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Adverse weather conditions impede odor-guided foraging of parasitoids and reduce their host-finding success

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ABSTRACT

Biological pest control depends on the ability of natural enemies to find herbivore-infested plants, which is often guided by herbivore-induced plant volatiles (HIPVs). While foraging behavior of natural enemies has been extensively studied under controlled conditions, little is known on how odor-guided foraging behavior is influenced by fluctuating weather conditions in the field.

Here we investigated how HIPV-guided foraging of *Cotesia glomerata* parasitoids is influenced by prevailing weather conditions in the field. *C. glomerata* females were released in 5 m radius circles of cabbage plants infested with *Pieris brassicae* caterpillars, and host finding success and direction of foraging activity was assessed by recapturing parasitoids on the host-infested plants. Wind speed and direction, humidity, barometric pressure and temperature was recorded and related to parasitoid foraging activity. Parasitoid foraging behavior was studied in more detail by observing individually released parasitoids in 0.5 m circles with host-infested cabbages.

Recapture rates and movement direction of parasitoids was influenced by an interaction between humidity, wind speed, temperature and change in barometric pressure. High humidity and low wind speed was generally positively associated with host finding success. Direct observations of parasitoid flight behavior confirmed the influence of humidity and wind speed. Successful host finding in upwind direction was only observed at wind speeds below 3 m/s.

Our study highlights the complex ways in which weather variables moderate parasitoid foraging behavior under field conditions. Since unfavorable weather conditions result in a strong reduction in parasitoid foraging efficiency, weather conditions are an important factor in the effectiveness of parasitoids as biocontrol agents.

1. Introduction

Insect pests can cause considerable crop losses. Economic costs that arise due to yield losses and expenses for crop protection were estimated to reach 18.8 billion US$ per year alone in the USA (Losey and Vaughan, 2006). These costs accrue despite the fact that the majority of potential pest species are successfully suppressed by naturally occurring predatory insects and parasitoids. The annual value of biocontrol services provided by natural enemies was estimated to 4.5 billion US$ in the USA (Losey and Vaughan, 2006). Although biocontrol can provide economic, agronomic and environmental benefits, effective biocontrol in crops requires recruitment of sufficient natural enemies from surrounding landscape and that natural enemies can find herbivore-infested plants.

While foraging of natural enemies has been extensively studied in small-scale experiments under controlled laboratory conditions (see references in Mumm and Dicke, 2010; Oudenhove et al., 2017), little is known how foraging behaviour is influenced by fluctuating weather conditions in the field. Some studies suggest that parasitoid behaviour can be influenced by weather conditions, such as changes in barometric pressure and wind speed (Steinberg et al., 1992; Fink and Völkl, 1995; Messing et al., 1997). High variability in precipitation decreased parasitism rates of field collected caterpillars (Stireman et al., 2005), and high wind speeds and rain decreased the foraging activity of parasitoids and associated reproductive success under field conditions (Weisser et al., 1997). Further insight in the way how fluctuating weather conditions influence the foraging efficiency of natural enemies

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will enhance our understanding of tri-trophic interactions and will be of great importance to predict how biological pest control will be affected by climate change.

Foraging parasitoids and predatory insects often rely on plant volatiles that are emitted upon insect feeding on a plant (Mumm and Dicke, 2010; Oudenhove et al., 2017). These so called herbivore-induced plant volatiles (HIPVs) serve as a reliable and highly detectable foraging cue (Vet and Dicke, 1992) and the majority of the tested parasitoid species used HIPVs to detect host-infested plants under laboratory conditions (Mumm and Dicke, 2010; Oudenhove et al., 2017). Oviposition-experience usually increases the responsiveness of parasitoids to HIPVs (Geervliet et al., 1998; Peñaflor et al., 2017; Vosteen et al., 2019) and parasitoids can learn to associate specific volatile blends with oviposition success (Smid and Vet, 2016). However, detecting and following an odour plume may be more challenging under field conditions, where wind speed and turbulences constantly change the shape and structure of odour plumes (Murlis et al., 2000; Riffell et al., 2008) and strong winds impede upwind flight.

Although attraction of parasitoids to herbivore-infested plants via HIPVs has been documented under field conditions (Poelman et al., 2009; Aartsma et al., 2019), it is not known how weather conditions influence the ability of parasitoids to detect volatiles and move towards an odour source. Due to the spatial constrains in laboratory experiments, most work on parasitoid foraging has focused on short range foraging on a single plant or within a plant patch, while only little is known about parasitoid foraging on larger spatial scales. HIPV-guided foraging has been intensively studied in the parasitoid *Cotesia glomerata* (Linnaeus). More than 30 wind tunnel studies document that *C. glomerata* uses HIPVs to detect caterpillar-infested plants from a distance when approaching herbivore-infested plants from the upwind direction (Steinberg et al., 1992; e.g. Poelman et al., 2009; Vosteen et al., 2019). Under field conditions *C. glomerata* can find host-infested cabbage plants from 20 m distance when the cabbage variety is attractive, while the attraction distance was only 10 m for a less attractive cultivar (Aartsma et al., 2019), revealing that cultivar attractiveness determines the attraction distance of HIPVs.

Since insects have to fly upwind in order to trace an odour source (Beyaert and Hilker, 2014) and show a reduced foraging efficiency during downwind flight (Vosteen et al., 2020), moderate or stronger wind speeds may disrupt HIPV-guided foraging in the field if they hamper upwind flight. In laboratory set-ups, several parasitoid species were unable to fly upwind at wind speeds of 1 m/s or lower and showed decreased take-off rates at wind speeds of 3 m/s or lower (Elzen et al., 1987; Keller, 1990; Fink and Völkl, 1995; Messing et al., 1997; Schwörer et al., 1999; Marchand and McNeil, 2000; McClure and McNeil, 2009; Kristensen et al., 2013). However, we lack understanding how HIPV-guided foraging behaviour unfolds under field conditions.

The aim of this study was to assess how HIPV-guided foraging behaviour of parasitoids under field conditions is influenced by weather variables, and how this interacts with oviposition experience of parasitoids. We conducted a release recapture study whereby inexperienced and oviposition experienced *C. glomerata* were released at a distance of 5 m from herbivore-infested plants to investigate which levels of humidity, wind speed, temperature and barometric pressure favour parasitoid activity (measured by high recapture rates) and upwind movement of parasitoids. To get a better understanding how different aspects of parasitoid host finding behaviour (responsiveness, host finding success, upwind movement and ignoring host-infested plants) are influenced by wind speed, temperature and humidity level, a more detailed observation study was conducted, whereby host finding behaviour of inexperienced and oviposition-experienced parasitoids was recorded at a distance of 0.5 m. Both experiments show that high wind speeds and low humidity conditions reduce the foraging efficiency of both inexperienced and oviposition experienced parasitoids.

2. Material & methods

2.1. Field site

Experiments were conducted on a meadow near Wageningen, The Netherlands, from mid-July until end of August in 2016, and from the beginning of June until the beginning of August in 2017. No brassicaceous plants were present on the experimental site and its direct vicinity, and therefore there were no naturally occurring *C. glomerata* (Aartsma et al., 2019). The meadow was mown each year before the start of the experiments and one time between trials. The maximum grass height was 30 cm.

2.2. Weather conditions

Data of wind speed and direction, humidity, temperature and barometric pressure at a temporal resolution of one minute were obtained from a weather station located about 4 km west of the experimental site. The weather station and experimental site do not differ in altitude and are located in an open agricultural landscape. We therefore assumed that the data from the weather station were representative for the field site. We checked this assumption by comparing the wind direction by a wind fan at the study site and weather station data. While the prevailing wind directions were consistent between the two sites, occasionally local turbulences close to the plant canopy resulted in a discrepancy between the wind directions at the field site at a height of 30 cm and the weather station that recorded wind direction at 2 m. Wind speed, temperature and humidity data from the weather station were averaged over the duration of the experiments from beginning of the first trial until termination of the last trial (release-recapture experiment: 180–230 min, depending on the number of trials conducted on the respective day, direct behavioural observations: 35–135 min, depending on the number of released parasitoids), resulting in one value per weather variable for each experimental day. To calculate the change in barometric pressure during the experiment, the average barometric pressure measured towards the end of the experiment (release-recapture experiment: 180–195 min after first parasitoid release, direct behavioural observation: 60–75 min after first parasitoid release) was subtracted from the average barometric pressure during the beginning of the experiment (0–15 min after first parasitoid release).

2.3. Model system

C. glomerata is a gregarious endoparasitoid that attacks caterpillars of cabbage white butterflies (*Pieris rapae* (Linnaeus) and *P. brassicae* (Linnaeus)) and has been used to study parasitoid foraging under laboratory and field conditions (e.g. Poelman et al., 2009; Aartsma et al., 2019; Vosteen et al., 2019). The parasitoid and its preferred host *P. brassicae* were obtained from cultures maintained at the Laboratory of Entomology, Wageningen University. Parasitoid cultures were restarted every summer with field-collected individuals to avoid any long-term rearing effects on parasitoid performance and behaviour. Insects were reared on Brussels sprouts plants (*Brassica oleracea* (Linnaeus) var. gemmifera cultivar Cyrus) under climate-controlled conditions (L16:D8 photoperiod, at 21 ± 1 °C and 50–70 % relative humidity). *C. glomerata* was reared on caterpillars of *P. brassicae*. Parasitoid cocoons were transferred to screen cages (30 × 30 × 30 cm, Bugdorm, Taiwan) in a climate cabinet at 24 ± 1 °C, LD12:D12 in the absence of plant odours. Emerging parasitoids were supplied with water and honey, and were used when they were 1–6 days old. Females used in the release-recapture experiment were separated from males one day before the experiment and were kept in groups of 10 females in small plastic vials closed with cotton wool, where they were provided with honey and moist filter paper.

Five-week old white cabbage plants of the highly attractive cultivar Christmas Drumhead (*Brassica oleracea* (Linnaeus) var. alba) were used

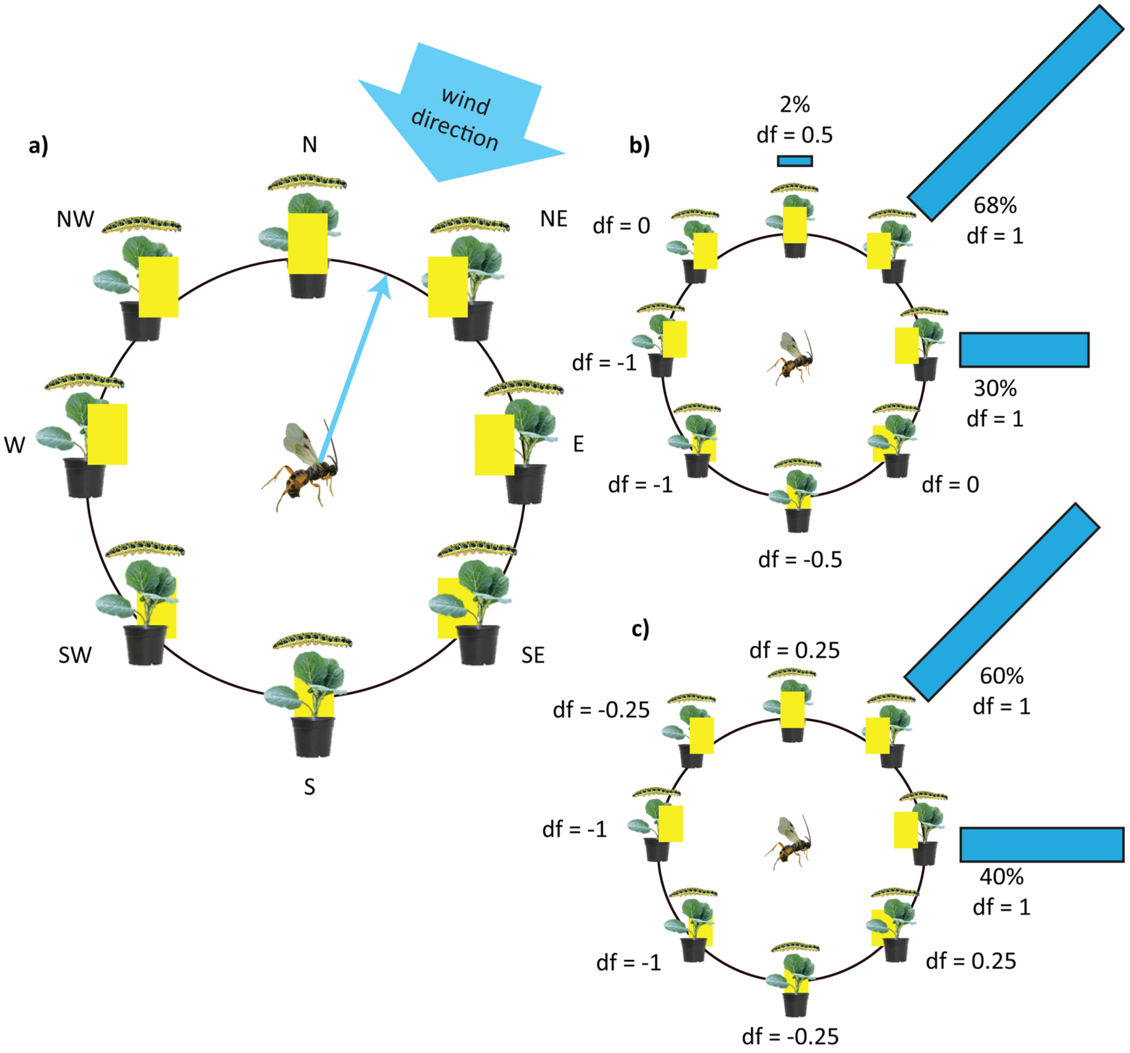

Fig. 1. Experimental design (a) and derivation of dispersal factor based on the wind direction (b, c). a) 50 parasitoids were released in a 5-m radius circle containing eight host-infested plants with yellow sticky traps. b, c) To calculate the dispersal direction index, a dispersal factor (df) was assigned to each cardinal direction, based on the prevailing wind directions. The blue bars and percentage values indicate the proportion of time the wind was coming from the respective upwind directions. b) df = 1 was assigned to the direction where the wind was coming from in 10 % of the time or more, df = 0.5 was assigned if the wind was coming from a direction in 0.1 to 9.9 % of the time, while negative dfs of the same magnitude were assigned to the corresponding downwind directions. df = 0 was assigned to crosswind directions. c) If the wind was coming only from two cardinal directions, dfs of 0.25 were assigned to the two directions facing towards the upwind directions, while the two directions facing towards the downwind directions were assigned −0.25. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

as odour sources in our experiments (Poelman et al., 2009; Aartsma et al., 2019). The plants were transported to the field one day before the experiment and were each infested with 10 one to two day old *P. brassicae* caterpillars to induce HIPV emission (Poelman et al., 2009; Vosteen et al., 2019). Caterpillars were always placed on one of the newly emerging leaves and were allowed to disperse freely on the plant. After infestation, plants were left in a shaded place and were placed on the experimental plots on the following day.

2.4. Experiment 1: Parasitoid recapture at 5 m distance

Foraging insects trace odour sources by flying upwind in odour plumes (Beyaert and Hilker, 2014). To test whether parasitoids are able to follow HIPV-plumes over distances of several meters to a host-infested plant under field conditions, we released parasitoids in a circle of eight host-infested plants (Fig. 1) and tried to recapture them at the host-infested plants. If parasitoids are able to perceive HIPVs emitted by upwind-located plants at the release site and if weather conditions permit upwind flights, we would expect to recapture the majority of parasitoids on upwind-located plants. If parasitoids cannot detect the HIPV-plumes at the release site or if strong winds prevent upwind flights, parasitoids may disperse downwind or crosswind and we would expect to recapture the majority of parasitoids on the plants located in the respective directions. Alternatively, parasitoids may take off in a random direction, which would result in a random or uniform distribution of the recaptured parasitoids.

Before the start of the experiment, eight caterpillar-infested plants were placed in cardinal directions in a 5-m radius circle around the parasitoid release point. One hour prior to the release of parasitoids, a yellow sticky trap (25 × 10 cm, Koppert Biological Systems, The Netherlands) was placed between the leaves of each plant, facing the release point. The traps were checked just before the parasitoids were released to ensure that there were no naturally occurring *C. glomerata* present. A maximum of six release circles was set-up in parallel and circles were spaced 50 m apart to minimize the risk of cross-trial movement of parasitoids (Aartsma et al., 2019). In each circle, 50 inexperienced or experienced female parasitoids were released by opening the transportation vials, which were placed next to a noninfested white cabbage plant in the centre of the circle. The different trials conducted on one experimental day (see below) were started 10 min after each other and sticky traps and plants were checked 1.5 and 3 h after parasitoids had been released. Parasitoids that were found foraging on a plant were captured to avoid double counts and the total number of parasitoids captured at each plant was recorded. The release plant and the vials were checked after 3 h, and any dead or non-responding parasitoids were recorded. Oviposition experienced parasitoids were conditioned on the day before the experiment by placing a Petri dish with a host-infested Brussel Sprouts leaf in the parasitoid cage. After approximately 5 min the Petri dish was removed and parasitoids were collected after they had finished their current oviposition. Thus, oviposition experienced parasitoids had at least laid eggs once and a few times at most to prevent egg depletion.

A maximum of six parallel trials were conducted per day, and the experiments were conducted once per week. The weather forecast was checked regularly in order to avoid days with high probability of rain and/or wind speeds exceeding 5 m/s, because rain and higher wind speeds may inhibit parasitoid flight activity (e.g. Weisser et al., 1997). In total, 63 trials with inexperienced parasitoids and 21 trials with oviposition experienced parasitoids were conducted during 23 experimental days. In 2016 all 24 trials were conducted with inexperienced parasitoids. However, since recapture rates of inexperienced parasitoids were often low, from mid-June 2017 onwards half of the trials in each experimental day were conducted with oviposition experienced parasitoids and the other half with inexperienced parasitoids, resulting in 7 experimental days on which both inexperienced and oviposition experienced parasitoids were released and two days in which only oviposition experienced parasitoids were released (see Appendix S1: Table S1 for number of trials conducted on each day).

2.4.1. Processing of the parasitoid recapture data

Recapture rates of each trial were calculated by dividing the number of parasitoids that were recaptured on sticky traps and plants by the number of parasitoids that took flight in the respective circle. Those plants located in any of the cardinal directions from which the wind was coming during the duration of the experiment were defined as upwind-located plants, while those plants located in the opposite direction were defined as downwind-located plants. Plants that were located neither in upwind nor in downwind direction were defined as crosswind-located plants. Depending on the variability of the wind direction, either two, three or four plants were considered as upwind-located. If the wind was coming from more than five directions, this experimental day was omitted from the analysis of dispersal and recapture directions.

To assess whether the parasitoids released in a trial moved in a upwind, downwind or random direction, we calculated a ‘dispersal direction index’ (*dd*) for each trial, which is a wind direction weighted index. First, the eight cardinal directions were assigned a dispersal factor (*df*) between -1 and +1, depending on the wind direction. The prevailing wind directions during the experiment were considered as upwind directions and assigned +1, while the opposite directions were considered as downwind directions and were assigned −1 (Fig. 1 b). Directions of wind that occurred in less than 10 % of the time were assigned a +0.5 and the opposite direction a −0.5. If the wind was coming from two cardinal directions, four directions remained, which were neither up- nor downwind directions. The two directions facing towards the upwind directions were assigned a +0.25, while the two directions facing towards the downwind directions were assigned a −0.25 (Fig. 1c). If the wind was coming from three cardinal directions, the remaining two directions were assigned a 0 (Fig. 1 b).

The dispersal direction index was then derived as the average of the dispersal factors weighted by the number of parasitoids recaptured in each direction. More specifically, the dispersal factor of each cardinal direction was multiplied by the number of recaptured parasitoids in that direction, summed up and divided by the total number of parasitoids recaptured in the respective circle. With this formula, the dispersal direction index was calculated for each circle. Values of $dd \geq 0.5$ indicate upwind dispersal, while $dd \leq -0.5$ indicates downwind dispersal. Values of *dd* close to 0 indicate random or crosswind dispersal. Dispersal direction indices were only calculated for trials with four or more recaptured parasitoids.

2.5. Experiment 2: Direct behavioural observations over 0.5 m distance

To get a better understanding which aspects of parasitoid foraging behaviour are influenced by the different weather conditions, direct behavioural observations were conducted in the field. For this, a total of 149 parasitoids were released individually in a 0.5 m circle of host-infested plants during 10 experimental days. As in the release-recapture experiment, the 8 plants in a circle were placed according to the cardinal directions.

Inexperienced and oviposition experienced females were used in this experiment. Female parasitoids were separated from the males ca. 30 min to 1 h before the experiment and oviposition experienced females were conditioned according to the same procedure as in the release-recapture experiment on the same day as the experiment. Before release, parasitoids were kept individually in glass vials closed with cotton wool. Parasitoids that did not take flight within 5 min were recorded as non-responsive, while parasitoids that took flight were observed until they left the plant circle or landed on a host-infested plant, which was scored as foraging success. At the moment the parasitoid took flight the wind direction was assessed with a wind fan at ca. 30 cm height directly at the release point. This allowed an accurate assessment of the landing plant in terms of upwind, downwind or crosswind direction. On some experimental days, several parasitoids approached caterpillar-infested plants, but instead of landing, they passed the plant in less than 15 cm distance and left the plant circle. This phenomenon was scored as plant-ignoring behaviour.

2.6. Statistical analysis

Data were analysed with generalized linear models (glm) in R version 3.1.1 (R Core Team, 2014). Due to overdispersion, recapture rates (proportions of recaptured parasitoids in each trial of the release-recapture experiment) were analysed using a glm with binomial error structure corrected for overdispersion (quasibinomial error structure) with parasitoid experience, wind speed, humidity, temperature and pressure change used as explanatory variables. The full model contained all two- and three-way interactions of the different weather variables, but no interactions of weather variables with parasitoid experience because only inexperienced parasitoids were released in 2016 and during the first experimental days in 2017. Model simplification was conducted by deleting individual explanatory variables (with the drop1 command), comparing the deviance of the more complex model with that of the simpler model with an F-test and removing the non-significant interactions from the model (Zuur et al., 2009).

GLMs with Bernoulli error structure were used to analyse response variables that were scored as presence-absence data: i) occurrence of upwind flight (i.e. main dispersal direction was upwind ($dd \geq 0.5$)) in the release-recapture experiment, as well as ii) parasitoid responsiveness (i.e. released parasitoids that took flight), iii) foraging success (i.e. parasitoids that landed on a host-infested plant), iv) upwind landing (i.e. parasitoids that landed on the upwind-located plant), and v) plant-ignoring behaviour (i.e. parasitoids that passed close to a host-infested plant without landing) in the direct behavioural observation experiment. Parasitoid experience, wind speed, humidity, temperature, and, in case of the release recapture experiment, pressure change were used as explanatory variables. The effect of pressure change could not be analysed in the direct behavioural observations because of collinearity between wind speed and pressure change during the experiments. Upwind landing could only be analysed for oviposition experienced parasitoids because foraging success of inexperienced parasitoids was very low.

The full model on the occurrence of i) upwind flight contained all two- and three-way interactions of the different weather variables, but no interactions between weather variables and parasitoid experience. The full models on ii) parasitoid responsiveness, iii) foraging success, iv) upwind landing, and v) plant-ignoring behaviour contained all possible two- and three-way interactions. Model simplification was conducted by deleting individual explanatory variables (with the drop1 command), comparing the deviance of the more complex model with that of the simpler model with a likelihood ratio test and removing the non-significant interactions from the model (Zuur et al., 2009). P-values for the parameters retained in the final models on data from the direct behavioural observations were obtained by the same procedure.

3. Results

3.1. Experiment 1: Parasitoid recapture at 5 m distance

In the release-recapture experiments, a total of 3200 inexperienced parasitoids were prepared for the release in plant circles in the field. Of these 2963 took flight (92.6 %) and 389 (12.2 %) were recaptured on the host-infested plants at 5 m distance. In the same experiments 1050 oviposition experienced parasitoids were prepared for the release, 820 took flight (78.1 %) and 319 were recaptured (30.4 %).

A large proportion of the variability in recapture rates was explained by parasitoid experience and by interacting effects of wind speed, humidity, temperature and barometric pressure change (Mc Fadden $R^2 = 0.710$). The interactions between humidity and wind speed, humidity and pressure change, wind speed and pressure change, pressure change and temperature as well as humidity, wind speed and pressure change were retained in the final model (Fig. 2, Appendix S1: Table S2), indicating that the effect of weather variables is not additive, and that all considered weather variables have to be in the favourable range to obtain high recapture rates. The effect of specific weather variables on parasitoid recapture rates was assessed by comparing recapture rates of trials in which all weather variables, except for the focal weather variable, were in the favourable range (Fig. 2). Recapture rates decreased with decreasing humidity and increasing wind speed and temperature, while decreasing barometric pressure resulted in low recapture rates. On experimental days when both inexperienced and oviposition experienced parasitoids were released, recaptures rates were usually higher for oviposition experienced (45.1 ± 5.2 %) than for inexperienced parasitoids (18.4 ± 2.1 %).

In order to determine if the majority of recaptured parasitoids moved to the upwind-located plants and thus displayed HIPV-guided upwind flight, the dispersal direction index was calculated (see Appendix S1: Fig. S1 for the relationship between the dispersal direction index and the number of parasitoids recaptured on upwind-, downwind- and crosswind-located plants). Upwind dispersal (dd > 0.5) was only detected in inexperienced parasitoids, and parasitoid experience was retained as an explanatory variable in the final model (Appendix S1: Table S3). Interactive effects between humidity and barometric pressure change, humidity and temperature, barometric pressure change and wind speed, wind speed and temperature as well as between barometric pressure change and temperature indicate that upwind dispersal of inexperienced parasitoids was only found under specific weather conditions. Upwind dispersal was observed when humidity was between 50 % and 70 %, temperature exceeded 20 °C, and wind speed was not higher than 4.5 m/s (Fig. 3). The effect of barometric pressure change was more difficult to grasp, but it may have a moderating effect on the influence of the other weather parameters. For example, when wind speeds exceeded 4 m/s, upwind flight was only observed when barometric pressure was increasing compared to situations with decreasing barometric pressure. However, even when weather conditions were highly favourable for odour-guided upwind flights, upwind dispersal could not be detected in all trials. Upwind dispersal of inexperienced parasitoids was found on 7 of the 21 experimental days, indicating that favourable conditions for upwind dispersal happened only in one out of three experimental days. A total of 16 trials with inexperienced parasitoids were conducted during these days and upwind dispersal was found in nine of the trials. A total of nine trials with oviposition experienced parasitoids was conducted during three days with favourable conditions for upwind flight, but upwind dispersal was not observed in any of the trials with oviposition experienced parasitoids.

3.2. Experiment 2: Direct behavioural observations over 0.5 m distance

Direct behavioural observations showed that parasitoid responsiveness was positively associated with humidity (binomial glm: LRT = 19.296, $p < 0.001$, Fig. 4a, Appendix S1: Table S4), negatively associated with wind speed (binomial glm: LRT = 27.817, $p < 0.001$, Fig. 4b) and temperature (binomial glm: LRT = 5.144, p = 0.023, Fig. 4c). Inexperienced parasitoids showed a higher responsiveness in terms of flight initiation than oviposition experienced parasitoids (binomial glm: LRT = 5.394, p = 0.020).

Oviposition experienced parasitoids were more successful in finding plants at 0.5 m distance than inexperienced parasitoids (binomial glm: LRT = 25.786, $p < 0.001$, Appendix S1: Table S5). Foraging success was positively associated with humidity and temperature, while it was negatively associated with wind speed (binomial glm - humidity: LRT = 9.815, p = 0.002, wind speed: LRT = 8.416, p = 0.004, temperature: LRT = 10.956, $p < 0.001$, wind speed x temperature: LRT = 5.687, p = 0.017, Fig. 4d–f). A decline in foraging success of inexperienced parasitoids was observed at lower wind speeds compared to oviposition experienced parasitoids (binomial glm - wind speed x experience: LRT = 6.798, p = 0.009).

Due to the low foraging success of inexperienced parasitoids the proportion of parasitoids that landed on the upwind-located plant could only be analyzed for oviposition experienced parasitoids. The proportion of responding oviposition experienced parasitoids that landed on the upwind-located plant negatively associated with wind speed (binomial glm: LRT = 3.146, p = 0.076, Fig. 4h, Appendix S1: Table S6) and temperature (binomial glm: LRT = 3.479, p = 0.062, Fig. 4i), while it was highest at medium humidity levels (binomial glm: LRT = 3.207, p = 0.073, Fig. 4g). A maximum of 62.5 % (5 out of 8) of the responding parasitoids landed on the upwind-located plants at wind speed of 1.7 m/s, while no landing on upwind-located plants was observed at wind speeds exceeding 3.2 m/s.

The direct behavioural observation of parasitoid foraging in the field revealed that some parasitoids approached caterpillar-infested plants, but instead of landing, they passed the plant. This ignoring behaviour was observed when humidity was below 55 % as well as when humidity was below 70 % and wind speed was above 2.5 m/s (binomial glm - humidity: LRT = 10.032, p = 0.002, wind speed: LRT = 4.751, p = 0.029, Fig. 4j, Appendix S1: Table S7). The final model for plant-ignoring behaviour also contained temperature (binomial glm: LRT = 10.437, p = 0.001), and significant interactions between wind speed and temperature as well as humidity and temperature, indicating that temperature has a mediation effect on plant-ignoring behaviour.

4. Discussion

In this study we show that HIPV-guided upwind flights of parasitoids over 0.5 and 5 m distance only occur during favourable weather conditions and that adverse weather conditions, such as low humidity or high wind speed, strongly reduce parasitoid foraging activity and foraging success. Weather conditions had an interactive effect on parasitoid foraging and high foraging success was only obtained when key weather variables were in the favourable range. Thus, weather conditions may influence the efficiency of parasitoids as biocontrol

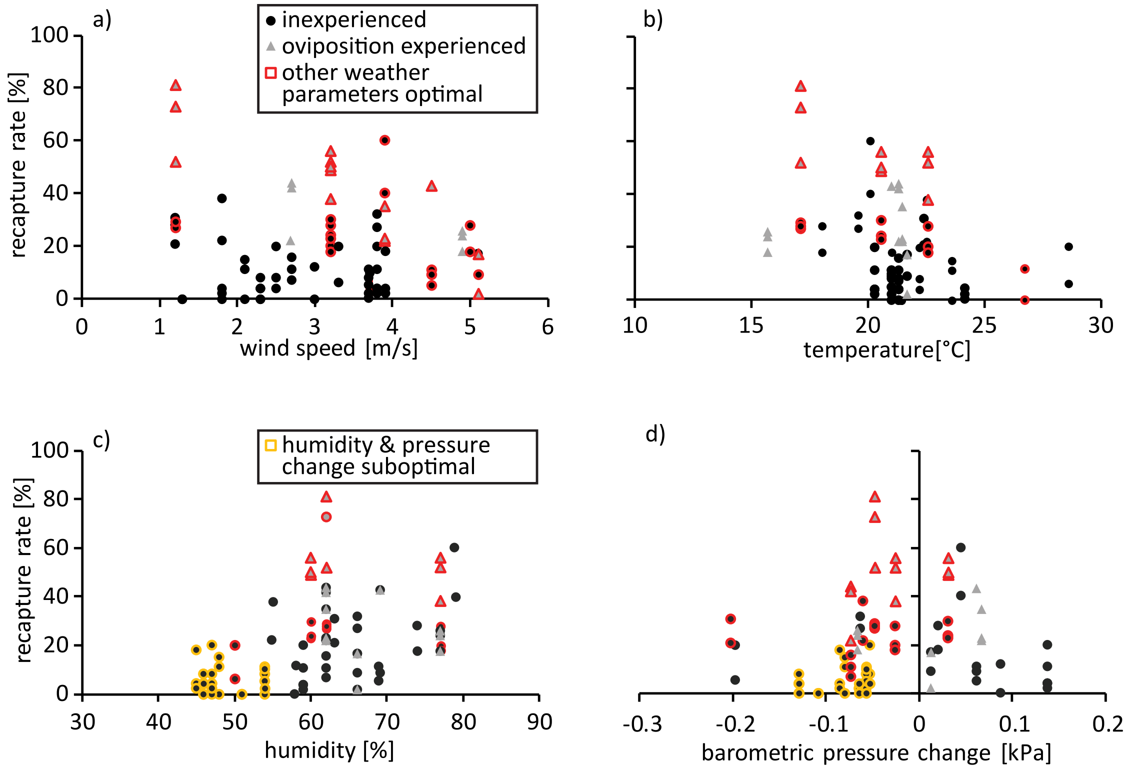

Fig. 2. Effect of a) wind speed, b) temperature c) humidity and d) change in barometric pressure on recapture rates during trials with inexperienced (black circles) and oviposition experienced *Cotesia glomerata* (grey triangles) on host-infested plants placed 5 m away from the release point. Parasitoid experience and the four tested weather variables have interactive effects on the recapture rate. To visualize the effect of the respective weather variable presented in each panel, red borders were used to indicate those trials were all other tested weather variables were in the optimal range. The markers with red border thus illustrate the main effect of each weather variable. Markers with yellow borders in c and d indicate those trials during which both humidity and pressure change were in the suboptimal range, which made it impossible to distinguish which of the two variables were causing the low recapture rates. Weather variables were considered to be in the optimal range if wind speed was lower than 3.5 m/s, temperature was below 24 °C, humidity was higher than 55 % and barometric pressure did not decline more than 0.05 kPa. The optimal range of weather variables was determined visually based on strong changes in recapture rate caused by small changes in the respective weather variable. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

agents.

Our findings suggest that limitation of foraging time by adverse weather conditions can be an important factor that influences *C. glomerata* foraging efficiency. Foraging activity and recapture rates of *C. glomerata* declined with decreasing humidity and increasing wind speed, while a decline in barometric pressure of 0.5 kPa or more resulted in low recapture rates. These results are in line with findings from laboratory studies with *C. glomerata*, which show that responsiveness decreased with increasing wind speed and was reduced in experiments that were conducted during decreasing barometric pressure when compared to experiments under stable or increasing barometric pressure conditions (Steinberg et al., 1992; Gu and Dorn, 2001). Decreasing or rapidly changing barometric pressure may be perceived by the parasitoid as an early warning signal for changing weather conditions and reducing foraging activity under decreasing or rapidly changing barometric pressure seems to be a common response of parasitoids (Steinberg et al., 1992; Roitberg et al., 1993; Roermund and Lenteren, 1995; Marchand and McNeil, 2000; Fournier et al., 2005). Thus, avoiding flight under adverse weather conditions may be a general strategy among parasitoids to reduce mortality risk, and may compromise foraging time and reproductive success.

Contrary to the other weather variables, temperature had a contrasting effect on parasitoid take-off rate and foraging success. Flight activity of *Cotesia glomerata* increased with increasing temperature in our field experiment, as it was also found in laboratory studies with other parasitoid species (Barbosa and Frongillo, 1977; Forsse et al., 1992; Langer et al., 2004; Yu et al., 2009; Fahrner et al., 2015; Jerbi-Elayed et al., 2015). This increase in flight activity did not result in increased foraging success in our experiment, as foraging success and recapture rates decreased with increasing temperature. Furthermore, increasing temperature led to decreasing proportions of parasitoids that landed on the upwind-located plants in 0.5 m distance, which suggests that parasitoid attraction towards HIPVs decreases with increasing temperature. HIPV emission of herbivore-infested maize and lima bean plants peaked at temperatures around 30 °C, but changes in blend composition may have resulted in a reduced attractiveness of HIPV blends emitted at high temperatures (Gouinguené and Turlings, 2002; Ozawa et al., 2012). Upwind flight was reduced at temperatures below 20 °C when the plants were located at 5 m distance. Since flight speed decreased with decreasing temperature (Yu et al., 2009; Jerbi-Elayed et al., 2015), it may be difficult for parasitoids to reach a plant located at 5 m distance through upwind flights when temperatures are low. Our results thus suggest that temperature differently affects different aspects of parasitoid foraging and additional studies are needed to disentangle these effects.

Parasitoid responsiveness and odour guided upwind flight were negatively associated with wind speed and no upwind flight was observed at average wind speeds exceeding 3.0 m/s in our field experiments. Laboratory studies report a decrease in flight activity of different parasitoid species already at wind speeds below 3 m/s (Elzen et al., 1987; Keller, 1990; Fink and Völkl, 1995; Messing et al., 1997; Schwörer et al., 1999; Marchand and McNeil, 2000), but it has to be noted that in our study, we could only assess the average wind speed during the experiments. The actual momentaneous wind speed at which parasitoids took flight in our study might have also been lower than 3 m/s. Our results thus confirm that already moderate wind speeds

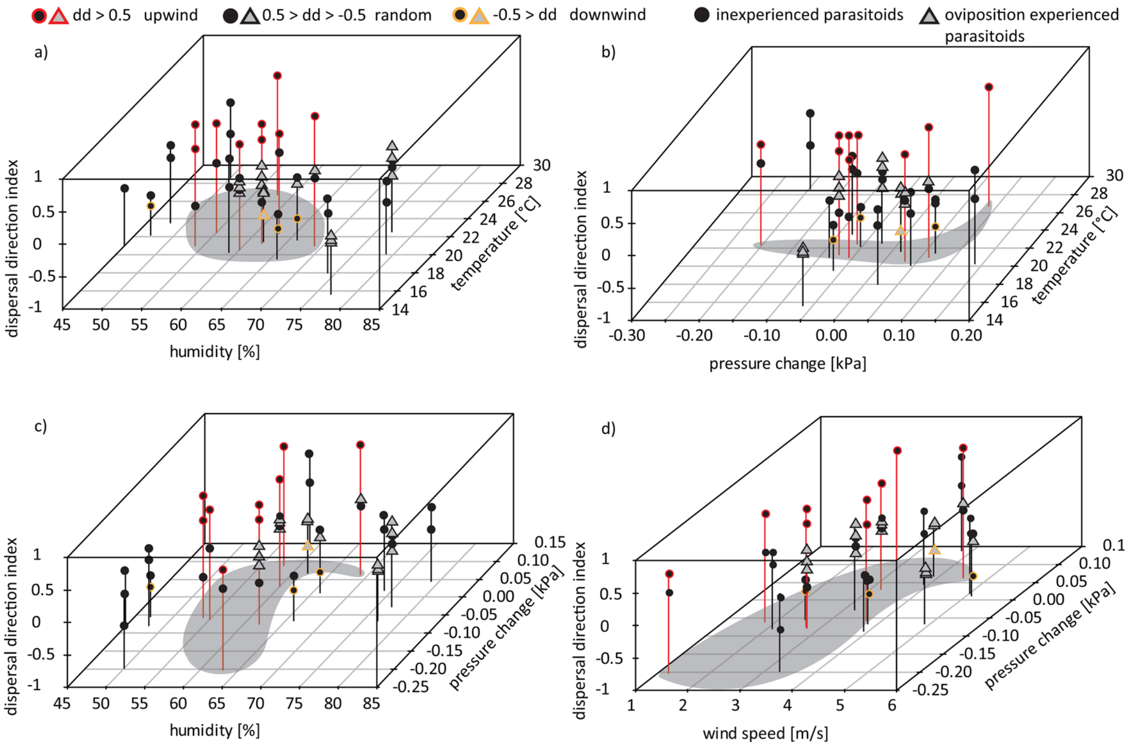

Fig. 3. Interactive effects of humidity, temperature and barometric pressure change (a, b, c), and of wind speed and barometric pressure change (d) on dispersal direction of inexperienced and oviposition-experienced *Cotesia glomerata* in the release-recapture experiment. Upwind dispersal is defined as direction dispersal index (dd) $>$ 0.5, while downwind dispersal is defined as dd $<$ $-$0.05. The grey area indicates weather conditions under which upwind flight was observed.

reduce parasitoid flight activity, which aligns with findings from other field studies (Casas, 1989; Kristensen et al., 2013). Strong winds may impede insect flight control (Marchand and McNeil, 2000) and we observed indeed that, when wind speeds increased, *C. glomerata* often attempted to fly upwind, but were blown downwind during wind gusts. The inability of parasitoids to follow an HIPV-plume to its source when wind speeds were high resulted in a decrease in foraging success and recapture rates. Similarly, *C. glomerata* that were forced to enter a plant patch in downwind flight showed a reduced foraging efficiency compared to upwind flying parasitoids, because in downwind foraging situations, volatile information only becomes available after parasitoids have passed a plant (Vosteen et al., 2020). These results stress the importance of odour-guided upwind flights for effective foraging. The foraging behavior of the aphid parasitoid *Aphidius rosae* is influenced by strong winds in a similar way: the number of colonies with parasitized aphids decreased with increasing duration of high wind speed conditions, while the number of parasitized aphids per colony increased (Weisser et al., 1997). Parasitoids may partly compensate their inability to fly upwind at high wind speeds by avoiding take-off during wind gusts and waiting for low wind conditions to fly upwind (Fink and Völkl, 1995; Messing et al., 1997). In wind tunnel experiments with continuous air flow, *C. glomerata* already showed a strongly reduced responsiveness at wind speeds exceeding 0.53 m/s (Gu and Dorn, 2001), while in our field experiments all released parasitoids still took flight at an average wind speed of 3.2 m/s. Upwind flight, however, was not observed during average wind speeds above 3 m/s and movement was either random or downwind. This finding may indicate that even if parasitoids are able to perceive HIPVs from an upwind plant, wind speeds exceeding 3 m/s inhibit upwind flights and thus limit the ability of parasitoids to use HIPVs as long-range cues. Under strong wind conditions, parasitoids either postpone their flight activities or may drift passively with the wind, as observed by Kristensen et al. (2013), until they perceive an HIPV-plume, which triggers landing on or close to the host-infested plant.

Recapture rates and flight initiation by parasitoids were positively associated with humidity. Insects are susceptible to dehydration due to their low storage capacity for water combined with a large surface area (Enjin, 2017). Reducing foraging activities during low humidity conditions may thus be a strategy of small insects to avoid water loss. Yet, the decline of recapture rates observed in our experiment at low humidity was stronger than the decline in flight initiation and may be explained by an alternative hypothesis. At low humidity conditions, *C. glomerata* often ignored host-infested plants in their direct vicinity, rarely performed upwind flights or found a host-infested plant. This may indicate that *C. glomerata* had difficulties to perceive HIPVs under low humidity conditions. While it is known that insects sense humidity with hygrosensory sensilla which are co-located with olfactory sensilla on the antennae (Enjin, 2017), the effect of humidity on odour-guided foraging has rarely been studied in insects, and insect responses to low humidity conditions seem to be species specific (Royer and McNeil, 1993; Bourchier and Smith, 1996; Smith, 1996; Bassett et al., 2011; Henderson et al., 2017). Our data do not allow making conclusive statements about whether the decreased host finding ability of parasitoids at low humidity is a general phenomenon, and whether this phenomenon is caused by a reduced ability of insects to perceive volatiles at low humidity, or by a reduced HIPV emission from the herbivore-attacked plant as the result of stomata closure (Gouinguené and Turlings, 2002; Niinemets et al., 2004; Harley, 2013; Seidl-Adams et al., 2015). Alternatively, parasitoids may simply ignore HIPVs at low humidity conditions to search for water or areas with a more humid microclimate. Experiments on volatile perception and foraging activity at different humidity levels are thus needed to determine the cause for the observed low recapture rates at low humidity.

Oviposition experienced parasitoids found the host-infested plants more often than inexperienced parasitoids during our field experiment. This may be explained by an increased responsiveness of oviposition experienced parasitoids to HIPVs as usually observed in wind tunnel studies (Geervliet et al., 1998; Peñaflor et al., 2017; Vosteen et al., 2019; Vosteen et al., 2020). Oviposition experience also influenced upwind flight behaviour of *C. glomerata*. Experienced parasitoids

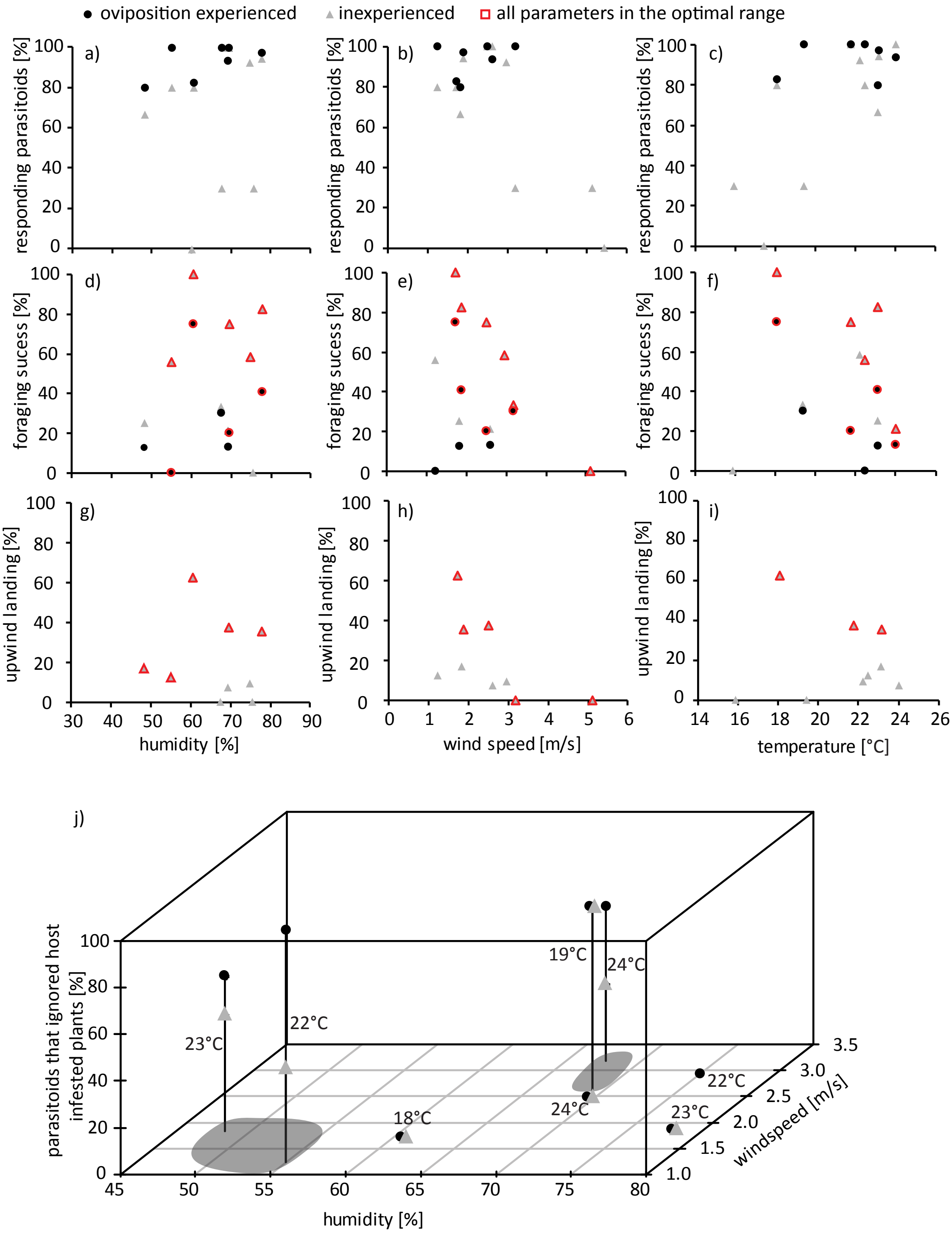

Fig. 4. Relationships between humidity, wind speed, temperature and parasitoid responsiveness (a, b, c), foraging success (d, e, f), upwind landing (g, h, i) and plant ignoring behaviour (j) in the direct observation trial where *Cotesia glomerata* parasitoids were released in 50 cm distance from the host-infested plants. Occurrence of these behavioural parameters was scored and analysed as presence-absence data for each individual parasitoid and is presented as the proportion of parasitoids that showed the respective behaviour. Panels d-i: To visualize the effect of the respective weather variable presented in a panel, red borders were used to indicate trials were all other weather variables were in the optimal range. Weather variables were considered to be in the optimal range if wind speed was lower than 3 m/s, temperature was lower than 24 °C and humidity was higher than 50 %. The optimal range of weather variables was determined visually based on strong changes in recapture rate caused by small changes in the respective weather variable. j) The grey areas indicate humidity and wind speed levels under which parasitoid ignoring behaviour of host-infested plants was observed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

performed upwind flights to host-infested plants located in 0.5 m distance, while inexperienced parasitoids usually left the release site in straight flights up, a behaviour that is also observed under laboratory conditions (Geervliet et al., 1994). Surprisingly, upwind movement over 5 m distance by the majority of the recaptured parasitoids was only observed in inexperienced parasitoids, while oviposition-experienced parasitoids mainly dispersed randomly. The absolute numbers of parasitoids recaptured on upwind-located plants at 5 m distance was similar between oviposition-experienced and inexperienced parasitoids, but higher recapture rates of oviposition-experienced parasitoids led to a relative increase of oviposition-experienced parasitoids on downwind- and crosswind-located plants. A possible explanation for this observation could be that two different mechanisms are involved in influencing parasitoid responsiveness to HIPVs. The first one is the motivation to start foraging and to respond to HIPVs. It has been shown repeatedly that foraging motivation is increased after oviposition-experience (e.g. Vosteen et al., 2019; Vosteen et al., 2020) and we also observed a higher foraging motivation in oviposition-experienced parasitoids, which were released in 0.5 m distance to the host-infested plants. The second mechanism is the HIPV concentration that needs to be reached to trigger upwind flight. We hypothesize that this concentration may be relatively low in inexperienced parasitoids, because they need to find distant herbivore-infested plants. Oviposition-experienced parasitoids on the contrary already found a plant stand, in which hosts occur. If they perceive volatiles from an upwind-located herbivore-infested plant, parasitoids leave the host-infested plant earlier than in the absence of HIPVs (Maeda et al., 1998; Mayland et al., 2000; Tentelier and Fauvergue, 2007; Vosteen et al., 2020). If oviposition-experienced parasitoids would be attracted by low concentrations of HIPVs from distant herbivore-infested plants, they would risk leaving before the current patch has been fully exploited. Oviposition-experienced parasitoids may thus have a higher HIPV-response threshold than inexperienced parasitoids, which would explain the observed lack of HIPV-guided upwind flight over 5 m in oviposition-experienced parasitoids. Vos et al. (1998) indeed showed that multiple oviposition experiences decreased the patch-leaving tendency of *C. glomerata* in an environment where HIPVs from other host-infested plants were present.

We show in this study that both low humidity and high wind speed reduce the foraging activity and efficiency of *C. glomerata*, which results in a strong decrease in foraging success. Most parasitoids and predatory insects use HIPVs to detect host-infested plants from a distance (Mumm and Dicke, 2010; Oudenhove et al., 2017), and HIPV-guided upwind flight may increase parasitoid foraging efficiency (Puente et al., 2008). Our understanding of the way in which abiotic conditions influence HIPV-guided foraging is relatively limited, especially on the effect of humidity and temperature, but it is likely that other natural enemies are similarly affected by conditions that hamper odour-guided foraging, such as high wind speeds and low humidity. Quantitative data on the effect of weather conditions on natural enemy foraging as reported in this study may inform recommendations for the release of natural enemies in augmentative biocontrol. For instance, wind speeds of 3 m/s seem to be a general threshold for upwind or downwind flight of several parasitoid species, and depending on wind speed, upwind- or downwind-located release sites may be preferable in augmentative biocontrol. Since both wind speeds and humidity levels change over the course of a day, natural enemies are likely to experience on most days at least a few hours with conditions that are favourable for odour-guided foraging and upwind flights. The resulting limitation in foraging time, however, may compromise biocontrol. Computer simulations show that foraging time limitation due to adverse weather conditions does not only reduce the number of host attacks, but also the efficiency of individual parasitoids and parasitoid fitness (Weisser et al., 1997), which may have negative consequences for the population development of these biocontrol agents. Better understanding the effect of weather conditions on biological pest control and multitrophic interactions in agroecosystems is especially important in the light of climate change. Climate change scenarios predict an increase in heat waves, which are accompanied by high temperatures, drought and decreases in average relative humidity (De Boeck et al., 2010). Natural enemies may codetermine the effect of climate change on herbivore abundance (Robinson et al., 2017), but changes in multitrophic interactions due to climate change are complex and difficult to predict (Jamieson et al., 2012; Wade et al., 2017; Rosenblatt, 2018). Even though our study is restricted to a relatively moderate envelope of weather conditions encountered during the experiments across two field seasons and does not include extreme conditions as predicted in future climate change scenarios, it suggests that changes in foraging efficiency of natural enemies may be anticipated under scenarios of climate change, which may influence outcomes of multitrophic interactions and biological control. Future work should focus on the effect of weather conditions on different natural enemy species in order to evaluate their potential as biocontrol agents under different climatic conditions and to obtain a more mechanistic understanding on the effects of weather conditions on the third tropic level.

Declaration of Competing 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 A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2020.107066.

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