosts or food depending on whether they are hungry or not (Lewis *et al.* 1998). These associations between stimuli and resources can be both innate (Wäckers 1994) and learnt (Lewis & Takasu 1990). Although we could not separate innate and learnt preferences for these wild collected parasitoids, we expected the starved parasitoids to be in food-seeking mode and to make no distinction between non-infested and infested plants. If anything, we might have expected a preference for uninfested plants. A possible explanation for the results is that both infested and non-infested plants contained flowers and released typical flower odours. It is possible that an odour blend advertising a resource providing both food and host is always preferred, regardless of hunger state.

A number of compounds were released at increased rates after larval feeding and detected by female parasitoids and thus can be important in discriminating between infested and non-infested oilseed rape. The most pronounced increase in emission after infestation was found for (Z)-3-hexenol and (Z)-3-hexenylacetate. These green leaf volatiles (GLVs) are released from most plants in response to all types of mechanical damage as a consequence of lipid degradation (Hatanaka 1993). In analysis of volatiles from

freshly artificially damaged buds of oilseed rape, these two compounds were among the most abundant (Borg 1996). A large increase in emission of one or both of these compounds has also been observed in Brussels sprouts and cabbage after larval feeding (Blaakmer *et al.* 1994; Mattiacci *et al.* 1994; 2001; Geervliet *et al.* 1997).

In the present study, 3-butenyl isothiocyanate was released in small but increased amounts from infested plants. This compound is derived from 3-butenyl glucosinolate, which is the most abundant glucosinolate in buds of oilseed rape (Clossais-Besnard & Larher 1991). The isothiocyanates are formed by hydrolysis of glucosinolates, a reaction catalyzed by myrosinase. The myrosinases are normally stored in separate cells and the reaction is activated upon tissue damage (Fahey *et al.* 2001). In contrast to indole glucosinolate production, the production of aliphatic glucosinolates has not been shown to be induced by insect feeding in oilseed rape seedlings (Bodnaryk 1992; Bartlet *et al.* 1999). However, we were unable to find any study on the effects of insect feeding on the levels of 3-butenyl glucosinolate or other glucosinolates in the buds or flowers. Therefore, we do not know to what degree the observed release of 3-butenyl isothiocyanate was a specific response to insect feeding or a general response to damage.

The emission of sesquiterpenes also increased due to pollen beetle feeding. In Brussels sprouts, two sesquiterpenes ((*E*)- β -caryophyllene and α -humulene) were the only compounds found to be specifically released after larval feeding and not after mechanical damage (Mattiacci *et al.* 2001). It is possible that the sesquiterpenes released, in contrast to the GLVs, are more specific indicators of the type of damage suffered by the plant. In the present study, as in other studies on crucifers (Blaakmeer *et al.* 1994; Agelopolous & Keller 1994; Geervliet *et al.* 1997; Mattiacci *et al.* 1994; 2001) observed differences between non-infested and infested plants were mainly quantitative. A more specific response has been found in other plants, for example maize (Turlings *et al.* 1990) and cotton (McCall *et al.* 1994), in which many volatiles, often terpenoids, are detected only from infested plants. The terpenoid that increased relatively most in response to infestation was β -elemene. This compound has earlier been identified as an oilseed rape volatile (Tollsten & Bergström 1988), but has in general been identified in head-space extracts from a smaller number of plant genera than the other terpenoids (Knudsen *et al.* 1993). One compound, indole, was released at a lower rate from infested plants than from non-infested. This compound is mainly released from flowers of oilseed rape (Jönsson *et al.* 2005) and therefore the emissions may decrease when the flowering parts are damaged.

In several plant species the emission of volatile compounds has been found to vary throughout the photoperiod (Dudareva *et al.* 2004). It is possible that the relative amounts of volatiles present in the oilseed rape field during parasitoid host location differ somewhat from the volatiles collected and used in this experiment. A rhythmic emission has been observed in floral emission of oilseed rape, two terpenes out of eight quantified were released at higher rate during daytime while the emission of other did not differ between day and night (Jakobsen *et al.* 1994). Thus, the

ratio between different compounds in the volatile blend from oilseed rape may differ during different times of the photoperiod.

The GC-EAD experiments showed that *P. morionellus* females responded to a variety of compounds. Such an ability to detect a broad spectrum of plant volatiles is common among hymenopterous parasitoids (e.g. Li *et al.* 1992; Park *et al.* 2001; Smid *et al.* 2002). The isothiocyanate detected here is almost exclusive for Brassicaceae and it may therefore be an important cue in a general location of plants possibly attacked by their specialized host. Results from field studies show that isothiocyanates are attractive to other hymenopterous parasitoids with hosts feeding on oilseed rape (Murchie *et al.* 1997; Bradburne & Mithen 2000). The aphid parasitoid *Diaeretiella rapae* preferred plants with high levels of 3-butenyl isothiocyanate (Bradburne & Mithen 2000). The GLVs (Z)-3-hexenylacetate and (Z)-3-hexenol seem to be detected by many parasitoid species, both Ichneumonids (Baehreke *et al.* 1989) and Braconids (Ramachandran *et al.* 1991; Li *et al.* 1992; Smid *et al.* 2002). These general damage indicators have been reported to be important for host-seeking parasitoids (Whitman & Eller 1990). Volatiles typical for flowering rape, such as phenyl acetaldehyde, 2-phenyl ethanol and indole (Tollsten & Bergström 1988; Jönsson *et al.* 2005), also elicited antennal responses. These compounds can be essential in location of flowers, either in foraging for host or food.

The observed release characteristics of compounds detected by female *P. morionellus* can as indicated by the behavioural results guide parasitoids in search for a suitable host. Clearly, plant odours are important for the behaviour of the studied parasitoid. There is a need to reduce the use of synthetic insecticide in control of pollen beetles (Alford *et al.* 2003). One possible sustainable strategy to control pollen beetles can be a trap-crop system (Cook *et al.* 2006). Biological control is important in these integrated pest management strategies and knowledge about plant chemicals involved in the parasitoids host search can be useful in development of methods that can augment the effectiveness of the pest's natural enemies.

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