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Root and shoot jasmonic acid induction differently affects the foraging behavior of *Cotesia glomerata* under semi-field conditions

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Abstract Plants can accumulate and release defensive chemicals by activating various signaling pathways when they are damaged by herbivores or pathogens. The jasmonic acid pathway is activated after damage by chewing herbivores. Here we used jasmonic acid (JA) as an exogenous elicitor to induce feral cabbage plants. In this study, the effects of root JA (RJA) and shoot JA (SJA) induction on the foraging behavior of *Cotesia glomerata*, a parasitoid of the large cabbage white butterfly *Pieris brassicae*, was investigated under semi-field conditions. In all combinations of differently induced plants (RJA, SJA and control plants), the percentages of shoot induced plants that were visited by at least one wasp were significantly higher than those of controls or root induced plants during 3 h of foraging. Consequently, parasitism rates of *P. brassicae* on shoot-JA induced plants were significantly higher than on plants induced with JA to the roots or control plants in all tests. However, this behavioral preference was not reflected in the allocation of offspring. The clutch sizes of *C. glomerata* eggs on control, root induced and shoot induced plants were not significantly different from each other in two-choice or three-choice experiments, but did differ with clutch size in the two-choice experiment of uninduced control plants versus SJA. This semi-field study helps to further understand the choice behavior and preferences of parasitoids in natural multitrophic communities in which plants induced with root or shoot herbivores occur together.

Keywords *Cotesia glomerata* · Jasmonic acid · Plant preference · Root- and shoot induction · Tritrophic interactions

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Introduction

Plants have evolved intricate direct and indirect defense systems during the course of their coevolution with herbivorous insects and pathogens (Turlings et al. 1995; Dicke and van Loon 2000). Indirect defenses, for instance, may consist of volatiles emitted by plants in response to damage from arthropod pests. These volatiles do not directly influence the performance of the herbivore but can serve as long-distance cues attracting parasitoids of the pests (Vet and Dicke 1992; Dicke 1999; Hilker and Meiners 2002). The emission of herbivore-induced plant volatiles (HIPV) is a general phenomenon. It has been demonstrated in many different plant species, and parasitic wasps, predatory insects and mites have been shown to use HIPV to locate their hosts or prey (Vet and Dicke 1992; Lou and Cheng 2003; Lou et al. 2005a, b). Most of the work on HIPV and their ecological roles have been performed on leaf herbivores and their aboveground natural enemies. However, belowground herbivores may also elicit HIPVs that attract specific natural enemies (Neveu et al. 2002, Ferry et al. 2007; Soler et al. 2007a, b). Interestingly, it was found that feeding activities of root herbivore *Delia radicum* on *Brassica nigra* may affect the plant preference in *C. glomerata*, an endoparasitoid of the leaf chewing herbivore *Pieris brassicae*, mediated by changes in plant volatiles (Soler et al. 2007a). This suggests that aboveground parasitoids are able to discriminate between aboveground and belowground induced plants.

Studies on the production of HIPV have demonstrated the role of herbivore-specific elicitors (Mattiacci et al. 1995; Alborn et al. 1997; Halitschke et al. 2001). These elicitors can activate various signaling pathways in the plant, resulting in the accumulation and release of specific HIPV bouquets by up-regulating a wide array of defense-related genes (Kessler and Baldwin 2002). Among the signaling pathways that can be activated by herbivores, the jasmonic acid (JA) pathway is the best studied. JA is a natural plant hormone that has been reported to play an important role in the induction of direct and indirect plant defenses after damage by chewing herbivores (Hopke et al. 1994; Dicke et al. 1999; Schmelz et al. 2003), especially for the induction of HIPV serving as cues for parasitoids and predators (Thaler et al. 2001; Moore et al. 2003). For example, exogenous application of JA or methyl-JA to tobacco and tomato plants increased the parasitism or predation rates of the herbivores in natural and agricultural fields (Kessler and Baldwin 2001; Thaler et al. 2001). In Lima bean plants, chemical and behavioral analyses have demonstrated that spider mite damage and JA treatment have similar, although not identical, effects on volatile induction (Dicke et al. 1999). Recently, JA has been used to mimic the induction by herbivores in above- and belowground multitrophic interaction studies (Qiu et al. 2009; van Dam et al. 2010). For studies analyzing the differences between root and shoot induction, the additional advantage of using JA is that the induction treatment is qualitatively and quantitatively more comparable for both organs than inductions with different species of real root and shoot herbivores (van Dam and Oomen 2008).

The effects of JA-induced responses on the development of herbivores and their parasitoids have been investigated in the laboratory (van Dam and Oomen 2008; Qiu et al. 2009). For example, when the large cabbage white butterfly *Pieris brassicae* (Lepidoptera: Pieridae) and its parasitoid *Cotesia glomerata* (Hymenoptera: Ichneumonidae) are tested in a JA shoot and root induction system with *Brassica oleracea* as the host plant, both the herbivore and wasp developed much slower on shoot JA (SJA) induced plants than on root JA (RJA) induced or uninduced control plants (CON). Moreover, the mass of *C. glomerata* offspring that developed in *P. brassicae* on SJA plants was significantly less than from those developed from RJA and control plants (Qiu et al. 2009). Interestingly, choice experiments conducted in the greenhouse showed that shoot-induced plants were significantly preferred over RJA or control plants. This was closely correlated with the elevated production of mono-, sesqui- and homoterpenes in SJA plants, whereas in root JA plants only monoterpene levels were induced (van Dam et al. 2010). Under natural field conditions, however, these terpenes may rapidly degrade under the influence of ozone and sunlight (Holopainen 2004). Thus, it remains questionable whether the observed preference in the lab will also be shown in the field. Therefore, we also studied the attraction of JA induced plant volatiles to the parasitic wasp *C. glomerata*, a parasitoid of foliar herbivore *P. brassicae*, under semi-field conditions. In addition, we also analyzed the effect on the oviposition decisions of the wasps in terms of egg clutch size. Even if the wasps are very much attracted to shoot induced plants which support lower quality hosts (Qiu et al. 2009) they may decide to allocate fewer eggs under these conditions. So far, few studies have explored the influence of these JA induced volatiles on the foraging behavior and oviposition decisions of hymenopteran parasitoids in field or semi-field conditions (Thaler 1999). This lack of knowledge limits the potential to apply JA and related jasmonates as elicitors of volatiles that can enhance the efficiency of biocontrol agents in cropping systems (Powell and Pickett 2003).

Materials and methods

Plants and insects

The plant species used in this study was a feral strain of *Brassica oleracea*. Seeds of *B. oleracea* were initially collected from a road side population near Heteren, The Netherlands in 2000. A subset of these seeds were used to grow ten plants at NIOO-KNAW in Heteren for seed production in 2004. The latter seeds were sown in 1.3 l plastic pots containing soil-sand mixture (30% sand, 5% clay and 65% peat, Potgrond 4, Lentse Potgrond B.V., Lent, NL) in a greenhouse at 21°C (day) and 16°C (night), R.H. 60%, and plants were watered as needed. Natural daylight was supplemented with sodium lamps to maintain the minimum PAR (photosynthetically active radiation) at 225 μmol m^{-1} s^{-1} with a photoperiod of 16:8 (L:D).

P. brassicae second instar larvae were obtained from an insect culture maintained at the Laboratory of Entomology, Wageningen University, The Netherlands, where it is reared on *B. oleracea* (Brussels sprouts cv. Cyrus) plants. *C. glomerata* was obtained from cultures maintained at the Netherlands Institute of Ecology, Heteren, The Netherlands.

Plant JA induction

B. oleracea plants were used for experiments at four weeks of age when they had five to six fully expanded leaves. Plants were assigned to three treatment groups as described in van Dam and Oomen (2008), i.e., control (CON), root JA application (RJA) and shoot JA application (SJA). Here we used 500 µg JA (Sigma, St Louis, MO, USA) per plant to induce the test plants to mimic the response to chewing root and shoot herbivores. In the RJA group, 500 µg JA per plant was applied in 10 ml 0.1% Triton and 0.5% EtOH in demineralized water (pH 4.0) by injecting the solution in the soil near the root-shoot interface. SJA plants were treated by gently rubbing 0.25 ml of a 2.0 mg ml^{-1} JA solution in 0.1% Triton and 0.5% EtOH (pH 3.3) in water on the oldest two leaves. Plants in the control group received similar amounts of 0.1% Triton and 0.5% EtOH in acid water (pH 3.7 with HCl) on both roots and shoots. After JA application, each plant was supplied with 50 ml nutrient solution (0.5 Hoagland solution). When 500 µg JA is applied to these *B. oleracea* plants, the level of secondary compounds (e.g. glucosinolates) significantly increased in *B. oleracea* 3–14 days after induction (van Dam et al. 2004; van Dam and Oomen 2008) whereas volatile emissions increase within 2–3 days (van Dam et al. 2010).

Experimental set-up

Experiments were performed outdoors (July 2008) in a semi-transparent tent (8 × 4 × 2.5 m) covered with fine-meshed nylon gauze (70 mesh). We considered the tents as semi-filed conditions, as most of the conditions (temperature, humidity, as well as photoperiod) are the same as those in the field, except light quality and the search range of the wasps. In the two-choice experiments (CON vs. RJA, CON vs. SJA, RJA vs. SJA), 12 plants from two treatments (six for each treatment) were alternately placed in the tents (Fig. 1a). In the three-choice experiments, 12 plants from three treatments (four for each treatment) were placed in the tent as depicted in Fig. 1b. The distance between two plants was approximately 0.8 m. All the plants were of similar height and shape to avoid any potential effects of plant morphological characteristics on parasitoid behavior.

Three days before the choice experiments, plants were induced by JA (as described above) in a greenhouse at 21°C (day) and 16°C (night), R.H. 60%, with a photoperiod of 16:8 (L:D). On the day of the experiment, the SJA, RJA and CON plants were moved to the test tents, and ten second instar larvae of *P. brassicae* were placed on the two untreated leaves of all plant (SJA, RJA and CON plants) at 8:00 am. They were allowed to feed on the plants for at least 3 h. From 11:00 am onwards the plants with the caterpillars were used for testing parasitoid preference. The experiments were repeated five times within five days and on each day the SJA, RJA and CON plants were tested simultaneously with new plants.

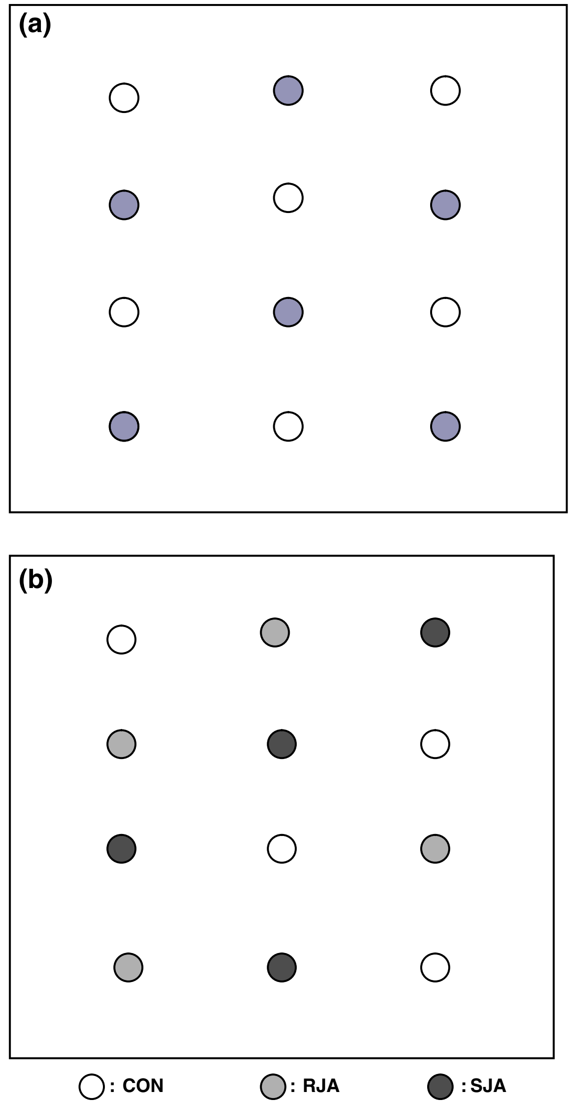

Fig. 1 Scheme of the two-choice experiment. **a** circles with a different color represent two of the three differently treated plants (RJA, SJA and CON); **b** circles with different colors represent the three differently treated plants (RJA, SJA and CON)

Parasitoid preference and oviposition decisions in semi-field tests

Parasitoid preference was investigated using experienced *C. glomerata*. To obtain experienced *C. glomerata*, a 3–6 days old female wasp was offered a neonate *P. brassicae* larva on a fine paint brush for an oviposition experience and then kept separate in a small plastic Petri dish until the experiment started. Two kinds of choice experiments were investigated in the current study: the first consisted of two-choice experiments (RJA-SJA, SJA-CON, and RJA-CON), and the second consisted of three-choice (SJA-RJA-CON) experiments, so parasitoids could select the preferred plants when two or three different treated plants were offered. At the start of the experiment, ten experienced *C. glomerata* females were released in the middle of a tent, 2 m above the ground. The wasps were allowed to forage freely during 3 h and were then recaptured. Subsequently, *P. brassicae* larvae were collected from the plants, and dissected to determine the number of parasitized and unparasitized larvae per plant. Based on these counts, we calculated (i) the percentage of RJA, SJA and CON plants selected by at least one parasitoid female among the 12 plants in total, (ii) the percentage of parasitized caterpillars on each plant among the ten larvae in total and (iii) the clutch sizes of eggs, i.e., the mean number of parasitioid eggs in each *P. brassicae* larva. Clutch sizes in *C. glomerata* were determined by counting the number of parasitoid eggs under a stereo-microscope. Briefly, five caterpillars were randomly selected and the wasp eggs in their body were determined in each replicate of SJA, RJA and CON treatments, and, as above, five replicates were performed.

Statistical analysis

For the statistical analyses we used Statistica 8.0 software (Statsoft Inc., Tulsa, OK, USA). The percentage of host plants that were visited by the wasps, and percentage parasitism in each treatment were analyzed with non-parametric Kruskal-Wallis ANOVA (Tukey unequal N HSD). The number of parasitioid eggs per host larva on the different plant treatments in each experiment was analyzed using two-way ANOVA (repeat × treatment) with SAS 8.2 software (SAS Institute, Cary, NC, USA). Means were separated using the Student–Newman–Keuls multiple range test at a significance level of $\alpha = 0.05$.

Results

Plant preference of *C. glomerata*

When experienced *C. glomerata* wasps were initially released into the tents, all of them showed intensive searching behavior and high responsiveness. In the choices between CON versus SJA, RJA versus SJA and CON versus RJA versus SJA, the percentages of SJA plants that were visited by at least one wasp were 66.7, 56.7 and 80.0%, respectively, which were significantly higher than those of CON or RJA plants during the 3 h foraging (Fig. 2a, $F_{1,8} = 12.07$, $P = 0.0084$; Fig. 2c, $F_{1,8} = 33.33$, $P = 0.0004$ and Fig. 2d, $F_{2,12} = 13.29$, $P = 0.0009$). In the RJA versus CON experiment, on average more RJA than CON plants were chosen by the *C. glomerata* wasps, but the difference was not statistically significant (43.3% vs. 56.7%, Fig. 2b, $F_{1,8} = 1.03$, $P = 0.3394$).

Parasitism rates of *P. brassicae* on different plants

Dissection of the ten second instar *P. brassicae* larvae per plant showed that the percentage parasitism of *P. brassicae* on CON, RJA and SJA plants was different (Fig. 3). In both two-choice experiments (CON vs. SJA, RJA vs. SJA) and the three-choice experiment, parasitism rates of *P. brassicae* on SJA plants were similar, 55.2, 57.0 and 57.5%, respectively, and these rates were all significantly higher than those observed on CON and RJA plants (Fig. 3a, $F_{1,8} = 17.15$, $P = 0.0033$; Fig. 3c, $F_{1,8} = 17.80$, $P = 0.0029$; Fig. 3d, $F_{2,12} = 16.47$, $P = 0.0124$). While in the CON versus RJA test, the parasitism

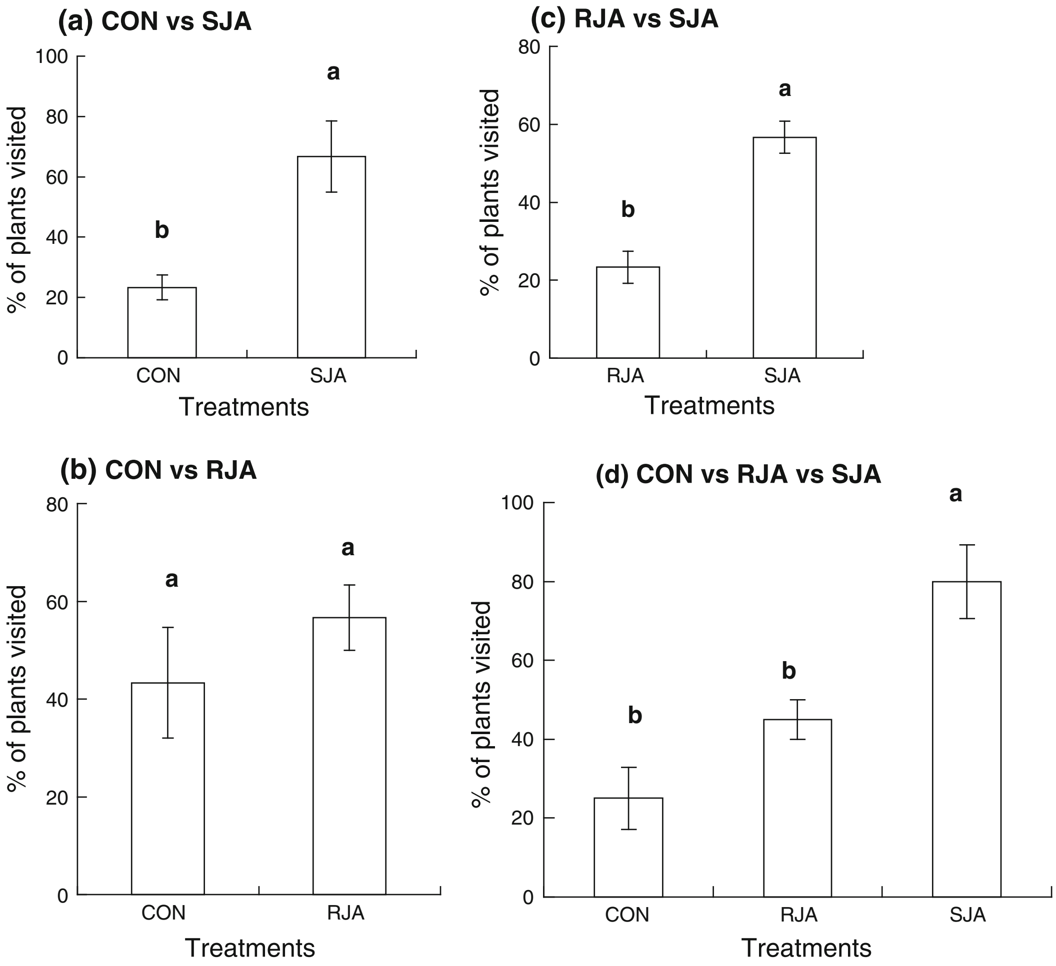

Fig. 2 Average (±SE) percentage of plants visited by parasitoids in different choice experiments **a** CON vs. SJA, $F_{1,8} = 12.07$, $P = 0.0084$; **b** CON vs. RJA, $F_{1,8} = 1.03$, $P = 0.3394$; **c** RJA vs. SJA, $F_{1,8} = 33.33$, $P = 0.0004$; **d** CON vs. RJA vs. SJA, $F_{2,12} = 13.29$, $P = 0.0009$

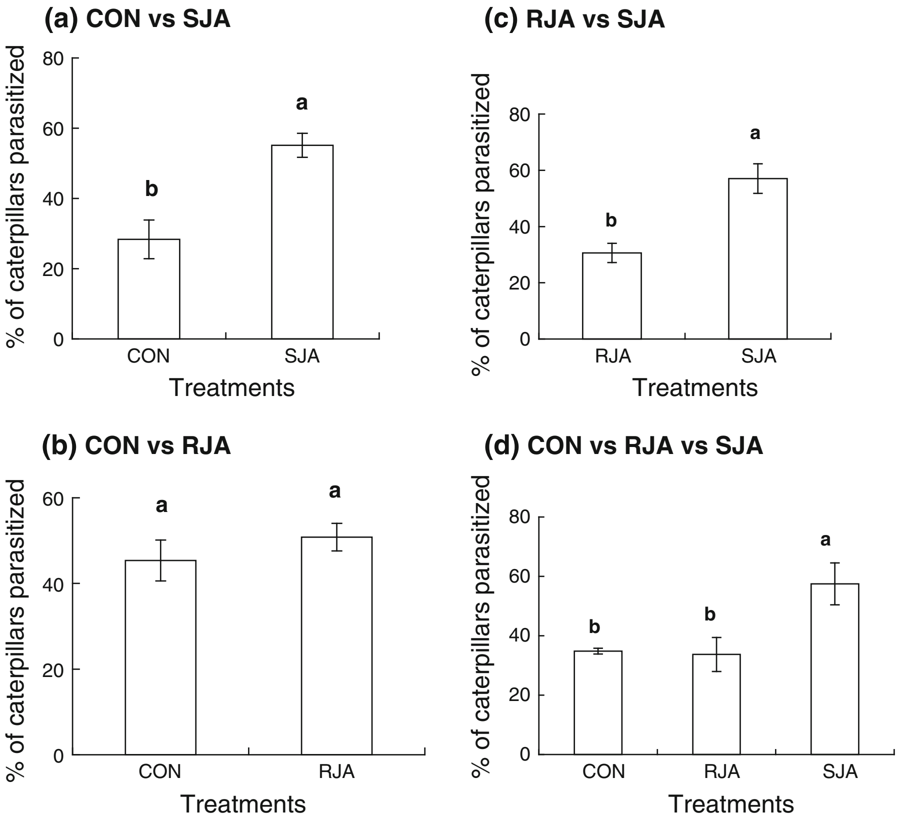

Fig. 3 Average (±SE) parasitism of *P. brassicae* larvae in different choice experiments **a** CON vs. SJA, $F_{1,8} = 17.15$, $P = 0.0033$; **b** CON vs. RJA, $F_{1,8} = 0.9016$, $P = 0.3702$; **c** RJA vs. SJA, $F_{1,8} = 17.80$, $P = 0.0029$; **d** CON vs. RJA vs. SJA, $F_{2,12} = 16.47$, $P = 0.0124$

rates were 45.4% and 50.8% on CON and RJA plants, respectively, which were not significantly different from each other (Fig. 3b, $F_{1,8} = 0.9016$, $P = 0.3702$).

Clutch sizes of *C. glomerata* on different plants

C. glomerata females laid a mean of 36.4 eggs per host. The egg clutches laid by *C. glomerata* in *P. brassicae* larvae on the differently treated plants were not significantly different to each other in the two-choice of CON versus RJA, RJA versus SJA, nor in the three-choice experiment of CON versus RJA versus SJA (Table 1). However, significant differences were found in the clutch sizes of *C. glomerata* eggs in *P. brassicae* larvae on SJA plants compared with those on CON plants ($F_{1,40} = 4.52$, $P = 0.0398$).

Discussion

The results of this study showed that the location of JA induction can influence the preference and oviposition behavior of an aboveground parasitoid also under semi-field conditions. In greenhouse experiments with the same species, we found significant differences in the induced volatile blends emitted by the plants (van Dam et al. 2010). In the current study, *C. glomerata* females also exhibited a similarly clear preference for SJA plants over RJA and CON plants under semi-field conditions as observed earlier in a flight-cage experiment under greenhouse conditions (Qiu et al. 2009; van Dam et al. 2010). Other than in the greenhouse (van Dam et al. 2010), the wasps in the field cages did not show a clear preference for RJA plants when they were next to control plants. However, Soler et al. (2007a) reported that, both in flight-cage and semi-field experiments with root-damaged

Table 1 Average egg clutch sizes (±SE) laid by *C. glomerata* in *P. brassicae* larvae feeding on differently treated plants

Plants	CON versus RJA	CON versus SJA	RJA versus SJA	CON versus RJA versus SJA
CON	36.48 ± 3.27	32.60 ± 2.08	–	35.52 ± 2.62
RJA	42.88 ± 3.54	–	30.64 ± 2.25	36.04 ± 3.12
SJA	–	39.68 ± 2.82	32.68 ± 2.99	39.36 ± 4.13
F	1.77	4.52	0.27	0.41
df	1, 40	1, 40	1, 40	2, 60
P	0.1903	0.0398	0.6077	0.6680

and root-undamaged *Brassica nigra* (black mustard) plants, *C. glomerata* females were found to prefer plants without root induction. Even though it has been shown that root herbivore feeding may involve the induction of JA synthesis (Erb et al. 2009), the additional mechanical damage and the contact with regurgitant or microbes from the herbivore cannot be fully mimicked by JA application. This may explain the observed differences in volatile blends induced by JA or real herbivores. In a confined setting like the one that was used in this experiment, it is possible that all the plants in a test can be visited and every host can be parasitized if the experimental duration is prolonged beyond a certain temporal threshold (Soler et al. 2007a). In the present study, the rate of parasitism of *P. brassicae* on SJA plants was remarkably higher than those on CON and RJA plants in the time allowed for foraging (3 h). Our data showed that the foraging efficiency of experienced parasitoids on SJA plants was much higher than of wasps foraging in an environment consisting of RJA and CON plants.

In the present study, we found that *C. glomerata* was able to recognize plants treated with jasmonic acid at different positions, as SJA plants were preferred over RJA plants and the controls by parasitoid females. Interestingly, the primary clutch size was not significantly different on CON, RJA and SJA plants in either two- or three-choice experiments although it did differ in the two-choice experiment with CON vs SJA plants. Hence, the female's preferences did not always match with the hosts that yield the best performance for their offspring. Our earlier study has shown that the masses of both male and female adult wasps that developed from *P. brassicae* reared on SJA plants were significantly less than those that developed from *P. brassicae* on CON and RJA plants, thus hosts feeding on SJA plants are not the most profitable for *C. glomerata* (Qiu et al. 2009). Theoretical models predict that oviposition decisions by parasitoid females lead to the selection of the most profitable host for their offspring (van Alphen and Visser 1990; Godfray 1994), but *C. glomerata* exhibited the strongest preference for SJA plants which are the least profitable. Generally, parasitoids and especially females with oviposition experience, use herbivore induced-volatiles as cues to identify plants with potential hosts (Steidle and van Loon 2003). Only after landing on the plant and physically contacting the host are they able to assess its suitability as an oviposition site. Here, the caterpillars had been feeding on the plants for a very short time before parasitism (∼3 h). Consequently, there may have been insufficient time for the plant to mount a defensive response, explaining why potential differences in host quality were not detected by the parasitoid. Qiu et al. (2009) reported that, although the overall development time of *C. glomerata* larvae in *P. brassicae* hosts on SJA plants was less than in wasps developing in *P. brassicae* hosts on RJA and CON plants, the parasitoid's pupal stage was shortest on SJA plants. According to the slow-growth, high-mortality hypothesis (Benrey and Denno 1997), choosing a host on SJA plant may shorten the pupal stage period of *C. glomerata*, thus reducing the probability of being parasitized by secondary hyperparasitoids or predators. It has been reported that cocoons of *C. glomerata* harbor a diverse number of pupal hyperparasitoids, i.e. *Gelis* spp., *Lysibia nana*, *Acrolyta nens* and *Pteromalus semotus* (Tanaka et al. 2007; Harvey 2008; Harvey et al. 2009, 2011). The suitability of *C. glomerata* cocoons for the development of hyperparasitoids decreases linearly with time (Harvey 2008). If these higher trophic levels cause high mortality rates, fast pupal development may be advantageous.

In the field, plants are constantly being exposed to above- and below-ground herbivores, and it has become evident that root and shoot herbivores can influence each other through changes in the shared host plants (Bezemer and van Dam 2005). Other workers have suggested that jasmonates may be used as novel crop protectants enhancing the efficacy of biocontrol agents in cropping systems (Thaler 1999; Powell and Pickett 2003). Our study shows that the way that JA is applied determines to a large extent how JA influences the behavior of natural enemies such as parasitoids. Moreover, our results may help to explain the ecology and evolution of above- and below-ground interactions whilst increasing our understanding of decision-making processes and preferences of key players in communities over several trophic levels.

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Jeffrey A. Harvey explores links between above-below ground multitrophic interactions, life-history evolution in hyperparasitoid wasps, the effects of secondary plant chemistry on host-parasitoid interactions and the biology of invasive plants and their insect communities.

Louise E. M. Vet is interested in the chemical, behavioural and molecular ecology of plants and insects in a multitrophic and community context. This work was carried out in NIOO-KNAW, The Netherlands.