

Selecting volatiles to protect brassicaceous crops against the cabbage root fly, *Delia radicum*

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Abstract

Volatiles resulting from plant–herbivore interactions play an important role in the behavioral decisions of phytophagous, predatory, and parasitoid insects and could be used for managing pest insects. However, to date and after about 40 years of research, documented studies on applications in the field remain extremely scarce. *Delia radicum* L. (Diptera: Anthomyiidae), the cabbage root fly, is a major pest of brassicaceous crops for which classical control strategies are currently lacking. Our previous studies showed that dimethyl disulfide (DMDS), a compound emitted by roots heavily infested by *D. radicum* larvae, was attractive for the fly's main natural enemies and could lead to a reduction of 60% in number of eggs laid on treated plants in the field. As a follow-up of this work, we conducted another field study to select additional volatiles that could be used in a push–pull approach. Several synthetic herbivore-induced plant volatiles, selected on the basis of their potential action on the behavior of both the fly and its natural enemies, were placed in odor dispensers in experimental broccoli plots and their influence on oviposition by *D. radicum* and egg predation by ground-dwelling predators was assessed. Our results confirmed the role of DMDS in reducing *D. radicum* egg numbers on broccoli plants and revealed that (*Z*)-3-hexenyl acetate, a green leaf volatile released by recently damaged plants, strongly stimulated fly oviposition. Also, two of the compounds tested slightly modified predation activity of ground-dwelling predators: acetophenone decreased the proportion of predated patches, whereas methyl salicylate increased it. This study is a first step in designing a push–pull strategy to control the cabbage root fly.

Introduction

Volatiles resulting from plant herbivore interactions play a major role in resource foraging by predators and parasitoids. They have been shown to be involved in orientation processes, oviposition decisions, feeding site acceptance, or patch quality estimation by natural enemies (e.g., Geervliet et al., 1998; Meiners & Hilker, 2000; Dicke et al., 2003; Turlings & Wäckers, 2004; Rasmann et al., 2005; Tentelier & Fauvergue, 2007; Fatouros et al., 2008; Allmann & Baldwin, 2010). These volatiles can be used by predators or parasitoids as reliable cues to find their host

or prey and are usually considered as part of indirect defense strategies of plants (Dicke et al., 2003; Turlings & Wäckers, 2004). However, herbivore-induced plant volatiles (HIPVs) can also be used by phytophagous insects to optimize their resource use. They can be important signals to locate suitable host plants (Bolter et al., 1997; Reddy & Guerrero, 2000; Turlings & Wäckers, 2004; Halitschke et al., 2008), can stimulate oviposition (Baur et al., 1998; Agrawal & Sherriffs, 2001; Johné et al., 2006), host acceptance (Landolt, 1993), or feeding by larvae (Halitschke et al., 2004; Carroll et al., 2006), and serve as aggregation cues for conspecifics (Loughrin et al., 1995; Johné et al., 2006). On the other hand, as they are emitted once the plant has been attacked, these volatiles can also give indications of poor-quality oviposition or feeding sites (because

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of high competition or natural enemy risk) and repel herbivores (Bernasconi et al., 1998; De Moraes et al., 2001; Kessler & Baldwin, 2001; Sanchez-Hernandez et al., 2006).

The discovery of these multiple and important effects of HIPVs on insect behavior (and particularly natural enemies) opened new perspectives for managing pest insects (Degenhardt et al., 2003; Pickett et al., 2006; Turlings & Ton, 2006; Khan et al., 2008; Rodriguez-Saona & Stelinski, 2009). However, to date and after about 40 years of research on this topic, documented studies on applications in the field remain extremely scarce. The effect of synthetic HIPVs on attraction of predators and parasitoids was demonstrated in hop yards and vineyards by a series of field studies (James, 2003a,b; James & Price, 2004; James & Grasswitz, 2005). Furthermore, for one of the HIPVs [viz., methyl salicylate (MeSA)], increases in natural enemy numbers were also associated with a reduction below threshold levels of important pests like spider mites and aphids (James & Price, 2004). Field application of synthetic volatiles gave similar promising results in sweet maize, broccoli, wine grapes, and cotton (Yu et al., 2008; Simpson et al., 2011). An approach which combines the use of volatiles to manipulate both insect pests and their natural enemies has led to real applications in the field: the push–pull (sometimes also termed stimulo–deterrent diversion) strategy (Cook et al., 2007; Hassanali et al., 2008; Khan et al., 2008). This strategy is the only one practiced by farmers and is currently used for the control of the cereal stem borers *Chilo partellus* (Swinhoe) and *Busseola fusca* Fuller on cereal crops in Africa (Khan et al., 2008). It is based on the use of plant species that naturally release deterring (push) volatiles for the pests, intercropped with cereals. In addition, other plant species that release volatiles attractive to the pest (pull) are placed around the crop field. Volatiles released by plants repelling adult stem borers also appear to stimulate parasitoid foraging and result in increased levels of parasitism in the crop (Khan et al., 1997).

Delia radicum L. (Diptera: Anthomyiidae), the cabbage root fly, is a major pest of brassicaceous crops in countries of the north of the Holarctic region. Females aggregatively lay their eggs near plant stems and the larvae crawl in the soil to feed on the roots before pupating in the soil surrounding the roots. Root damage can result in important crop losses if pesticides are not used (e.g., Klein-Gebbinck & Woods, 2002). In northern Europe, the main insecticide against *D. radicum*, the organophosphorous chlorfenvinphos [2-chloro-1-(2,4-dichlorophenyl)vinyl diethyl phosphate] has been banned since 2008 due to human health risks (e.g., Heudorf et al., 2004). Therefore, new strategies for controlling this severe cabbage pest are needed. A

recent study by our group investigated the potential of dimethyl disulfide (DMDS) in a control strategy against *D. radicum* (Ferry et al., 2009). This compound is emitted in large amounts by roots heavily infested by larvae and has been found to be attractive to the main natural enemies of the fly in the field (Ferry et al., 2007): carabids belonging to the genus *Metallina* (*Bembidion*), which are generalist predators of eggs and larvae of insects, and two staphylinid beetles, *Aleochara bilineata* Gyllenhal and *Aleochara bipustulata* (L.), which are both predators of the eggs and larvae of the fly and parasitoids of its pupae. Furthermore, DMDS was also found to lower the number of eggs laid on treated plants in the field by 60% (Ferry et al., 2009). These two coupled effects (i.e., repel the pest and attract its predators) opened new perspectives for utilization of DMDS in a push–pull strategy against the cabbage root fly.

As a sequel to the work of Ferry et al. (2009), we conducted another field study to select additional volatiles that could be used in a push–pull approach. Several compounds were selected on the basis of their potential action on the behavior of both the fly and its natural enemies, including (1) allyl isothiocyanate (AITC), a breakdown product of glucosinolates characteristic of *Brassica* plants (Bones & Rossiter, 2006) and found to be attractive to *D. radicum* females in wind tunnel experiments (Nottingham & Coaker, 1985), (2) MeSA, a volatile emitted after herbivore attack and attracting beneficial insects in the field in different crops, including *Brassica* (James & Price, 2004; James & Grasswitz, 2005; Orre et al., 2010; Simpson et al., 2011), (3) hexenyl acetate, a compound previously used singly or in mixtures as an attractant of herbivores and/or their natural enemies (James & Grasswitz, 2005; von Arx et al., 2011; Simpson et al., 2011), and (4) acetophenone (ACPH), a flower-derived compound attractive to fruit fly parasitoids (Rohrig et al., 2008a) and emitted by flowering plants attractive to *D. radicum* (Rännbäck, 2008). Dimethyl disulfide, which influences the behavior of the fly and its natural enemies as shown by our previous studies (Ferry et al., 2007, 2009), was also included. These volatiles were placed in experimental broccoli plots in the field and their influence on oviposition by *D. radicum* and egg predation by ground-dwelling predators was assessed.

Materials and methods

Field setup

Cultivated broccoli plants, *Brassica oleracea* L. var. *Italica* (cv. Marathon) (Brassicaceae), were used in the experiment. Seeds were sown individually in peat soil cylinders and grown for 6 weeks in a plastic tunnel (Thomas Plant,

Ploubazlanec, France). The experimental site was located in the 'Domaine experimental de la Motte' (INRA Center, Le Rheu, France; 48°06'07"N, 01°47'44"W). The soil was fertilized at 63.5 kg nitrogen per ha before plantation. One week later (7 April 2011), the broccoli seedlings were transplanted in the field at a density of 1.7 plants m^{-2} . No insecticide was used, neither as a seed coating nor as a spray in the field.

We used a randomized block design consisting of four blocks. Each block included nine randomized plots corresponding to the treatments. A plot comprised 25 plants (five rows of five plants each, planted on a 0.8 × 0.8 m grid). The plots were separated from each other by four rows (i.e., 5 m) of untreated broccoli plants. Blocks were separated from each other by 5 m of uncultivated soil. Treatments consisted of two controls and seven different volatiles supplied by means of odor dispensers (Natural Plant Protection, Pau, France) positioned at the center of the plots (Figure 1).

Volatiles tested

Volatiles likely to play a role in the behavior of the cabbage root fly or its natural enemies were tested: AITC, (Z)-3-hexenyl acetate (HA), MeSA, ACPH, and DMDS. Two additional treatments were originally planned but later excluded from the analyses: Z-3-hexenol was out of supply during the experiment and benzaldehyde crystallized inside the dispensers and did not volatilize properly.

Products were obtained from Sigma-Aldrich (St Louis, MO, USA). Pure product (2–3 ml) was deposited in the dispensers. Depending on the product volatility dispensers were replaced every week (AITC, DMDS) or every other

week (HA, MeSA, ACPH). Two dispensers were used for all volatiles except for MeSA, which is not very volatile and was applied using four dispensers per plot. The quantity of product volatilized was checked by weighing the dispenser before it was installed in the field and after it was replaced. The mean volatility of the compounds was 95.00 ± 9.54 (AITC), 26.43 ± 2.15 (MeSa), 31.75 ± 7.70 (HA), 31.75 ± 3.36 (ACPH), and 234.00 ± 7.76 mg per day (DMDS).

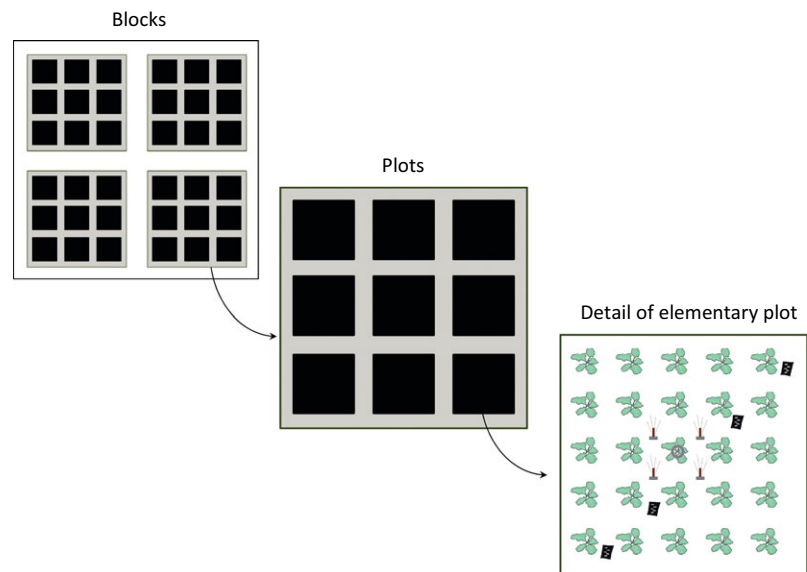
Oviposition

Egg laying by *D. radicum* was monitored using felt traps (for a description, see Bligaard et al., 1999) positioned around the stem of the plants, where flies deposit their eggs. These traps are used by farmers as an indicator of pest prevalence. Felt traps were placed on one plant in the middle of each plot surrounded by the odor dispensers (Figure 1). Traps were collected every week and the eggs found inside were counted and removed. Emptied traps were then replaced on the same plants (or on the nearest plant when this plant had died). Egg deposition was monitored from 12 April to 10 May 2011.

Egg predation

Egg predation in the plots was assessed using artificial patches of eggs. These patches consisted of a 1-cm² piece of black paper pinned down to the soil surface and protected from the rain using a small plastic cover. Five *D. radicum* eggs collected in our rearing facility were glued onto the paper with gum arabic. Four patches were placed next to the stem of four plants in each elementary plot and maintained in the plots for 48 h, after which egg predation was recorded. We measured the percentage of patches in

Figure 1 Schematic representation of the experimental field consisting of four blocks as repetitions, each block of nine randomized plots corresponding with the nine treatments. A plot comprised 25 plants (five rows of five plants each, planted on a 0.8 × 0.8 m grid). The plots were separated from each other by four rows of untreated broccoli plants. Blocks were separated from each other by 5 m of uncultivated soil. Treatments consisted of two controls and seven different volatiles supplied by means of odor dispensers. Two to four dispensers were positioned at the centre of the plots. ○ felt trap; ■ artificial egg patch; ⌊ odor dispenser; 🌱 broccoli plant.



which predation occurred (at least one egg predated per patch) and the mean number of predated eggs when predation occurred. This experiment was repeated in two consecutive weeks (starting on 2 and 9 May). The presence of *Aleochara* spp. in the experimental field was assessed using two pitfall traps placed in each block and monitored weekly. Predation tests were carried out when more than 15 adults were found per trap.

Statistical analysis

All statistical analyses were carried out with R software, version 2.12.1 (R Development Core Team, 2010). The number of *D. radicum* eggs laid and the number of eggs predated on in the artificial patches were analyzed using generalized linear mixed models (GLMM) with a Poisson distribution for errors and using blocks as a random factor. Comparison between treatments was carried out using an analysis of contrast (function 'esticon' of the package 'doBy'; Højsgaard, 2004). Egg predation was also analyzed by comparing the proportion of artificial patches where predation occurred with a χ^2 test (basic assumption: balanced proportion of artificial patches predated and not predated) followed by an exact binomial test (function 'binom.test', $P = 0.5$).

Results

Oviposition

Delia radicum colonized experimental plots soon after plantation and the number of eggs per trap in control plots

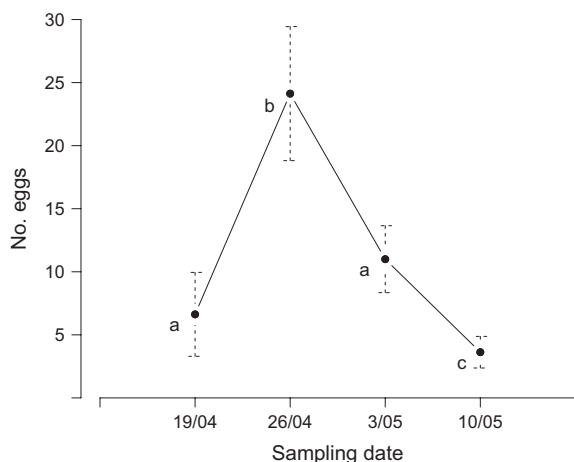


Figure 2 Mean (\pm SE) number of *Delia radicum* eggs found per felt trap on control broccoli plants on four sampling dates. Broccoli seedlings were transplanted in plots on 7 April. Means with different letters are significantly different (GLMM Poisson and analysis of contrast: $P < 0.05$).

rapidly exceeded the threshold level of seven eggs per felt trap per week, which is habitually used by farmers to decide whether or not to spray against the pest (Figure 2). The presence of two synthetic HIPVs influenced the egg laying activity of *D. radicum* on broccoli plants (GLMM: $\chi^2 = 46.71$, d.f. = 5, $P < 0.001$; Figure 3). (*Z*)-3-hexenyl acetate significantly increased the number of eggs laid on plants (GLMM: $\chi^2 = 5.99$, d.f. = 1, $P < 0.05$), whereas DMDS significantly decreased it (GLMM: $\chi^2 = 7.00$, d.f. = 1, $P < 0.01$). The other compounds, AITC, MeSA, and ACPH, did not modify the number of eggs laid compared to the control (GLMM: $P > 0.1$ for each comparison with control). The number of eggs was well over the threshold of seven eggs per felt trap per week (i.e., 28 eggs per month) for all treatments except for DMDS (Figure 3).

Egg predation

The presence of some synthetic HIPVs influenced predation activity of *D. radicum* eggs on artificial patches ($\chi^2 = 11.47$, d.f. = 5, $P < 0.05$; Figure 4). Acetophenone significantly decreased the proportion of predated patches (10 patches predated upon out of 32 in total; exact binomial test: $P < 0.05$), whereas MeSA significantly increased it (22 patches predated upon out of 32 in total; exact binomial test: $P < 0.05$). The other compounds, AITC, DMDS,

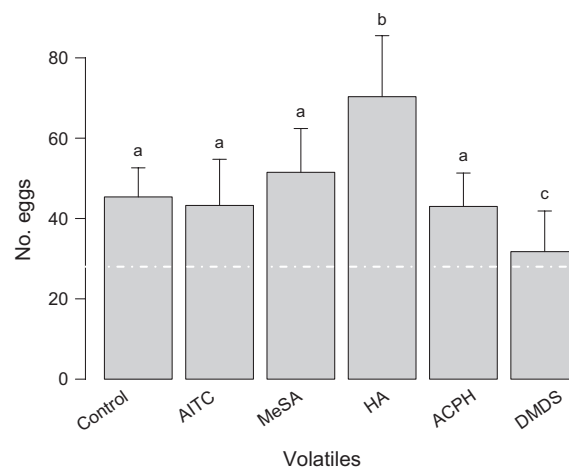


Figure 3 Mean (\pm SE) cumulative number of *Delia radicum* eggs found per felt trap on four sampling dates (19 and 26 April, 3 and 10 May) in control plots and plots where various synthetic herbivore-induced plant volatiles (HIPVs) were released: allyl isothiocyanate (AITC), methyl salicylate (MeSA), (*Z*)-3-hexenyl acetate (HA), acetophenone (ACPH), or dimethyl disulfide (DMDS). Volatiles were supplied with odor dispensers placed in the middle of the plots. The dashed line corresponds to the threshold of 28 eggs per felt trap per month, which is habitually used by farmers to decide whether or not to spray against the pest. Means with different letters are significantly different (GLMM Poisson and analysis of contrast: $P < 0.05$).

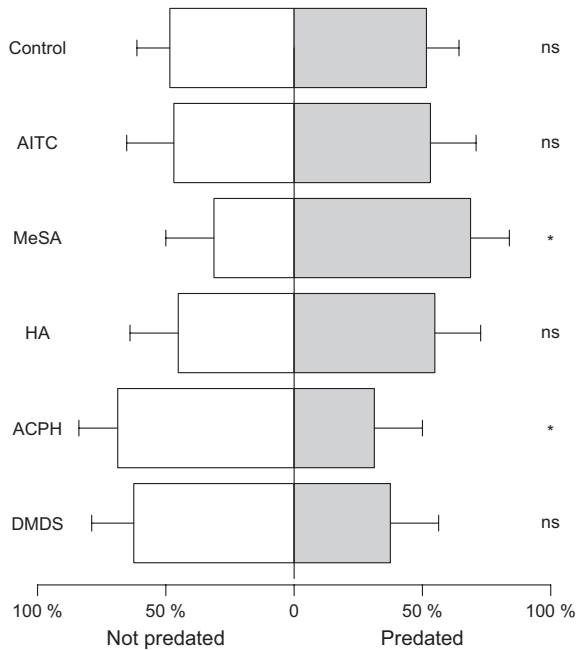


Figure 4 Mean (+ SE) percentage of *Delia radicum* artificial egg patches predated in control plots and plots to which various HIPVs were added: allyl isothiocyanate (AITC), methyl salicylate (MeSA), (*Z*)-3-hexenyl acetate (HA), acetophenone (ACPH), or dimethyl disulfide (DMDS). Volatiles were supplied with odor dispensers placed in the middle of the plots. * $P < 0.05$; ns, not significant (exact binomial test).

and HA, did not influence the proportion of predated patches. However, none of the HIPVs significantly influenced the number of eggs predated on artificial patches (GLMM: $\chi^2 = 0.76$, d.f. = 5, $P > 0.05$). The mean number of eggs predated on all plots was 2.87 ± 0.14 .

Discussion

The role of HIPVs in the behavioral decisions of phytophagous, predatory, and parasitoid insects has been demonstrated in many laboratory studies. However, demonstrations of the usability of HIPVs to manipulate pest and natural enemy behavior in the field and to reduce crop damage remain scarce (but see Khan et al., 2008). In the present paper we aimed at selecting volatiles that could influence the behavior of both a pest of brassicaceous crops, *D. radicum*, and its main natural enemies in the field. Our results confirmed the role of DMDS in reducing egg laying by *D. radicum* on broccoli plants but also revealed that HA strongly stimulated oviposition by this fly in the field. Moreover, some of the test compounds slightly modified (either positively or negatively) the predation activity of ground-dwelling predators.

Among the HIPVs tested in our experiments, HA was the only compound that stimulated oviposition by *D. radicum*. (*Z*)-3-hexenyl acetate is a green leaf volatile emitted by many plants including cabbage crops (Reddy & Guerrero, 2000; Shiojiri et al., 2001, 2010) and it is attractive to other pests of cabbage crops such as the diamondback moth, *Plutella xylostella* (L.), in the field (Reddy & Guerrero, 2000; Dai et al., 2008). To our knowledge, it is the first report of HA to have an effect on the behavior of *D. radicum*.

In *D. radicum*, several compounds present on the surface of cabbage plants are perceived by specific receptor cells in the tarsal sensilla and they have been shown to stimulate oviposition. These compounds include glucosinolates and thia-triaza-fluorenes (Roessingh et al., 1992; Hurter et al., 1999; Gouinguen e & St adler, 2006). Host plant acceptance by the cabbage root fly seems to result from a synergistic response to simultaneously perceived olfactory and contact chemostimulation (de Jong & St adler, 1999). The presence of HA could have enhanced the effect of the contact cues, naturally present on broccoli plants. Further laboratory experiments need to be performed to determine whether this compound attracts *D. radicum* or stimulates (alone or in combination with other known compounds) its oviposition.

Surprisingly, plants surrounded by odor dispensers containing AITC did not receive more *D. radicum* eggs than control plants. This volatile results from the hydrolysis of glucosinolates and is typically released by damaged brassicaceous plants containing high levels of 2-propenyl glucosinolate or sinigrin (Bones & Rossiter, 2006). It was previously shown to be attractive to the cabbage root fly and has been used in bait traps to monitor populations (adults) in the field (Wallbank & Wheatley, 1979; Finch & Skinner, 1982; Nottingham & Coaker, 1985) but has never been shown to influence oviposition. Methyl salicylate and ACPH did not have any effect on plant infestation levels either. Although all these compounds could have no effect on *D. radicum* oviposition behavior, it is also possible that we applied biologically irrelevant concentrations. To avoid differences in compound volatility using solvents, we placed pure products in our dispensers and obtained different evaporation rates for each compound, but rather stable for a given compound. Variations in concentrations of volatile compounds have been shown to influence the behavior of *D. radicum* in previous studies (Wallbank & Wheatley, 1979; Ferry, 2007). Therefore, concentrations other than those evaluated here might have different effects on the behavior of the fly.

Consistent with our previous studies, DMDS reduced egg laying by *D. radicum*, although we applied higher doses here. This compound is emitted by brassicaceous

roots heavily infested by *D. radicum* larvae for an extended period of time (i.e., 3 weeks). Therefore, it may be an indicator of a poor-quality oviposition site and play an important role in patch quality assessment by the fly. Reducing clutch sizes on plants emitting high amounts of DMDS may be adaptive for *D. radicum* as it helps reducing intraspecific competition among larvae and can also avoid choosing plants providing limited food resources for the offspring. Moreover, as it attracts the main predators of the fly (Ferry et al., 2007), DMDS may also indicate a high predation risk for the eggs. Our results confirm the importance of DMDS in reducing infestation levels of brassicaceous plants in the field.

As for natural enemy activity in the field in HIPV-enriched broccoli plots, we were only able to demonstrate marginal effects. Methyl salicylate tended to stimulate predation activity, whereas ACPH tended to decrease it. These two compounds modified predator visits to artificial egg patches but none of the compounds tested influenced the number of eggs predated in these patches. Although some studies demonstrated the impact of artificial HIPVs on natural enemy recruitment in the field, studies documenting the effect of these compounds on predatory activity are still scarce (Khan et al., 2008; Rodriguez-Saona et al., 2011). Yet, predation is of utmost importance for crop protection. Here we focused on the influence of artificial odors on predation activity, rather than on natural enemy presence.

Previous laboratory experiments have shown that one of the compounds tested here, DMDS, can stimulate egg predation by *A. bilineata* (Ferry, 2007). However, this effect could not be confirmed in the field, neither here nor in previous experiments (Ferry et al., 2009). It highlights that laboratory studies conducted under controlled conditions cannot always be validated under field conditions. The absence of any effect of artificial HIPV on predation levels in the field could be due to disruption of natural enemy behavior because of false information: artificial HIPVs could indicate the presence of high levels of prey resource but actual resources present may not match the signal perceived. Also, the artificial egg patch setup we used may not be optimal for testing activity of ground-dwelling predators in the field as less than 50% of *D. radicum* eggs were eaten in all our treatments. Indeed, egg patches were placed at some distance from odor dispensers and they may have been difficult to find if predators first oriented toward the artificial odor sources because the detectability of isolated eggs may be very low. Our results may also indicate that all the odors tested, except MeSA, do not enhance global prey searching in the field. Methyl salicylate is by far the most tested HIPV in field studies for its influence on natural enemy attraction (Rodriguez-Sa-

ona et al., 2011). It has been shown to attract a wide range of predatory and parasitic arthropods in as many as nine crops and is considered as a broad-spectrum attractant (Rodriguez-Saona et al., 2011). However, the influence of MeSA on ground-dwelling predators has rarely been tested.

Delia radicum females are synovigenic and need to feed on carbohydrates and proteins to mature their eggs (Finch & Coaker, 1969; Finch, 1971). These nutrients can be found on flowering plants surrounding brassicaceous crops and are regularly visited by females (Finch & Coaker, 1969). Acetophenone is emitted by flowering plants including alyssum, *Lobularia maritima* (L.) Desv. (Rohrig et al., 2008a), a brassicaceous species of which the flowers are particularly attractive to *D. radicum* females (Rännbäck, 2008). In our experiments, we found no effect of ACPH on egg laying by *D. radicum* but this compound negatively affected the activity of ground-dwelling predators. Such an effect has not been described before, but this compound has been found attractive to some parasitoid species (Rohrig et al., 2008a) and *L. maritima* has been shown to attract numerous species of parasitoids and predators of several insect pests under field conditions (Rohrig et al., 2008b; Sivinski et al., 2011).

This study is a first step in designing a push-pull method to control the cabbage root fly, but many steps need to be investigated before it can be implemented. We have found two volatiles with opposing effects on the oviposition behavior of the fly in the field and one that slightly enhanced predation activity. The next step would be to combine them in the field in a push-pull type disposition – i.e., DMDS and MeSA in the target crop, hexenyl acetate in neighboring field edges – to check whether they can be used to limit crop damage in broccoli fields. In parallel experiments (A Kergunteuil, S Dugravot & AM Cortesero, unpubl.), we also investigated the effect of several species and varieties of Brassicaceae on fly and natural enemy behavior. Like for the synthetic compounds tested here, we have found plants that stimulate egg laying and others that reduce egg laying by *D. radicum*. The addition of both specific plant species and synthetic volatiles affecting the colonization of plants by the pest would be interesting to combine in future field experiments.

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