

Close-Range Host Searching Behavior of the Stemborer Parasitoids *Cotesia sesamiae* and *Dentichasmias busseolae*: Influence of a Non-Host Plant *Melinis minutiflora*

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Accepted July 26, 2004; revised September 30, 2004

Studies were conducted on the host searching behavior of the larval parasitoid Cotesia sesamiae (Cameron) (Hymenoptera: Braconidae) and the pupal parasitoid Dentichasmias busseolae Heinrich (Hymenoptera: Ichneumonidae), both of which attack lepidopteran (Crambidae, Noctuidae) cereal stemborers. The behavior of D. busseolae was observed in a diversified habitat that consisted of stemborer host plants (maize, Zea mays L. and sorghum, Sorghum bicolor (L). Moench (Poaceae)) and a non-host plant (molasses grass, Melinis minutiflora Beauv. (Poaceae)), while C. sesamiae was observed separately on host plants and molasses grass. In previous olfactometer studies, C. sesamiae was attracted to molasses grass volatiles while D. busseolae was repelled. The aim of the present study was to investigate the influence of molasses grass on close-range foraging behavior of the parasitoids in an arena that included infested and uninfested host plants.

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Dentichasmias busseolae strongly discriminated between host and non-host plants, with female wasps spending most of the time on infested host plants and least time on molasses grass. Likewise, *C. sesamiae* spent more time on uninfested and infested host plants than it did on molasses grass in single choice bioassays. While on infested plants, the wasps spent more time foraging on the stem, the site of damage, than on other areas of the plant. Overall, the results indicate that presence of the non-host plant does not hinder close range foraging activities of either parasitoid.

KEY WORDS: *Cotesia sesamiae*; *Dentichasmias busseolae*; *Melinis minutiflora*; stemborer parasitoids; foraging behavior; intercropping; diversified habitat.

INTRODUCTION

Foraging behavior is an important factor that influences the effectiveness of a parasitoid as a biological control agent (Jervis and Kidd, 1996). During foraging, the parasitoid must first locate a host plant, then an infested plant, and finally the host. Parasitoids use chemical, visual, mechanical and acoustic cues, or a combination of two or more of these to locate host habitats and hosts within the habitat (Godfray, 1994; Vet *et al.*, 2002). A sequence of responses to different stimuli brings the parasitoid closer to its potential host. Plants are a major source of information and their role in the host selection process of parasitoids has become increasingly clear (Turlings *et al.*, 1995; Dicke and Vet, 1999; Vet, 1999).

With insect pests becoming increasingly resistant to conventional chemical pesticides, and heightened concern about possible environmental and human health effects of pesticides, research is now directed towards more effective, environmentally sustainable approaches to combat pests. Habitat management is one such approach that has recently gained attention (Gurr *et al.*, 2000; Landis *et al.*, 2000). In this approach, the habitat is altered to improve the availability of resources required by natural enemies for optimal performance. Intercropping, a component of habitat management, may improve parasitoid activity because, among other advantages, one of the plants of the intercrop may provide allelochemical attraction to natural enemies (Verkerk *et al.*, 1998). In their studies on habitat management to control cereal stemborers (Lepidoptera: Crambidae, Noctuidae), Khan *et al.* (1997a,b) devised a system in which molasses grass (*Melinis minutiflora* Beauv. (Poaceae)), a non-host plant of stemborers, repelled gravid stemborer moths away from a maize crop. The moths were in turn attracted by a trap crop, reducing infestation and damage on maize. This approach has been referred to as a 'push-pull' or stimulo-deterent diversionary strategy (Pickett *et al.*, 1997; Agelopoulos *et al.*, 1999). An advantage

noted in the same study was the positive effect of the intercropping on the performance of a larval stemborer parasitoid, *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae). Higher parasitism was found in the intercrop than in the maize monocrop. This observation was attributed to the attraction of the parasitoid to the intercrop by chemical volatiles produced by molasses grass.

Olfactometric Y-tube studies confirmed that molasses grass volatiles attracted *C. sesamiae* (Khan *et al.*, 1997a; Gohole *et al.*, 2003a). In contrast, the volatiles were repulsive to another parasitoid species, *D. busseolae* (Gohole *et al.*, 2003b). Whether they were attracted or repelled, the question that remains is: what happens once parasitoids have entered such a diversified habitat? When attracted, do they land and search on the molasses grass, thereby wasting valuable foraging time? When repelled, do they recognize the non-host plant at short range and consequently are diverted to the infested host plants? To link results from laboratory olfactometer studies to field results on parasitism rates, it is crucial to understand the influence of plant diversity on short-range foraging activities of parasitoids. This is an area that has received limited attention in spite of the numerous theories that have been put forward to explain why some diversified systems harbor more arthropod natural enemies than simple cropping systems.

Cotesia sesamiae is a gregarious endoparasitoid of larvae of several stemborers (Ngi-Song *et al.*, 1995). It employs an 'ingress and sting' foraging strategy, where it locates the entrance hole of the tunnel, contacts the frass, starts antennating and then enters the tunnel by crawling through the frass (Smith *et al.*, 1993). During foraging, *C. sesamiae* uses chemical cues to locate its host, with the most attractive chemical compounds coming from infested host plants and frass (Ngi-Song *et al.*, 1996; Ngi-Song and Overholt, 1997; Rutledge and Wiedenmann, 1999). *Dentichasmias busseolae* Heinrich (Hymenoptera: Ichneumonidae) is a solitary pupal endoparasitoid with a narrow host-range that is limited to *Chilo* species (Lepidoptera: Crambidae) (Mohyuddin and Greathead, 1970; Zhou *et al.*, 2003). Most collections of the parasitoid have been from *Chilo partellus* (Swinhoe). *Dentichasmias busseolae* is attracted to the vicinity of its host mainly by chemical cues resulting from the interaction of the host and host plant (Gohole *et al.*, 2003b). It prefers to oviposit in young pupae (one to two days old) in which development is optimal (Bahana, 1989). Once on the infested plant, the parasitoid is arrested by cues from frass and possibly by mechanosensory and visual cues because it concentrates its antennating at the stem region harboring the pupa. The parasitoid gains entry into the tunnel by biting off the membranous moth exit window. This window is constructed by the last larval instar of the stemborer prior to pupation to facilitate egress of the adult moth from the stem. Like *C. sesamiae*, *Dentichasmias*

busseolae also attacks its host using an 'ingress and sting' tactic (Smith *et al.*, 1993).

The objective of the present work was to examine the foraging behavior of the stemborer parasitoids *C. sesamiae* and *D. busseolae* on hosts and the non-host plant molasses grass. The investigations will be useful in predicting the influence of the non-host plant on the foraging process of these parasitoids in an intercrop.

MATERIALS AND METHODS

Plants

The host crop plants sorghum (cv Seredo) and maize (H-511) were planted in plastic pots (\varnothing 20 cm). The non-host plant molasses grass, derived from Thika ($37^{\circ}5' E$, $1^{\circ}3' S$) situated 35 km from Nairobi, Kenya, was also planted in plastic pots (\varnothing 25 cm) from root splits. Both sorghum and maize were thinned to one plant per pot after 7 days of emergence (DAE). The plants were kept at the International Centre of Insect Physiology and Ecology (ICIPE) in Nairobi, under large cages covered with 400-micron mesh netting to protect them from natural insect attack.

Insects

Chilo partellus larvae were obtained from a laboratory colony reared on artificial diet (Ochieng *et al.*, 1985), and maintained at ICIPE. *Cotesia sesamiae* were also obtained from a laboratory colony maintained at ICIPE ($25 \pm 2^{\circ}C$, 70–80% RH) according to the method described by Overholt *et al.* (1994). Females used in the bioassays were 1–2 days old and naive with regard to host plant and ovipositional experience.

A laboratory culture of *D. busseolae* was established with adults reared from *C. partellus* pupae collected from Mbita Point in western Kenya ($34^{\circ}10' E$, $0^{\circ}25' S$). The parasitoids were reared using a slightly modified version of Mohyuddin's (1972) method. Maize stems of 15 cm length were split longitudinally into two, and then three depressions, 3 cm apart, were excavated in one of the longitudinal sections. Holes (\varnothing 0.4 cm) were bored through the other longitudinal section at locations corresponding to the depressions. The depressions were filled with frass from fifth instar *C. partellus* larvae but ensuring there was space for the parasitoid to maneuver its way around the pupae. Two one-day-old *C. partellus* pupae were placed in each depression. The longitudinal sections were rejoined and secured at each end using elastic bands. The holes were lightly sealed with frass

to simulate an exit hole. The stem pieces containing the pupae were offered to the *D. busseolae* females in acrylic cages ($30 \times 30 \times 30$ cm) at a ratio of 1 female:2 pupae. Stems were presented in an upright position and held in place by standing them in plasticine. Pupae were extracted from the stems after 24 h and placed on moistened filter paper in Petri dishes. After emergence, both male and female parasitoids were released in a cage and allowed 48 h for mating after which the females were separated from the males and placed in separate cages. The parasitoids were provided a diet of 20% honey/water solution, supplied in Petri dishes containing cotton wool pads. The pads were renewed every two days to avoid fermentation. The parasitoids also had access to water supplied on wet cotton wool pads. Females used in the experiment were 5–7 days old and naïve.

Bioassay with *D. busseolae*

The experiments were conducted in a screen-house at $26 \pm 2^\circ\text{C}$, 45–65% RH. A steel-framed cage, measuring $2 \text{ m} \times 2 \text{ m} \times 2 \text{ m}$ and covered with fine white mesh ($400 \mu\text{m}$) net material, was constructed. The experimental arena consisted of four potted plants placed in a square arrangement on a table centrally positioned in the cage (Fig. 1). Two fans were placed at one end of the table to provide an air stream. The wind speed was measured using an anemometer and set at $0.2\text{--}0.3 \text{ m s}^{-1}$. The foraging behavior of *D. busseolae* was observed in the following crop arrangements:

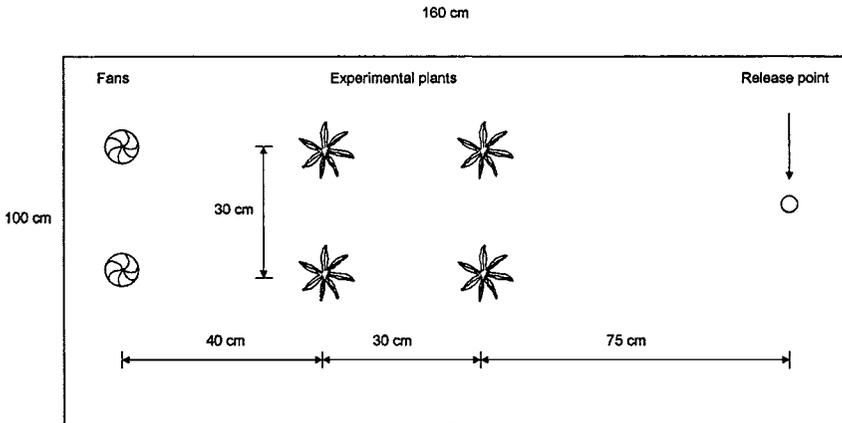


Fig. 1. Layout of the semi-field experiment testing close range behavior of *D. busseolae* in host and non-host plants.

| | |
|---|--|
| (I) Maize monocrop (MM)... | Two uninfested maize + two infested maize plants |
| (II) Uninfested maize intercrop (UMI)... | Two uninfested maize + two molasses grass plants |
| (III) Infested maize intercrop (MI)... | Two infested maize + two molasses grass plants |
| (IV) Sorghum monocrop (SM)... | Two uninfested sorghum + two infested sorghum plants |
| (V) Uninfested sorghum intercrop (USI)... | Two uninfested sorghum + two molasses grass plants |
| (VI) Infested sorghum intercrop (ISI)... | Two infested sorghum + two molasses grass plants |

Host plants were artificially infested by introducing two fifth instar *C. partellus* larvae into the whorl of each host plant. The larvae were allowed to feed and tunnel into the stem for a period of 5–8 days during which they constructed a moth exit window and pupated in the plant stem. At the start of each observation, a single naive *D. busseolae* female was released from a vial 75 cm downwind from the plants. From the moment it flew away from the vial, observations and recording of its behavior and location were started. Observations were terminated after 30 min or when the parasitoid walked or flew away and landed elsewhere (not on plants) and remained there for more than 5 min. For each crop arrangement, 15 females were tested and each wasp was used once. Plants were changed after every three individuals, or when the parasitoid bit off the exit hole window. The following behavioral activities were recorded using the computer software package, The Observer (Noldus, 1991):

| | |
|------------------|--|
| Flying... | When the wasp was in flight either within the vicinity of the plants or away from the plants and not in touch with any object. |
| Walking... | When the wasp walked constantly on any substrate, with antennae swinging but not palpating the substrate. |
| Standing... | The wasp remained motionless with very minimal antennal movements. |
| Grooming... | The wasp repeatedly drew antennae through forelegs and brushed wings and abdomen with the other legs. |
| Antennating... | The wasp walked with irregular speed or stopped, with antennae forward and palpating the substrate. |
| Window biting... | The wasp bit through the stemborer exit window using her mandibles while frequently probing into the tunnel with her antennae. |

Tunnel entry. . . The wasp entered the tunnel headfirst or if pupa was close to entrance, she turned and probed at the tunnel entrance with her ovipositor.

Throughout the experiment, the plant treatment on which the wasp was located was recorded, and all non-plant positions were recorded as elsewhere.

Bioassay with *C. sesamiae*

Preliminary experiments showed that the bioassay used for *D. busseolae* would not work with *C. sesamiae* due to its small size (~3 mm long), which made observations problematic. Thus, the arena was modified and experiments were conducted in a temperature-controlled room at $25 \pm 2^\circ\text{C}$, 60–75% RH. The host plants were 5 weeks old. Observations were made on single plants. The following plants were used:

- (I) Infested maize
- (II) Uninfested maize
- (III) Infested sorghum
- (IV) Uninfested sorghum
- (V) Molasses grass

To obtain infested plants, a hole was bored in the stem of a host plant 10 cm above soil level. A single third instar *C. partellus* larva was introduced into the hole and allowed 36 h to bore into the plant stem. At the start of an observation, a single wasp was placed on a host plant's stem 15 cm above soil level. In case of molasses grass, it was placed 5 cm above soil level on one of the centrally positioned stems. The behavior and location of the wasp on the plant were recorded using The Observer. A total of 20 female wasps were observed for each treatment and each wasp was used only once. The experimental plants were changed after every three wasps or when the wasp entered the tunnel. The durations (in s) of the following parameters were recorded.

- (a) Behavior of the parasitoid: fly, walk, stand, groom, antennate and tunnel entry (see bioassay with *D. busseolae* for explanations of behaviors).
- (b) Position of the parasitoid: stem, leaves, whorl, tunnel entrance, inside tunnel and elsewhere.

Observations were terminated after 20 min or when the parasitoids flew or walked away from the plant and stayed elsewhere for more than 2 min.

Data Analysis

Since data were not normally distributed and variances were not equal, they were analyzed using non-parametric statistics. For each crop arrangement in the *D. busseolae* experiment, total time spent at each position by the wasp and average durations of behaviors were compared using the Friedman's test. When significant, the means were further compared using Wilcoxon's multiple pairwise comparison with Bonferroni correction. Residence time spent on similarly treated plants in the monocrop and intercrop (e.g., residence time on uninfested maize in the monocrop was compared with that on uninfested maize in the intercrop) were compared with the Mann-Whitney-*U* test. The time it took for the wasp to locate infested host plants in the monocrop and intercrop and frequency of visits to these plants was compared using the Mann-Whitney-*U* test.

Analyses of difference in time durations between treatments and duration of behavioral parameters in the *C. sesamiae* experiment were performed using the Kruskal-Wallis one-way ANOVA. In case of analyses being significant, the Mann-Whitney-*U* test for pairwise comparisons were used with a Bonferroni correction. The Wilcoxon signed rank test was used to compare time spent on the plant to time spent elsewhere (not on the plant), within the same treatment.

RESULTS

Dentichasmias Busseolae

In all crop arrangements that had infested host plants (MM, IMI, SM and ISI), *D. busseolae* wasps spent most of their time on the infested plant (Fig. 2). There was no difference in time spent on uninfested host plants and time spent elsewhere in the two crop arrangements containing uninfested host plants (UMI and USI). *Dentichasmias busseolae* spent significantly less time on molasses grass than on either infested or uninfested host plants (Fig. 2). Comparison of the amount of time spent on uninfested maize and sorghum in the monocrop with their counterparts in the intercrop revealed that the wasps spent more time on uninfested plants in the intercrop as compared to the monocrop ($U = 17, n_1 = 20, n_2 = 20, p < 0.0001$ and

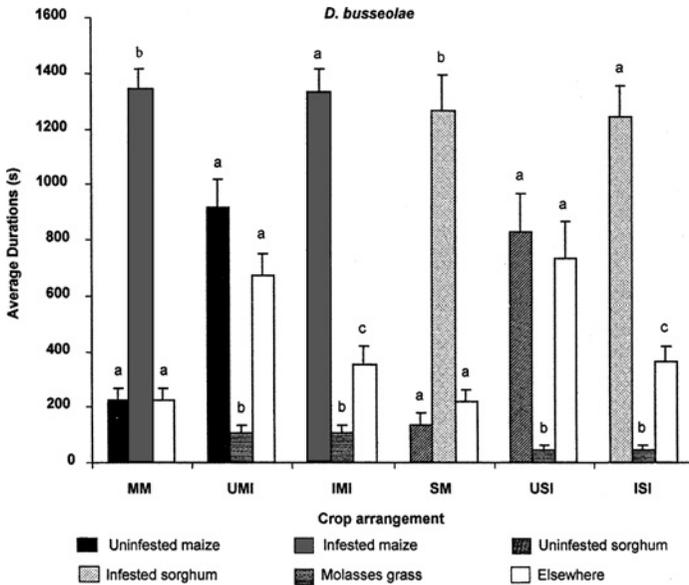


Fig. 2. Average residence times (mean \pm SE) of *D. busseolae* in a semi-field set-up of host and non-host plants. Within each crop arrangement, means sharing the same letter do not differ (Friedmann’s test (df = 2) followed by Wilcoxon’s multiple pairwise comparison with Bonferroni correction, $\alpha < 0.016$, for multiple pairwise comparison), $n = 15$. MM, maize monocrop; UMI, uninfested maize intercrop; IMI, infested maize intercrop; SM, sorghum monocrop; USI, uninfested sorghum intercrop; ISI, infested sorghum intercrop.

$U = 20.5$, $n_1 = 20$, $n_2 = 20$, $p < 0.0001$, for uninfested maize and sorghum, respectively). There was no difference in time spent on infested host plants in the monocrop and intercrop ($U = 110$, $n_1 = 20$, $n_2 = 20$, $p = 0.935$ and $U = 101$, $n_1 = 20$, $n_2 = 20$, $p = 0.653$ in infested maize and sorghum, respectively).

Durations of behavior at the three positions in each crop arrangement are shown in Table I. While on the host plants, the wasps were more involved in walking and standing. On the infested plants, the wasps were also occupied with activities related to close range host finding: antennating, window biting and tunnel entry. On encountering frass, the wasps were arrested and spent time antennating the frass.

When the wasp located the portion of the stem harboring the pupa, it walked around that area, drumming this part of the stem with its antennae until it located the moth exit window. The wasp then bit off part of the window occasionally inserting one of its antennae through the hole in the window and probed the tunnel. When it encountered a host, it continued biting

Table 1. Average Durations (s) (\pm SE) of Behaviors of *Dentichasmius busseolae* in Different Cropping Arrangements

| Crop arrangement | Position | Behavioral parameters | | | | | | |
|------------------------------|--------------------|-----------------------|-------------------|--------------------|-------------------|------------------|------------------|-----------------|
| | | Fly | Walk | Stand | Groom | Antennate | Window biting | Tunnel entry |
| Maize monocrop | Uninfested maize | 13.3 \pm 3.2a | 77.8 \pm 16.2a | 103.9 \pm 30.3ab | 29.6 \pm 10.9a | — | — | — |
| | Infested maize | 12.7 \pm 2.9a | 391.1 \pm 41.9b | 220.7 \pm 33.3b | 131.9 \pm 14.4b | 416.7 \pm 64.9 | 145.9 \pm 60.4 | 24.7 \pm 10.0 |
| | Elsewhere | 69.2 \pm 19.1b | 82.2 \pm 22.9a | 44.5 \pm 11.9a | 25.8 \pm 8.8a | — | — | — |
| Uninfested maize intercrop | Uninfested maize | 22.6 \pm 6.6a | 260.0 \pm 54.5a | 508.7 \pm 89.4a | 123.6 \pm 23.4a | 0.9 \pm 0.8 | — | — |
| | Molasses grass | 9.6 \pm 2.6a | 27.9 \pm 6.2b | 49.2 \pm 17.4b | 19.2 \pm 8.2b | — | — | — |
| | Elsewhere | 86.7 \pm 9.2b | 296.9 \pm 52.1a | 202.3 \pm 31.8c | 86.0 \pm 17.1a | — | — | — |
| Infested maize intercrop | Infested maize | 10.9 \pm 2.0a | 400.2 \pm 52.4a | 335.9 \pm 57.9a | 81.0 \pm 10.0a | 413.5 \pm 52.3 | 47.5 \pm 21.5 | 42.6 \pm 31.7 |
| | Molasses grass | 9.5 \pm 2.2a | 38.6 \pm 14.8b | 51.5 \pm 17.0b | 6.0 \pm 3.9b | — | — | — |
| | Elsewhere | 42.3 \pm 10.9b | 148.0 \pm 28.8c | 103.4 \pm 26.1b | 57.5 \pm 19.4a | — | — | — |
| Sorghum monocrop | Uninfested sorghum | 9.2 \pm 5.7a | 70.8 \pm 31.2a | 42.5 \pm 17.8a | 13.7 \pm 7.5a | — | — | — |
| | Infested sorghum | 11.8 \pm 4.2a | 384.7 \pm 56.1b | 143.6 \pm 35.9b | 169.3 \pm 28.2b | 370.9 \pm 48.4 | 135.6 \pm 53.6 | 51.6 \pm 19.0 |
| | Elsewhere | 34.9 \pm 7.0b | 89.7 \pm 21.0a | 49.6 \pm 14.9ab | 44.2 \pm 11.9a | — | — | — |
| Uninfested sorghum intercrop | Uninfested sorghum | 17.0 \pm 7.7ab | 392.0 \pm 84.3a | 346.1 \pm 60.5a | 69.7 \pm 20.9a | 3.8 \pm 2.7 | — | — |
| | Molasses grass | 5.2 \pm 1.4a | 9.4 \pm 4.1b | 27.3 \pm 11.7b | 4.7 \pm 3.1b | — | — | — |
| | Elsewhere | 44.5 \pm 9.3b | 284.0 \pm 68.4a | 279.5 \pm 66.8a | 127.4 \pm 31.1a | — | — | — |
| Infested sorghum intercrop | Infested sorghum | 14.3 \pm 1.9a | 505.1 \pm 51.5a | 225.2 \pm 43.0a | 160.9 \pm 21.4a | 266.0 \pm 46.6 | 56.0 \pm 24.7 | 15.6 \pm 7.6 |
| | Molasses grass | 5.2 \pm 1.6b | 6.8 \pm 2.9b | 26.3 \pm 11.6b | 6.0 \pm 3.1b | — | — | — |
| | Elsewhere | 47.3 \pm 10.0c | 161.3 \pm 32.8c | 88.7 \pm 21.7ab | 67.4 \pm 15.4c | — | — | — |

Note. Means followed by the same letter in a column within a crop arrangement group are not significantly different (Friedman's test followed by a Wilcoxon test with Bonferroni correction, $\alpha < 0.016$, for multiple pairwise comparisons). $N = 15$.

Table II. Behavioral Durations (s \pm SE) of *D. busseolae* on Infested Host Plants in Different Crop Arrangements

| Parameter | Crop | | Arrangement | |
|--|-----------------------------|----------------------------|-------------------------------|------------------------------|
| | Infested maize in intercrop | Infested maize in monocrop | Infested sorghum in intercrop | Infested sorghum in monocrop |
| Mean time to first landing on infested plant | 111.7 \pm 34.6a | 153.6 \pm 59.1a | 93.8 \pm 26.8A | 131.7 \pm 38.7A |
| Frequency of visits | 3.8 \pm 0.5a | 3.3 \pm 0.6a | 3.7 \pm 0.5A | 2.5 \pm 0.3A |
| Mean latency time to window biting | 799.7 \pm 152.1a | 720.4 \pm 162.6a | 433.6 \pm 58.7A | 454 \pm 94.4A |
| Percentage locating window | 53% ($n = 15$) | 60% ($n = 15$) | 47% ($n = 15$) | 80% ($n = 15$) |
| Percentage entering | 20% ($n = 15$) | 33% ($n = 15$) | 27% ($n = 15$) | 47% ($n = 15$) |

Note. Means followed by the same case letter in a row are not significantly different (Mann-Whitney-*U* test, $p < 0.05$).

the window until the hole was big enough for the wasp to enter the tunnel. If the pupa was close to the window, the wasp would turn, start probing with its ovipositor until it detected the pupa, and then oviposit. A comparison of duration of various behaviors in uninfested host plants in monocrop and intercrop arrangements revealed that wasps spent more time walking, standing and grooming in the intercrops than monocrops (Mann-Whitney-*U* test, $n_1 = 20$, $n_2 = 20$, $p < 0.05$). There was no difference in duration of behaviors (fly, walk, stand, groom, antennate, window biting and tunnel entry) on infested host plants in monocrop and intercrop arrangements. The same observation was noted for duration of behaviors on the non-host plant, molasses grass, when in combination with uninfested and infested host plants (Mann-Whitney-*U* test, $n_1 = 20$, $n_2 = 20$, $p > 0.05$).

The time taken to locate a window and to bite the window was not different between the two crop arrangements for infested maize or sorghum (Table II). More than 45% of the wasps released in each of the four crop arrangements with infested plants were, able to locate the stemborer exit window. In both the intercrop and monocrop arrangements, 20–47% of the wasps bit off the window and entered the tunnel. In 63% of cases where the wasps entered the tunnel (for both maize and sorghum), oviposition was successful as evidenced by adult parasitoid emergence from the host. Generally, *D. busseolae* spent less time on molasses grass compared to uninfested and infested host plants. Its foraging behavior while on molasses grass typically followed the sequence: walk, stand, groom, and then fly to another location. It was never observed antennating any part of the plant.

There was no difference in time taken by *D. busseolae* until its first encounter with a host plant in the monocrop arrangement compared to the

first encounter of a similarly treated host plant in the intercrop arrangement (Table II). There was also no difference in frequency of visits to infested plants in the two types of crop arrangement. Frequency of visits to uninfested host plants in intercrops was higher than for the uninfested host plants in the monocrop (UM in UMI = 4.6 ± 0.5 , UM in MM = 2.3 ± 0.46 , Mann–Whitney- U test, $U = 41.5$, $n_1 = 20$, $n_2 = 20$, $p = 0.002$ for uninfested maize and US in USI = 3.5 ± 0.7 , US in SM = 1.0 ± 0.3 , Mann–Whitney- $U = 37$, $n_1 = 20$, $n_2 = 20$, $p < 0.001$ for uninfested sorghum).

Case of *Sesamiae*

Cotesia sesamiae spent more time on the host plants as compared to the non-host plant, molasses grass (Fig. 3). None of the parasitoids tested in the molasses grass bioassay stayed in the experimental arena for more than 50% of the observation time. On average, parasitoids spent a total of 329.6 ± 29.9 s in this arena before abandoning it completely. Residence times on infested host plants were higher than on uninfested host plants (Fig. 3), with 40–55% of the wasps spending more than half of their time on the infested plants compared to 15–25% on uninfested plants. The wasps spent more time on the plant than elsewhere in the case of infested maize, uninfested maize, infested sorghum and uninfested sorghum. Mean times spent on molasses grass and elsewhere did not differ (Fig. 3).

While on the infested plants, the wasps spent most of their time on the stem, which also includes time spent at the tunnel entrance (Fig. 4). Of the observed wasps, 70 and 85% were able to locate the tunnel entrance on the infested maize and sorghum, respectively. Of the wasps that located the tunnel entrance, 40% entered maize tunnels, and 25% entered tunnels in sorghum. Of all the wasps that entered the tunnels, only one managed to leave during the time allocated for the bioassays. The movements of the rest were hindered because their bodies and wings adhered to the wet fresh frass.

The average percentages of time of the different foraging behaviors of *C. sesamiae* on different plants are shown in Fig. 5. The wasps were mostly engaged in walking while on host and non-host plants and least in flying. Comparisons were made of the common behavioral elements (fly, walk, stand and groom) on all the plants. The mean duration of flying did not differ among the plants. Durations of walking, standing and grooming did not differ among host plants but were less on molasses grass (Table III). There was no difference in the amount of time spent on the behaviors related to host location between the infested plants. *Cotesia sesamiae* spent the same amount of time antennating and in the act of entering the borer tunnel in

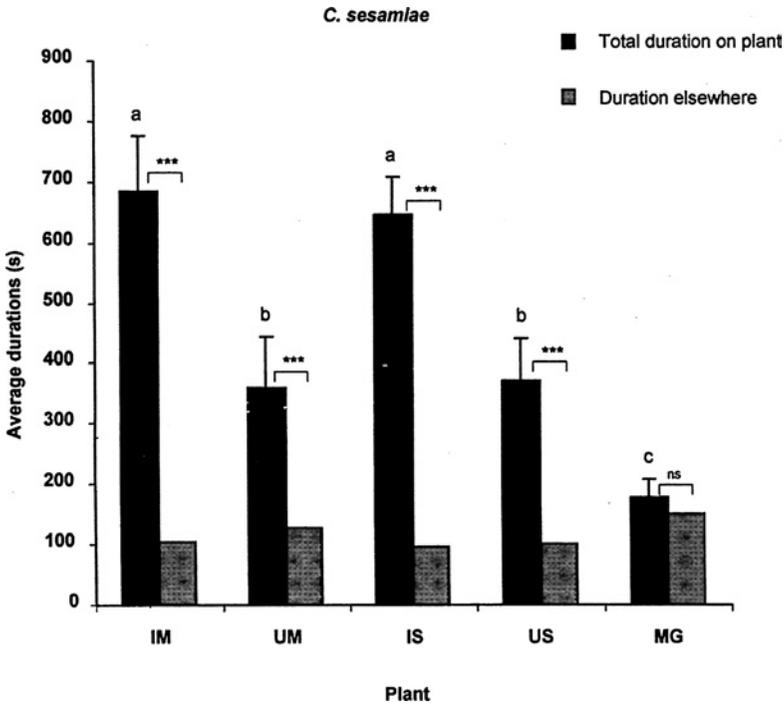


Fig. 3. Average residence times (mean \pm SE) of *C. sesamiae* on host plants and a non-host plant and time spent elsewhere. Same letters above black bars (duration on plant) indicate no significant difference between means (Kruskal-Wallis (df = 4) test followed by Mann-Whitney-U test with Bonferroni correction, $\alpha < 0.005$, for multiple pairwise comparison). Within a treatment, asterisks indicate significant differences between time spent on plant and time spent elsewhere. *** $P < 0.0001$; ns, not significant (Wilcoxon test); $n = 20$. IM, infested maize; UM, uninfested maize; US, uninfested sorghum; IS, uninfested sorghum; MG, molasses grass.

both infested maize and infested sorghum. Analyses on behaviors within a plant treatment revealed that walking was the dominant activity followed by standing and grooming with flying occupying the least time (Table III). *Cotesia sesamiae* spent the least time on molasses grass.

DISCUSSION

Previous laboratory olfactometer studies have shown that *C. sesamiae* and *D. busseolae* are attracted to the host habitat by volatiles emanating from host plants (Ngi-Song *et al.*, 1996; Rutledge and Wiedenmann, 1999; Gohole *et al.*, 2003a,b). Volatiles from the non-host plant, molasses grass, were shown to be attractive to *C. sesamiae* but repellent to *D. busseolae*

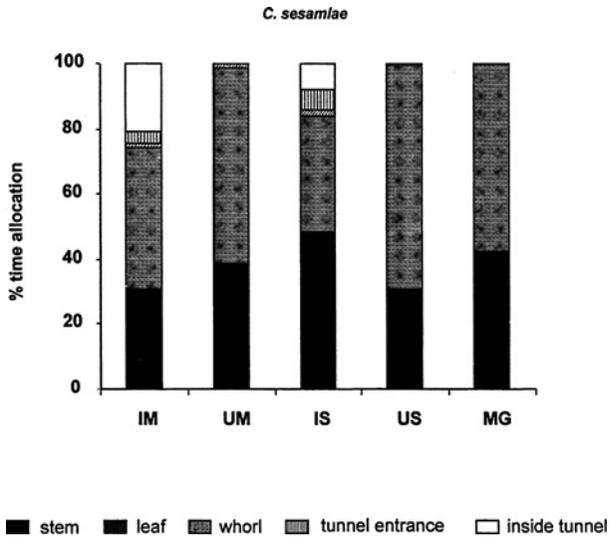


Fig. 4. Relative time allocation of *C. sesamiae* at various locations while foraging on host and non-host plants. IM, infested maize; UM, uninfested maize; US, uninfested sorghum; IS, uninfested sorghum; MG, molasses grass.

(Khan *et al.*, 1997a; Gohole *et al.*, 2003a,b). The present work was designed to determine whether the presence of molasses grass would interfere with close-range foraging of parasitoids once they arrive in the vicinity of the plants. We set out to investigate whether *C. sesamiae* was likely to search on molasses grass, thus wasting time on an unrewarding plant, and if *D. busseolae* was repelled from the intercrop. The results show that both parasitoids behaved differently on host and non-host plants. *Cotesia sesamiae* was not arrested on molasses grass and the presence of the grass did not interfere with foraging of *D. busseolae* on infested host plants. As part of their search for host plants, insects go through a sequence of predictable behavioral acts, called reaction chains (Atkins, 1980), which eventually lead them to suitable host plants. Part of this sequence involves making a decision on whether to stay on a plant on which it has landed or leave. This has recently been described by Finch and Collier (2000) as the 'appropriate/inappropriate landings' theory. The decision is based on visual, olfactory and tactile cues. Variations in color, size and shape of plants play an important role in host selection behavior of insects, especially at close range (Prokopy *et al.*, 1983; Schoonhoven *et al.*, 1998). Molasses grass has slender leaves and thin stems. While walking on this grass, the parasitoids may perceive from the size of the stem that the plant could not

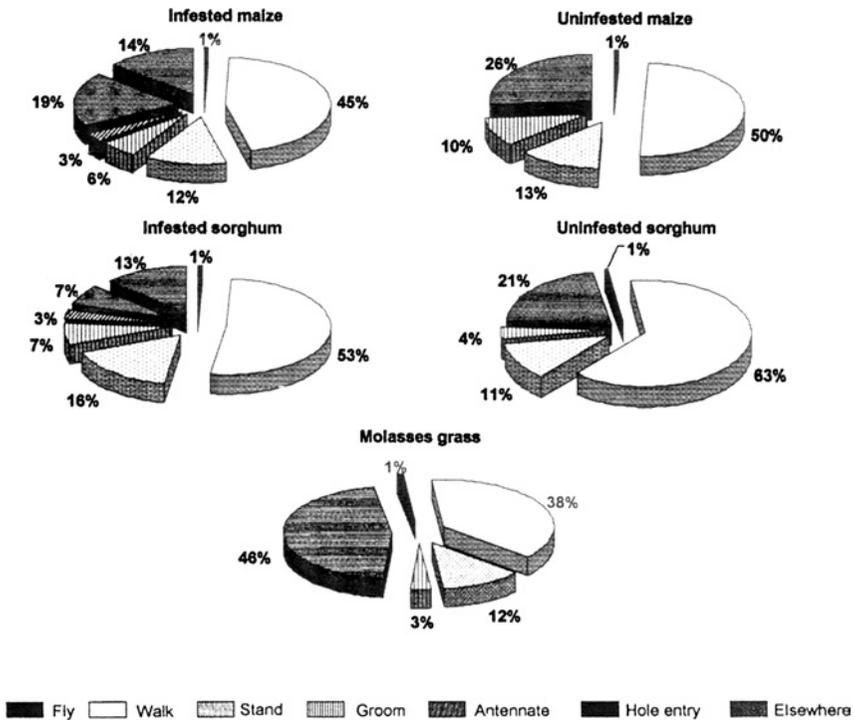


Fig. 5. Foraging activities of *C. sesamiae* on host and non-host plants. Numbers next to pie slices indicate % duration of each behavior while on plant and % duration spent elsewhere.

harbor its hosts. It has been reported that size of leaves was one of the factors influencing residence time of *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) on different plant species (van Roermund and van Lenteren, 1995; Sutterlin and van Lenteren, 1999). While on a plant, a parasitoid also evaluates the chemical traits of the plant that could not be perceived at a distance. The insect, using tarsal receptors, assesses whether the chemical stimuli are acceptable or not (Kostal and Finch, 1994). It is most likely that the parasitoid’s decision to leave the unsuitable molasses grass in search of a more appropriate patch was based on contact chemicals and/or visual cues.

Leaving tendency of *C. sesamiae* and *D. busseolae* on molasses grass was high. Of the total time allotted for observation, *C. sesamiae* spent 27% of the time in the experimental arena with molasses grass, while 63% of the total foraging time was spent in the infested plants arena. *Dentichasmias busseolae* on average spent 5% of its time on molasses grass and 72% on infested plants, in intercrop arrangements.

Table III. Average Durations (s ± SE) of Behavioural Parameters of *Cotesia sesamiae* on Uninfested and Infested Host Plants and a Non-Host Plant

| Behavioural parameters | Treatment | | | | | |
|------------------------|------------------------------|------------------|----------------------------|--------------------|-----------------|--|
| | Infested maize | Uninfested maize | Infested sorghum | Uninfested sorghum | Molasses grass | |
| Fly | 3.8 ± 1.5a A | 4.7 ± 1.6a A | 6.8 ± 3.6a A | 2.9 ± 0.7a A | 3.8 ± 0.9a A | |
| Walk | 350.7 ± 53.4a B | 241 ± 41.1ab B | 382.5 ± 52.3a B | 298.6 ± 56.1a B | 125.2 ± 17.0b B | |
| Stand | 94.2 ± 27.5ab C | 62.3 ± 12.1ab C | 121.6 ± 20.3a C | 52.6 ± 11.7ab C | 39.5 ± 11.5b C | |
| Groom | 46.2 ± 11.4a C | 49.3 ± 11.4a C | 54.7 ± 20.8a AC | 17.4 ± 4.7a A | 9.8 ± 4.9b A | |
| Antennate | 23.8 ± 4.8 ^a AC | – | 23.3 ± 7.2 ^a A | – | – | |
| Tunnel entry | 142.8 ± 69.6 ^b BC | – | 53.8 ± 44.7 ^b A | – | – | |
| Elsewhere | 105.5 ± 17.1ab | 127.9 ± 12.5ab | 96.9 ± 14.5a | 99.5 ± 10.6ab | 151.3 ± 8.7b | |

Note. Mean times in a row followed by the same lowercase letter are not significantly different (Kruskal–Wallis test followed by a Mann–Whitney–*U* test with Bonferroni correction, $\alpha < 0.005$, for multiple pairwise comparisons), $n = 20$. Means in a column followed by the same uppercase letter are not significantly different (Friedman's test followed by Wilcoxon's test with Bonferroni correction, $\alpha < 0.003$, for multiple pairwise comparisons).

^aMann–Whitney–*U* test, $p = 0.54$.

^bMann–Whitney–*U* test, $p = 0.13$.

Availability of hosts and the correct type of stimuli play a major role on whether a parasitoid should leave a patch or not (Vos *et al.*, 1998; Wang and Keller, 2002). In the present case, molasses grass did not harbor hosts and close-range stimuli must have been unsuitable for further searching by the parasitoids. Cereal stemborers are often found aggregated in single plants in the field (Overholt *et al.*, 1994; Sallam *et al.*, 2001). Searching for infested patches is an energy-consuming venture and it may be more efficient to stay longer in a favorable patch resulting in longer residence time. Therefore, infested host plant patches surrounded by non-host plants should be less abandoned than those surrounded by host plants. This might also explain the longer residence time on infested plants.

More time was spent on the uninfested host plant than on molasses grass, probably because it provided some of the correct stimuli. Several studies have shown the attractiveness of uninfested host plants to parasitoids (Ngi-Song *et al.*, 1996; Rutledge and Wiedenmann, 1999; Ockroy *et al.*, 2001). However, the parasitoids spent more time on infested than uninfested host plants. This finding concurs with several similar studies (Wiskerke and Vet, 1994; van Roermund and van Lenteren, 1995; Potting *et al.*, 1999b; Shiojiri *et al.*, 2000; Wang and Keller, 2002). The parasitoids were clearly arrested by the host-damaged plants. Injury to the plant and the presence of frass played a major role in this arrestment. Of the total foraging time of *C. sesamiae*, more than 50% was spent on the stem, including time spent at the tunnel entrance and inside the tunnel. *Cotesia flavipes* was attracted to infested stem pieces, which were more attractive than leaves from an infested plant (Potting *et al.*, 1995). This was attributed to close-range volatiles produced by the injured stem, which guided the parasitoid to the right host microhabitat. Though a large percentage of *C. sesamiae* females located the tunnel entrance, only a small fraction managed to enter the tunnel. This appeared to be due to difficulties in penetrating the frass, which was fresh and wet. Chinwada and Overholt (2001) speculated that *C. sesamiae* performed poorly in the early part of the maize growing season because stemborer frass produced in young vegetatively growing plants was wet and impeded parasitoid movement. There was low success in parasitoids leaving the tunnel, probably due to the wet frass and also the parasitoids being killed by aggressive borers. Aggressive behavior of borers during stinging by *Cotesia flavipes* has been observed (Potting *et al.*, 1997, 1999a; Takasu and Overholt, 1997).

Dentichasmias busseolae dedicated a large percentage of its time to antennating frass and drumming parts of the stem that harbored the host. Stemborer frass is attractive to *D. busseolae* and plays a role in host microhabitat location (Mohyuddin, 1972; Bahana, 1989). Frass is an attractive component and is used by searching parasitoids to detect presence of a host

(Hailemichael *et al.*, 1994; Potting *et al.*, 1997; Ngi-Song and Overholt, 1997; Tanaka *et al.*, 2001). Arrestment by frass is mediated by both non-volatile contact chemical and volatile chemical cues. Pupal parasitoids often employ mechanosensory cues to locate their hosts. They may detect sounds or vibrations produced by their hosts (Meyhöfer and Casas, 1999). The parasitoids may also produce their own vibrations by drumming the substrate (vibrational sounding) to scan substrate for hidden host pupae (Wäckers *et al.*, 1998; Otten *et al.*, 2001). *Dentichasmias busseolae* was most likely cueing in on mechanosensory stimuli when it was involved in the drumming of the stem with its antennae.

In conclusion, *D. busseolae* clearly discriminated between host plants, maize and sorghum, and the non-host plant, molasses grass in a diversified habitat. Foraging behavior of *D. busseolae* in intercrop arrangements with infested host plants was not different from that of monocrop arrangements. Due to this discrimination of host and non-host plants, we do not expect molasses grass to hinder the foraging behavior of either parasitoid in an intercrop situation. *Cotesia sesamiae* spent much less time on non-host plants compared to host plants in single choice experiments, suggesting that the wasp will not waste time searching on non-host plants even though the molasses grass was earlier shown to produce volatiles that were attractive to the parasitoid at long-range. However, these predictions need to be confirmed in a more realistic field situation.

ACKNOWLEDGMENTS

The International Centre of Insect Physiology and Ecology (ICDPE), is acknowledged for providing the working space, facilities and supply of insects. Financial support was provided by MHO/NUFFIC of the Netherlands to L.S. Gohole, under a collaborative project between Wageningen University and Moi University, entitled “Strengthening Research and Teaching at the Faculty of Agriculture, Moi University, Kenya” (MHO/MU/WAU/Seed Technology/I). This is Florida Experiment Station Research Journal Series no. R-09721.

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