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THE DISTRACTING POWER OF FLOWERS : FLORAL VOLATILES CAN INTERFERE WITH THE HOST-SEARCHING BEHAVIOUR OF PARASITOIDS

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RÉSUMÉ

LE POUVOIR DISTRACTIF DES FLEURS : LES PARFUMS FLORAUX PEUVENT INTERFERER AVEC LE COMPORTEMENT DE RECHERCHE D'HOTES DES PARASITOIDES

Les composés organiques volatils (COVs) émis par les plantes appartiennent à plusieurs catégories : les parfums floraux dont le but est d'attirer les pollinisateurs, et les composés induits par l'attaque d'herbivores, qui sont attractifs pour les ennemis naturels des herbivores, en particulier les parasitoïdes. Ici, nous émettons l'hypothèse que les parfums floraux ont un effet négatif sur l'attractivité des plantes infestées d'herbivores pour les parasitoïdes. En utilisant comme modèle la plante *Brassica rapa*, nous avons testé l'attractivité de plantes infestées d'herbivores, avec ou sans l'addition de parfums floraux de *B. rapa*, pour le parasitoïde *Cotesia glomerata* dans un olfactomètres à 4 bras. Les résultats montrent que les parfums floraux diminuent fortement l'attractivité des plantes pour le parasitoïde testé. Ces résultats ont d'importantes implications pour l'utilisation de fleurs et bandes fleuries dans la lutte biologique par conservation.

Mots-clés : parasitoïdes, défense indirecte, odeurs des fleurs, ecologie comportementale, COVs

ABSTRACT

Volatile organic compounds (VOCs) emitted by plants belong to different categories: floral odors are signals attracting pollinators, and herbivore-induced plant volatiles are attractive to natural enemies of insect herbivores, including parasitoids. Here we formulate the hypothesis that floral odors have a negative effect on the attractiveness of herbivore-infested plants to parasitoids. Using the plant *Brassica rapa* as a model system, we tested the attractiveness of herbivore-infested plants with and without the addition of floral odors to the parasitoid *Cotesia glomerata* in a four-arm olfactometer. Results showed that floral odors strongly reduce the attractiveness of herbivore-infested plant for the parasitoid tested. These results have important implications for the use of flowers and floral strips in conservation biological control.

Keywords: parasitoids, indirect defence, floral odors, behavioural ecology, VOCs

INTRODUCTION

Plants produce a wide range of chemically-diverse volatile organic compounds (VOCs) under various circumstances (Dudareva, Negre et al. 2006), and the evolution and ecological functions of these volatile emissions are long-standing debates in Ecology (Dicke and Loon 2000, Holopainen 2004, Heil and Karban 2010). Plant volatiles can be perceived by a variety of organisms, including neighboring plants, pollinators, herbivores, and natural enemies of herbivores such as predators and parasitoids. This prompted the idea that plant volatiles may have evolved to serve as signals conveying information to mutualists. It is very clear for floral odors, whose main function is to attract pollinators (Raguso 2008, Schiestl 2010). Floral scents have been shown to convey informations about the quality of the nectar reward (Knauer and Schiestl 2015) and to promote specialization in plant–pollinator relationships, which may lead to speciation and diversification events (Waser and Ollerton 2006, Raguso 2008). It is also thought that herbivore-induced plant volatiles (HIPVs) have evolved as a means to attract members of the third trophic level (i.e. predators and parasitoids), which in turn reduce herbivore damage by killing or displacing herbivores, a phenomenon referred to as indirect defense (Dicke, van Poecke et al. 2003, Turlings and Wäckers 2004). It is clear that HIPVs are important cues for natural enemies in search of prey items/hosts and play a critical role in the foraging behaviour of many parasitoid species (Hare 2011). However, whether or not attracting natural enemies is the main ecological function of HIPVs is still debated, and several alternative ecological functions have been proposed (Heil and Karban 2010, Hare 2011). Floral odors and HIPVs typically involve different types of VOCs or different ratios of VOCs (Raguso 2008), and their interactions in the atmosphere may potentially “pollute” the infochemicals conveyed to specific mutualists (Desurmont, Harvey et al. 2014). In other words, floral odors could potentially interfere with the cues contained in HIPVs bouquets and affect the foraging behaviour of natural enemies. In parallel, HIPVs may interfere with floral odors and affect the attraction of pollinators. Ultimately, such interference effects may have direct consequences for plant fitness. It has been frequently found that flowering plants attacked by herbivores become less attractive to pollinators than undamaged plants (Adler, Karban et al. 2001, Kessler and Halitschke 2009, Schiestl, Kirk et al. 2014), but the part played by direct interference between floral odors and HIPVs in such effects is often difficult to assess. Similarly, it has been documented that herbivores can suffer less parasitism when feeding on flowering plants than on vegetative plants (Lucas-Barbosa, Poelman et al. 2014), but the importance of floral odors in such effects has yet to be clearly evaluated (Patt, Hamilton et al. 1997). It is important to note that floral odors can also be attractive to parasitoids (Wäckers 2004). Indeed parasitoids can feed on the nectar and pollen of flowers, and food-limited parasitoids have been shown to be attracted to floral odors in olfactometer settings (Belz, Kölliker et al. 2013, Géneau, Wäckers et al. 2013). Therefore, the effects of floral odors on the foraging behaviour of parasitoids may depend on what parasitoids are foraging for: food such as nectar and pollen, advertised by floral odors, or hosts, advertised by HIPVs. Because flowering plants can provide food and refuges to natural enemies of herbivores, the implementation of floral strips in the vicinity of agricultural fields is often recommended as an effective method to reduce herbivore damage in conservation biological control programs (Pontin, Wade et al. 2006, Jonsson, Wratten et al. 2008).

In a previous study involving the plant *Brassica rapa*, we showed that plants become less attractive to parasitoids when they reach the flowering stage (Desurmont, Laplanche et al. 2015). Here, we test the hypothesis that the addition of synthetic floral odors of *B. rapa* directly decreases the attractiveness of plants to parasitoids. In order to test this hypothesis, we measured the preferences of the parasitoid *Cotesia glomerata* in three series of tests in a 4-arm olfactometer. In this setting, parasitoids were given the choice between: 1) First series: a plant without herbivores (P Ctrl), a plant infested with herbivores (P Inf), and two blank odor sources; 2) Second series: a plant infested with herbivores (P Inf), a plant infested with herbivores with the addition of synthetic floral odors (P Inf + F), and two blank odor sources; 3) Third series: a plant without herbivores (P Ctrl), a plant infested with herbivores with the addition of synthetic floral odors (P Inf + F), and two blank odor sources.

MATERIAL AND METHODS

PLANT MATERIAL

Plant material used for the experiments came from a wild accession of *Brassica rapa* whose seeds were collected in Maarssen, the Netherlands. Plants were grown in controlled growth chambers under 16/8 L:D light regime at 25°C, light intensity 240-260 µmol. Plants were grown in cylindrical plastic pots (4*10 cm), with fertilized commercial soil (Ricoter Aussaaterde, Aarberg, Switzerland). Plants were watered every other day without supplemental nutrients. Plants used for experiments were three to four weeks old and had and had three to five fully expanded leaves.

INSECT MATERIAL

The host herbivore of the parasitoid used in the study, the large cabbage white *Pieris brassicae* (Lepidoptera: Pieridae) is a Eurasian butterfly that specializes on plants containing glucosinolates and is a very common pest of cultivated and wild crucifers. The caterpillars of *P. brassicae* used in the study came from a laboratory rearing kept at the university of Neuchâtel (Switzerland) started with field-collected individuals from various parts of Switzerland. In the rearing, *P. brassicae* individuals were maintained on *B. rapa* (for oviposition) and *B. oleracea* (for larval development). Adult butterflies were given sugar water as food and kept in larges insect tents (60 × 60 × 90 cm, Vermandel entomology material, The Netherlands).

The parasitoid *Cotesia glomerata* (Hymenoptera: braconidae) was used in this study. It is the main specialist parasitoid of *P. brassicae* through its native range, and parasitizes young *P. brassicae* caterpillars (first to third instar). It is a gregarious koinobiont endoparasitoid, which means that females can lay many eggs within one host and that the parasitoid does not stop the development of its host once parasitized. The parasitoids used in the study came from a laboratory rearing kept at the University of Neuchâtel that was initiated with field-collected individuals from the Wageningen area (The Netherlands), later complemented with individuals from the Neuchâtel and Zürich areas (Switzerland). Adult parasitoids were kept in plastic rearing containers (30 × 30 × 30 cm, BugDorm insect cages, Taïwan) and were provided water and droplets of honey as food. The rearing containers were kept in an incubator at 25°C for 48 hours after emergence of the parasitoids to allow successful mating, then were transferred in an incubator at 13˚C until needed for experimental purposes. Mated naive females that were 2-4 weeks old were used for all experiments. Parasitoids were only used once in olfactometer tests.

SYNTHETIC FLORAL ODORS

The synthetic floral odors used in the study were based on the most abundant compounds found in the floral bouquet of the *B. rapa* population used in the study (Knauer and Schiestl unpublished): phenylacetaldehyde (≥ 90 %, Sigma-Aldrich, Buchs, Switzerland) 3 µL/mL, nonanal (Givaudan, Dübendorf, Switzerland) 9 µL/mL, decanal (Givaudan) 4 µL/mL, acetophenone (Givaudan) 24.5 µL/mL, p-Anisaldehyde (Sigma Aldrich) 27 µL/mL, and α-Farnesene (mixture of isomers, Sigma Aldrich) 492 µL/mL, diluted in dichloromethane (HPLC grade). Before olfactometer tests, rubber septa (GR-2, 5 mm Supelco, Bellefonte, PA, USA) were left to soak in the solution of synthetic floral odors for a duration of one hour, then were allowed to dry for four hours. One septum with floral odors was placed above the treatment plant inside the olfactometer just prior to the tests of the second series of olfactometer tests, so the floral odors would mix with the volatile compounds emitted by the plant. Preliminary trials conducted prior to the experiments showed that rubber septa soaked only in solvent (dichloromethane) do not have an effect on parasitoid foraging behavior under the same experimental conditions. For the second series of olfactometer tests, the concentration of each compound in the solution was adjusted so that the emission rate of each compound from one septa was comparable to one inflorescence (ca. 30 flowers) of *B. rapa* (Schiestl, Kirk et al. 2014). For the third series of olfactometer tests, a stronger concentration of floral odors was used so that the emission rate of each compound from one septum was comparable to four inflorescences (ca. 120 flowers).

OLFACTOMETER SETTING

The preferences of parasitoids were investigated using a 4-arm olfactometer setting. In this setting, wasps were given the choices between four odor sources (=treatments), each belonging a glass bottle associated with one arm of the olfactometer. Individual air flows were connected to each odor source, and all air flows converged to a central glass piece, where the wasps were released. A source of light was placed just above the central glass piece in order to insure that parasitoids would not converge to one arm due to differences in light conditions. For all olfactometer tests, herbivore-infested plants were prepared by letting 20 1st instar caterpillars feed on the plants during 24h before the tests. The herbivores were not removed from the plants during the tests. After 30 minutes spent in the olfactometer, wasps were recollected and the treatment they chose was recorded. Wasps that did not make a choice were noted as "no-choice" in the analysis of the results. An olfactometer test (=1 replicate) consisted in 5 consecutive releases of 5 wasps (wasps were replaced between releases; total wasps tested per replicate = 25). We conducted a minimum of 4 replicates for each series of olfactometer tests (first series: 11 replicates; second series: 9 replicates; third series: 4 replicates). To avoid potential branch position effects, a same branch of the olfactometer was never chosen for the same treatment for two consecutives replicates. The plants were changed and the glassware of the olfactometer was cleaned between replicates. The cleaning process consisted in rinsing the glassware sequentially with three solvents: water, acetone, and pentane, and putting the glassware in an oven at 250°C for a minimum of two hours.

STATISTICAL ANALYSIS

Preferences of *C. glomerata* females were analyzed for each test using a generalized linear model (GLM) with a poisson distribution fitted by maximum quasi-likelihood estimation in accordance with a method developed by Turlings et al. (Turlings, Davison et al. 2004), with the number of wasps counted in the different branches of the olfactometer as the dependent variable. Means were compared using a Chi-square test and a multiple comparison post hoc Wilcoxon test ($\alpha = 0.01$, JMP12). Results are presented as percentages in the figures illustrating olfactometer tests for easier comprehension: percentage attractiveness of a given treatment was calculated as the number of wasps that chose that particular treatment divided the total number of wasps that made a choice during the test *100 (wasps that did not make a choice were excluded from the calculations of percentage attractiveness). The attractiveness values for the two empty odor sources (Blank1 and Blank2) were averaged for each series of olfactometer tests to

RESULTS

OLFACTOMETER TESTS

In the first series of olfactometer tests, parasitoids showed significant preferences among the treatments (d.f. = 3, $\chi^2 = 70.0$, $P < .0001$): herbivore-infested plants (P Inf) were highly attractive to parasitoids (84.8 ± 8.4)(% attractiveness, mean ± SE). On the other hand, plants without herbivores (P Ctrl) and empty odor sources (Blank) were not attractive to parasitoids (Fig. 1A). In the second series of olfactometer tests, parasitoids showed the following preferences among the treatments (d.f. = 3, $\chi^2 = 119.5$, $P < .0001$): herbivore-infested plants (P Inf) were the most attractive treatment (52.1 ± 9.5), followed by herbivore-infested plants with the addition of floral odors (31.7 ± 8.6), and empty odor sources (8.0 ± 2.4). In other words, the addition of floral odors decreased the attractiveness of an herbivore-infested plant by 39.1% for the parasitoid *C. glomerata* (Fig. 1B). In the third series of olfactometer tests, parasitoids showed the following preferences among the treatments (d.f. = 3, $\chi^2 = 7.8$, $P < .0001$): herbivore-infested plants with the addition of floral odors (P Inf + F) (46.1 ± 7.3) and plants without herbivores (P Ctrl) (37.2 ± 9.6) were comparably attractive and were more attractive than empty odor sources (16.7 ± 4.1) (Fig. 1C). The percentage motivation of parasitoids (i.e. number of parasitoids making a choice divided by the number of parasitoids tested * 100) was as follows for the three series of tests: first series: 76.4%; second series: 85%; third series: 78%.

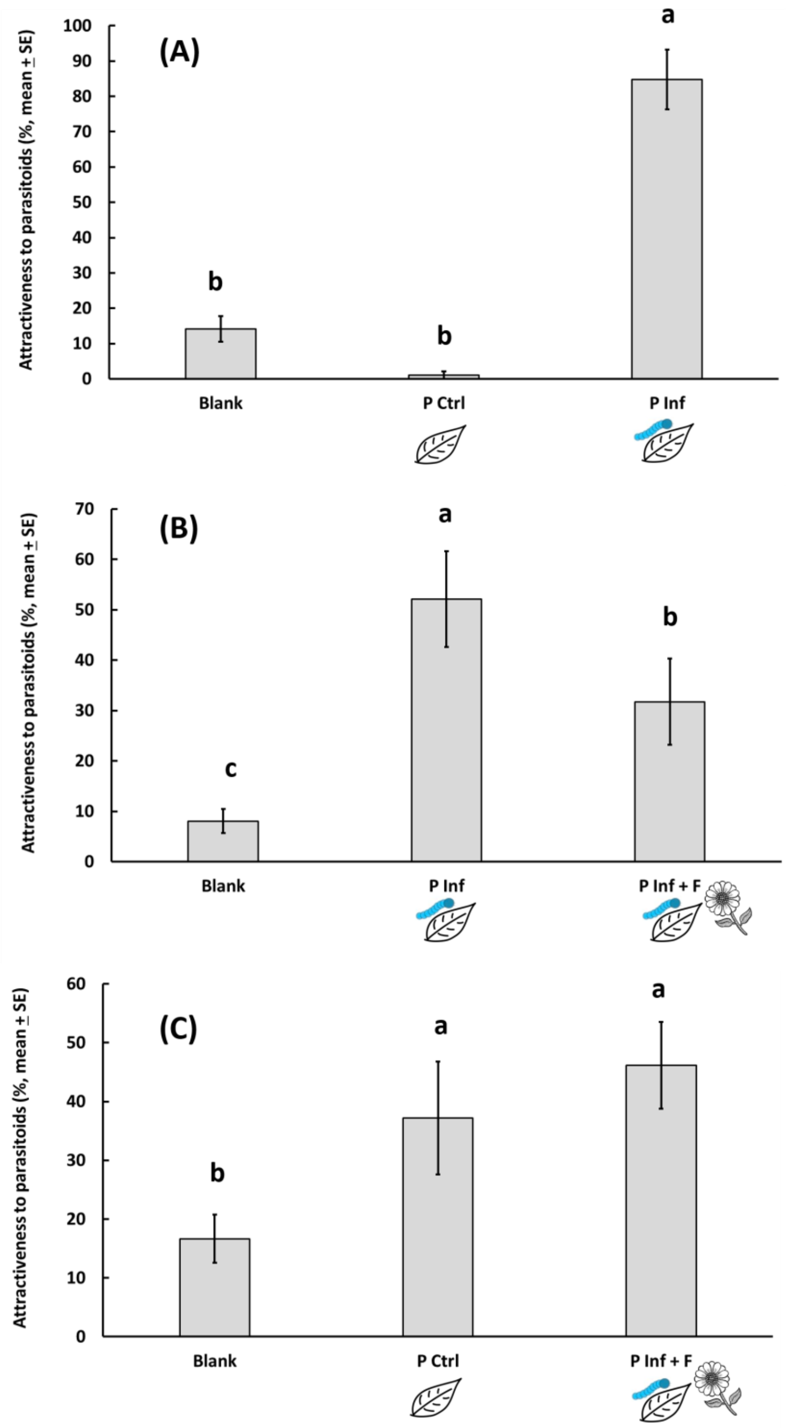

Figure 1 : ATTRACTIVENESS OF *B. RAPA* PLANTS WITHOUT HERBIVORES (P CTRL), WITH HERBIVORES (P INF), AND WITH HERBIVORES WITH THE ADDITION OF FLORAL ODORS (P INF + F) TO THE PARASITOID *COTESIA GLOMERATA* (%, MEAN ± SE). (A) FIRST SERIES OF TESTS (B) SECOND SERIES OF TESTS (C) THIRD SERIES OF TESTS. BLANK = EMPTY ODOR SOURCE.

ATTRACTIVITE DE LA PLANTE *B. RAPA* SANS HERBIVORES (P CTRL), AVEC DES HERBIVORES (P INF) ET AVEC DES HERBIVORES ET L'ADDITION D'ODEURS FLORALES (P INF + F) POUR LE PARASITOIDE *COTESIA GLOMERATA* (%, MEAN ± SE) (A) PREMIERE SERIE DE TESTS (B) DEUXIEME SERIE DE TESTS (C) TROISIEME SERIE DE TESTS. BLANK = SOURCE D'ODEUR VIDE.

DISCUSSION

The chemical nature of floral odors and herbivore-induced plant volatiles is often dissimilar, and the interactions between these two types of plant volatiles may have consequences for infochemical networks and plant fitness in nature. Here we tested the hypothesis that floral odors can interfere with the foraging behavior of parasitoids in an olfactometer setting. Our results show unambiguously that the addition of floral odors significantly diminishes the attractiveness of *B. rapa* plants infested by *P. brassicae* to the main parasitoids of *P. brassicae* in nature, the braconid wasp *C. glomerata* (Fig.1 B&C). This decrease in attractiveness implies that parasitoids may be less likely to forage on plants surrounded by floral odors of *B. rapa* in nature, and that *P. brassicae* may be more likely to escape parasitism in such microhabitats. Floral odors of *B. rapa* may thus create a temporary "enemy-free space" for the herbivore (Jeffries and Lawton 1984) through chemical interference with herbivore-induced plant volatiles (Desurmont, Harvey et al. 2014). This type of "enemy-free space" is likely to be highly dynamic and context-sensitive in nature, and the consequences of such interference effects with herbivore and parasitoid fitness remain to be explored. It should be noted that we used a high concentration of floral scents (ca. 120 flowers) in the third series of olfactmeter tests, which corresponds to the "extreme" situation of a herbivore-infested plant entirely surrounded by large numbers of flowers. Other data (unpublished) show that the effects of floral odors on plant attractiveness are dose-dependent and are only detectable passed a certain threshold of floral odor concentrations (ca. 30 flowers). In absence of floral odors (Fig. 1A), parasitoids showed a very strong attraction to herbivore-infested plants compared to control plants without herbivores, which confirms that they rely on herbivore-induced plant volatiles to detect their hosts from a distance.

Parasitoids can be attracted to floral odors when they are looking for food (nectar and pollen). Therefore, it could be argued that the addition of floral odors to a blend of HIPVs should make the blend more attractive, as it advertises a "double reward" (food + host) to parasitoids. However, in the light of our results, it seems more likely that parasitoids looking for hosts are targeting HIPVs specifically, and that the addition of floral odors just create "noise" that mask the infochemicals parasitoid are searching for. It should be noted that we only used well-fed parasitoids in our olfactometer tests: starved parasitoids may have primarily searched for food and may have shown a stronger preference for floral odors. In addition, we should keep in mind that the compounds emitted by *B. rapa* flowers represent a minuscule fraction of the diversity of compounds produced by flowering plants (Dudareva, Negre et al. 2006, Raguso 2008): further studies using other plant systems would be needed in order to determine how commonly floral odors interfere with parasitoid foraging behavior.

Our results were obtained under laboratory conditions and require field validation. Odor plumes originating from flowers and originating from herbivore-infested plant parts may be easier to distinguish for a parasitoid foraging under natural conditions than in an olfactometer setting (Beyaert and Hilker 2014). Therefore floral odor interferences may be uncommon and/or limited to patches with high densities of flowers located near herbivore-infested plants under natural conditions. The use of flower strips in agricultural fields as sources of food and refuges for natural enemies has proven a highly effective method to enhance the natural regulation of insect pests in conservation biological control programs (Bianchi and Wäckers 2008, Jonsson, Wratten et al. 2008). Our results suggest, however, that floral odors may not always be beneficial for the foraging efficiency of parasitoids, and should remind practitioners that the choice of flower species contained in flower strips and the distance and positioning of flower strips from the plants to protect are critical factors for the efficacy of this biological control method.

CONCLUSION

Floral odors and HIPVs have evolved to specifically attract two types of beneficial insects: pollinators and natural enemies. Our study shows that these two types of plant volatiles can interact and that floral odors can directly impact the foraging behavior of parasitoids and decrease plant attractiveness to parasitoids. These results indicate that floral odor interferences are a factor to keep in consideration for practioners using flowers and floral strips as a conservation biological control method, and need to be further explored under natural conditions.

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