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Dispersal behaviour of *Trichogramma brassicae* in maize fields

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Abstract

Glue-sprayed maize plants were used to study dispersal behaviour of the egg parasitoid *Trichogramma brassicae* Bezdenko (Hymenoptera Trichogrammatidae) in maize fields. To estimate the distance covered during an initial flight, *T. brassicae* were studied in a field cage with 73 glue-sprayed plants. Most of the parasitoids were found close to the release point, but several reached plants at distances up to 180 cm showing that walking and jumping are not the only mechanisms involved in initial dispersal. Mean distance of recapture from the release point was 60 cm. In a second experiment, glue-sprayed plants were placed in a maize field in a cross-pattern with 1.5 m distance between plants. On plants neighbouring the glue-sprayed plants, egg masses were fixed to measure parasitism. Only 0.7 to 3% of the released parasitoids were recaptured in the field. During the first day there was a sharp gradient with distance in the numbers of parasitoids recaptured, but during the second and third day there was no longer a significant gradient. The numbers captured on the second and third day were much lower than those captured on the first day. There was little correlation between the number of wasps landing on a plant and parasitism. In the field, apparently 75% of the wasps had left the area within 7.5 meter of the release point at the end of the first day, and 95% had left this area at the end of the second day. It is concluded that *T. brassicae* disperses in maize fields mainly by short flights.

Key words: *Trichogramma brassicae*, *Ostrinia nubilalis*, egg parasitoid, European corn borer, dispersal behaviour, flight, biological control.

Introduction

The egg parasitoid *Trichogramma brassicae* Bezdenko (Hymenoptera Trichogrammatidae) is being used worldwide for the control of Lepidopterous pests. An estimated area of 32 million hectares was treated in 1993 with *T. brassicae* and other parasitoids of the family *Trichogramma* (Li, 1994), but recent estimates state that currently 15 million hectares are treated with *Trichogramma* (van Lenteren, 2000; van Lenteren and Bueno, 2003). Although extensive applied research has been carried out on *Trichogramma*, the information on the behaviour of the individual parasitoids in the field is scanty (Smith, 1996; Thomson *et al*., 2003).

One of the factors which has a clear influence on the efficiency of biocontrol release systems is the dispersal and host-location behaviour of the released wasps (e.g. Bigler, 1994). Which behaviour, walking or flying, is most important for dispersal of *Trichogramma*, is still a matter of controversy (Flanders, 1937; Smits, 1982; Pak *et al*., 1985). After mating at the site of emergence, which is the first priority for arrhenothokous *Trichogramma*, the female will start searching for hosts. If suitable hosts are not present in the immediate vicinity, the parasitoid has to move away from the place of emergence and locate a host patch. After the females have mated and left, the males will also have to disperse if they are to mate again (Keller *et al*., 1985).

Speed of dispersal is influenced by many factors, such as crop type and architecture, wind and total leaf area of the crop. For example, in releases of *T. brassicae* for control of the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera Crambidae) in Switzerland, 50 release points per hectare were initially used, which assumes that the wasps will be able to parasitize egg masses of *O. nubilalis* effectively within an eight metre radius (Bigler, 1983). The distance from the release point at which a sufficient level of parasitism is found varies from 5 to 50 m, depending on the *Trichogramma* species and the crop (Franz and Voegelé, 1974). Low rates of dispersal were reported for several *Trichogramma* spp. (3 m, Torgovetski *et al*., 1988), for *Trichogramma minutum* Riley in cotton (4-8 m in several days, Fye and Larsen, 1969), for *Trichogramma* spp. (probably *Trichogramma dendrolimi* Matsumura) and *Trichogramma embryophagum* (Hartig) in apple trees (3 m in one day, Kolmakova and Molchanova, 1981) and *Trichogramma* spp. in orchards and cabbage (50 m in one week, Kot, 1964). High rates of dispersal were found for *T. brassicae* in maize (400 m in one week, Bigler *et al*., 1990), *Trichogramma* spp. (probably *Trichogramma pretiosum* Riley or *Trichogramma deion* Pinto et Oatman) in alfalfa (maximum 1000 m in 62 hours, Stern *et al*., 1965) and *Trichogramma* spp. in cotton (130 m in two days, Stinner *et al*., 1974). Apparently, dense crops, especially trees, inhibit dispersal (Meyer, 1941; Kot, 1964; Kolmakova and Molchanova, 1981). Strong winds in a fixed direction can increase dispersal of *T. brassicae* (Bigler *et al*., 1990).

Many dispersal studies of *Trichogramma* have been made (see e.g. Keller *et al*., 1985). The usual method to determine dispersion consists of using parasitism data from natural eggs or artificial egg cards, but this method has a clear flaw in that finding of parasitized eggs indicate that wasps have been present, but not how many. Also, finding unparasitized eggs does not guarantee that wasps have not been present, because generally not all eggs are accepted, even under optimal circumstances (Cerutti and Bigler, 1991). Some authors used sticky traps, which show where wasps have been present (Kolmakova and Molchanova, 1981; van den Berg *et al*., 1987). Keller and Lewis (1985) used a combination of egg cards and sticky traps in cotton to study behaviour of *T.*

pretiosum. They did not use a point release, so their results only indicate density of *Trichogramma* present in the field. It is unknown how *Trichogramma* reacts to colours and therefore it is unclear whether the number of wasps caught on sticky cards represents the number normally landing on plants. Sweep nets and vacuum suction samplers may give a better picture of the number of wasps present. Stern *et al*. (1965) could show high maximum rates of dispersal in alfalfa fields using these devices in combination with radio-actively marked wasps. Such methods are labour-intensive to use and cannot collect wasps continuously over a longer period. Using glue-sprayed plants, on which wasps have shown to land normally (Suverkropp, 1994), will give a clear indication of the number of wasps that visit a plant. This technique is used in the experiments described in this paper.

The objectives of this research are (a) to establish the distance covered during the first flight from a release point by *T. brassicae* and (b) to see how spatial and quantitative aspects of landing correlate with parasitism of *O. nubilalis* egg masses.

Materials and methods

Materials

Plants

The experiments were carried out in maize fields (cultivar Atlet) with normal planting density (75 cm between rows, 15 cm between plants). The fields used for the field dispersal experiments were normally managed maize fields with a size of 0.2 to 0.6 ha. The experiments always took place at least 10 m from the field edge.

Parasitoids

T. brassicae was used in all experiments. The stock material was obtained in 1975 from Antibes (strain 16), which was imported from the former Soviet Republic of Moldavia, and has been maintained on *O. nubilalis* eggs since. The rearing system is described in Bigler (1994). To obtain the numbers of egg masses necessary for mass releases, the wasps were reared for two or three generations on *Ephestia kuehniella* Zeller, creating so-called F2 and F3 material.

Moth egg masses

Egg masses of *O. nubilalis* were used in the field dispersal experiment. Egg masses were deposited by the moths on wet filter paper placed in the rearing cages in the laboratory. For use in the field, cut strips of filter paper (1 by 3 cm) with one egg mass were used.

Glue

Soveurode® aerosol glue for sticky insect traps sold in pressurized spray cans was used on the plants. This had neither an attractive nor a repellent effect on *T. brassicae* (Suverkropp, 1994).

Methods

Initial flight distance

In a full-grown maize field, an area of nine m^2 containing a total of 73 plant in four rows was enclosed in a wooden-frame cage with fine netting (Scrynel® 110 HC). Plants and netting were sprayed with glue. In the middle of the cage a plant without glue was placed, and a release container with parasitized *E. kuehniella* eggs producing about 5,000 *T. brassicae* females was fastened with tape to this plant about 60 cm from the ground. These eggs were timed to emerge on the first day of the experiment. Outside the cage a similar container, closed with netting, was fastened to a plant to check the emergence rate and the sex ratio of the emerged wasps. The wasps were allowed to emerge and fly for three days, then the cage was opened, the release container and the control container were stored in a freezer and all plants were potted and inspected for the presence of parasitoids in the laboratory. The location and sex of each *T. brassicae* captured on the plants was recorded. The release container was checked, all wasps that had not left were counted. The experiment was run on July 22-24 and August 16-18, 1993. In the first replicate, the first day was relatively cool with only eight hours above 18 °C and 5.4 mm of rain. The second and third days were warm and dry. In the second replicate all days were warm with at least eleven hours above 18 °C.

Dispersal in the field

Twenty maize plants were potted and sprayed with glue. The plants were placed in a cross pattern in a maize field at 1.5, 3, 4.5, 6 and 7.5 m from a central release point. On a plant next to each glue-sprayed plant, an egg mass on filter paper was clipped to one of the middle leaves. At the central plant, a release container with about 10,000 female and 7,000 male one day old or emerging *T. brassicae* was placed on the ground. The glue-sprayed plants and egg masses were left in the field overnight. The next two mornings, the glue-sprayed plants and egg masses were replaced by fresh ones. After the experiment, the egg masses were incubated at 25 °C until the parasitized eggs turned black. To measure parasitism, white and black eggs in each egg mass were counted. The glue-sprayed plants were checked under the microscope and the number, sex and position of the wasps captured on the plants were recorded. The experiment was run three times, on June 8-10, June 19-21 and June 30-July 2, 1993. In the first replicate, the experiment was stopped after only two days. During all days there were at least ten daylight hours with temperatures above 18 °C. During the second day of the second replicate, there was a short rainstorm with 2.9 mm of rain. The glue-sprayed plants had an average of 4.4 leaves in the first replicate (mean height 40 cm) and 6.6 leaves in the second (mean height 100 cm) and third (mean height 120 cm) replicate. There were no other releases of *T. brassicae* close to the experimental fields and *Trichogramma* spp. did not occur naturally in these fields.

Statistics

The numbers of wasps landing per plant in the experiment on dispersal in the field were compared using ANOVA and the Duncan test. Data were square-root transformed to meet the assumptions of ANOVA. If the wasps move out from the centre in a random diffusion process in the experiment on dispersal in the field, the proportion in numbers landing on the glue-sprayed plants at 1.5, 3, 4.5, 6 and 7.5 m is expected to be 5.00: 2.50: 1.67: 1.25: 1.00. The numbers of wasps that actually landed per plant at different distances were compared with the expected numbers, using a χ^2 test. For the analysis of the rates of parasitism, the data were arcsine transformed and tested with an ANOVA and Duncan test.

Results

Initial flight distance

Of the 73 plants in the cage, 51 were checked for *T. brassicae* in the first replicate. The actual number of females which had emerged was about 4,000, of which 575 were found on the checked glue-sprayed plants, a recapture of 14.3%. In the second replicate, 53 of the 73 plants were checked and 838 of the about 3,900 emerged females were recaptured, which is 21.1%. The number of females that landed on the plants is presented in figure 1. Most females were recaptured on the two

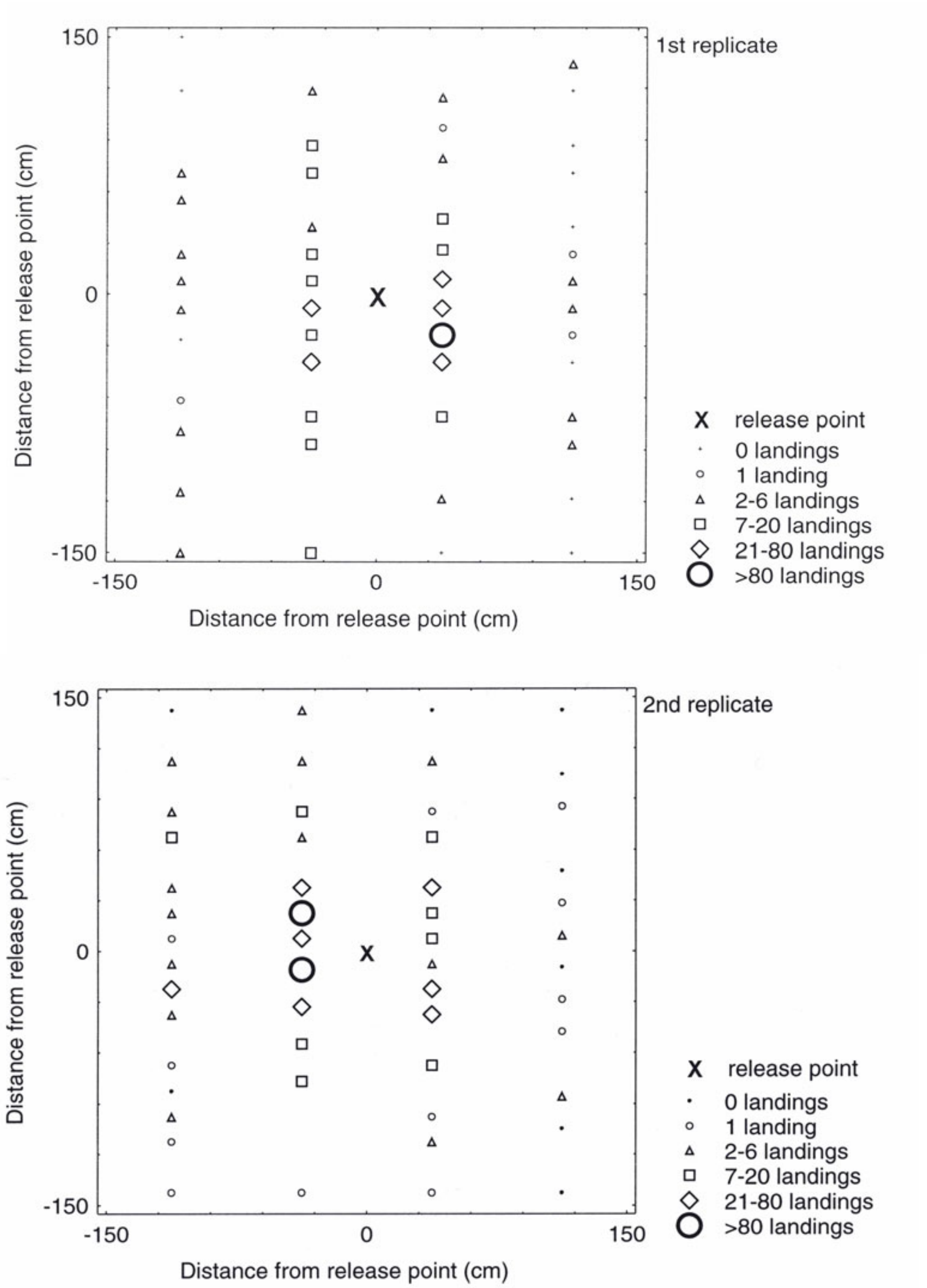

Figure 1. Number of female *T. brassicae* landing on glue-sprayed plants in a field cage.

middle rows, and the number of landings decreased sharply with increasing distance from the release point. However, some managed to reach the outer plants. Since the netting touched the tops of the plants, the wasps were forced to fly between the plants and not over them, which might have reduced mean flight distance. The mean flight distance was 59.4 ± 0.6 cm, and the median was 43.7 cm.

Part of the netting was checked for *T. brassicae*, especially the part directly above the release point, but none could be found. The netting was found to be not very sticky, so wasps that landed on the netting might have left again. The soil under the release plants was not checked for presence of parasitoids.

Dispersal in the field

L a n d i n g

Of 17,000 wasps released, 92 (0.54%), 381 (2.24%) and 333 (1.96%) were recaptured on the spray-glued plants in the first, second and third replicate, respectively. Of the released females, 0.67, 3.07 and 2.89% were recaptured. The actual numbers of females landing on the spray-glued plants during the first, second and third days are shown in figure 2. It is clear that the number of females landing on the first day was always much higher than on the second and third days.

On the first day, there was a clear gradient with significantly more females landing on the plants closest to the release point. The shape of the first-day landing curve was similar for the three replicates. On the second and third day, there was no relation between distance from the release point and numbers of wasps that had landed on the spray-glued plants. If we compare the number of actual landings with the expected number of landings based on diffusion dispersal, it can be concluded that dispersal is similar to what one expects based on random dispersal (at 1.5, 3, 4.5, 6 and 7.5 meter the actual average numbers of wasps landing on the spray-glued plants were respectively 25.6, 8.3, 5.3, 3, and 1.9, while the expected numbers based on random distribution were 19.2, 9.6, 6.5, 5, and 3.8; this results in a χ^2 value of 3.68 and a P value > 0.05). The average distance flown by the more than 500 wasps that were caught on a spray-glued plant on the first day was 2.74 meters.

The number of males found on the spray-glued plants was lower on the first days than what would be expected from the sex-ratio of the release material (table 1). On the second and third days, the proportion of males increased and came often close to the expected 0.6 sex-ratio of the released material. Vertical landing distributions over the leaf levels of both males and females were similar to those found in the experiments of Suverkropp (1994).

The parasitism of the egg masses placed in the field is shown in figure 3. In the first two replicates, mean parasitism was 37 and 40% on the first day. On the second day, mean parasitism was 24 and 4%, respectively. On the third day of the second replicate, 6% of the eggs were parasitized. In the third replicate, there was only 3% mean parasitism on the first day and even less (2%) or none on the second and third day. There was no correlation between parasitism and distance from the re-

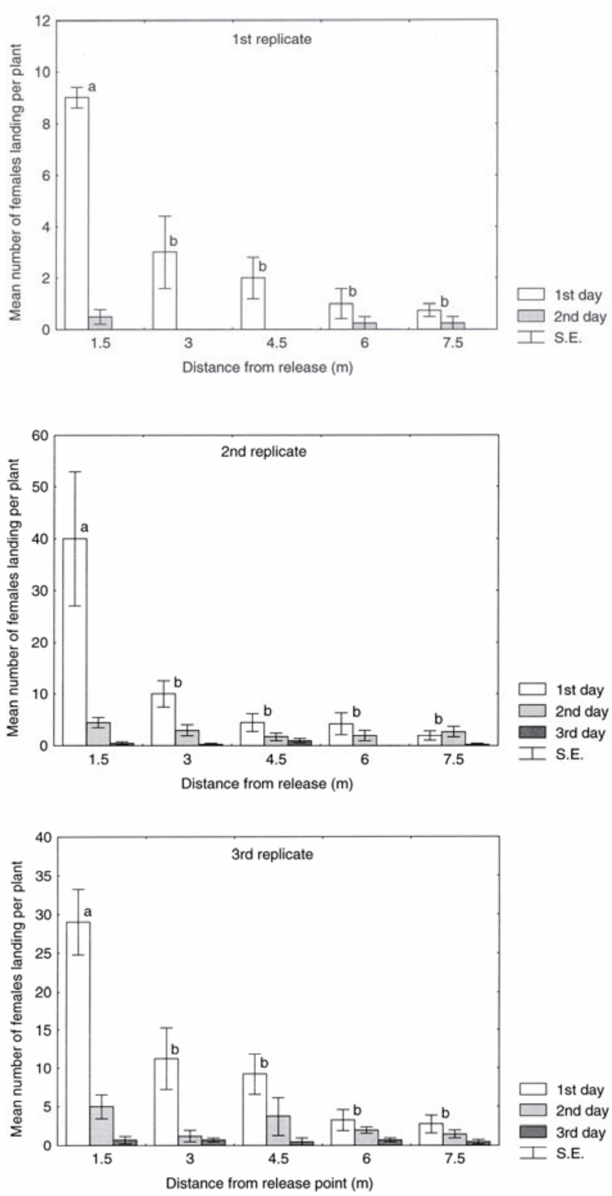

Figure 2. Mean number of female *T. brassicae* landing on glue-sprayed plants at different distances from the release point one, two and three days after release. Different letters indicate significant differences (P < 0.05) in a Duncan test of square-root transformed data. No significant differences on second and third days.

Table 1. Number and percentage of females of total number of released *T. brassicae* landed on glue-sprayed plants one, two and three days after release.

Replicate	Day	No.	Percentage females
1	1	86	0.73
	2	6	0.66
2	1	267	0.91
	2	100	0.56
	3	14	0.57
3	1	241	0.92
	2	71	0.76
	3	21	0.61

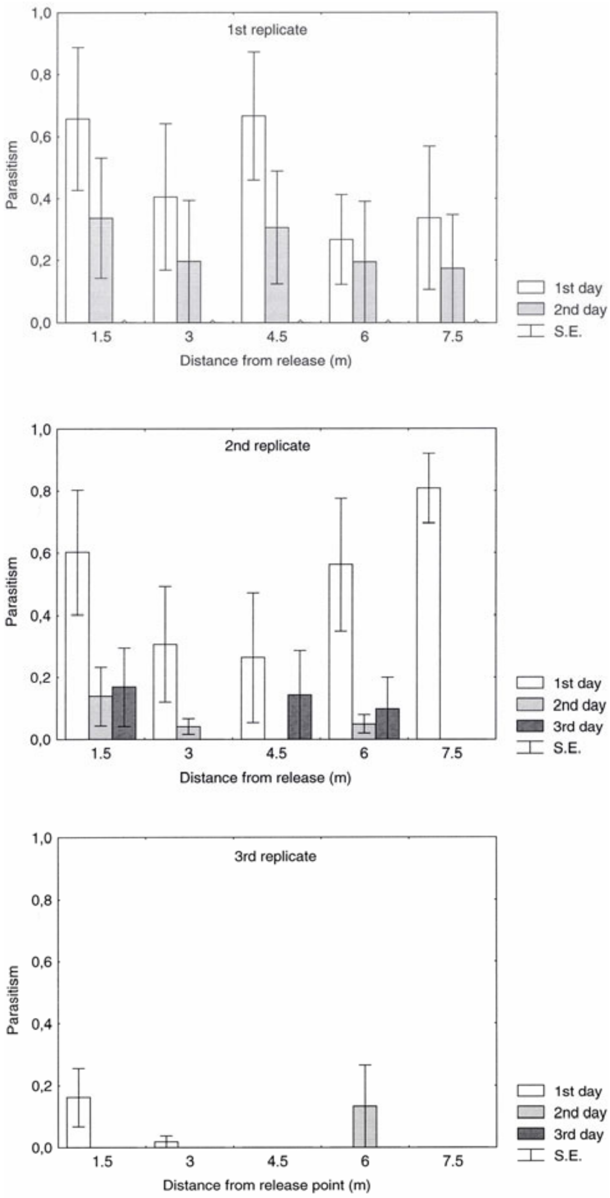

Figure 3. Mean percentage of parasitism of *O. nubilalis* egg masses at different distances from the release point one, two and three days after release. No significant differences ($P < 0.05$) in a Duncan test of arcsine transformed data.

lease point in any of the replicates (ANOVA of arcsine transformed percentages). Most of the egg masses were only partly parasitized, on average 52.2% of the eggs in an egg mass were parasitized, and this was markedly lower on the second and third day.

Also, no correlation was found between the number of wasps on the glue-sprayed plants and the parasitism of the egg masses at the same location.

Discussion

The experiment for estimating the distance covered during an initial flight showed that most of the wasps were found on plants close to the release plant. Since plants within rows were only 15 cm apart, and the plants had leaves that were up to 95 cm, short jumps (<5 cm) from the release plant to the spray-glued plants could account for some of the dispersal measured.

This would mean that most of the wasps should have been found at those spots where the leaves of the spray-glued plants were closest the release plant. However, this is not what we found in our experiment, indicating that walking and short jumps were not, as suggested by Pak *et al*. (1985), the main mechanisms of dispersal. A small part of the wasps reached plants that were either too far away for jumping or in the two outer rows, which shows that *T. brassicae* does fly between plants without intermittent landings and that not all movement is by flights of only a few centimetres. A problem in these experiments is the low percentage of wasps recaptured. Since the plants were all sprayed with glue, all the wasps that landed on the plants were captured. No wasps were found on the parts of the netting that were checked. Since the netting was checked thoroughly directly above the release point, it is unlikely that many wasps flew straight upwards. Apparently, most wasps fly between the plants in a crop of this height. Keller and Lewis (1985) found that most flight activity of *T. pretiosum* also takes place within the cotton crop and not above it. In an empty cage of the same size as used in the current experiment with a release container hanging free in the centre, up to 24 to 40% of the wasps were found on the ground directly under the release point, and only 2% or less on the top (Dutton and Bigler, 1995). In the current experiment, we have not sampled for wasps on the soil.

The experiment on landing and oviposition in the field indicated fast dispersal behaviour. On the first day a clear decrease was found between the number of wasps on spray-glued plants and the distance from the release point. On the second and third day, this gradient was no longer observed. The high number of wasps on the plants closest to the release point is supposed to be the result of many wasps moving away from the release points with short flights. This confirms our observations from the initial flight experiment.

The minimum temperature at which *T. brassicae* still flies is 18 °C (Suverkropp, unpublished data) and *T. brassicae* is only active during daylight (Pompanon *et al*., 1994). This means that the wasps had at least ten hours each day to disperse by flight in the experiments. The mean time spent between flights is about 20 minutes (Suverkropp, 1997), so about thirty flights could have been made each day. If the mean distance of the first flight (60 cm) is a good indication for the distance of flights in general, this should cause most wasps to leave the experimental area in three days, even if flight was undirected. We assume that the number of wasps caught on the glued plants was proportional to the number of wasps present in the experimental area. This means that only 25% of the wasps were still in the experimental area on the second day and only 5% on the third day. The mean life-span of the *T. brassicae* adults used in these experiments was at least ten days in the laboratory when fed on diluted honey (Bigler *et al*., 1987). As weather conditions in the field were not extreme, we expect that disappearance was due to combined effects of dispersal and mortality. The only carbohydrate source for adult wasps in maize would be honeydew from sap sucking insects (e.g. aphids). However, in our experiments, no or very few aphids and other sap suckers were present and, thus, honeydew was not available. This fact could have resulted in high adult wasp mortality within the first two to three days.

In the first replicate where the plants were small, the number of *T. brassicae* landing was significantly lower than in the other replicates. This might be an effect of the plant landing area available, but it is also possible that the dispersal speed is influenced by plant size. Residence time of *T. brassicae* is lower on smaller plants (Suverkropp, 1997), so the number of flights per day is higher. The open space between the plants also means that the wind is stronger inside the crop, which might influence speed of passive movement out of the experimental area.

Males dispersed slower than females. *Trichogramma* males emerge on average earlier than females (Waage and Ng, 1984; Lee *et al*., 1988; Forsse *et al*., 1992). Apparently, males spend a longer time close to the area where they emerged than the females. Slow dispersal of *Trichogramma* males was also found by Stern *et al.* (1965) for *Trichogramma semifumatum* (Perkins).

Parasitism was low throughout the experiment. The very low parasitism on the second and third days is the result of the very low numbers of *T. brassicae* still present. The numbers landing on the adjacent glue-sprayed plants on the first day suggest that substantial numbers of wasps must have landed on the plants with egg masses closest to the release point. The fact that not all egg masses were parasitized at this distance means that the chances of an individual female to find an egg mass on a plant on which it landed are not very high. However, the fact that the egg masses were on cards clipped to the leaves makes it more difficult for the females to find the egg masses (Chernyshev *et al*., 1988; Suverkropp *et al*., 2008). A gradient in parasitism around the release point was found in maize (Bigler *et al*., 1988; Maini *et al*., 1991), but not in cabbage (van der Schaaf *et al*., 1984). Van den Heuvel (1986) measured a parasitism gradient in low maize crops but not in high ones. The absence of correlation between landing and oviposition in this experiment shows that parasitism is not a good indicator of dispersal as such.

Parasitism was just as high in the first as in the second replicate, although the number landing was significantly higher in the second replicate. This is most likely a result of the smaller leaf area of the plants in the first replicate. In theory, searching success of *Trichogramma* is directly correlated with leaf area, because *Trichogramma* searching is assumed to be mostly random (Kanour and Burbutis, 1984; Knipling and McGuire, 1968). In many field studies, this was also observed (Ables *et al*., 1980; Burbutis and Koepke, 1981; van den Heuvel, 1986; Kot, 1979; Maini *et al*., 1991; Need and Burbutis, 1979). However, this assumes that dispersal and disappearance are the same in crops with plants of different size. In a point release, there will be no such clear correlation, because dispersal has a much stronger effect on the number of wasps actually available for parasitization in the testing area. Parasitism by *Trichogramma evanescens* Westwood was also higher after plants became larger (and the leaf canopy closed) in small cabbage plots (van Heiningen *et al*., 1985). The reason for the very low parasitism in the third replicate is unclear, since the difference in size of the plants with the second replicate was not large and weather conditions were good.

We realize that the use of eggs laid on wet filter paper and then attached to the host plant may have influenced the degree of parasitism in the field, as host scales and host kairomones may not be present in and around egg batches in the same manner as when directly laid on the host plant (e.g. Smits, 1982; Suverkropp, 1997; Suverkropp *et al*., 2008). However, our main goal of this experiment was not to determine the efficacy of parasitism by *T. evanescens,* but how this parasitoid disperses, and it is known that egg scales and semiochemicals present near host egg batches do not influence flight and landing behaviour of *T. evanescens* (Suverkropp, 1997).

In conclusion, both experiments show that flight, and not walking or jumping, is the most important mechanism in between-plant movement for *T. brassicae*. This is supported by the fact that there is little effect of planting distance (van Alebeek *et al*., 1986; Neuffer, 1987; Suverkropp, 1994) on dispersal. The second experiment clearly shows that parasitism is not a very good measure of dispersion. Host location, host recognition, host acceptance and host availability are all involved in determining the level of parasitism. If the object of study is purely the dispersal behaviour and not the performance of *T. brassicae* as a biocontrol agent, the use of trap plants will yield clear and unambiguous information.

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