Intraspecific plant variation and nonhost herbivores affect parasitoid host location behaviour

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Parasitoids need to find their hosts in patchy environments that differ in profitability. To maximize foraging efficiency, parasitoids use volatile information of plants on which their hosts feed. The blend of plant volatiles emitted is affected by genetic variation in plants and by the herbivore species feeding on the plant. How parasitoids deal with variation in plant volatiles induced by host or nonhost herbivores on various plant genotypes in a plant stand is unclear. In a wind tunnel, we examined foraging behaviour of the parasitoid *Cotesia glomerata* in mixes of white cabbage cultivars with host (*Pieris brassicae*) and nonhost herbivores (*Mamestra brassicae* or *Delia radicum*). We specifically studied the efficiency of parasitoids in locating a host-infested plant when having to pass three other plants that varied in volatile emission by cultivar and herbivore identity. We show that foraging decisions of *C. glomerata* are affected by the apparency of volatile cues from upwind host-infested plants. We found that parasitoids flew over the first three plants more often when the last plant was a host-infested attractive cultivar and the first three plants were a less attractive cultivar, regardless of the presence of host or nonhost herbivores. Furthermore, parasitoids spent more time on the first three plants if these were infested with host or nonhost larvae, and this effect was stronger when the first three plants were of the attractive cultivar. Our results suggest that parasitoids may more easily locate host herbivores on plant genotypes with more apparent volatile information. However, host location efficiency is affected by the contrast with other plumes of plant volatiles derived from genotypic variation in plants and induction of volatiles by nonhost herbivores. Apparency of information on upwind patches influences patch residence time and patch choice and is an important component of optimal foraging in parasitoids.

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According to optimal foraging theory, animal foraging decisions should be made economically, reducing energy expenditure and increasing energy gain or reproductive success (Charnov, 1976). If food sources can be found on distinct patches within a landscape, two decisions strongly impact foraging efficiency: which food patch to enter and when to leave a patch. To maximize foraging efficiency in a patchy habitat, animals use (indirect) information from the environment to find potential patches and to assess patch quality (Finnerty et al., 2017; Heil, 2014; Webster & Cardé, 2017). After a patch is perceived as profitable, it is entered, and optimal foraging is determined by local efficiency in food location and processing. The time spent searching within a patch is dependent, among other things, on the odds and rate of finding more prey within the patch, the time to locate new patches (Cassini et al., 1990; Muratori et al., 2008), previous experience with other patches (Charnov, 1976; Vos et al., 1998) and the apparency of cues from more profitable patches against the background of cues from less profitable patches (Heydari et al., 2017). Parasitoid wasps that lay their eggs in or on herbivorous insects are good examples of animals that need to locate their prey in a patchy environment.

In complex environments information may be more difficult to detect, and hierarchical foraging steps might help parasitoids to optimize foraging (Aartsma et al., 2017). First, parasitoids select habitats using landscape-scale cues, after which plant assemblages that may contain hosts are localized within the chosen habitat. Thereafter, individual plants within the assemblage are selected to find hosts. Lastly, host searching using direct cues from the hosts and host handling precede the final parasitism step. Thus, the

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individual plant can be considered as a patch from the perspective of the parasitoid.

To assess patch profitability, parasitoids use plant volatiles as reliable cues for host presence (Geervliet et al., 1994). Plants release herbivore-induced plant volatiles in response to herbivory, which are specific within and between plant species and dependent on the identity of herbivores (Heil, 2014; Webster & Cardé, 2017). However, parasitoid wasps need to select patches based on complex information from volatiles of genetically diverse plants under herbivory by many insect species (Aartsma et al., 2017). Although parasitoids discriminate host-infested plants from undamaged plants, plant volatiles induced by nonhost herbivores may not be innately discriminated from host-induced volatiles (De Rijk et al., 2013; Vosteen et al., 2019). Nonhost herbivores feeding on different plants or alongside host herbivores on the same plant may reduce host location efficiency of parasitoids (Desurmont et al., 2016; Hu et al., 2020; Li et al., 2017; Moujahed et al., 2014; Peñaflor et al., 2017; Pierre et al., 2011). Plants also show both inter- and intraspecific variation in volatile composition, which affects the apparency of cues from individual host-infested plants through herbivore-induced plant volatiles (Bukovinszky et al., 2005; Degen et al., 2012; Kuramitsu et al., 2019; Lamy et al., 2018; Li et al., 2018; Mody et al., 2017; Ode & Crompton, 2013). Also, plumes of plant volatiles from neighbouring plants might mix to create new odour blends, further affecting parasitoid host location efficiency (Bukovinszky et al., 2007; Kostenko et al., 2015; Kruidhof et al., 2015). Apparency of profitable patches for parasitoids is thus determined by how well plant volatile cues stand out in the context of other cues derived from the plant community and is determined by plant genotypic variation in volatile emission as well as its relative difference from volatile emissions by neighbouring plants. Moreover, the time parasitoids spend on a patch should be carefully balanced between the profitability of the currently visited patch and the availability of potentially more profitable patches (Vos et al., 1998). Interactions with (non)host herbivores and information from neighbouring patches might aid in making informed leaving decisions (Bukovinszky et al., 2012; Vosteen et al., 2019, 2020). The direction of information flow is vital here, as volatiles are transported downwind and might have mixed by the time they reach the parasitoid (Vosteen et al., 2020). Furthermore, parasitoids might learn to recognize patch profitability from previous experience (Geervliet et al., 1998). Yet, it remains unclear how innate patch choice and patch residence time are affected when parasitoids are confronted with information from upwind plant mixes that differ in plant genotypic variation for volatile emission and how this variation interacts with the presence of host and nonhost herbivores.

Foraging behaviour has been well studied for the parasitoid *Cotesia glomerata* and its tritrophic interactions with host and nonhost insect species and different food plant species, accessions or cultivars. *Cotesia glomerata* is a specialist, gregarious, koinobiont endoparasitoid that parasitizes larvae of the large and small cabbage white butterflies, *Pieris brassicae* and *Pieris rapae*, which in turn are specialist herbivores of brassicaceous plants (Brodeur et al., 1996). *Cotesia glomerata* uses herbivore-induced plant volatiles to locate host-infested plants (Geervliet et al., 1994, 1996, 1998), after which it switches to direct cues left by the larvae to find and parasitize its host (Aartsma et al., 2017). These herbivore-induced plant volatiles are known to differ not only between *Brassica* species (Gols et al., 2012), but also between varieties and cultivars of *Brassica* species (Poelman et al., 2009). For example, *C. glomerata* showed a clear preference for host-induced plants of the white cabbage, *Brassica oleracea* var. *capitata*, cultivar Christmas Drumhead over the cultivars Rivera and Badger Shipper (Aartsma, Hao, et al., 2020; Poelman et al., 2009). Moreover, *C. glomerata*

responded to volatiles from Christmas Drumhead from a longer distance than to volatiles from Rivera (Aartsma, Leroy, et al., 2019). Complexity in the landscape might, however, reduce host-finding chances for *C. glomerata* (Aartsma, Pappagallo, et al., 2020; Kruidhof et al., 2015; Perfecto & Vet, 2003). Nonhost herbivory can also complicate *C. glomerata* optimal patch decisions when nonhost-induced plant volatiles resemble host-induced plant volatiles (De Rijk, Wang, et al., 2016; De Rijk, Yang, et al., 2016; De Rijk, Zhang, et al., 2016; Desurmont et al., 2016, 2018; Soler, Harvey, & Bezemer, 2007; Soler, Harvey, Kamp, et al., 2007). Similarly, *C. glomerata* patch residence time was increased and parasitoids initially chose patches without hosts more often when the nonhost intraguild herbivore *Mamestra brassicae* was present upwind (Vosteen et al., 2019). When host-infested plants were placed downwind from the parasitoid release point, distraction by nonhost herbivores was even greater (Vosteen et al., 2020). Moreover, parasitoids regularly lost time investigating nonhost cues on the plant and even oviposited in nonhosts (Bukovinszky et al., 2012; Vosteen et al., 2019, 2020). A better understanding of how plant genetic variation interacts with the presence of host and nonhost herbivores to alter host-searching behaviour of a common agroecological control agent is paramount for any intraspecific crop diversification strategy aimed at enhancing conservation biocontrol.

Here we studied how *C. glomerata* patch choice and patch residence time are affected by cultivar identity and (non)host herbivore presence on rows of white cabbage plants upwind from the parasitoid release point. We focused on these behavioural components of optimal foraging to infer how behavioural decision making may have evolved to maximize foraging efficiency in complex habitats. We considered each plant as a single entity, referred to as a patch. Two white cabbage cultivars with known differences in parasitoid recruitment were used: the relatively less attractive cultivar Rivera and the relatively more attractive cultivar Christmas Drumhead (Poelman et al., 2009). *Pieris brassicae* was used as host herbivore, whereas the foliar herbivore *M. brassicae* and the root herbivore *Delia radicum* were used as nonhost herbivores. We specifically addressed (1) whether foraging decisions are affected by the cultivar identity of an upwind host-infested plant and the cultivar identity of undamaged plants in complex multiplant stands. Here we were specifically interested in whether parasitoids can distinguish differences between plant cultivars and host presence even when volatile profiles of individual plants were mixed. We also investigated (2) how parasitoid patch choice and patch residence time are affected by cultivar mixes and host presence. Here we specifically addressed how host presence and cultivar identity interact to affect parasitoid foraging efficiency and decisions. Finally, we addressed (3) how nonhost presence affects host finding in mixed cultivar stands. Here we tested how nonhost presence and cultivar identity interact to affect parasitoid foraging efficiency and decisions.

METHODS

Organisms

Adult female *C. glomerata*, larvae of its host *P. brassicae* and its nonhosts *M. brassicae* and *D. radicum* were acquired from stock maintained at the Laboratory of Entomology, Wageningen University, The Netherlands. The larvae of *P. brassicae* and *M. brassicae* were reared on Brussels sprouts plants, *B. oleracea* var. *gemmifera* cultivar Cyrus, and the larvae of *D. radicum* on swede, *Brassica napobrassica*, in a climate-controlled room (16:8 h light:dark photoperiod, at 21 ± 1 °C and 50—60% relative humidity). Larvae of *P. brassicae* were used as host to rear *C. glomerata*. First-instar *P. brassicae* were placed into the cage of adult parasitoids, which

were allowed to oviposit for 5–10 min. Parasitized larvae were fed with Brussels sprouts plants to complete parasitoid development. After the parasitoid larvae egressed from the host to pupate, the parasitoid cocoons were placed into screen cages (30 × 30 × 30 cm, Bugdorm) in a climate-controlled room at 24 ± 1 °C, 12:12 h light:dark. Adult parasitoids were fed with honey and water. The stock *C. glomerata* is replaced yearly with new specimens collected from the vicinity of Wageningen University. Two–five-day-old, mated females were used in all experiments.

Five-week-old white cabbage, *B. oleracea* var. *alba*, plants of the less attractive cultivar Rivera (Bejo Zaden BV, Warmenhuizen, The Netherlands) and the more attractive Christmas Drumhead (Centre for Genetic Resources, CGN-Wageningen, The Netherlands) were used for the experiments (Poelman, Oduor, et al., 2009). These two white cabbage cultivars are known to differ in their (herbivore-induced) volatile profiles, with Rivera producing more of eight different types of monoterpenes and one ester than Christmas Drumhead (Poelman, Oduor, et al., 2009). However, when infested by *P. rapae* both plants upregulate their production of methyl salicylate. Christmas Drumhead also increases emission of ketones, a furan and two unknown compounds (Poelman, Oduor, et al., 2009). In both controlled, wind tunnel, two-choice assays and open field studies, *C. glomerata* parasitoids are found to prefer host-induced Christmas Drumhead plants over induced plants of other cultivars (Poelman, Oduor, et al., 2009). Plants were grown in 1.45-litre pots containing potting soil ('Lentse potgrond nr. 4') in a greenhouse (16:8 h light:dark photoperiod with SON-T light, 500 µmol/m^2 per s in addition to daylight, at 18–26 °C and 40–70% relative humidity).

Ethical note

No licence was required for work with insects. A total of about 2500 female *C. glomerata* parasitoids, 9000 *P. brassicae* larvae, 800 *M. brassicae* larvae and 480 *D. radicum* larvae were used in the three experiments in this study. Larvae were handled gently with a fine paint brush when moving them to new plants. Parasitoids were taken from the cage by moving a glass vial over them and waiting for the parasitoid to crawl into the vial. Overcrowding in parasitoid cages was reduced by making sure the number of individuals per cages was kept below 150. Directly after use in any of the experiments, insects were killed by freezing them.

Experimental Set-up

All experiments were performed in a wind tunnel (200 × 60 cm and 60 cm high; for a detailed description see Geervliet et al., 1994). The wind tunnel was climate controlled at 23.6–25.1 °C and 50–68% relative humidity. Wind speed in the wind tunnel was 0.1 m/s. Single parasitoid females were released into a horizontal glass cylinder (30 cm long, 15 cm diameter) with two open sides. In all experiments, this glass cylinder was placed 75 cm downwind from any of the plant rows; within these plant rows, plants were placed at 20 cm distance from stem to stem (Fig. A1). We marked the spots where the plants were placed with tape, to ensure that plants were always at the same distance from the release point of the parasitoid. Plant stands were left for at least 5 min before a parasitoid was released into the wind tunnel.

Experiment 1: Cultivar Mixes in Two-choice Situations

To test whether the mix and host infestation of cultivars affect the foraging preference of *C. glomerata*, we placed two rows of four plants in the wind tunnel. Here, the focus was on whether parasitoids can still distinguish between mixes of plants that differ in their combined odour profiles. The rows differed in the number and

position of the more attractive Christmas Drumhead (C) and less attractive Rivera (R) cultivars, including the cultivar of the most upwind plant that was infested by 10 larvae of the host (H) herbivore (*P. brassicae*). First, we tested whether the known preference for herbivore-induced plant volatiles of Christmas Drumhead over those of Rivera persisted in more complex, simulated habitats, in which the first three plants in a row were undamaged Rivera plants (treatment A0, Fig. 1). Second, we tested whether addition of undamaged Christmas Drumhead plants in the row with host-infested Rivera plants increased the attraction of parasitoids to this row. We replaced either one, two or three plants and investigated whether the position of replacement in a row affected parasitoid preference (treatments A1–A3, Fig. 1). Third, we also tested whether replacing undamaged Rivera plants by the more attractive Christmas Drumhead plants resulted in a higher attraction to that row if the fourth plant in both rows was a host-infested Rivera plant. In these treatments, we also replaced one to three plants and tested for an effect of replacing specific plants in a row (treatments B1–B3, Fig. 1). Plants were placed upwind from the parasitoid release point in such a way that the two rows were separated 40 cm from stem to stem (Fig. A1b). Here, we acknowledge that the odour profiles of these plant rows might have overlapped, especially further downwind. Nevertheless, odour plumes of individual plants were more likely to overlap within a row than across rows due to the constant airflow. Under these conditions, we tested whether parasitoids would respond to subtle differences in odour plumes of groups of plants, even if the plumes of two rows may have partly overlapped.

Parasitoid choices for each row were monitored by visual observation. After initiating upwind flight, a parasitoid was considered to have made a choice for a row once it landed on one of the plants in a row and stayed on that plant for more than 15 s. The
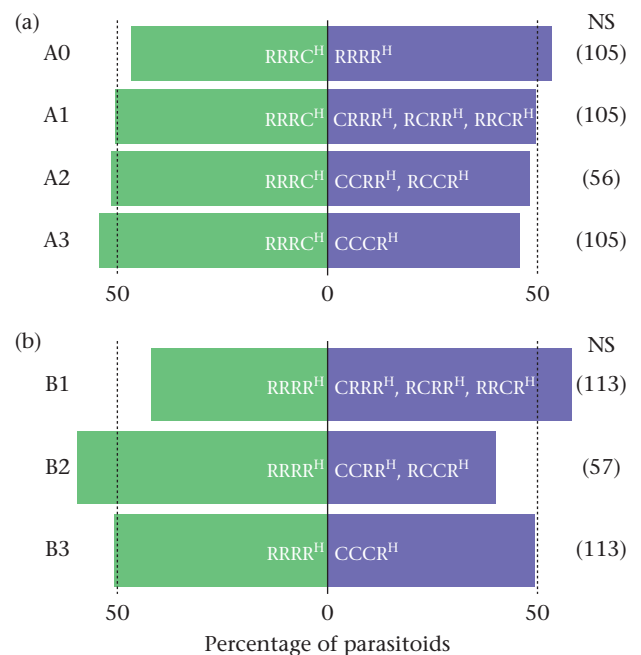
Figure 1. Influence of undamaged Christmas Drumhead plants on parasitoid (*Cotesia glomerata*) choice for plant rows with (a) a host-infested Christmas Drumhead at the end of one row and an induced Rivera plant at the end of the other row and (b) a host-infested Rivera plant at the end of both rows. Letters in the treatment codes indicate cultivar identity from downwind to upwind plants (R = Rivera; C = Christmas Drumhead). The 'H' in superscript indicates herbivore presence on the respective plant. The dotted vertical line indicates 50% choice. Numbers in parentheses indicate the number of replications for each treatment. The sample sizes of A2 and B2 are lower than those of other rows as these treatments were included later.

15 s rule ensured that parasitoid choices could be assigned to individual rows, excluding the few observations of nondistinct choices of parasitoids that were hovering between rows and that made short landings in this choice process. When the parasitoid remained in the glass cylinder or on one of the sides of the wind tunnel for over 5 min, the parasitoid was considered nonresponsive and the observation was terminated.

Experiment 2: Cultivar Mixes and Presence of Host Herbivores

In a second experiment, we studied the movement pattern of parasitoids when locating hosts in a single row of four plants. We tested how variation in host herbivore presence and cultivar identity affected parasitoids in reaching the hosts on the final, fourth plant of a row. First, we compared parasitoid searching behaviour when the fourth plant was either the attractive Christmas Drumhead or the less attractive Rivera cultivar and the first three were undamaged Rivera plants, either with or without hosts present on the fourth plant (last plant treatments: RRRR, RRRC, RRRR[H] and RRRC[H], Fig. 2). Next, we tested how the cultivar identity of the first three plants, the cultivar identity of the last plant and hosts on the first three plants affected foraging behaviour of the parasitoid (all plant treatments: RRRR[H], RRRC[H], CCCR[H], CCCC[H], R[H]R[H]R[H]R[H], R[H]R[H]R[H]C[H], C[H]C[H]C[H]R[H], C[H]C[H]C[H]C[H]; Fig. 2).

We used a hand-held computer with the 'The Observer XT 10.1' software (Noldus Information Technology) to track parasitoid behaviour. We recorded five behavioural parameters: the proportion of parasitoids that initiated flight and landed in the plant row (Response); the proportion of parasitoids that flew directly to the last plant in a row (Direct Flight); the time the parasitoid took to reach the last plant from the first time it took flight (Searching Time); the time the parasitoid spent on the first three plants in a row (Plant 123 Time); and the time it took the parasitoid to attack the hosts after landing on the last plant for the first time (Attack

Latency). We started recording time from the release of the parasitoid into the glass cylinder. The time the parasitoid spent on each plant was tracked separately until the parasitoid successfully parasitized a larva on the last plant (if no larvae were present at all, recording was stopped once the parasitoid reached the last plant), or until 30 min had elapsed. Any parasitoids that were responsive but did not reach the last plant within 30 min were considered to have taken the full 30 min to get to the last plant, thus underestimating time to reach the last plant. If a parasitoid remained motionless on a plant for more than 5 min, it was recorded as an 'unsuccessful forager' and the recording was terminated. If the parasitoid stayed in the glass cylinder or on one of the sides of the wind tunnel for more than 5 min without touching one of the plants, the recording was terminated, and the parasitoid was considered 'unresponsive'.

Experiment 3: Cultivar Mixes and Presence of (Non)Host Herbivores

To investigate how nonhosts affect foraging behaviour of *C. glomerata* females searching for their host *P. brassicae*, we either induced all plants within a row with five *M. brassicae* larvae (Mamestra), three *D. radicum* larvae (Delia), or plants were left without nonhost herbivores (Control). To examine whether these nonhosts affected attraction by the two cultivars Christmas Drumhead and Rivera, we subjected each of the nonhost regimes to four cultivar mixes always with a plant that was infested with 10 *P. brassicae* larvae at the end of the row (RRRR[H], RRRC[H], CCCR[H], CCCC[H]; Fig. 3). For all recordings, 'The Observer XT 10.1' software was used, and recorded variables were the same as in experiment 2.

Statistical Analysis

All analyses were performed using R version 3.6.3. The package 'lme4' was used for all mixed-effects models (Bates et al. 2020). As
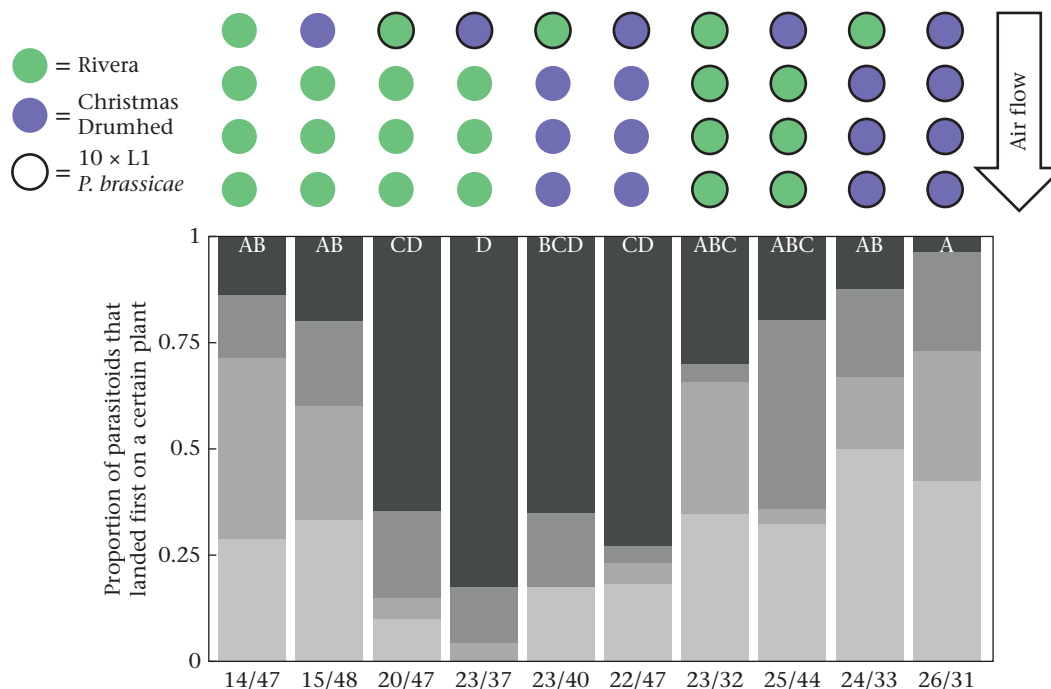
Figure 2. Influence of host presence and cultivar identity of four white cabbage plants in a row on the proportion of parasitoids that landed on certain plants. The coloured dots at the top illustrate the set-up of plants with the topmost plant indicating the most upwind (last) plant in the row; black circles indicate the presence of first-instar (L1) hosts. Plants landed on are indicated in different shades of grey (light to dark is down- to upwind). Below the X-axis the response rate is indicated as parasitoids that landed on any plant/total parasitoids. Different capital letters indicate significant differences in the proportion of parasitoids that flew directly to the last plant.
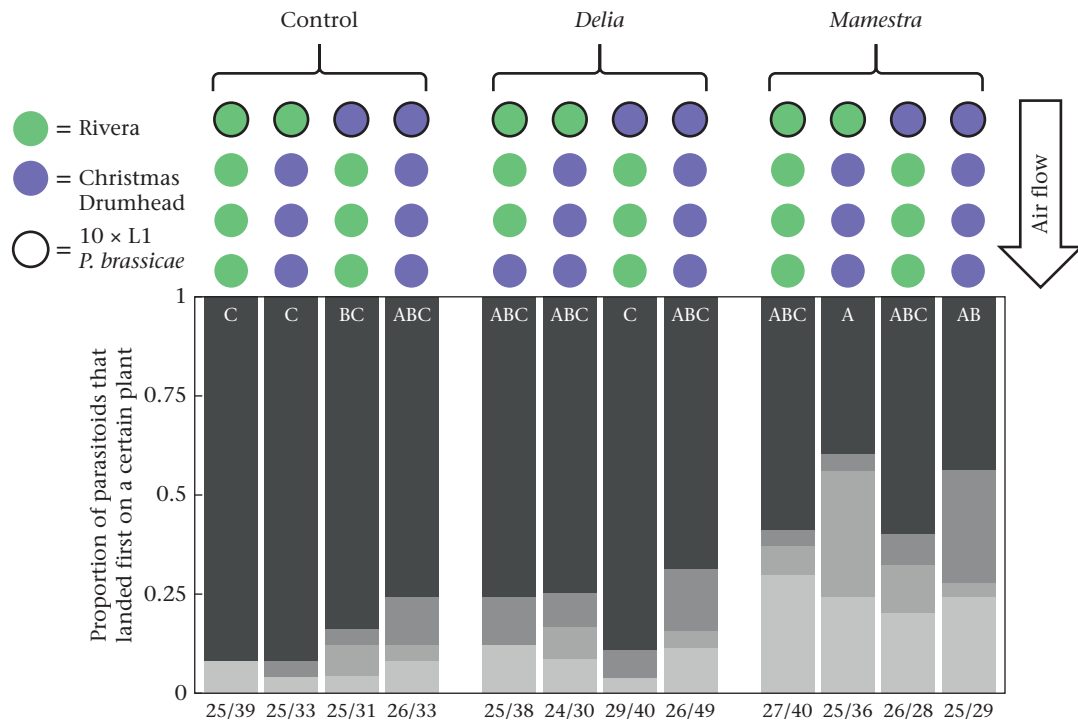
Figure 3. Influence of cultivar identity of the first three and last three plants and nonhost herbivores on the proportion of parasitoids that landed on a certain plant. Nonhost treatments were no nonhosts (Control), three larvae of *D. radicum* (*Delia*) or five larvae of *M. brassicae* (*Mamestra*). The coloured dots at the top illustrate the set-up of plants with the topmost plant indicating the most upwind (last) plant in the row; a dark circle around a dot indicate the presence of first-instar (L1) hosts. Plants landed on are indicated in different shades of grey (light to dark is down- to upwind). Below the X-axis the response rate is indicated as parasitoids that landed on any plant/total parasitoids. Different capital letters indicate significant differences in the proportion of parasitoids that flew directly to the last plant.

hypothesis testing with all fixed effects and any two-way in-teractions regularly resulted in an imbalance between observations and the variables we included, model selection was performed. To avoid arbitrariness, model selection happened in two a priori decided steps: (1) using the 'Dredge' function of the 'MuMIn' package (Barton 2020), only models with a ΔAIC (Akaike information criterion) of 2 or lower were retained; (2) within the retained models, those that contained most main factors were selected. When a tie between models occurred, the model with the lowest AIC value was chosen. Parameter estimates of all variables included in the models with a ΔAIC < 2 are reported in Tables A1-A14.

Experiment 1: cultivar mixes in two-choice situations

To test whether replacing undamaged, less attractive Rivera plants with undamaged, more attractive Christmas Drumhead plants increased attraction to a row of four plants, we used generalized linear mixed models (GLMMs). We tested whether the choice distribution deviated significantly from a 50% choice distribution for each treatment separately. Those treatments where one of the last plants was a host-infested Christmas Drumhead plant and the other was a host-infested Rivera plant (treatments A0–A3, Fig. 1) were separately analysed from the treatments that had a host-infested Rivera plant in both rows (treatments B1–B3, Fig. 1). Here we tested for the Bernoulli distribution with a logit link function. We made a binary, dependent variable that was equal to 1 when the parasitoid chose the row where the cultivar of the first three, undamaged plants was varied, whereas a choice for the constant row with three undamaged Rivera plants was given a 0. We included the orientation of the two rows within the wind tunnel and the observation date as random effects.

Experiment 2: cultivar mixes and presence of host herbivores

To investigate the role of host herbivory and cultivar identity on parasitoid foraging behaviour in a row of four plants we used a GLMM with a Bernoulli distribution and a logit link function for Response and Direct Flight. We applied linear mixed models (LMM) for continuous variables, such as Searching Time, time spent on the first three plants (Plant 123 Time) and Attack Latency, to natural log-transformed data. We tested the effect of cultivar identity of the first three plants in a row (Cultivar Plant 123) and the last plant in a row (Cultivar Plant 4), host herbivore presence on the first three plants (Hosts Plant 123) and the last plant (Hosts Plant 4) and any potential interactions between these variables on the five behav-ioural parameters mentioned above. In all analyses, the date was used as a random effect. These analyses were performed on two groups of treatments: the treatments that varied in cultivar identity and host presence of plant four and all treatments that had at least hosts on the last plant. All the models with a ΔAIC < 2 are presented in Tables A1-A9.

Experiment 3: cultivar mixes and presence of (non)host herbivores

To investigate how nonhosts affect foraging behaviour of *C. glomerata* females searching for their host *P. brassicae* and whether these nonhosts affect patch choice and residence time by interacting with the two cultivars Christmas Drumhead and Rivera, we used similar statistical methods as mentioned for experiment 2. We tested the effect of cultivar identity of the first three plants in a row (Cultivar Plant 123) and the last plant in a row (Cultivar Plant 4), nonhost treatment (Control, Delia, Mamestra) and any potential interactions between these variables on the same five behavioural parameters mentioned above. We also included the date as a random effect. All the models with a ΔAIC < 2 are given in Tables A10-A14.

RESULTS

Experiment 1: Cultivar Mixes in Two-choice Situations

In a wind tunnel in which we simulated a complex habitat in the form of two plant rows with different mixes of cultivars, parasitoids did not prefer a plant row with a host-infested plant of the attractive cultivar Christmas Drumhead over a plant row with a host-infested Rivera plant when they were accompanied by three undamaged Rivera plants (binomial GLMM: treatment A0: $z = 0.477$, $P = 0.633$; Fig. 1a). Attraction to the row with a host-infested Rivera plant could not be increased by adding undamaged Christmas Drumhead plants, regardless of the number of undamaged Rivera plants that were replaced (binomial GLMM: treatment A1: $z = -0.068$, $P = 0.946$; treatment A2: $z = -0.214$, $P = 0.831$; treatment A3: $z = -0.624$, $P = 0.532$; Fig. 1a). Similarly, when both host-infested plants at the end of the row were the less attractive Rivera cultivar, replacing the downwind three undamaged Rivera plants with Christmas Drumhead plants did not increase attraction, again regardless of the number of less attractive Rivera plants replaced (binomial GLMM: treatment B1: $z = 1.227$, $P = 0.220$; treatment B2: $z = -1.163$, $P = 0.245$; treatment B3: $z = -0.064$, $P = 0.949$; Fig. 1b).

Experiment 2: Cultivar Mixes and Presence of Host Herbivores

In a simulated complex habitat using a single row of four white cabbage plants with different cultivar mixes and host herbivore presence, parasitoids initiated more upwind flights when the last plant in a row was herbivore-induced, but cultivar identity of the last plant had no effect (Tables 1, 2, Fig. A2). When variation in cultivar identity and host presence of the first three plants was considered, only hosts on the first three plants significantly increased Response, whereas cultivar identity did not (Tables 1, 2, Fig. A2). Parasitoids that initiated flight towards the row of four plants spent less time on the first three plants and less time to get to the last plant and more frequently made a direct flight to the last plant in the row when the last plant was herbivore-induced (Figs 2, 4, A3, Tables 1, 2). The cultivar identity of the last plant affected none of these behaviours (Figs 2, 4, A3, Tables 1, 2). When the first three plants in the row were induced with host herbivores, parasitoids made fewer direct flights to the last host-infested plant in the row (Figs 2, 4, A3a, Tables 1, 2). The cultivar identity of the first three plants in the row and of the last plant interacted in an effect on the frequency of direct flights to the last plant in the row. When the last plant was a host-infested attractive Christmas Drumhead plant, parasitoids landed more frequently on the fourth plant when the first three plants were of the less attractive cultivar Rivera. However, when the first three plants were the more attractive Christmas Drumhead plants, the parasitoids landed more frequently on the first plants in a row and thus fewer direct flights to the last host-infested plant were observed. This was independent of whether the last plant was an attractive or less attractive cultivar.

Parasitoids spent more time on the first three plants and took significantly longer to get to the last plant when hosts were present on the first three plants, but the parasitoids took less time to find their hosts once they landed on the fourth plant (Fig. 4, A3, Tables 1, 2). The cultivar of the first three plants or of the last plant did not significantly affect any of these variables (Tables 1, 2).

Experiment 3: Cultivar Mixes and Presence of (Non)Host Herbivores

Nonhost herbivory by larvae of M. brassicae on all plants decreased the frequency of direct flights to the last plant in the row that was host-infested and increased both time spent on the first three plants and time spent to get to the host-infested plant (Figs 3, 4, A4, Tables 3, 4). Nonhost herbivory by larvae of D. radicum on all plants had a similar effect on time spent on the first three plants and the time to get to the last plant, but direct flight frequency was not different from the treatments without nonhosts (Figs 3, 4, A4, Tables 3, 4). When the first three plants were Christmas Drumhead, the frequency of direct flights to the last plant was reduced, and the time spent on the first three plants and to reach the host-infested plant at the end of the row was longer, regardless of the presence of nonhosts (Figs 3, 4, A4, Tables 3, 4). The cultivar identity of the last, host-infested plant did not affect direct flight frequency and time spent on the first three plants (Figs 3, 4, A4, Tables 3, 4). However, surprisingly, if the last plant was the more attractive cultivar Christmas Drumhead, the parasitoids took longer to get to it (Fig. 4, A4b, Tables 3, 4). The time taken to attack the host, once the parasitoid had landed on the last, host-infested plant, was reduced by the presence of D. radicum but was unaffected by the presence of M. brassicae or the cultivar identity of all the plants (Fig. A4d, Tables 3, 4). Response increased when the last, host-infested plant was a Christmas Drumhead plant, but only if the first three plants were Rivera plants or if the plants were not induced with D. radicum (Fig. A5, Tables 3, 4).

DISCUSSION

Our study identifies that differences in attraction between white cabbage cultivars affected parasitoid foraging behaviour in a small plant stand when plants were undamaged, host-infested or nonhost-infested. While the cultivar of the host-infested plant

Table 1
Effect of different cultivar mixes and host presence on five behavioural response variables of C. glomerata

Treatment	df	Response	Direct Flight	Searching Time (s)	Plant 123 Time (s)	Attack Latency (s)
RRRR	14/47	0.27 (± 0.076) A	0.07 (± 0.069) AB	355 (± 137) BC	34.8 (± 23.1) ABC	N/A
RRRC	15/48	0.27 (± 0.077) A	0.07 (± 0.064) AB	431 (± 161) C	51.1 (± 32.6) BCD	N/A
RRRR[H]	20/47	0.41 (± 0.089) AB	0.55 (± 0.111) CD	61.3 (± 19.7) A	3.82 (± 2.60) AB	93.7 (± 29.7) A
RRRC[H]	23/37	0.68 (± 0.089) BCD	0.78 (± 0.086) D	39.7 (± 11.8) A	2.73 (± 1.87) A	78.0 (± 21.8) A
CCCR[H]	23/40	0.59 (± 0.093) ABCD	0.44 (± 0.103) BCD	76.7 (± 22.9) AB	6.66 (± 3.83) AB	182 (± 53.8) A
CCCC[H]	22/47	0.47 (± 0.091) ABC	0.59 (± 0.105) CD	50.6 (± 15.5) A	2.90 (± 2.00) A	86.4 (± 25.7) A
R[H]R[H]R[H]R[H]	23/32	0.75 (± 0.086) BCD	0.30 (± 0.096) ABC	422 (± 126) C	139 (± 70.0) CD	40.6 (± 15.8) A
R[H]R[H]R[H]C[H]	25/44	0.64 (± 0.087) BCD	0.20 (± 0.080) ABC	320 (± 91.7) C	234 (± 113) CD	56.1 (± 24.3) A
C[H]C[H]C[H]R[H]	24/33	0.79 (± 0.076) CD	0.13 (± 0.068) AB	616 (± 180) C	352 (± 172) CD	38.8 (± 20.5) A
C[H]C[H]C[H]C[H]	26/31	0.89 (± 0.055) D	0.04 (± 0.038) A	679 (± 190) C	517 (± 243) D	25.7 (± 16.7) A

Response: proportion of parasitoids that landed on any plant; Direct Flight: proportion of parasitoids that flew directly to the last plant in a row; Searching Time: time until landing on the last plant; Plant 123 Time: time spent on the first three plants; Attack Latency: time until the parasitoid attacks the host after landing on the last host-infested plant. Letters in the treatment codes indicate cultivar identity from downwind to upwind plants (R = Rivera; C = Christmas Drumhead). The 'H' in superscript indicates herbivore presence on the respective plant. Means and SEs are given per treatment for each behavioural variable. Different capital letters indicate significant differences between treatments. Degrees of freedom are given as number of responders/total parasitoids tested.

Table 2
Effect of plant cultivar and host presence on five behavioural response variables of *C. glomerata*

Response variable	Distribution	Random effects	Subset	Fixed effects	Parameter estimate (SE)	P
Response	Binomial	Date	LP	Cultivar plant 4	0.43 (0.32)	0.169
				Hosts plant 4	0.91 (0.32)	**0.004**
			AP	Cultivar plant 123	0.33 (0.25)	0.193
				Hosts plant 123	0.93 (0.26)	**<0.001**
Direct Flight	Binomial	Date	LP	Cultivar plant 4	1.00 (0.69)	0.147
				Hosts plant 4	4.01 (1.17)	**<0.001**
			AP	Cultivar plant 123	−0.92 (0.36)	**0.010**
				Hosts plant 123	−1.34 (0.48)	**0.005**
				Cultivar plant 4	0.84 (0.45)	0.064
				Hosts plant 123 * Cultivar plant 4	−1.57 (0.73)	**0.032**
Log (Searching Time)	Gaussian	Date	LP	Hosts plant 4	−2.09 (0.26)	**<0.001**
			AP	Cultivar plant 123	0.42 (0.21)	0.052
				Hosts plant 123	2.18 (0.21)	**<0.001**
				Cultivar plant 4	−0.24 (0.21)	0.255
Log (Plant 123 Time + 1)	Gaussian	Date	LP	Cultivar plant 4	0.39 (0.80)	0.626
				Hosts plant 4	−2.01 (0.75)	**0.010**
				Cultivar plant 4 * Hosts plant 4	−0.65 (1.04)	0.534
			AP	Cultivar plant 123	0.57 (0.35)	0.108
				Hosts plant 123	3.61 (0.51)	**<0.001**
				Cultivar plant 4	−0.46 (0.51)	0.375
				Hosts plant 123 * Cultivar plant 4	0.91 (0.71)	0.201
Log (Attack Latency)	Gaussian	Date	AP	Hosts plant 123	−0.93 (0.28)	**0.001**
				Cultivar plant 4	−0.33 (0.25)	0.190

Influence of cultivar identity of the first three plants (Cultivar Plant 123), cultivar identity of the last plant (Cultivar Plant 4), host presence on the first three plants (Hosts Plant 123), host presence on the last plant (Hosts Plant 4) and any retained interactions between these variables on five foraging behaviours of *Cotesia glomerata*. Response: proportion of parasitoids that landed on any plant; Direct Flight: proportion of parasitoids that flew directly to the last plant in a row; Searching Time: time until landing on the last plant; Plant 123 Time: time spent on the first three plants; Attack Latency: time until the parasitoid attacks the host after landing on the last host-infested plant. The analyses were performed on two subsets of the data set: the treatments that varied in cultivar identity and host presence of plant four (last plant; LP) and all treatments that had at least hosts on the last plant (all plants; AP). Parameter estimates are given with SEs in parentheses. Significant *P* values ($\alpha < 0.05$) are shown in bold.
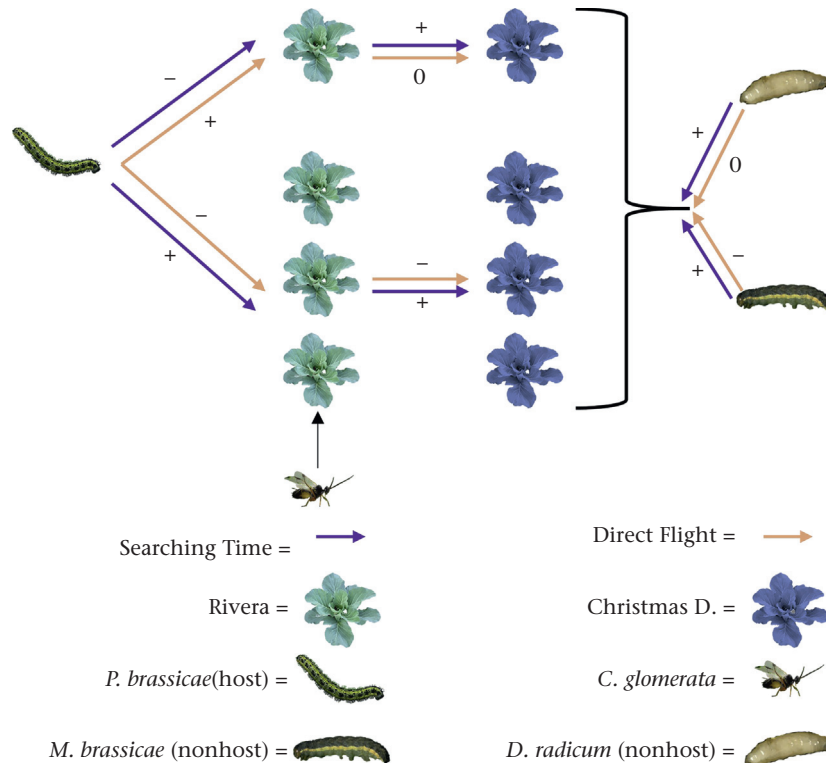
Figure 4. Schematic representation of the effects of switching the cultivar of the first three or the last plant from Rivera to Christmas Drumhead, host herbivore presence on the first three or the last plant and nonhost presence on all four plants on the fraction of parasitoids that first landed on the last plant (Direct Flight) and the time taken by parasitoids to reach the last plant (Searching Time). A (+) indicates a positive effect, a (−) a negative effect and a (0) no significant effect ($\alpha < 0.05$). The vertical black arrow indicates the flight direction of the parasitoids.

Table 3
Effect of different cultivar mixes and nonhost presence on five behavioural response variables of *C. glomerata*

Nonhost	Treatment	df	Response	Direct Flight	Searching Time (s)	Plant 123 Time (s)	Attack Latency (s)
Control	RRRR[H]	25/39	0.65 (± 0.093) AB	0.93 (± 0.051) C	30.5 (± 6.67) AB	1.83 (± 1.07) A	105 (± 34.8) A
	CCCR[H]	25/33	0.78 (± 0.082) AB	0.92 (± 0.055) C	37.2 (± 8.16) AB	1.80 (± 1.06) A	67.2 (± 22.0) A
	RRRC[H]	25/31	0.82 (± 0.077) AB	0.84 (± 0.077) BC	28.4 (± 6.22) A	2.57 (± 1.34) A	68.2 (± 22.7) A
	CCCC[H]	26/33	0.79 (± 0.080) AB	0.77 (± 0.092) ABC	78.2 (± 16.8) BC	5.41 (± 2.37) AB	54.8 (± 18.5) A
Delia	RRRR[H]	25/38	0.69 (± 0.089) AB	0.75 (± 0.094) ABC	39.8 (± 8.71) AB	5.08 (± 2.29) AB	31.3 (± 10.2) A
	CCCR[H]	24/30	0.81 (± 0.078) AB	0.76 (± 0.094) ABC	41.5 (± 9.24) ABC	5.17 (± 2.36) AB	25.7 (± 8.50) A
	RRRC[H]	29/40	0.72 (± 0.072) AB	0.94 (± 0.043) C	60.0 (± 12.2) ABC	2.77 (± 1.33) A	66.0 (± 21.2) A
	CCCC[H]	26/49	0.54 (± 0.090) A	0.70 (± 0.104) ABC	82.8 (± 17.9) BC	10.8 (± 4.38) ABC	47.0 (± 15.8) A
Mamestra	RRRR[H]	27/40	0.68 (± 0.089) AB	0.62 (± 0.109) ABC	61.3 (± 12.9) ABC	12.8 (± 5.02) ABC	45.6 (± 15.1) A
	CCCR[H]	25/36	0.73 (± 0.085) AB	0.36 (± 0.107) A	110 (± 24.0) C	27.0 (± 10.5) BC	48.4 (± 15.8) A
	RRRC[H]	26/28	0.92 (± 0.053) B	0.61 (± 0.110) ABC	71.7 (± 15.4) ABC	18.2 (± 7.11) ABC	82.1 (± 27.8) A
	CCCC[H]	25/29	0.88 (± 0.064) B	0.45 (± 0.116) AB	112 (± 24.5) C	34.9 (± 13.5) C	50.1 (± 17.4) A

Response: proportion of parasitoids that landed on any plant; Direct Flight: proportion of parasitoids that flew directly to the last plant in a row; Searching Time: time until landing on the last plant; Plant 123 Time: time spent on the first three plants; Attack Latency: time until the parasitoid attacks the host after landing on the last host-infested plant. Letters in the treatment codes indicate cultivar identity from downwind to upwind plants (R = Rivera; C = Christmas Drumhead). The 'H' in superscript indicates herbivore presence on the respective plant. Means and SEs are given per treatment for each behavioural variable. Different capital letters indicate significant differences between treatments. Degrees of freedom are given as number of responders/total parasitoids tested.

Table 4
Effect of plant cultivar and nonhost presence on five behavioural response variables of *C. glomerata*

Response variable	Distribution	Random effects	Fixed effects	Parameter estimate (SE)	P
Response	Binomial	Date	Delia on plants	0.34 (0.38)	0.378
			Mamestra on plants	0.24 (0.31)	0.445
			Cultivar plant 123	0.49 (0.32)	0.135
			Cultivar plant 4	1.39 (0.42)	**<0.001**
			Delia on plants * Cultivar plant 4	−1.44 (0.49)	**0.003**
			Cultivar plant 123 * Cultivar plant 4	−1.04 (0.49)	**0.033**
Direct Flight	Binomial	Date	Delia on plants	−0.50 (0.39)	0.199
			Mamestra on plants	−1.83 (0.37)	**<0.001**
			Cultivar plant 123	−0.72 (0.29)	**0.014**
Log (Searching Time)	Gaussian	Date	Delia on plants	0.30 (0.15)	**0.047**
			Mamestra on plants	0.76 (0.15)	**<0.001**
			Cultivar plant 123	0.43 (0.12)	**<0.001**
			Cultivar plant 4	0.33 (0.12)	**0.008**
Log (Plant 123 Time + 1)	Gaussian	Date	Delia on plants	0.54 (0.25)	**0.032**
			Mamestra on plants	1.82 (0.25)	**<0.001**
			Cultivar plant 123	0.52 (0.20)	**0.011**
			Cultivar plant 4	0.30 (0.20)	0.147
Log (Attack Latency)	Gaussian	Date	Delia on plants	−0.80 (0.27)	**0.003**
			Cultivar plant 4	0.00 (0.22)	0.987
			Delia on plants * Cultivar plant 4	0.68 (0.38)	0.077

Influence of cultivar identity of the first three plants (Cultivar Plant 123), cultivar identity of the last plant (Cultivar Plant 4), *D. radicum* presence on all plants (Delia), *M. brassicae* presence on all plants (Mamestra) and any retained interactions between these variables on five foraging behaviours of *Cotesia glomerata*. Response: proportion of parasitoids that landed on any plant; Direct Flight: proportion of parasitoids that flew directly to the last plant in a row; Searching Time: time until landing on the last plant; Plant 123 Time: time spent on the first three plants; Attack Latency: time until the parasitoid attacks the host after landing on the last host-infested plant. Parameter estimates are given with SEs in parentheses. Significant *P* values (α < 0.05) are shown in bold.

directly influenced parasitoid foraging, that of the plants downwind of it also affected the efficiency in reaching host-infested plants. Parasitoids were more efficient at locating the host, as indicated by flying over nonprofitable patches, when the first three plants were of the less attractive Rivera cultivar and the last plant was the more attractive Christmas Drumhead. Moreover, even when host distribution was equal on all four plants, parasitoids still showed a similar preference for more upwind plants. Furthermore, parasitoid patch residence time on the first three plants was higher when these were of the attractive Christmas Drumhead cultivar, even when they had no hosts on them and especially when they had nonhosts from the same feeding guild as the host (*M. brassicae*). The presence of nonhost herbivores on the attractive cultivar Christmas Drumhead, but not on the less attractive Rivera cultivar, led to an up to twofold increase in time spent on the plants without hosts and a decrease in direct flights to the host-infested plant, indicating distraction of *C. glomerata*. Below, we discuss how variation in (herbivore-induced) plant volatiles caused by variation in plant traits (cultivars) and nonhost herbivores affects parasitoid foraging in (agro)ecological communities.

Patch Selection

We found that *C. glomerata* chose upwind plants more often when their volatiles were more apparent, and that nonhost herbivory could lead to nonrewarding patch choices. For example, when only the last plant was herbivore infested or was the attractive Christmas Drumhead cultivar, parasitoids initially landed on this last plant more often than when all plants had herbivores on them or were the same cultivar. Furthermore, our two-choice assay might have resulted in (partly-)overlapping odour profiles that were not sufficiently distinguishable to the parasitoid, which could have made patch choice more difficult or even absent. Selection of profitable patches containing hosts is important for parasitoid foraging success, but finding them might be complicated in nature by the complexity of available information (Aartsma, Cusumano, et al., 2019). Parasitoids clearly distinguish between differently profitable patches in relatively simple foraging situations in Y-tube olfactometers, wind tunnels and simple greenhouse or field set-ups (Aartsma, Leroy, et al., 2019; Bukovinszky et al., 2005; Degen et al., 2012; Geervliet et al., 1994; Kos et al., 2011; Li et al., 2018, 2017;

Poelman et al., 2009, 2013; Thanikkul et al., 2017). However, when subjected to a greater variation of available information in more complex habitats such as in our current study, parasitoid foraging decisions might be constrained depending on the ecological context of plant community, abiotic conditions and presence of other nonhost herbivores (Aartsma, Hao, et al., 2020; Aartsma, Pappagallo, et al., 2020; Bukovinszky et al., 2007, 2012; Li et al., 2016). Genetic variation in plant traits might influence the quality of hosts or the chance of encountering hosts, which might be indicative of patch profitability (Bustos-Segura et al., 2017; Gaillard et al., 2018; Lamy et al., 2018). Optimal patch finding might also be complicated when information from different patches combine or when information is physically obstructed (Bukovinszky et al., 2007). Also, herbivory by nonhosts might further complicate optimal patch selection, as parasitoids might wrongly interpret patches including nonhosts as patches containing hosts (Moujahed et al., 2014), especially if these nonhosts induce similar volatile cues (Gols et al., 2012; Peñaflor et al., 2017; Thanikkul et al., 2017), or distort information from hosts (Desurmont et al., 2016; Hu et al., 2020; Moujahed et al., 2014; Pierre et al., 2011).

Patch Leaving

According to the marginal value theorem, a parasitoid would be expected to leave a patch when the host encounter rate within it drops below the average encounter rate for the habitat (Charnov, 1976). For parasitoids this means balancing the risks and time expenditure of initiating flight in search of a more profitable patch with continuing the search for more hosts on a patch (Muratori et al., 2008). Information available to the parasitoid might regularly lack reliability, which might result in suboptimal patch choices (Vet et al., 1995). The effect of a suboptimal foraging choice on foraging efficiency might depend on the detectability of profitability of the current patch and the apparency of signals from better patches. When a patch contains no direct information potentially indicating host presence, a choice to leave is evident and rapidly made (Vosteen et al., 2019). However, when a patch contains nonhost cues resembling host cues, a parasitoid might lose time on a nonhost-infested patch (Bukovinszky et al., 2012) or even suffer detrimental losses through nonhost oviposition (Carrasco et al., 2018; Steven et al., 2019; Vosteen et al., 2019) and defence mechanisms employed by such nonhosts (Brodeur et al., 1996; Desurmont et al., 2017). Alternatively, infestation of both hosts and nonhosts on a patch might also lead to the parasitoid prematurely leaving the patch if direct cues of a nonhost are picked up prior to those of a host (De Rijk, Wang, et al., 2016; De Rijk, Yang, et al., 2016). A decision to leave also depends on the contrast of available information from the environment indicating potentially more profitable patches upwind (Soler, Harvey, & Bezemer, 2007; Vosteen et al., 2019), whereas profitable patches downwind are not detected (Vosteen et al., 2020). Indeed, we found that parasitoids spent less time on the first three plants when the contrast with the last plant was greatest: when only the last plant was either host-infested or was the more attractive Christmas Drumhead cultivar. Finally, experience can aid optimal patch selection as parasitoids learn to distinguish honest patch quality information from noise (Desurmont et al., 2018; Gols et al., 2012; Vet et al., 1995). Furthermore, experience can optimize leaving tendencies based on prior information on patch qualities within the habitat (Vos et al., 1998). Especially for a parasitoid of gregarious hosts, like *C. glomerata*, patch quality varies markedly, as the number of hosts on a patch can vary from a few to hundreds of individuals. This increases the benefit of reliably assessing patch quality through prior experience and adjusting leaving decisions accordingly (Vos et al., 1998).

Conclusion and Future Perspectives

Cotesia glomerata patch choice and patch residence time is affected by the apparency of available information. This apparency is influenced by intraspecific variation among plants in volatile emission used by parasitoids as the primary information source to locate profitable patches, like the difference between Christmas Drumhead and Rivera in this study, or by the presence of host and/or nonhost herbivores. We conclude that optimal foraging decisions by animals foraging in a patchy environment are affected by variation in the apparency of information on patch profitability and how such information is often incomplete, distorted by noise or conflicting information or even mixed into complex volatile information blends. In agroecosystems, increasing parasitoid foraging efficiency to maximize biological control through careful selection of plant cultivars with apparent volatile blends might protect crops. Such conservation biological control measures might reduce crop injury and increase crop quality (Juventia et al., 2021). Future studies should take the natural complexity of available information into account and further investigate how animal behaviour is affected by incoming information.

Author Contributions

Luuk Croijmans: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing − original draft, Writing − review & editing, Visualization, Supervision. **Reinier T. Valstar**: Methodology, Investigation. **Lien Schuur**: Methodology, Investigation. **Isabelle Jacobs**: Methodology, Investigation, Writing − review & editing, Visualization. **Dirk F. van Apeldoorn**: Conceptualization, Writing − review & editing, Supervision. **Erik H. Poelman**: Conceptualization, Methodology, Writing − review & editing, Supervision, Project administration, Funding acquisition.

Data Availability

Data will be made available on request.

Declaration of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

Table A1
Model selection on the effect of plant cultivar and host presence of the last plant on response rate

Model	Cultivar 4	Host 4	Cultivar 4 * Host 4	df	logLik	AIC	ΔAIC	Weight
3	NA	**0.870**	NA	2	−116.7	237.3	0.00	0.379
4	0.434	**0.908**	NA	3	−115.7	237.4	0.09	0.362
8	0.069	0.557	0.728	4	−115.0	238.1	0.77	0.259

Model selection table for the effect of switching the last (fourth) Rivera plant for a Christmas Drumhead plant (Cultivar 4), host presence on the last plant (Host 4) and any interactions on parasitoid response rate. AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A2
Model selection on the effect of plant cultivar and host presence on Response

Model	Cultivar 123	Cultivar 4	Host 123	Cultivar 123 * Cultivar 4	Cultivar 123 * Host 123	Cultivar 4 * Host 123	Cultivar 123 * Cultivar 4 * Host 123	df	logLik	AIC	ΔAIC	Weight
22	−0.007	NA	0.565	NA	0.826	NA	NA	5	−196.5	403.0	0.00	0.256
5	NA	NA	**0.908**	NA	NA	NA	NA	3	−198.6	403.2	0.21	0.231
128	0.659	**0.999**	**1.323**	**−1.439**	−0.471	**−1.528**	**2.700**	9	−192.7	403.4	0.46	0.204
6	0.330	NA	**0.928**	NA	NA	NA	NA	4	−197.7	403.5	0.51	0.199
24	−0.020	0.143	0.548	NA	0.856	NA	NA	6	−196.3	404.7	1.69	0.110

Model selection table for the effect of switching the first three Rivera plants for Christmas Drumhead plants (Cultivar 123), switching the last Rivera plant for a Christmas drumhead plant (Cultivar 4), host presence on the first three plants (Host 123) and any interactions on parasitoid Response. AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A3
Model selection on the effect of plant cultivar and host presence of the last plant on Direct Flight

Model	Cultivar 4	Host 4	Cultivar 4 * Host 4	df	logLik	AIC	ΔAIC	Weight
4	1.002	**4.007**	NA	4	−33.0	73.9	0.00	0.416
3	NA	**3.775**	NA	3	−34.1	74.2	0.30	0.358
8	−0.215	**3.256**	1.537	5	−32.6	75.1	1.23	0.226

Model selection table for the effect of switching the last (fourth) Rivera plant for a Christmas Drumhead plant (Cultivar 4), host presence on the last plant (Host 4) and any interactions on the proportion of parasitoids that flew directly to the last plant without landing on another plant (Direct Flight). AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A4
Model selection on the effect of plant cultivar and host presence on Direct Flight

Model	Cultivar 123	Cultivar 4	Host 123	Cultivar 123 * Cultivar 4	Cultivar 123 * Host 123	Cultivar 4 * Host 123	df	logLik	AIC	ΔAIC	Weight
40	**−0.925**	0.841	**−1.344**	NA	NA	**−1.568**	6	−97.0	206.1	0.00	0.390
56	−0.673	0.833	−1.057	NA	−0.695	**−1.581**	7	−96.6	207.3	1.16	0.218
6	**−0.919**	NA	**−2.093**	NA	NA	NA	4	−99.6	207.3	1.17	0.217
48	−0.729	1.098	**−1.317**	−0.455	NA	**−1.667**	7	−96.9	207.7	1.61	0.174

Model selection table for the effect of switching the first three Rivera plants for Christmas Drumhead plants (Cultivar 123), switching the last Rivera plant for a Christmas drumhead plant (Cultivar 4), host presence on the first three plants (Host 123) and any interactions on Direct Flight. AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A5
Model selection on the effect of plant cultivar and host presence of the last plant on Searching Time

Model	Cultivar 4	Host 4	df	logLik	AIC	ΔAIC	Weight
3	NA	**−2.090**	4	−108.3	224.6	0.00	1.00

Model selection table for the effect of switching the last (fourth) Rivera plant for a Christmas Drumhead plant (Cultivar 4), host presence on the last plant (Host 4) and any interactions on the time the parasitoid took to get to the last plant (Searching Time). AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A6
Model selection on the effect of plant cultivar and host presence on Searching Time

Model	Cultivar 123	Cultivar 4	Host 123	Cultivar 123 * Cultivar 4	Cultivar 123 * Host 123	Cultivar 4 * Host 123	df	logLik	AIC	ΔAIC	Weight
6	**0.422**	NA	**2.181**	NA	NA	NA	5	−334.5	679.0	0.00	0.381
5	NA	NA	**2.181**	NA	NA	NA	4	−335.8	679.7	0.64	0.276
22	0.254	NA	**2.018**	NA	0.320	NA	6	−334.2	680.3	1.30	0.199
8	0.417	−0.243	**2.183**	NA	NA	NA	6	−334.5	681.0	1.95	0.144

Model selection table for the effect of switching the first three Rivera plants for Christmas Drumhead plants (Cultivar 123), switching the last Rivera plant for a Christmas drumhead plant (Cultivar 4), host presence on the first three plants (Host 123) and any interactions on the time the parasitoid took to get to the last plant. AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A7
Model selection on the effect of plant cultivar and host presence of the last plant on time spent on the first three plants

Model	Cultivar 4	Host 4	Cultivar 4 * Host 4	df	logLik	AIC	ΔAIC	Weight
3	NA	**−2.345**	NA	4	−156.5	321.0	0.00	0.497
8	0.394	**−2.006**	−0.650	6	−155.1	322.3	1.21	0.271
4	0.005	**−2.344**	NA	5	−156.3	322.6	1.52	0.232

Model selection table for the effect of switching the last (fourth) Rivera plant for a Christmas Drumhead plant (Cultivar 4), host presence on the last plant (Host 4) and any interactions on the time parasitoids spent on the first three plants (Plant 123 Time). AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A8
Model selection on the effect of plant cultivar and host presence on time spent on the first three plants

Model	Cultivar 123	Cultivar 4	Host 123	Cultivar 123 * Cultivar 4	Cultivar 123 * Host 123	Cultivar 4 * Host 123	Cultivar 123 * Cultivar 4 * Host 123	df	logLik	AIC	ΔAIC	Weight
6	0.578	NA	**4.074**	NA	NA	NA	NA	5	−426.2	862.3	0.00	0.22
22	0.270	NA	**3.776**	NA	0.584	NA	NA	6	−425.2	862.5	0.18	0.20
5	NA	NA	**4.073**	NA	NA	NA	NA	4	−427.4	862.8	0.44	0.18
40	0.568	−0.456	**3.607**	NA	NA	0.906	NA	7	−424.9	863.8	1.46	0.11
56	0.249	−0.471	**3.290**	NA	0.606	0.921	NA	8	−423.9	863.9	1.56	0.10
128	0.462	−0.257	**3.368**	−0.417	0.462	0.775	0.283	10	−422.0	864.0	1.72	0.09
39	NA	−0.482	**3.593**	NA	NA	0.931	NA	6	−426.1	864.1	1.80	0.09

Model selection table for the effect of switching the first three Rivera plants for Christmas Drumhead plants (Cultivar 123), switching the last Rivera plant for a Christmas drumhead plant (Cultivar 4), host presence on the first three plants (Host 123) and any interactions on the time parasitoids spent on the first three plants. AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A9
Model selection on the effect of plant cultivar and host presence on Attack Latency

Model	Cultivar 123	Cultivar 4	Host 123	Cultivar 4 * Host 123	df	logLik	AIC	ΔAIC	Weight
5	NA	NA	**−0.902**	NA	4	−177.0	362.5	0.00	0.53
7	NA	−0.327	**−0.932**	NA	5	−176.6	363.9	1.42	0.26
39	NA	−0.486	**−1.203**	0.585	6	−175.8	364.4	1.95	0.20

Model selection table for the effect of switching the first three Rivera plants for Christmas Drumhead plants (Cultivar 123), switching the last Rivera plant for a Christmas drumhead plant (Cultivar 4), host presence on the first three plants (Host 123) and any interactions on the time parasitoids took to attack their host since they initially landed on the last plant (Attack Latency). AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A10
Model selection on the effect of plant cultivar and nonhost presence on Response

Model	Cultivar 123	Cultivar 4	Delia	Mamestra	Cultivar 123 * Cultivar 4	Cultivar 123 * Delia	Cultivar 4 * Delia	Cultivar 4 * Mamestra	df	logLik	AIC	ΔAIC	Weight
152	0.486	**1.369**	0.214	NA	**−1.033**	NA	**−1.418**	NA	7	−232.6	479.5	0.00	0.295
135	NA	**0.829**	0.199	NA	NA	NA	**−1.399**	NA	5	−234.9	479.9	0.44	0.237
160	0.485	**1.388**	0.336	0.236	**−1.036**	NA	**−1.435**	NA	8	−232.3	481.0	1.50	0.139
143	NA	**0.844**	0.318	0.231	NA	NA	**−1.415**	NA	6	−234.6	481.4	1.94	0.112
416	0.486	**1.035**	0.192	−0.046	**−1.050**	NA	−1.078	0.839	9	−231.5	481.5	1.99	0.109
184	0.529	**1.341**	0.272	NA	**−1.000**	−0.143	**−1.393**	NA	8	−232.6	481.5	2.00	0.109

Model selection table for the effect of switching the first three Rivera plants for Christmas Drumhead plants (Cultivar 123), switching the last Rivera plant for a Christmas drumhead plant (Cultivar 4), presence of *D. radicum* on all four plants (Delia), presence of *M. brassicae* on all four plants (Mamestra) and any interactions on parasitoid Response. AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A11
Model selection on the effect of plant cultivar and nonhost presence on Direct Flight

Model	Cultivar 123	Cultivar 4	Delia	Mamestra	Cultivar 123 * Cultivar 4	Cultivar 123 * Delia	Cultivar 4 * Delia	Cultivar 4 * Mamestra	df	logLik	AIC	ΔAIC	Weight
152	0.486	**1.369**	0.214	NA	**−1.033**	NA	**−1.418**	NA	7	−232.6	479.5	0.00	0.295
135	NA	**0.829**	0.199	NA	NA	NA	**−1.399**	NA	5	−234.9	479.9	0.44	0.237
160	0.485	**1.388**	0.336	0.236	**−1.036**	NA	**−1.435**	NA	8	−232.3	481.0	1.50	0.139
143	NA	**0.844**	0.318	0.231	NA	NA	**−1.415**	NA	6	−234.6	481.4	1.94	0.112
416	0.486	**1.035**	0.192	−0.046	**−1.050**	NA	−1.078	0.839	9	−231.5	481.5	1.99	0.109
184	0.529	**1.341**	0.272	NA	**−1.000**	−0.143	**−1.393**	NA	8	−232.6	481.5	2.00	0.109

Model selection table for the effect of switching the first three Rivera plants for Christmas Drumhead plants (Cultivar 123), switching the last Rivera plant for a Christmas drumhead plant (Cultivar 4), presence of *D. radicum* on all four plants (Delia), presence of *M. brassicae* on all four plants (Mamestra) and any interactions on the proportion of parasitoids that flew directly to the last plant without landing on another plant (Direct Flight). AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A12
Model selection on the effect of plant cultivar and nonhost presence on Searching Time

Model	Cultivar 123	Cultivar 4	Delia	Mamestra	Cultivar 123 * Cultivar 4	Cultivar 123 * Delia	Cultivar 4 * Delia	Cultivar 4 * Mamestra	df	logLik	AIC	ΔAIC	Weight
16	**0.433**	**0.329**	**0.304**	**0.764**	NA	NA	NA	NA	7	−467.2	948.4	0.00	0.17
12	**0.429**	**0.333**	NA	**0.610**	NA	NA	NA	NA	6	−468.2	948.5	0.04	0.17
48	**0.560**	**0.326**	**0.487**	**0.767**	NA	−0.375	NA	NA	8	−466.6	949.2	0.80	0.12
268	**0.432**	**0.454**	NA	**0.795**	NA	NA	NA	−0.367	7	−467.7	949.4	0.95	0.11
272	**0.436**	**0.447**	**0.300**	**0.943**	NA	NA	NA	−0.358	8	−466.7	949.4	1.00	0.10
144	**0.435**	0.216	0.129	**0.763**	NA	NA	0.336	NA	8	−466.8	949.6	1.20	0.09
32	0.278	0.178	**0.305**	**0.764**	0.306	NA	NA	NA	8	−466.9	949.9	1.44	0.08
28	0.277	0.184	NA	**0.610**	0.301	NA	NA	NA	7	−468.0	949.9	1.53	0.08
304	**0.563**	**0.444**	**0.483**	**0.945**	NA	−0.374	NA	−0.357	9	−466.1	950.2	1.80	0.07

Model selection table for the effect of switching the first three Rivera plants for Christmas Drumhead plants (Cultivar 123), switching the last Rivera plant for a Christmas drumhead plant (Cultivar 4), presence of *D. radicum* on all four plants (Delia), presence of *M. brassicae* on all four plants (Mamestra) and any interactions on the time the parasitoid took to get to the last plant (Searching Time). AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

Table A13
Model selection on the effect of plant cultivar and nonhost presence on time spent on the first three plants
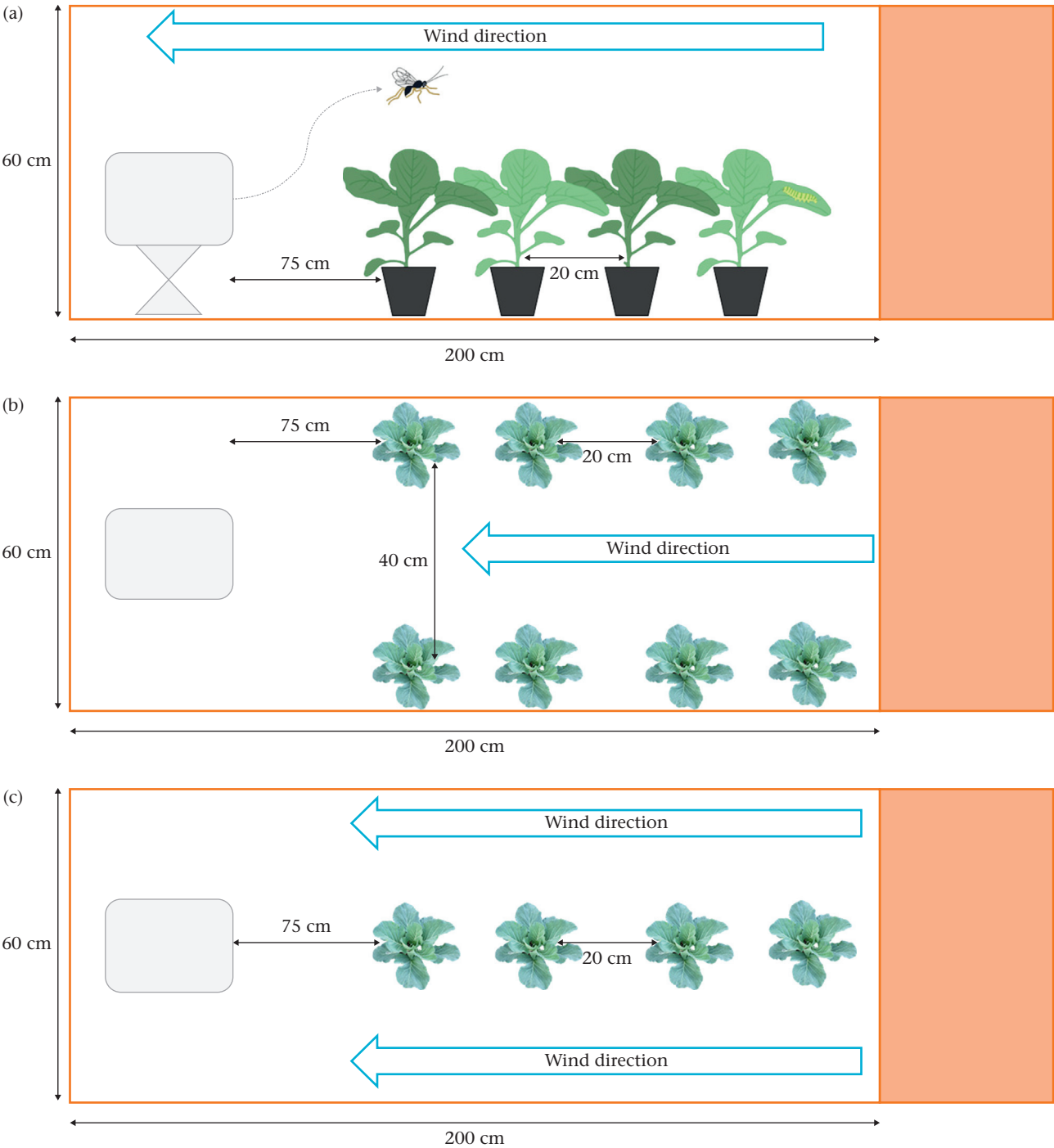
Model	Cultivar 123	Cultivar 4	Delia	Mamestra	Cultivar 123 * Cultivar 4	Cultivar 123 * Delia	Cultivar 123 * Mamestra	df	logLik	AIC	ΔAIC	Weight
14	**0.525**	NA	**0.548**	**1.817**	NA	NA	NA	6	−621.8	1255.6	0.00	0.30
16	**0.523**	0.298	**0.541**	**1.820**	NA	NA	NA	7	−621.4	1256.8	1.23	0.16
32	0.240	0.024	**0.544**	**1.820**	0.556	NA	NA	8	−620.5	1256.9	1.33	0.15
78	0.452	NA	**0.546**	**1.709**	NA	NA	0.217	7	−621.6	1257.2	1.58	0.14
46	0.483	NA	0.488	**1.816**	NA	0.123	NA	7	−621.7	1257.3	1.76	0.12
10	**0.518**	NA	NA	**1.538**	NA	NA	NA	5	−623.7	1257.4	1.83	0.12

Model selection table for the effect of switching the first three Rivera plants for Christmas Drumhead plants (Cultivar 123), switching the last Rivera plant for a Christmas drumhead plant (Cultivar 4), presence of *D. radicum* on all four plants (Delia), presence of *M. brassicae* on all four plants (Mamestra) and any interactions on the time parasitoids spent on the first three plants (Plant 123 Time). AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.

**Table A14**
Model selection on the effect of plant cultivar and nonhost presence on Attack Latency

| Model	Cultivar 123	Cultivar 4	Delia	Mamestra	Cultivar 4 * Delia	df	logLik	AIC	ΔAIC	Weight
5	NA	NA	−**0.454**	NA	NA	4	−541.8	1091.6	0.00	0.34
135	NA	0.004	−**0.797**	NA	0.678	6	−540.2	1092.4	0.86	0.22
6	−0.270	NA	−**0.455**	NA	NA	5	−541.5	1092.9	1.37	0.17
13	NA	NA	−**0.585**	−0.267	NA	5	−541.7	1093.3	1.73	0.14
7	NA	0.234	−**0.459**	NA	NA	5	−541.7	1093.5	1.92	0.13

Model selection table for the effect of switching the first three Rivera plants for Christmas Drumhead plants (Cultivar 123), switching the last Rivera plant for a Christmas drumhead plant (Cultivar 4), presence of *D. radicum* on all four plants (Delia), presence of *M. brassicae* on all four plants (Mamestra) and any interactions on the time parasitoids took to attack their host since they initially landed on the last plant (Attack Latency). AIC: Akaike information criterion. All models with a ΔAIC lower than 2 are given. Significant effects on attraction by specific plants are indicated in bold. The chosen model is indicated in bold; see Methods for the model selection procedure. NA indicates that the variable in question was not retained in the model.
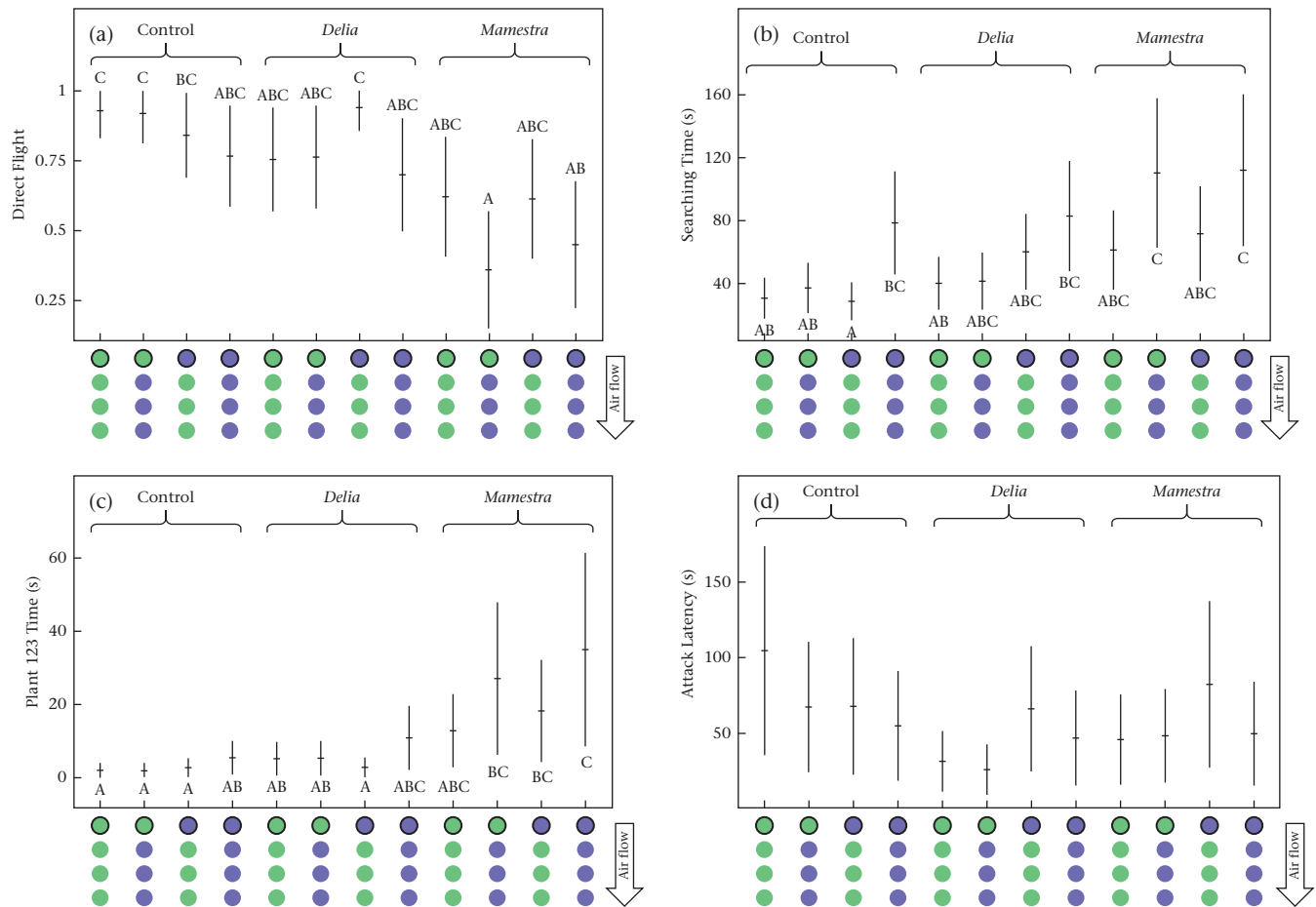

Figure A1. Experimental set-up in the wind tunnel. On the left is the glass cylinder in which parasitoids were released, and which was 75 cm from the first plant in a row. Plants were placed 20 cm apart. The wind direction was always towards the glass cylinder, in the figure from right to left. (a) Side view of the wind tunnel. (b) Top view of the wind tunnel for experiment 1, the two-choice assay with rows of four plants. The two plant rows were placed 40 cm apart. (c) Top view of the wind tunnel for experiments 2 and 3.
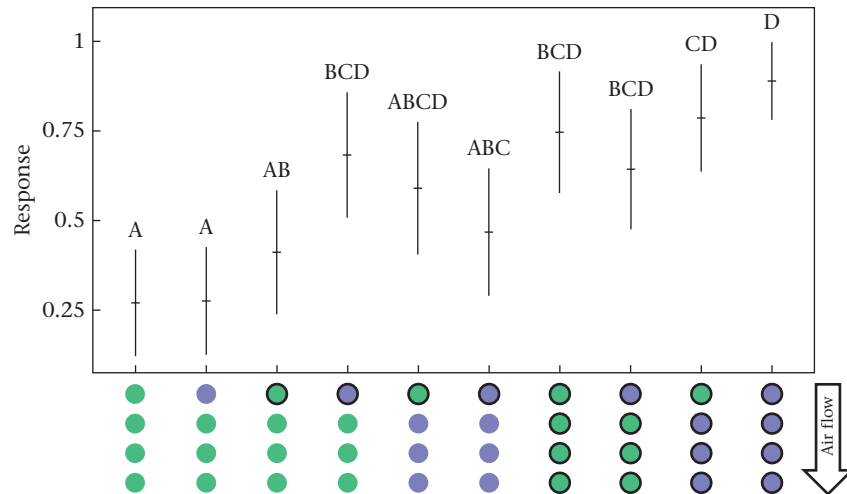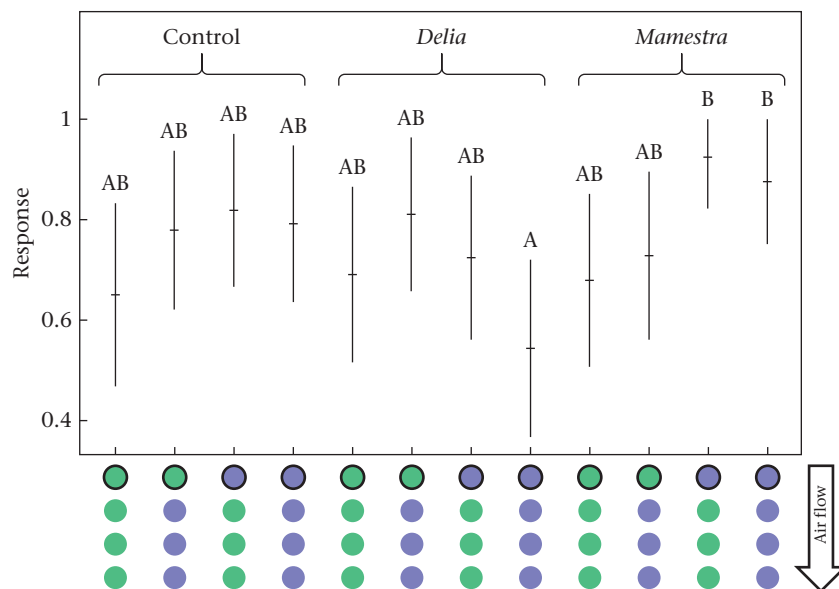
Figure A2. Influence of different cultivar mixes and host presence on the proportion of parasitoids that took flight and landed on a plant (Response). Different capital letters indicate significant differences between groups. The coloured dots at the bottom of each graph illustrate the set-up of plants with the topmost plant indicating the most upwind (last) plant in the row: green is Rivera, blue is Christmas Drumhead, and a dark circle around a dot indicates the presence of 10 first-instar host larvae (*P. brassicae*).
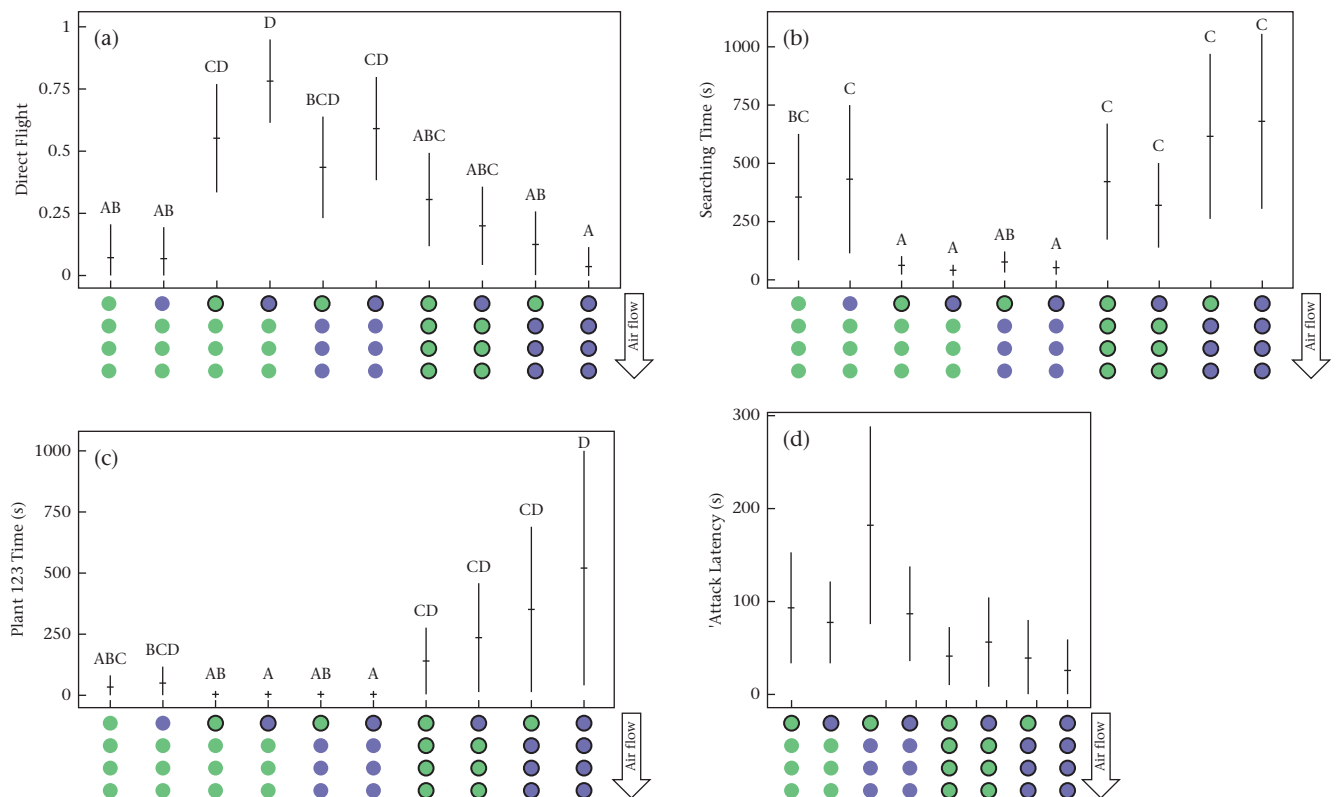
Figure A3. Influence of different cultivar mixes and host presence on (a) the proportion of parasitoids that flew directly to the last plant in a row (Direct Flight), (b) the time parasitoids took to reach the last plant (Searching Time), (c) the time parasitoids spent on the first three plants (Plant 123 Time) and (d) the time it took parasitoids to attack a host after landing on the last plant (Attack Latency). Different capital letters indicate significant differences between groups. The coloured dots at the bottom of each graph illustrate the set-up of plants with the topmost plant indicating the most upwind (last) plant in the row: green is Rivera, blue is Christmas Drumhead, and a dark circle around a dot indicates the presence of 10 first-instar host larvae (*P. brassicae*).

Figure A4. Influence of different cultivar mixes and nonhost presence on (a) the proportion of parasitoids that flew directly to the last plant in a row (Direct Flight), (b) the time parasitoids took to reach the last plant (Searching Time), (c) the time parasitoids spent on the first three plants (Plant 123 Time) and (d) the time it took parasitoids to attack a host after landing on the last plant (Attack Latency). Different capital letters indicate significant differences between groups. The coloured dots at the bottom of each graph illustrate the set-up of plants with the topmost plant indicating the most upwind (last) plant in the row: green is Rivera, blue is Christmas Drumhead, and a dark circle around a dot indicates the presence of 10 first-instar host larvae (*P. brassicae*).

Figure A5. Influence of different cultivar mixes and nonhost presence on the proportion of parasitoids that took flight and landed on a plant (Response). Different capital letters indicate significant differences between groups. The coloured dots at the bottom of each graph illustrate the set-up of plants with the topmost plant indicating the most upwind (last) plant in the row: green is Rivera, blue is Christmas Drumhead, and a dark circle around a dot indicates the presence of 10 first-instar host larvae (*P. brassicae*).