

Parasitism of *Bemisia tabaci* (Homoptera: Aleyrodidae) by *Eretmocerus mundus* (Hymenoptera: Aphelinidae) on cassava

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Abstract. Parasitism rates of *Bemisia tabaci* (Gennadius) and searching and oviposition behaviours of its parasitoid *Eretmocerus mundus* Mercet were compared on two cassava varieties: a glabrous variety, Nase 4 and a hirsute variety, MM97/0245 with *c.* 88 leaf hairs/cm². Parasitism was assessed after potted plants of both varieties were exposed in open fields to natural infestation by *B. tabaci* and its natural enemy. For the behavioural studies, naive, less than 24-h-old females were individually observed on infested cassava leaflets under a microscope for a maximum of 1 h each. The different foraging behaviours were recorded using the computer software 'The Observer 5.0' (Noldus Ltd, Wageningen, The Netherlands). Total per cent parasitism and parasitism by *E. mundus* did not differ significantly between varieties. Upon encounter with leaf hairs, the parasitoids stopped and groomed before resuming the host search. The frequency of repeat probing, host feeding and antennation after probing and host feeding were higher on the glabrous than on the hirsute variety, while the converse was observed when feeding on liquids on the leaf. The duration of host assessment, initial probing, grooming and resting on the leaf was higher on the glabrous than on the hirsute variety. Leaf hairiness at the density investigated caused some changes in the behaviour of the parasitoids, but did not have an overall effect on field parasitism. Since cassava is generally considered to have glabrous leaves and the variety MM97/0245 is one of the most hirsute varieties, we discount leaf hairiness as a factor in determining levels of parasitoid activity.

Key words: *Bemisia tabaci*, *Eretmocerus mundus*, behaviour, *Manihot esculenta*, parasitism, Uganda

Introduction

Cassava is an important root crop in sub-Saharan Africa for more than 200 million people. Its production is affected by many factors including

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insect pests and diseases, weeds and poor agronomic practices (Anonymous, 1994). These factors result in lower yields (< 10 t/ha) in farmers' fields, in comparison with 25 t/ha at experimental stations and a potential of 80 t/ha (Fauquet and Beachy, 1989). Among the biotic constraints, the whitefly *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) counts as an important insect pest of cassava in the tropics and subtropics (Oliveira *et al.*, 2001). It transmits cassava mosaic geminiviruses that cause cassava mosaic disease (CMD), which is estimated to cause loss of cassava of between 12 and 23 million tonnes in Africa per annum (Thresh *et al.*, 1997). The disease, whose presence often causes total crop loss, may be overcome through the use of virus-resistant varieties. Unfortunately, these same varieties are often acting as hosts to high whitefly populations, which damage them by feeding, and by reduction of photosynthesis due to leaf distortion and sooty mould growth on the honeydew. Such damage may amount to 34–50% of the tuberous yield reduction depending on the variety (Legg *et al.*, 2003). Moreover, *B. tabaci* has recently gained new prominence since the cassava brown streak disease (CBSD) has been confirmed to be caused by *B. tabaci* transmitted viruses (Maruthi *et al.*, 2005). This disease occurs widely on most of the CMD-resistant varieties in Uganda (Alicai *et al.*, 2007). Thus given the increasing importance of *B. tabaci* and, in light of the fact that no control method is effective when used alone, there is an urgent need to develop a balanced approach to CMD/CBSD/vector management, which can combine the deployment of CMD/CBSD/whitefly-resistant cultivars and alternative control methods, such as the use of *B. tabaci* natural enemies.

There have been many attempts to find efficient natural enemies of *B. tabaci* in different parts of the world. Parasitoids have been more widely studied than predators and fungi as they are more easily followed and have been successful in the control of whitefly infestations on other crops (Gerling *et al.*, 2001). In Uganda, *B. tabaci* is attacked by three aphelinid parasitoid species: *Eretmocerus mundus* Mercet, *Encarsia sophia* Girault and Dodd and a so far undescribed black-headed *Encarsia* sp. (Otim, 2007). Although the parasitoids do not seem to be effectively reducing *B. tabaci* populations early in the season (Otim *et al.*, 2006), studies by Asiimwe *et al.* (2007) revealed that parasitism is a key mortality factor in the fourth instar stage, calling for a need to enhance parasitism at this stage. This requires the knowledge of factors that affect parasitism, and conducting research to enhance the positive factors, while at the same time minimizing the effect of those factors that negatively impact parasitoids.

Parasitoid efficiency, as reflected in parasitism rates, is dependent, in part, on the host plant morphology and parasitoid foraging abilities. These occur in a tritrophic environment in which the host plant and host insect have a profound effect on the parasitoid's behaviour and success (Price *et al.*, 1980). Host plant morphology, especially leaf pubescence, may affect the searching efficiency of parasitoids by slowing or inhibiting their movements, or by enhancing parasitism. For instance, van Lenteren *et al.* (1995) and van Roermund and van Lenteren (1995) found that leaf hairs interfered with the locomotion and parasitism efficiency of *E. formosa* on cucumber and tomato, while McAuslane *et al.* (1995) found reduced parasitism of *B. argentifolii* Bellows and Perring by *Encarsia* and *Eretmocerus* spp. on soya bean. Likewise, Rajam *et al.* (1988) reported that dense, stout and spine-like hairs on prickly chaff precluded parasitism on this plant. Contrarily, Headrick *et al.* (1996a) reported higher parasitism levels on melon than on cotton and sweet potato because the hairs on melon leaves raised the nymphs and made it easier for *E. eremicus* Rose and Zolnerowich (reported as *E. sp. nr. californicus*) to place its eggs under the nymphs than on cotton and sweet potato. Thus knowledge and understanding of parasitism levels and the causes for a particular foraging behaviour are important in developing a successful biological control approach. In our investigations, we looked at the roles of weeds and cassava component crops, and the biological and behavioural attributes of the parasitoids in influencing the population dynamics of *B. tabaci*. In the present study, we investigated parasitism levels and searching behaviour of *E. mundus*, which is a predominant parasitoid of *B. tabaci* on cassava in the country (Otim *et al.*, 2006; Otim, 2007).

Materials and methods

Choice of plants

Both cassava varieties used in this experiment support high whitefly populations. In addition, variety Nase 4 is glabrous and MM97/0245 is hirsute. Leaf hair characteristics were determined by counting the number of trichomes on the underside of 1 cm diameter leaf discs under a stereoscopic microscope. Leaf hair length was measured individually using a micrometer fitted in the microscope objective. A sample of 20 discs and 20 leaf hairs per disc was used. Leaf hair density on the hirsute variety averaged $88 \pm 7.85/\text{cm}^2$ (mean \pm SE; range 13–163/ cm^2). Hair length averaged 3.3 ± 0.21 mm (2–4.9 mm) on the hirsute variety. The hairs occurred more on the midribs than on the smaller veins.

Parasitism of B. tabaci

This experiment was carried out in the field plots of the National Crops Resources Research Institute (NaCRRI), Namulonge, Uganda. To determine the influence of leaf pubescence on *B. tabaci* parasitism, potted plants raised from stem cuttings were grown in a screenhouse until they reached the three-leaf stage. The leaves were tagged with tape and the plants placed in a cassava field to allow *B. tabaci* and its parasitoids to colonize. This was done twice, each time with 12 sets of each variety, randomly placed in the field. The plants were left until the first pupal parasitoids were observed on any of the three leaves. The marked leaves were then harvested and taken to the laboratory for observations of parasitism. Counts were made of the healthy and parasitized fourth instar *B. tabaci* nymphs. Parasitoid pupae were recognized as follows (Otim *et al.*, 2005): *E. mundus* had an orange pupa and no meconia, whereas *E. sophia* had black pupal cases with meconia symmetrically located on both sides posteriorly. The hosts of the yet undifferentiated younger parasitoid stages on the other hand showed displaced bacteriomes (mycetomes) or contained banana-shaped larvae as opposed to the unparasitized nymphs that were either translucent or mildly opaque and yellowish with yellow symmetrically located bacteriomes.

Bemisia tabaci colony and source of parasitoids

Cassava plants obtained through cuttings of the variety Nase 4 were grown in 1 l buckets containing sterilized soil. When the plants reached the four-leaf stage, adults of *B. tabaci* were introduced to initiate colonies. To obtain adults used in initiating the colony, nymphs were collected from cassava fields at NaCRRI in June 2004 and held in emergence bottles. Emerged adults were collected daily and introduced on clean plants in the screenhouse. The colony was maintained on cassava under natural fluctuating conditions (means \pm SD: 22.8 ± 5.4 °C (range 15.6–34 °C); $64 \pm 20.2\%$ relative humidity (RH) (range 25.3–91.7% RH); 12 h light-12 h dark photoperiod).

The parasitoids used in this study were reared from parasitized nymphs collected from the same fields as the *B. tabaci* nymphs. Parasitoid pupae were collected a few days before use and the parasitized nymphs were placed in emergence bottles. Upon emergence, one <24-h-old *E. mundus* female was picked at a time using an aspirator and observed. The females used did not have access to hosts and water before observation, and were assumed to be mated as they were mixed with males in the same emergence bottles. Putting females directly without food was done because

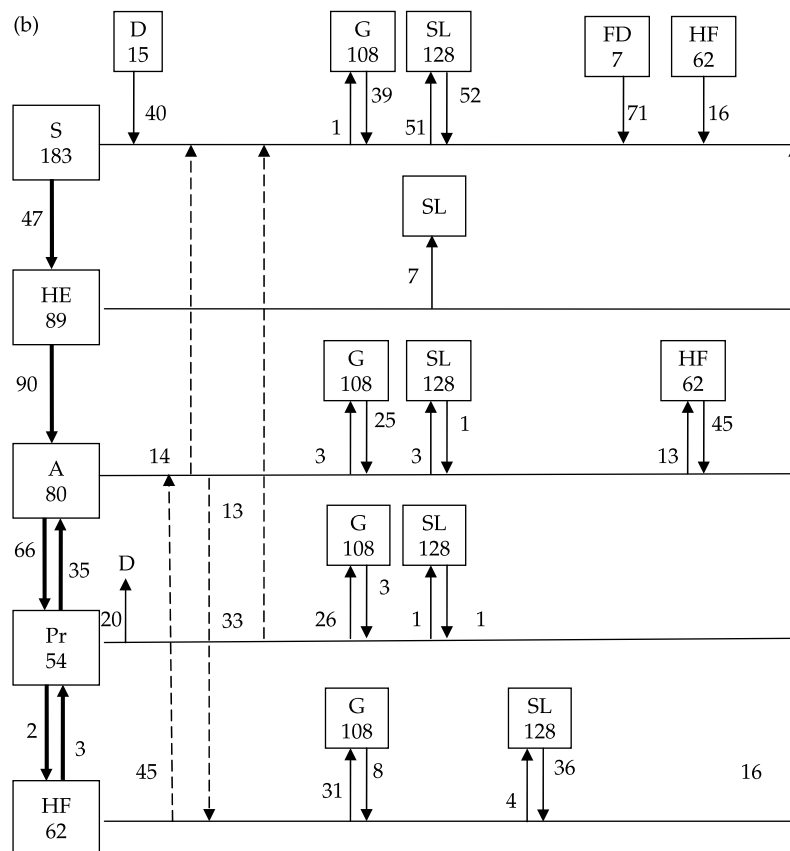
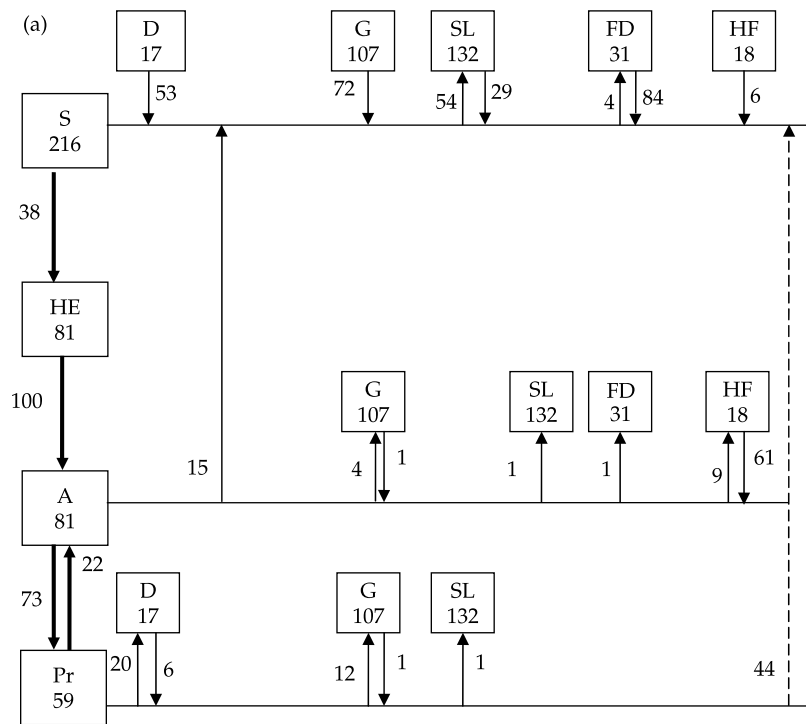
dissect studies showed that they are provigenic. The conditions in the laboratory were: 25.5 ± 1.7 °C (range 21.7–31.9 °C); $60.2 \pm 8.4\%$ RH (range 23.8–79.3% RH); 12 h light-12 h dark photoperiod.

Searching behaviour

Studies on the behaviour of the parasitoids were conducted between November and December 2004. The searching behaviour of *E. mundus* was studied using methods developed by Headrick *et al.* (1995, 1996a,b), in which parasitoids were allowed access to nymphs in a Petri dish. Direct visual observations were made, unlike those of Headrick *et al.* (1995, 1996a,b) in which the females were videotaped and the duration of events recorded using a built-in recorder. Our experimental arena consisted of cassava leaflets bearing 50–60 mainly third instar nymphs, placed abaxial side up on moist filter paper in an 8.8 cm diameter Petri dish. The leaflets were held in position by a piece of masking tape. Prior to the onset of the experiment, the behaviours of five female *E. mundus* were observed, recorded and assigned unique keyboard keys. Single (0 to 24-h-old), naïve female parasitoids were picked from emergence bottles and placed individually on a leaflet in the Petri dish, which was observed under a stereomicroscope and illuminated by a fibre-optic cold light source. Once exposed to the leaflet, the female had a choice of remaining to search, walking or flying away. The behaviours of each female were monitored under a microscope and the appropriate key was pressed when an activity was performed. All the recordings were done using 'The Observer[®]' software (version 5.0; 2003; Noldus Ltd, Wageningen, The Netherlands), for a maximal period of 1 h, or until the parasitoid left the leaflet. The frequency and duration of the following behavioural elements were recorded: searching, host encounter, antennation, probing, host feeding, feeding (on liquids on the leaf), standing (resting) on leaflet and host, and grooming. About 15 females were observed per cassava variety.

Data analysis

Total parasitism was expressed as a percentage of the total number of parasitoids to the total nymphs (both parasitized and unparasitized fourth instar *B. tabaci* nymphs combined), while that due to *E. mundus* was calculated as a percentage of observed *E. mundus* pupae to total nymphs (Otim *et al.*, 2006). Data on per cent parasitism values were transformed using arcsine square root transformation. These were then subjected to a two-factor ANOVA in a completely randomized design using GenStat Release 7.2 DE (PC/Windows XP) (Copyright 2007,



Lawes Agricultural Trust, Rothamsted, UK). The treatment factors were trial and cassava variety. On the other hand, data generated from 'The Observer[®]' were entered into Microsoft Excel spreadsheets, summarized and exported for statistical analysis using Genstat. Mean durations of the different behaviours were square root transformed and differences among mean durations were examined using *t*-statistics. The frequencies of behaviours were subjected to chi-square analysis to test whether the observed numbers deviated from the expected 1:1 fixed ratio. Interpretations are based on the transformed values.

Results

Parasitism of B. tabaci on the two cassava varieties

Total per cent parasitism per plant ranged from 10.7 to 67% and 0 to 42% on the hirsute and glabrous varieties, respectively, in the first trial. The corresponding values for the second trial were 0–45.8% and 0–66.7% per plant, respectively. There was neither a significant interaction in total parasitism between the trials and cassava varieties ($F = 0.1$; $df = 1$; $P = 0.748$), nor a significant difference between varieties ($F = 2.01$; $df = 1$; $P = 0.164$). However, the first trial registered a significantly higher total parasitism ($F = 12.99$; $df = 1$; $P < 0.001$) and parasitism by *E. mundus* ($F = 18.35$; $df = 1$; $P = 0.006$) compared with the second trial. Total parasitism averaged 31.7 and 15.2% in the first and second trials, respectively. Total parasitism averaged 36.4 and 27% on the hirsute and glabrous varieties, respectively, in the first, and 16.1 and 14% on the hirsute and glabrous varieties in the second trials, respectively. Parasitism by *E. mundus* averaged 23.9 and 12.8% in the first and second trials, respectively. Parasitism by *E. mundus* averaged 27.2% on the hirsute and 20.5% on the glabrous variety during trial 1 and 13.6 and 12% on the hirsute and the glabrous varieties during trial 2, respectively. Parasitism due to *E. sophia* and undifferentiated parasitoids accounted for the difference between total per cent parasitism and parasitism due to *E. mundus*.

Search behaviour

When females were placed on whitefly-infested leaflets, six females walked off the leaves of the hirsute and two from the glabrous variety. Therefore, the numbers that remained to search on the hirsute and glabrous varieties were 9 and 13, respectively. Searching females walked on the whitefly-infested leaflet, drumming with their antennae, i.e. alternately raising and lowering the tip of each flagellum to the leaflet surface as they walked. A host encounter was recorded when any part of the parasitoid's body came into contact with the whitefly nymph. Upon encountering a host, a female antennated it by drumming the lateral margins of the host with the antennae (antennation), while making clockwise and counterclockwise movements. Antennation was followed either by walking away from a host (antennal rejection) or by probing the host using the ovipositor. Probing involved a female positioning herself either perpendicular to the margin of the host or on top of the host and contacting it with the basal portion of her abdomen. The ovipositor was then inserted either between the nymph and the leaflet or into the nymph through the vasiform orifice (all referred to as probing). Probing of hosts in *E. mundus* is for two purposes: the first probing between the host and the leaflet is for oviposition, while probing in the vasiform orifice is to wound the host such that the females feed on the haemolymph to mature more eggs (Gerling *et al.*, 2001). Following probing, host feeding was recorded and this typically involved feeding on the haemolymph from the injured part of the host. Host feeding was interjected with grooming, probing the wound (repeat probing), and then either feeding from the host or turning again for a new attempt to make a wound, or walking away. Occasionally, the females withdrew their ovipositors and drummed the dorsal part of the host with the hindlegs. Feeding on liquids on the leaf was also recorded. The other behaviours that frequently occurred were grooming, which involved using the front legs to remove accumulated liquids from the antennae or using the hindlegs to clean the wings and the metasoma, and standing still (resting) on the leaflet or host without

Fig. 1. Ethograms for behaviours of *Eretmocerus mundus* attacking *Bemisia tabaci* on (a) the hirsute cassava variety, MM97/0245 and (b) the glabrous variety, Nase 4. The main behavioural pathway begins at the top left, and moves down the left margin. The figures in the boxes represent the total number of times a particular behaviour occurred. The horizontal lines are extensions to show which behaviours were followed by, or led to the associated main behaviour in the left margin. Arrows indicate subsequent behavioural events and the associated numbers indicate the per cent frequency of each observation, summed for all females observed. A, antennation; D, drumming on host; FD, feeding liquids on the leaf; G, grooming; HE, host encounter; HF, host feeding; Pr, probing; S, searching; SL, standing (resting) on leaflet. Dotted lines are used for arrows that cross lines of the main behavioural events. Other sequences not associated with the main behavioural pathway account for the situations where the percentages do not add up to 100.

performing any activity. Upon encounter with leaf hairs, the females stopped to groom before proceeding with the search.

Behavioural pathway

Ethograms for *E. mundus* females were drawn from the recorded sequences. Frequencies are reported as a per cent of the total number of times a particular behaviour was recorded (Fig 1a and b). For instance, in Fig. 1a, there were 216 cases of searching; of which 81 (38%) were followed by host encounters; of the 81 cases of host encounters, all of them (100%) led to antennation. On the same figure, the 53 associated with the arrow pointing from the rectangle labelled D to the horizontal line from the rectangle labelled S means that 9 of the 17 cases (53%) of drumming were followed by searching. The numbers without letters, for instance 44 in the bottom right-hand corner of Fig. 1a associated with the dotted line running from the horizontal line from rectangle HF to the horizontal line from the rectangle S, mean that probing was followed by searching 26 times (44%) out of the 59 probing cases.

When placed on leaflets of the hirsute variety, females of *E. mundus* began searching, which was followed by resting on the leaflet, host encounters and feeding on liquids on the leaf, which represented 54, 38 and 4% of the total search frequencies, respectively (Fig. 1a). All host encounters led to antennation 100% of the time and antennation led to probing 73% of the time. Antennation led to resumption of searching 15% of the time, grooming 4% of the time and to standing still on the leaf and feeding on liquids on the leaf 1% each. Probing was followed by searching 44% of the time, antennation 22% of the time,

grooming 12% of the time, drumming 18% of the time and resting on the leaflet 1% of the time.

On the glabrous variety, searching by *E. mundus* females was followed by resting on the leaflet 51% of the time and host encounters 47% of the time (Fig. 1b). Host encounter was followed by antennation and resting on the leaflet in 90% and standing still on the leaf 7% of the time. Antennation led to probing and searching for 66 and 14% of all antennations, respectively. The probed hosts were antennated 35% of the time, or the females resumed searching 23% of the time, or drummed 20% of the time. Antennation also led to host feeding 13% of the time, and grooming and resting on the leaflet 3% of the time. Host feeding followed probing 2% of the time and led to antennation, grooming, searching and resting on the leaflet 45, 31, 16 and 2% of the time, respectively.

Frequency and duration of events

In total, 826 and 881 behavioural events were recorded for *E. mundus* on the hirsute and glabrous varieties, respectively.

The observed frequency of feeding on liquids on the leaf was significantly higher ($P < 0.05$) on the hirsute than on the glabrous variety when compared with an expected 1:1 ratio (Table 1). On the other hand, the frequency of repeat probing and host feeding, and antennation following each of these activities was significantly higher ($P < 0.05$) on the glabrous than that on the hirsute variety.

The mean duration of antennation (before probing, after probing and after host feeding), initial probing, grooming and resting on the leaf was significantly ($P < 0.05$) higher on the glabrous than that on the hirsute variety, while the duration

Table 1. Frequency (in number of observations) and chi-square statistics for behaviours of *Eretmocerus mundus* females on a hirsute and glabrous cassava variety

Behaviour	Frequency		Statistics	
	Hirsute variety	Glabrous variety	Chi-square*	P-value
Searching	216	183	2.73	0.099
Host encounter	81	89	0.385	0.539
Antennation	83	80	0.06	0.814
Grooming	107	108	0.005	0.946
Initial probing	59	54	0.22	0.638
Repeat probing	37	59	5.04	0.025
Antennation after probing	29	60	10.8	0.001
Feeding on liquids on the leaf	31	7	15.16	<0.001
Host feeding	18	62	24.2	<0.001
Antennation after host feeding	16	36	7.69	0.006
Drumming	17	15	0.13	0.724
Standing still	132	128	0.06	0.804

* df = 1 for all tests.

of searching, host feeding, feeding on liquids on the leaf and resting on the host did not differ significantly ($P > 0.05$) between the varieties (Table 2).

Time budget

The time budget for females did not differ markedly between the varieties. *Eretmocerus mundus* females spent most of their time probing and host feeding (Fig. 2), followed by searching and grooming on leaves of the hirsute, and searching, antennation, grooming and resting on leaves of the glabrous variety. There were similarities in the per cent of time spent searching, antennating and grooming between the two varieties.

Discussion

This study was conducted to assess parasitism and the behaviour of *E. mundus* on cassava varieties with different hair densities. There were no significant differences between cassava varieties in parasitism levels in the field. However, differences occurred between the varieties in the numbers of females remaining to search on the leaves, and the duration and frequency of some of the behaviours. While 60% of the females remained on the leaves of the hirsute variety, 87% remained on the leaves of the glabrous variety. Also, the parasitoids antennated, rested on the leaf, groomed and probed for longer durations on the glabrous than that on the hirsute variety. The observed frequencies of repeat probing and host feeding, and antennation after each of these behaviours were higher on the glabrous than on the hirsute variety, while the

reverse was observed for females feeding on liquids on the leaf.

The greater propensity of *Eretmocerus* spp. to leave hairy than smooth leaves was also noted by Headrick *et al.* (1996b) and may be attributed to the more favourable habitat that the smooth leaf offers to the parasitoids. However, females of *E. mundus* that remained spent almost 80% of their time budget searching, assessing hosts, probing and host feeding on each cassava variety. Although host feeding is considered a prerequisite for maturation of a full complement of eggs in *Eretmocerus* and *Encarsia* spp. (Flanders, 1935; Gerling, 1990), the females that we used began searching immediately they were placed on the leaves. This was probably because they emerge with mature eggs ready to be laid (Otim, 2007). By contrast, Headrick *et al.* (1996b) noted that *E. eremicus* are synovigenic and their earlier behaviours are focused on nutrition and not oviposition. This calls for more experiments to ascertain whether the *E. mundus* studied is indeed provigenic.

The apparent lack of influence of leaf pubescence on parasitism efficiency between the two cassava varieties may be attributed to the arrangement of leaf hairs on cassava leaves where hairs are more numerous on the main veins than on the smaller veins, between which most of the search occurred. Clearly, there was no observable hindrance of leaf hairs on parasitoid movement, only affecting the parasitoids when they came into direct contact with leaf hairs. Then they rested and groomed for a short time before resuming the search. By contrast, however, other studies have shown that leaf pubescence affects the searching efficiency of parasitoids by slowing or inhibiting their movements (Gerling, 1990;

Table 2. Mean duration (in seconds \pm SE) and *t*-statistics for behaviours of *Eretmocerus mundus* females on a hirsute and glabrous cassava variety

Behaviour	Mean duration (s)		Statistics	
	Hirsute (<i>n</i> = 826)	Glabrous (<i>n</i> = 887)	<i>t</i> -value*	<i>P</i> -value
Searching	12.5 \pm 0.6	11.0 \pm 0.6	1.79	0.074
Antennation	6.0 \pm 0.6	10.0 \pm 1.1	-3.4	<0.001
Grooming	15.7 \pm 2.0	21.8 \pm 1.9	-2.25	0.026
Initial probing	55.9 \pm 5.7	111.7 \pm 10.9	-4.53	<0.001
Repeat probing	58.2 \pm 8.0	66.2 \pm 8.7	-0.68	0.498
Antennation after probing	6.0 \pm 0.5	11.4 \pm 1.1	-4.43	<0.001
Feeding on liquids on the leaf	25.4 \pm 5.7	48.2 \pm 14.6	-1.65	0.107
Host feeding	201.3 \pm 131.7	149.3 \pm 24.4	0.39	0.702
Antennation after host feeding	5.7 \pm 0.6	14.1 \pm 1.6	-4.97	<0.001
Drumming	10.0 \pm 1.5	10.7 \pm 1.7	-0.31	0.755
Resting	7.3 \pm 0.3	23.5 \pm 3.3	-4.75	<0.001

* *df* = 1 for all tests.

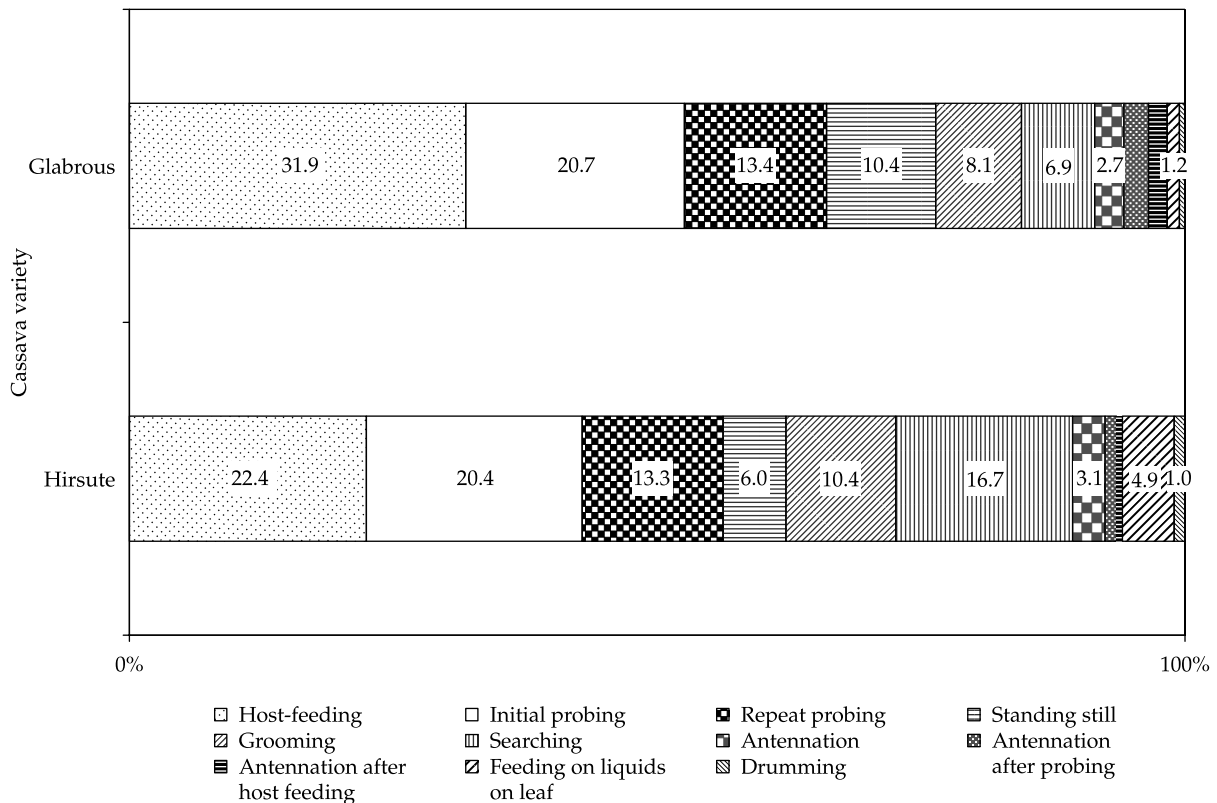


Fig. 2. Percentage of total time spent by *Eretmocerus mundus* attacking *Bemisia tabaci* on different cassava varieties

Headrick *et al.*, 1996a) and reducing parasitism efficiency (McAuslane *et al.*, 1995; van Lenteren *et al.*, 1995; van Roermund and van Lenteren, 1995).

Similar to parasitism, the searching and oviposition pathways described for *E. mundus* in this study were similar on both cassava varieties. The pathways described for *E. eremicus* on smooth sweet potato, cotton and hairy melon plants (Headrick *et al.*, 1995; 1996a,b) resembled our findings, except that no mention was made as to what the parasitoid did upon encountering hairs on melon leaves. The higher frequencies of repeat probing and antennation after probing observed on the glabrous compared with the hirsute variety may be due to either difficulty in locating a suitable place for inserting the ovipositor between the nymph and leaf surface, or the presence of extra honeydew on the glabrous variety. The difference in leaf surface structure may also explain the longer duration of initial probing on the glabrous than that on the hirsute variety. This made the females make many attempts, alternatively probing (repeat probing) and reassessing the host on the glabrous than that on the hirsute variety. The observations of longer probing duration on the glabrous than that on the hirsute variety contrast with those of Headrick *et al.* (1996a,b) who observed longer duration of probing on melon (a hairy plant) than on cotton and sweet potato because melon has

dense trichomes, covering the entire leaf surface when compared with the other crops and the glabrous cassava variety used in this study. The reason for the longer duration of resting on the leaf of the glabrous variety is not clear. However, the longer duration of grooming on the glabrous than that on the hirsute variety might be because there were more liquids on the former than on the latter.

Host drumming with the hindlegs reported by Foltyn and Gerling (1985) and McAuslane and Nguyen (1996) was also observed in this study. Although host drumming was considered a host-marking activity, Foltyn and Gerling (1985) and McAuslane and Nguyen (1996) found that eggs were laid under the hosts that had been drummed and not under those that had not. During the present study, drumming frequency and duration did not differ between the two varieties, implying that there is no effect of pubescence on this activity. However, oviposition under the drummed hosts was not assessed. Further studies are recommended to elucidate the role of drumming in *E. mundus* and oviposition under probed hosts.

Conclusion and recommendation

One of the hairiest cassava varieties was used in this study and the results suggest that leaf hairs at the

density investigated caused only minor changes in parasitoid behaviour in *E. mundus*. Since most cassava varieties are less hairy than the hirsute variety that was used, leaf pubescence in cassava seems to have an insignificant effect on *E. mundus*' ability to parasitize *B. tabaci*. This first report on the behaviour of *E. mundus* attacking *B. tabaci* on cassava provides useful information regarding the possible effect of leaf hairiness on parasitoid behaviour and parasitism. It has been demonstrated that leaf hair may affect *E. mundus*' readiness to search, but did not translate to differences in parasitism levels in the field. As such, it appears that the most critical factor in this case is the propensity to remain and search on the leaves as postulated by Headrick *et al.* (1996b). Similar types of behavioural observations should be conducted to examine the effect of other variables such as leaf shape, i.e. broad versus narrow, and CMD-disease-affected versus CMD-free leaves. Further studies on the influence of leaf pubescence on cassava or any other crop should take into account the arrangement of leaf hairs or trichomes on the leaf, in addition to hair density.

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References

- Alicai T., Omongo C. A., Maruthi M. N., Hillocks R. J., Baguma Y., Kawuki R., Bua A., Otim-Nape G. W. and Colvin J. (2007) Re-emergence of cassava brown streak disease in Uganda. *Plant Disease* 91, 24–29.
- Anonymous (1994) *Cassava Growers' Guide*. Agricultural Communication Centre, National Agricultural Research Organization, Entebbe. 18 pp.
- Asiimwe P., Ecaat J. S., Otim M., Gerling D., Kyamanywa S. and Legg J. P. (2007) Life-table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda. *Entomologia Experimentalis et Applicata* 122, 37–44.
- Fauquet C. and Beachy R. N. (1989) *Cassava Viruses and Genetic Engineering*. International Cassava Trans Project. Department of Biology, Washington University, St. Luis. 30 pp.
- Flanders S. E. (1935) An apparent correlation between the feeding habits of certain pteromalids and the condition of the ovarian follicles. *Annals of the Entomological Society of America* 28, 438–444.
- Foltyn S. and Gerling D. (1985) The parasitoids of the aleyrodid *Bemisia tabaci* in Israel: development, host preference and discrimination of the aphelinid wasp *Eretmocerus mundus*. *Entomologia Experimentalis et Applicata* 38, 255–260.
- GenStat (2007) GenStat for Windows. Release 7.2 DE Discovery Edition. VSN.
- Gerling D. (1990) Natural enemies of whitefly: predators and parasitoids, pp. 147–185. In *Whitefly: Their Bionomics, Pest Status and Management* (Edited by D. Gerling). Intercept, Andover, Hants, UK.
- Gerling D., Alomar O. and Arnó J. (2001) Biological control of *Bemisia tabaci* using predators and parasitoids. *Crop Protection* 20, 779–799.
- Headrick D. H., Bellows T. S. and Perring T. M. (1995) Behaviours of female *Eretmocerus* sp. nr. *californicus* (Hymenoptera: Aphelinidae) attacking *Bemisia argentifolii* (Homoptera: Aleyrodidae) on sweet potato. *Environmental Entomology* 24, 412–422.
- Headrick D. H., Bellows T. S. and Perring T. M. (1996a) Host-plant effects on the behaviour of *Eretmocerus* sp. nr. *californicus* raised from melon. *Entomophaga* 41, 15–26.
- Headrick D. H., Bellows T. S. Jr. and Perring T. M. (1996b) Behaviours of female *Eretmocerus* sp. nr. *californicus* (Hymenoptera: Aphelinidae) on cotton, *Gossypium hirsutum* (Malvaceae) and melon, *Cucumis melo* (Cucurbitaceae). *Biological Control* 6, 67–75.
- Legg J. P., Mallowa S. and Sseruwagi P. (2003) First report of physical damage to cassava caused by the whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Sternorrhyncha: Aleyrodidae). *Book of Abstracts, 3rd International Bemisia Workshop*, 17–20 March 2003. p. 41. Institut de Recerca i Tecnologia Agroalimentàries, Barcelona, Spain.
- McAuslane H. J. and Nguyen R. (1996) Reproductive behaviour and biology of a thelytokous species of *Eretmocerus* (Hymenoptera: Aleyrodidae) parasitizing *Bemisia argentifolii*. *Annals of Entomological Society of America* 89, 686–693.
- McAuslane H. J., Johnson F. A., Colvin D. L. and Sojack B. (1995) Influence of foliar pubescence on incidence and parasitism of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on soybean and peanut. *Environmental Entomology* 24, 1135–1143.
- Maruthi M. N., Hillocks R. J., Mtunda K., Raya M. D., Muhanna M., Kiozia H., Rekha A. R., Colvin J. and Thresh J. M. (2005) Transmission of cassava brown streak virus by *Bemisia tabaci* (Gennadius): progress and problems. *Journal of Phytopathology* 152, 307–312.
- Noldus Information Technology (2003) *Professional Software for Collection and Analysis of Observational Data*. Wageningen, The Netherlands.
- Oliveira M. R. V., Henneberry T. J. and Anderson P. K. (2001) History, current status and collaborative research projects for *Bemisia tabaci*. *Crop Protection* 20, 709–723.

- Otim M. (2007) The distribution, biology and behaviour of the major natural enemies of *Bemisia tabaci* on cassava in Uganda. PhD Thesis. 114 pp.
- Otim M., Legg J. P., Kyamanywa S., Polaszek A. and Gerling D. (2005) Occurrence and activity of *Bemisia tabaci* parasitoids on cassava in different agro-ecologies in Uganda. *Biocontrol* 50, 87–95.
- Otim M., Legg J. P., Kyamanywa S., Polaszek A. and Gerling D. (2006) Population dynamics of *Bemisia tabaci* (Homoptera: Aleyrodidae) parasitoids on cassava mosaic disease resistant and susceptible varieties. *Biocontrol Science and Technology* 16, 201–214.
- Price P. W., Bouton C. E., Gross P., McPherson B. A., Thompson J. N. and Weis A. E. (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecological Systems* 11, 41–65.
- Rajam B., Peter C. and David B. V. (1988) Influence of host plants on the parasitism of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) by *Encarsia* sp. *Current Science* 57, 1246–1247.
- Thresh J. M., Otim-Nape G. W., Legg J. P. and Fargette D. (1997) African cassava mosaic disease: the magnitude of the problem. *African Journal of Root and Tuber Crops* 2(1), 13–19.
- van Lenteren J. C., Li Z. H., Kamerman J. W. and Rumei X. (1995) The parasite-host relationship of *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). XXVI. Leaf hairs reduce the capacity of *Encarsia* to control whitefly on cucumber. *Journal of Applied Entomology* 119, 553–559.
- van Roermund H. J. W. and van Lenteren J. C. (1995) Residence times of the whitefly parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) on tomato leaflets. *Journal of Applied Entomology* 119, 465–471.