

Plant characteristics mediated by growing conditions can impact parasitoid's ability to attack host aphids in winter canola

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Abstract Winter canola (*Brassica napus*) is an important crop in various parts of the world. It is planted in fall, vernalized during winter and offers higher yields than spring canola. One of the key aphid pests of this crop is *Myzus persicae* Sulzer (Homoptera: Aphididae). Recent surveys in Europe showed that *M. persicae* in winter canola is parasitized by *Aphidius matricariae* and *Diaeretiella rapae*, but not by other aphidiine parasitoid species known to attack *M. persicae* in other crops. During vernalization, winter canola plants acclimatize to survive specific climatic conditions of winter, e.g. through the formation of epicuticular waxes on leaves. These waxes could affect efficiency on natural enemies. In this study, we characterized (1) the ability of aphidiine parasitoids to locate and attack *M. persicae* on winter canola, and (2) how plant vernalization influences parasitoid ability to attack suitable hosts. In the laboratory, the ability of *A. ervi*, *A. matricariae* and *D. rapae* to orient toward odors of the *M. persicae*-winter canola complex was studied in an olfactometer, as well as their ability to attack *M. persicae* on winter canola. In addition, the impact of plant species and plant vernalization on the ability of

A. colemani to attack and locate *M. persicae* was evaluated. The results show that *A. matricariae* and *D. rapae* readily locate and attack *M. persicae* on winter canola as does *A. ervi*, albeit to lesser extent. *Aphidius colemani* shows low ability to parasitize *M. persicae* on this plant species. Vernalization of canola is an important factor mediating the ability of *A. colemani* to attack *M. persicae* and it likely results from the presence of *Brassica*'s waxes that reduce parasitoid mobility and impact foraging behavior. These results show that aphid parasitoids differ in their ability to locate and attack *M. persicae* on winter canola, the latter being a function of parasitoids' capacity to cope with plant characteristics that are mediated by growing conditions.

Keywords Aphid parasitoid · Winter canola · Host location · Olfactometer · Oviposition · *Aphidius colemani* · *Brassica* wax

Introduction

Canola is grown on a large scale around the world (>27.7 million ha in 2006, United Nations, Food and Agriculture Organization data). Winter canola (*Brassica napus*) is planted in fall and harvested in early summer, and is predominantly grown in Europe. Through vernalization (i.e. plants subjected to low temperature during winter), winter canola offers higher yields than regular canola planted in spring. One of the dominant aphid species infesting winter canola crops is *Myzus persicae* Sulzer (Homoptera: Aphididae). This insect pest weakens plants, transmits viruses, and decreases yields (van Emden et al. 1969; Buntin and Raymer 1994; Schliephake et al. 2000).

Various parasitoid species attack *M. persicae* in cruciferous crops (Schlinger and Mackauer 1963; van Emden et al. 1969)

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and more specifically, two aphidiine parasitoids: *Aphidius matricariae* Haliday (Hymenoptera: Braconidae) and *Diaeretiella rapae* McIntosh (Hymenoptera: Braconidae) (Desneux et al. 2006b; Desneux N. unpublished data) which are dominant in winter canola fields. Although both species differ in their behavioral responses to *M. persicae* on canola (Desneux et al. 2004b), both appear well-adapted to this specific host–plant complex (Wilson and Lambdin 1987; Desneux et al. 2005). In contrast, *Aphidius ervi* Haliday and *A. colemani* Viereck (Hymenoptera: Braconidae), both parasitoids of *M. persicae* that are abundant in European agricultural landscapes (Kavallieratos et al. 2004; Lumbierres et al. 2007), are respectively rarely found and not found at all to attack *M. persicae* in winter canola (Desneux et al. 2006b; Desneux N. unpublished data). Yet, *A. colemani* is able to parasitize *M. persicae* on other cruciferous plants, such as cabbage (Kalule and Wright 2004; Langhof et al. 2005) and can be reared successfully on *M. persicae* on winter canola under laboratory conditions (Storeck et al. 2000; Colinet et al. 2006).

We suggest two non-exclusive hypotheses to explain low population densities of *A. ervi* and absence of *A. colemani* in winter canola. First, these two aphidiines may be unresponsive to volatiles of the *M. persicae*–winter canola complex (MPWC). Herbivore-induced plant volatiles are detectable and reliable host location cues (Vet and Dicke 1992) that are known to be important for parasitoid foraging in many tritrophic systems. Many parasitoid species are able to distinguish odors from different plant species or even cultivars of a given species (Elzen et al. 1986; Ding et al. 1989; Vet and Dicke 1992). Second, low parasitism of *M. persicae* may result from a poor ability of *A. ervi* and *A. colemani* to attack aphids on winter canola. During vernalization, winter canola plants acclimatize to survive the dehydrative effects of cold (Kacperska 1984), e.g. through an increase in the formation of epicuticular waxes on leaves (Baker 1982; Hadley 1985). These crystalline surface waxes (waxblooms) impact insect movement (Eigenbrode and Espelie 1995) and can affect efficiency of aphid parasitoids (Chang et al. 2004; Gentry and Barbosa 2006).

We aimed to evaluate the ability of four aphid parasitoids (*A. colemani*, *A. ervi*, *A. matricariae* and *D. rapae*) to (1) orient toward odors of the *M. persicae*-infested winter canola (MWPC) in an olfactometer, and (2) to attack *M. persicae* on leaves of winter canola. However, we were unable to successfully rear *A. colemani* on *M. persicae* fed on vernalized winter canola plants and had to use parasitoids from mummified *Rhopalosiphum padi* on wheat instead. Because emergence conditioning can occur in aphid parasitoids (during contact with the mummy at the time of emergence) and this potentially affects parasitoid behavior (Douloumpaka and van Emden 2003), studies on *A. colemani* were conducted

separately and we were not able to directly compare the results of the four parasitoid species. We assessed the impact of *Brassica* plant species and vernalization (i.e. vernalized winter canola versus ‘greenhouse-grown’ winter canola plants) on the ability of *A. colemani* to attack *M. persicae*. Our objective was to provide insight on the ability of aphidiine parasitoids to attack *M. persicae* on winter canola and on the effect of plant vernalization on aphid parasitoid efficiency.

Materials and methods

Plants and insects

Winter canola (*Brassica napus*, var. Goéland) plants were grown individually in 6 cm diameter pots and kept under greenhouse conditions (22 ± 2°C and 16:8 L:D.). At the five-leaf stage, plants were transferred to cold climatic chambers for 2 months (6°C, 45% R.H. and 16:8 L:D.) for vernalization (i.e. to mimic the exposure of canola plants to cold temperatures during winter). At the end of this treatment, plants obtained large, thick and waxy leaves (epicuticular lipids are known to vary with environmental conditions, Baker 1982; Eigenbrode and Espelie 1995), typical characteristics of winter canola plants observed in the field.

All insects were reared in environmental chambers at 23°C, 55% R.H. and 16:8 L:D. *Myzus persicae* was reared on *B. napus* (var. Goéland). *Aphidius matricariae* and *D. rapae* colonies were initiated from canola field-collected individuals (124 and 167 individuals, respectively) and were reared on the *M. persicae*–winter canola complex (MPWC) for ~20 generations before experiments. Mummified *R. padi* aphids containing *A. colemani* and mummified *Sitobion avenae* aphids containing *A. ervi* were provided by Biobest (Belgium) (both aphids on wheat). *Aphidius ervi* was reared for three generations on the MPWC before experiments. We were unable to successfully rear *A. colemani* on the MPWC hence we used parasitoids directly from mummified *R. padi*. As mentioned above, *A. colemani* was therefore studied separately from the other parasitoid species. For all parasitoid species, parasitoid mummies were removed from the leaves and kept individually in Petri dishes until adult emergence.

Female parasitoids were mated within 24 h of emergence, kept individually in Petri dishes (supplied with a 80% honey solution as a food source) and used in experiments when 24–48 h old. Wasps were considered naive as they had not been in contact with plants or aphids before the experiments. Each female was used only once in an experiment.

Experiment 1: olfactometer assay

Orientation responses of *A. ervi*, *A. matricariae* and *D. rapae* toward MPWC odors were observed in a four-arm olfactometer (described by Desneux et al. 2004a; 2006a), at 25°C and 70% R.H. In brief, in this apparatus, pressurized and humidified air flows into the central chamber through four arms (200 ml/min per arm) and is extracted from the center of the chamber, so that four fields of equal area are established. The odor source consisted of two winter canola stems (kept in water) with a total of eight leaves infested by *M. persicae* (500 aphids, plants infested for 7 days before the experiment). Stems were cut just prior to the start of experiments and the odor source was placed in an air-tight glass jar (h: 25 cm; d: 11 cm). The glass jar was then connected to one arm of the olfactometer to deliver the odor into that field, whereas other fields received clean air. In a pilot experiment, naive parasitoids showed significant attraction to odors from *M. persicae*-infested canola stems, but not toward clean canola stems (Desneux N. unpublished data). A female wasp was introduced into a vial connected to the center of the olfactometer and allowed freely to enter the apparatus (~12.5 s after the introduction into the olfactometer, Desneux et al. 2006c). Observations started when the wasp entered the chamber, and lasted for a minute. This time period has been demonstrated to be sufficient to observe parasitoid attraction toward odors of aphid-infested canola plants (Desneux et al. 2004a). The position of the female was recorded and time spent in each field was determined. After every 15 observations, the olfactometer was washed with ethanol and the position of the odorized field was changed to prevent any directional bias. Thirty-one to 43 replicates were done per parasitoid species, and observations were carried out in a randomized fashion.

Friedman analysis of variance on ranks was performed for each parasitoid species to test the null hypothesis, i.e. equal time spent in each field of the olfactometer (no attraction). We also compared time spent in the odor field among parasitoid species using a generalized linear model with a log-link function (Proc Genmod, SAS).

Experiment 2: oviposition experiment

Parasitoid females of *A. ervi*, *A. matricariae* and *D. rapae* were placed individually on a 5.3 cm dia. winter canola leaf disc (placed on sand + water in a Petri dish), with 100 *M. persicae* of mixed instars. Observations were done using a stereomicroscope. For 5 min, we recorded the frequency of the following behaviors: ‘antennal contact’ (contact with the aphid by at least one parasitoid antenna), ‘antennal palpation’ (antennal drumming of the aphid by the parasitoid), ‘failed sting’ (when the ovipositor was extruded next to an aphid or into an aphid exuvia) and

‘successful sting’ (ovipositor insertion into an aphid) (Wyckhuys et al. 2008; Desneux et al. 2009a). Parasitoid activity was further categorized as time spent ‘grooming’ (parasitoids rubbing their legs together or using their tarsi to remove wax from their bodies) and time spent ‘foraging’ (i.e. walking and attacking aphids). Pilot experiments showed that *Brassica* cuticular wax can accumulate on parasitoid legs when foraging on winter canola leaves, and that wax pellets can appear on parasitoid legs upon grooming (Desneux N. personal obs.). Therefore, we also noted the occurrence of wax pellets on parasitoid legs. For each parasitoid species, we observed 19–30 females, with each female tested on a new *M. persicae*-infested winter canola leaf disc.

We compared behaviors among parasitoid species using ANOVA followed by a Tukey’s post hoc test for multiple comparisons. Percentages of time spent ‘grooming’ and percentages of ‘failed sting’ were square root-transformed prior to analysis. Finally, we compared wax pellet occurrence on parasitoid legs using pairwise Fisher’s exact tests (Dunn–Sidak adjustment for multiple comparisons, adjusted $\alpha = 0.0169$).

Experiment 3: impact of canola vernalization on *A. colemani* performance

In a third series of experiments, we assessed how *Brassica* plant species and plant growing conditions can affect the ability of *A. colemani* to attack *M. persicae*. First, we tested attraction of *A. colemani* toward odors of *M. persicae*-infested (1) winter canola (vernalized *B. napus*) plants, (2) ‘greenhouse-canola’ plants (winter canola that was grown in a greenhouse without vernalization), and (3) cabbage (*B. oleracea*) plants (20, 21 and 20 replicates respectively). Parasitoid attraction to volatiles was determined in a four-arm olfactometer (as described in Exp. 1). Second, oviposition behavior of *A. colemani* was studied on these three host–plant complexes (15 replicates per group). Protocols and statistical analyses were as described above.

Results

Experiment 1: olfactometer assay

The parasitoids *A. ervi*, *A. matricariae* and *D. rapae* showed significant attraction to odors of *M. persicae*-infested winter canola plants (Fig. 1; Friedman statistics: $\chi^2_3 = 8.740$, $P = 0.033$; $\chi^2_3 = 56.083$, $P < 0.001$; $\chi^2_3 = 35.244$, $P < 0.001$, respectively). Time spent in the odor field differed among parasitoid species (Fig. 1; GLM: $\chi^2_2 = 12.717$, $P < 0.001$) with *A. matricariae* and *D. rapae* females spending significantly greater amounts of time in this field than *A. ervi*.

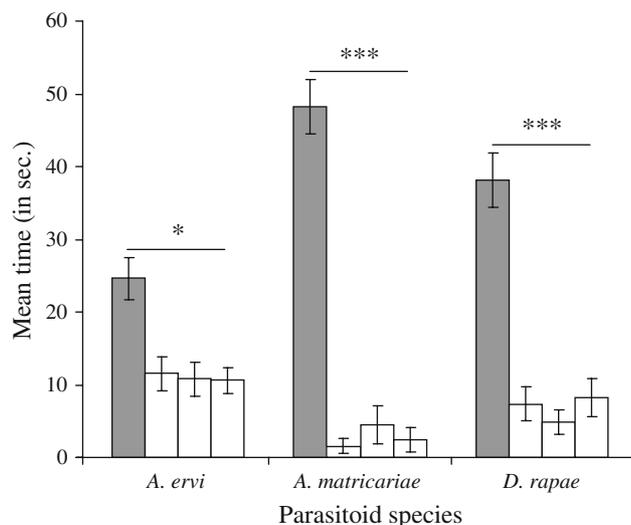


Fig. 1 Mean time (\pm SE) spent *A. ervi*, *A. matricariae* and *D. rapae* in the odor (odors of *Myzus persicae*-infested winter canola) (gray) and in three control (white bars) fields of the four-arm olfactometer. Horizontal lines indicate results of Friedman statistics (n.s. not significant; * $P < 0.05$, *** $P < 0.001$)

Experiment 2: oviposition experiment

The three parasitoid species did not differ in frequency of ‘antennal contact’ and ‘antennal palpation’, although *A. ervi* showed these two behaviors more often than *A. matricariae* and *D. rapae* (Table 1). *Aphidius matricariae* and *D. rapae* stung significantly more aphids than *A. ervi*, which showed the highest frequency of ‘failed sting’. *Aphidius ervi* and *A. matricariae* spent up to a third of their time grooming (36.1 and 32.3%, respectively), and this behavior was primarily observed following aphid attack. In contrast, *D. rapae* spent significantly less time grooming (<20%) than the two other species. Finally,

almost half (43%) of *A. ervi* females had wax pellets on their legs after grooming. The occurrence of these wax pellets tended to be lower for *A. matricariae* and was significantly lower for *D. rapae* (pairwise Fisher’s exact tests, all $P < \alpha$).

Experiment 3: impact of canola vernalization on *A. colemani* performance

Aphidius colemani did not orient significantly toward MPWC odors (Fig. 2; Friedman statistics: $\chi^2_3 = 1.839$, $P = 0.606$), while orientation toward *M. persicae*-infested ‘greenhouse-canola’ odors was marginally significant ($\chi^2_3 = 6.503$, $P = 0.090$). Odors from *M. persicae*-infested cabbage were attractive for *A. colemani* ($\chi^2_3 = 9.173$, $P = 0.027$). Time spent in the odor field differed significantly among host–plant complexes (Fig. 2; GLM: $\chi^2_2 = 7.720$, $P = 0.021$).

Host plants significantly affected *A. colemani* oviposition behavior on *M. persicae*, with parasitoids performing better on cabbage and ‘greenhouse-canola’ than on winter canola (Table 2). *Aphidius colemani* exhibited significantly fewer ‘successful sting’ and higher percentage of ‘failed sting’ when foraging on winter canola than on the other host plants. On winter canola, *A. colemani* spent 62.6% of time grooming, which was significantly higher than when foraging on the other host plant treatments, and the majority (87%) of the parasitoids on winter canola had wax pellets on their legs after grooming compared with 47 and 20% on the other treatments.

Discussion

Parasitoids go through a series of behavioral responses to parasitize their hosts: (1) host habitat finding, (2) host finding,

Table 1 Mean number (\pm SE) of parasitoid behaviors observed during the 5-min observation period

	Antennal contact ^a	Antennal palpation ^a	Successful sting ^a	Failed sting ^a	Percentage of failed sting/total sting ^b	Percentage of time spent ‘grooming’ ^b	Prop. of parasitoids with wax pellets ^c
<i>A. ervi</i>	8.97 \pm 1.15 a	14.07 \pm 1.28 a	6.30 \pm 0.57 b	24.27 \pm 1.86 a	80.0 \pm 1.3 a	36.1 \pm 2.9 a	0.43 a
<i>A. matricariae</i>	6.38 \pm 0.71 a	10.31 \pm 1.13 a	10.48 \pm 0.95 a	14.07 \pm 1.11 b	58.2 \pm 2.3 b	32.3 \pm 3.7 a	0.17 ab
<i>D. rapae</i>	6.42 \pm 1.14 a	11.26 \pm 1.57 a	8.05 \pm 1.22 a	14.74 \pm 1.93 b	65.7 \pm 3.0 b	17.5 \pm 5.1 b	0.05 b
Statistics	$F_{2,75} = 2.30$ $P = 0.108$	$F_{2,75} = 2.50$ $P = 0.089$	$F_{2,75} = 13.02$ $P < 0.001$	$F_{2,75} = 6.39$ $P = 0.003$	$F_{2,75} = 30.12$ $P < 0.001$	$F_{2,75} = 9.28$ $P < 0.001$	

The percentages of failed sting on total stings, mean percentages of time spent as ‘grooming’, and proportions of individuals with wax pellets are also reported

The different letters indicate significant differences among parasitoid species (at $P < 0.05$ or adjusted α for pairwise Fisher’s exact tests)

^a ANOVA followed by Tukey’s post hoc test

^b ANOVA (on squared root transformed data) followed by Tukey’s post hoc test

^c Pairwise Fisher’s exact tests (with Dunn–Sidak adjustment for multiple comparisons, $\alpha = 0.0169$)

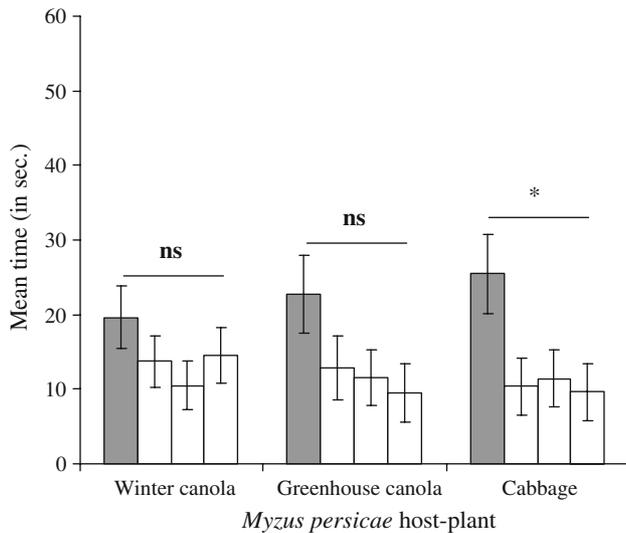


Fig. 2 Mean time (\pm SE) spent by *A. colemani* in the odor (gray) and in three control (white bars) fields of the four-arm olfactometer when tested for attraction to odors of *Myzus persicae*-infested (1) vernalized winter canola (*B. napus*), (2) ‘greenhouse-canola’, and (3) cabbage (*B. oleracea*) plants. Horizontal lines indicate results of Friedman statistics (n.s. not significant; * $P < 0.05$)

and (3) host acceptance and oviposition (Vinson 1984). Our results show that various parasitoid species differ in their performance in locating and attacking *M. persicae* on winter canola. *Aphidius matricariae* and *D. rapae* readily locate and attack the aphid on winter canola. Whereas *A. ervi* attacks *M. persicae* on winter canola to some extent, *A. colemani* shows low ability to parasitize the aphids on that plant (i.e. low attraction toward MPWC odors and low ability to attack it). However, an impact of pre-emergence conditioning (on *R. padi*—wheat) in the case of *A. colemani*

could not be completely ruled out as the tested wasps were not reared previously on the MPWC. Nevertheless, our results clearly show that *A. colemani* from *R. padi* on wheat can locate and attack *M. persicae* on other *Brassica* plants (cabbage) (i.e. without pre-emergence or emergence experiences on that aphid–plant complex), and that vernalization of canola plants reduces this parasitoid’s ability to attack *M. persicae* on canola. Plant characteristics, especially *Brassica*’s waxblooms, reduce parasitoid mobility and impact foraging behavior on the leaves.

Many aphid parasitoids respond weakly to plant and aphid odors alone (Guerrieri et al. 1993; Reed et al. 1995; Wyckhuys and Heimpel 2007), but use synomones to locate aphid-infested plants (Du et al. 1998; Battaglia et al. 2000). MPWC odors were attractive to variable degree to *D. rapae*, *A. matricariae* and *A. ervi*. Differences in degree of attraction may result from varying responsiveness among the parasitoid species to the MPWC odor blend. *Diaeretiella rapae* is attracted by characteristic odors from aphid-infested cruciferous plants (i.e. allylisothiocyanate) (Reed et al. 1995). *Aphidius matricariae* attacks aphids on a wide range of host plant species, and is a particularly important natural enemy of *M. persicae* (Schlinger and Mackauer 1963), which is consistent with its response toward *M. persicae*-related odors. *Aphidius ervi* showed the weakest response toward MPWC odors. This parasitoid does not commonly attack *M. persicae* and does not occur widely in cruciferous crops, but rather occurs in wheat crops (Kröber and Carl 1991; Lumbierres et al. 2007). Thus, it might be more responsive to characteristic odors associated with cereal plants (Wickremasinghe and van Emden 1992). However, *A. ervi* has previously been reported preferring odors of the host–plant complex on

Table 2 Mean number (\pm SE) of parasitoid behaviors observed during the 5-min observation period for *A. colemani* foraging on *Myzus persicae*-infested (1) winter canola (vernalized *B. napus*, var. Goéland), (2) greenhouse-canola, and (3) cabbage (*B. oleracea*) leaves

	Antennal contact ^a	Antennal palpation ^a	Successful sting ^a	Failed sting ^a	Percentage of failed sting/total sting ^b	Percentage of time spent ‘grooming’ ^b	Prop. of parasitoids with wax pellets ^c
<i>M. persicae</i> / winter canola	5.07 \pm 0.78 a	4.73 \pm 0.76 a	1.73 \pm 0.30 a	7.07 \pm 0.30 a	80.9 \pm 2.6 a	62.6 \pm 4.0 a	0.87 a
<i>M. persicae</i> / greenhouse canola	6.07 \pm 0.68 a	7.87 \pm 0.92 b	4.53 \pm 0.45 b	9.67 \pm 1.32 a	65.2 \pm 3.0 b	41.6 \pm 4.8 b	0.47 ab
<i>M. persicae</i> / cabbage	6.53 \pm 0.58 a	10.07 \pm 0.97 b	7.07 \pm 0.85 c	10.73 \pm 1.46 a	60.4 \pm 2.3 b	40.3 \pm 3.9 b	0.20 b
Statistics	$F_{2,42} = 1.19$ $P = 0.312$	$F_{2,42} = 9.13$ $P = 0.001$	$F_{2,42} = 20.99$ $P < 0.001$	$F_{2,42} = 2.16$ $P = 0.127$	$F_{2,42} = 16.31$ $P < 0.001$	$F_{2,42} = 58.21$ $P < 0.001$	

The percentages of failed sting on total stings, mean percentages of time spent as ‘grooming’, and proportions of individuals exhibiting wax pellets are also reported

The different letters indicate significant differences among the groups (at $P < 0.05$ or adjusted α for Pairwise Fisher’s exact tests)

^a ANOVA followed by Tukey’s post hoc test

^b ANOVA (on squared root transformed data) followed by Tukey’s post hoc test

^c Pairwise Fisher’s exact tests (with Dunn–Sidak adjustment for multiple comparisons, $\alpha = 0.0169$)

which it was reared (Daza-Bustamante et al. 2002), which was the MPWC in our study. The weak response to *M. persicae*-induced canola odors and relatively high percentage of failed attacks therefore suggests that *A. ervi* may not be used successfully for biological control against *M. persicae* in canola fields.

Aphidius colemani was not attracted by MPWC volatiles, which could explain its lack of parasitism of *M. persicae* in winter canola fields. As *A. colemani* was not reared on the MPWC complex prior to the experiment, this may have limited its responsiveness to host–plant complex-related odors as well as behavioral responses to *M. persicae*. Such differences in behavior could be ascribed to pre-emergence conditioning (Dukas 2008) but we deem it unlikely because *A. colemani* was attracted to odors of *M. persicae*-infested cabbage (Fig. 2) without previous pre-emergence conditioning on that host–plant complex. Its lack of attraction to MPWC odors is surprising, as this parasitoid has been reared on *M. persicae* on winter canola varieties in other studies (Storeck et al. 2000; Colinet et al. 2006). Also, other parasitoid species such as *A. ervi* showed significant attraction to MPWC odors even when reared on a different host–plant complex (*S. avenae* on wheat, i.e. when used directly from the biocontrol company, Desneux et al. 2006a). Even though *Aphidius colemani* exhibits high levels of specificity to certain host–plant complexes or habitats under natural conditions, it can switch from *R. padi* on barley to *M. persicae* on radish to some extent in laboratory conditions (Ode et al. 2005). As we were unable to rear *A. colemani* on the MPWC, it may be likely that the tested population is unable to switch to that host–plant complex. In addition, the degree of attraction of parasitoids to a certain host–plant complex-related odor blend can depend on plant variety (Kalule and Wright 2004; Elzen et al. 1986; Vet and Dicke 1992). In our study, differences in attraction of *A. colemani* to MPWC odors hint at the effects of plant growing conditions (like vernalization).

Upon landing on an aphid-infested plant, the number of hosts encountered and parasitized likely depends on the parasitoid mobility and on its capacity to detect available hosts (Mackauer et al. 1996). Overall, *A. colemani* on vernalized winter canola exhibited few behavioral responses, was less efficient when foraging, and spent more than 60% of its time ‘grooming’. Thus, *A. colemani* appeared to be less mobile on winter canola than the other parasitoid species because of vernalization-induced waxblooms (i.e. increase in epicuticular waxes on the leaves, Kacperska 1984; Hadley 1985). The presence of wax pellets on parasitoid legs likely reflects the inability of certain parasitoids to prevent wax accumulation when foraging on winter canola. *Diaeretiella rapae* is a specialist natural enemy of *Brassica*-feeding aphids (Gabrys et al. 1998; Desneux et al. 2005) and may have adaptations to deal with waxblooms.

The percentage of time spent grooming may reflect how fast wax accumulates on parasitoid legs and thus indirectly the degree of adaptation to forage on waxy *Brassica* leaves. *Aphidius ervi* and to a lesser extent, *A. matricariae*, indeed spent more time grooming than *D. rapae*.

Host detection and recognition rely on multiple sensory cues (Battaglia et al. 2000; Powell et al. 1998). Upon host encounter, effective detection of the host (e.g. aphid) occurs when ‘antennal palpation’ follows ‘antennal contact’ (Desneux et al. 2004b) and is based on the physical and chemical cues acting at short range or by contact (Battaglia et al. 2000). In our experiment, frequencies of ‘antennal palpation’ were always equal to or higher than frequencies of ‘antennal contact’, indicating that parasitoids easily detected *M. persicae*. Thus, despite the lack of attraction of *A. colemani* toward MPWC odors, this parasitoid effectively detects *M. persicae* proximal chemical cues, which is consistent with its acceptance and attack of *M. persicae* on other plant species (Messing and Rabasse 1995; Kalule and Wright 2004).

Overall, oviposition success differed among parasitoid species (Table 1) and among host–plant complex in case of *A. colemani* (Table 2). *Myzus persicae* is known to exhibit few defensive behaviors (Desneux et al. 2009b), thus failed attacks may result from parasitoids being hampered by *Brassica* wax to bring into a position that allows effective oviposition (see also Hare 1992; Inbar and Gerling 2008). The high percentage of failed attacks of *A. ervi* is consistent with its specialization on cereal aphids (Kröber and Carl 1991). Also, the comparatively low degree of attack by *A. colemani* of *M. persicae* on winter canola versus ‘greenhouse-canola’ or cabbage (Table 2) likely results from the wax characteristics of winter canola. Successful rearing of *A. colemani* on *M. persicae* on winter canola under laboratory conditions (Storeck et al. 2000; Colinet et al. 2006) might have resulted from a different canola variety (Kalule and Wright 2002, 2004), but more likely a result of plant growing conditions. In these studies, winter canola plants were grown under greenhouse conditions, and thus were not vernalized prior to rearing and experiments. We showed that growing conditions of winter canola affect *A. colemani* ovipositional success (Table 2). Plant growing conditions are of primary importance, as insect population growth could be reduced on waxy versus glossy *Brassica* sp. only on field-grown or water-stressed plants grown in greenhouse, but not when plants are grown in regular greenhouse conditions (Cole and Riggall 1992; Lamb et al. 1993).

Identification of *D. rapae* and *A. matricariae* as parasitoids of *M. persicae* on winter canola is of primary importance to successful initiation of pest management programs that aim to utilize conservation biological control instead of pesticides and thus help prevent negative side effects on beneficial arthropods (Desneux et al. 2007). Our study

shows that *A. colemani* and *A. ervi* are unlikely to be successful biological control agents against *M. persicae* in winter canola fields. This suggests that the strains of these two parasitoid species reared by European biocontrol companies are not adapted to attack aphids on winter canola (the waxes that accumulate on winter canola reduce parasitoid's foraging success). Our work shows that parasitoid ability to attack a given host species varies among parasitoid species according to parasitoid capacity to cope with plant characteristics mediated by growing conditions.

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