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FINAL REPORT

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Project Title

Management of *Bemisia tabaci* on virus-resistant cassava plants utilizing natural enemies

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3. EXECUTIVE SUMMARY:

The project was designed to study in depth the factors governing the outbreaks of the whitefly *Bemisia tabaci* on cassava in Uganda, especially in relation to new, virus-resistant, varieties. It was carried out in Uganda by the co-principal investigators, Prof. Kyamanyawa and Dr. Legg, and two students, one within his Ph.D. program and the other, his M.Sc. program. The preliminary idea was that these studies would enable us to manipulate the frequent association of cassava with sweet potatoes and to exploit the fact that both these crop support the same species: *Bemisia tabaci*, but of different biotypes, in which the whiteflies of one crop does not attack the other which they both share the same species of natural enemies. Thus, our studies in Uganda included surveying the whitefly and natural enemies in the fields, studying their relationships with cassava varieties and details of their life histories and behaviors and examining the possibilities of intercropping sweet potatoes and cassava for the purpose of having natural enemies of the former move on to the latter. Concurrently, the studies in Israel were designed to determine the technical details necessary for optimizing banker plant technology in our case, such as the relative attraction of cassava varieties to the whitefly and its natural enemies and the distances traveled by the parasitoids from a release plant. The studies in Uganda involved both field and laboratory work; In the field, we surveyed the pest and natural enemy situation and

conducted detailed studies of population dynamics. In the lab behavioral observations utilizing event recording and its computerized analysis were carried out.

The studies resulted in the conclusion that the intercropping of cassava with sweet potatoes would not be beneficial, since: 1. the former bear too small populations of whiteflies to support the necessary natural enemy fauna; and 2. intercropping always resulted in a significant reduction of the cassava yields. The extensive studies revealed which parasitoids and predators of *B. tabaci* exist in Uganda, their roles in the dynamics of this pest and pointed to the need for adding natural enemies (possibly parasitoids) if sustainable biological control is to be achieved. The studies in Israel have resulted in a greater understanding of some of the relationships between whiteflies, plants and parasitoids, they also demonstrated the efficacy and usefulness of the research methods that might and should be used for future plant-insect relationships. Finally, the training provided to the Ugandan personnel through this project can be seen as an important investment in the young generation, putting at its disposal new methodologies and techniques for furthering agricultural research in Uganda. .

4. RESEARCH OBJECTIVES:

Cassava mosaic virus disease (CMD) is arguably the economically most important whitefly-borne virus disease in Africa, not least since total annual production of cassava, at more than 91 million metric tons, is greater than that of any other crop (FAO, 2000). Continent-wide losses due to CMD have been estimated at 15-24% of total production (Thresh et al., 1997), equivalent to 16-29 million metric tons based on 2000 production levels. Furthermore, evidence obtained in recent years suggests that the situation may be deteriorating still further. In Uganda, in the late 1980s, reports were made from the north-central part of the country of an unusually severe form of CMD associated with large populations of B. tabaci. During the first half of the 1990s it became apparent that the zone of high incidence of severe CMD and abundant B. tabaci was 'moving' southwards at a rate of approximately 20-30km/yr (Legg and Ogwal, 1998). This pattern of movement seemed to be independent of agro-ecological environments.

With support from a wide range of both international and local partners, the national research system imported, evaluated, multiplied and disseminated in Uganda a series of CMD resistant varieties. Deployment of host plant resistance is now being

extended to the countries neighboring Uganda through the movement of CMD-resistant germplasm into these countries using open quarantine systems (Anon, 1999). Although the varieties have been instrumental in addressing the initial crisis posed by the CMD problem, two problems with their long-term usage have become apparent. Firstly, their organoleptic characteristics have yet to match those of traditionally grown CMD-susceptible cultivars; hence, farmers continue to grow local CMD diseased material. Secondly, populations of whiteflies have remained high in the so-called 'post-epidemic' zone (now all of Uganda and large areas of western Kenya and north-western Tanzania). In fact, whitefly population levels are 30-100 times higher than those recorded prior to the CMD epidemic (Legg, unpublished data), and are now causing both direct physical damage to cassava plants, and indirect damage through encouraging sooty mould development, most notably on the CMD-resistant varieties Nase 4 and Nase 12.

The primary objective of our research, as stated in the proposal for the grant, was to find ways to exploit the potential of natural enemies for reducing B. tabaci populations on cassava and through this to reduce physiological damage to cassava plants and the spread of cassava mosaic virus disease (CMD).

We planned to achieve this goal though following specific objectives:

1. Identify the natural enemies of *B. tabaci* (parasitoids and predators) in Uganda and determine their contribution to reducing pest populations in different climatic and agricultural zones of the country.
2. Characterize tritrophic interactions that could favor natural enemies of *B. tabaci*
3. Assess the control potential and shortcomings of the natural enemies present when acting on specific cassava varieties through field observations, with the support of laboratory experiments.
4. Implement biological control of cassava whiteflies in target zones using the information gained during our study, through enhancement of the agro-ecological environment by intercropping and using banker plants and through deploying plant varieties preferred by natural enemies. The identification of varietal characteristics preferred by natural enemies will also provide IITA and national program breeders with opportunities to incorporate these traits into new germplasm.

5. Train both academic and field-advisory personnel in the newly acquired techniques and skills, to assure their quick transferal to growers.

To our knowledge, no other scientists are conducting similar research, i.e. research that is aimed at better utilizations of natural enemy activity. However, other CDR-supported (and possibly other) projects aim at reducing whitefly damage to cassava. The CDR-supported projects are: (C22-003) and (C23-013), the first by Prof. Czosnek "Whitefly-transmitted Geminiviruses Affecting Cassava Production in the Southern Regions of Africa & Development of Cassava Resistant Lines," and the second by Prof. Gafni "Study of the Cassava Mosaic Disease in Ghana: Implications for Resistance".

The innovative aspects include the proposed use of the fact that two *B. tabaci* biotypes each specific to one host plant will be used in a way that one will serve as banker plants for natural enemies attacking the other. Moreover, the use of natural enemies, to control whiteflies of cassava, although not a novel concept, has never been attempted before and therefore may be considered novel.

In addition to being supported by USAID-CDR, the project was supported through salaries, equipment and facilities by Tel Aviv University, IITA and Makerere University. 1. Tel Aviv University paid for the salary of Prof. Dan Gerling who was the PI for the project and spent up to 1/3 of his research time on it. It also paid for the salary of Dr. Moshe Guershon, a principal technical assistant to Prof. Gerling. Likewise, the PhD. student, Ms. Shirly Sharon, whose salary was covered by the grant, was assisted in numerous material and equipment needs by the university, including the use of greenhouses and incubators. IITA...The faculty of agriculture at Makerere University supported the project through providing supervision to the student, laboratory facilities and equipment, office space and other necessary technical assistance during field and laboratory studies. The university also contributed to the day-to-day running of the project and administration of the finances.

5. METHODS AND RESULTS:

In order to reach our objectives, we embarked on the following series of activities:

1. Survey of field populations of *B. tabaci* and its enemies on cassava and adjacent weeds
2. Cataloguing predators of *B. tabaci* on a cassava mosaic disease resistant variety in Uganda
3. Life table analysis of mortality factors affecting populations of *B. tabaci* on cassava in Uganda.
4. Developmental duration and host-searching and oviposition behavior of the main parasitoids of *B. tabaci* in Uganda, *Eretmocerus mundus* and *Encarsia sophia.*
5. Biological studies (development duration, effect of leaf characteristics and prey consumption rate) of the coccinellid *Serangium* sp., a predator of *B. tabaci* on cassava and its dynamics in relationships to whitefly susceptibility of cassava varieties.
6. The whitefly and parasitoids dynamics were examined under an intercropping regime of cassava and sweetpotato.
7. Plant-whitefly-parasitoid relationship studies as a basis for effective intercropping and banker plant technology implementation.

Once it has been shown that sweetpotatoes are probably not suitable to serve as banker plants for the natural enemies of *B. tabaci* on account of the low levels of the pest and its parasitoids occurring on these plants, we branched off and intensified other studies, aimed at studying the potential and shortcomings of other natural enemies.

In order to assure maximal efficacy of the training obtained by local Ugandan personnel, we carried out all of the experiments directly associated with cassava and its ecosystem in Uganda. The role of research in Israel was to render support in solving basic scientific questions and in furnishing the training and support for the Ugandan students. Some of the work has been submitted in papers to scientific journals and others have been presented as lectures at scientific meetings. These will be summarized herein and the full publications or lecture abstracts are appended to this report. The still unpublished work is presented here as requested by CDR.

5.1 Survey of the natural enemies.

The preliminary work done on this subject by Otim *et al* (2005) before the present project was started, was supplemented with a study of the incidence of *B. tabaci* on cassava and associated weeds, abundance of its parasitoids and predators, and incidence of parasitism. A manuscript titled "Field populations of *B. tabaci* and its natural enemies on cassava, cassava component crops and weeds" has been prepared and the draft is attached. The main findings are summarized in the following abstract:

Monthly visit were made from November 2003 to December 2004 to Bukisa (Masindi district), Busukuma (Wakiso district) and Kyantonder (Rakai district) to assess the level of infestation of whitefly and its natural enemies on cassava, crops intercropped with cassava, and weeds within and around cassava files on crops. Three parasitoids species were recorded; *Eretmocerus mundus*, *Encarsia sophia* and an undescribed, black headed species of *Encarsia* (all Hymenoptera: Aphelinidae) at all locations. *E. mundus* was the most abundant, followed by *E. sophia* and the relatively rare black-headed *Encarsia* in all the locations. Parasitism was highest at Busukuma (41.7%), flowed by Bulisa (37.2%) and Lyantonde (32.2%). Parasitoids were also recorded from sweet potatoes, *Commelina* sp., *Melhania* sp., *Bidens* sp., and *Euphorbia* sp. Predators of *B. tabaci* recorded on cassava included: ants, predatory beetles, spiders, lacewings, hoverfly larvae and its predatory bugs. No component crops or weeds harbored high populations of whitefly and its natural enemies. The paper discusses the implications of the finings on the management of *B. tabaci* on cassava.

5.2 Cataloguing predators of *B. tabaci* on a cassava mosaic disease resistant variety in Uganda.

A field experiment was set up at Namulonge Agricultural and Animal Production Research Institute (NAARI) to determine the predators of *Bemisia tabaci* occurring on cassava. Two field trials were set up consisting of small uniform plantings of the virus-resistant variety Nase 4. These trials were set up during different rainfall regimes, with trial one planted during the dry season (August 2003) such that peak growth occurred during the wet season and trial two during the rainy season (November 2003) such that peak growth occurred during the dry season. The trials each consisted of a single 10m by 10m plot with cassava plants spaced at 1m intervals.

At 3 MAP (month after planting), ten plants were randomly selected from the trial plot. Each plant was then observed from the top to bottom including all leaves (both the top and underside), petioles and the stem. A count of every known whitefly predator present was made. The number of leaves on the plant was also counted to obtain a correlation between predator numbers and number of leaves on the plant. Data were collected once a week for a period of six months, i.e. from 3-8 MAP which is the active growth period of cassava and also the period when *B. tabaci* populations are highest. Each plant was sampled once and was only sampled again when all the plants in a particular trial had been sampled. This gave an average of two samplings per plant over the 6 month trial period, with a 10 week interval for each plant between samplings. All suspected predators were collected, taken to the laboratory and put in a petri dish with a single predator specimen and a moist filter paper on which a cassava leaf bearing whitefly eggs and nymphs was placed. Prior to introduction into the dish, the leaf was examined and the numbers of eggs and nymphs upon it were noted. The dishes were examined daily to determine whether feeding had occurred.

Results showed that six taxa of predators are found on cassava; spiders, ants, syrphid larvae, *Serangium* sp. larvae and adults, and syrphid larvae. The most abundant predators across both trials were *Serangium* larvae and adults. In both trials, predator numbers generally increased as the number of leaves on the plant increased. Highest predator numbers were observed in plants with over 100 leaves followed by plants with 51-75 leaves, while the least occurred on plants with 25 leaves or less.

5.3 Life-table analysis of mortality factors affecting populations of *B. tabaci* on cassava in Uganda

A manuscript entitled: "Life table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda" was accepted for publication by a peer-reviewed journal (*Entomologia experimentalis et Applicata*), a copy is attached. The following constitutes an abstract of the findings:

A study was set up to determine the sources and rates of mortality of *Bemisia tabaci* on field grown cassava in Uganda. Using a cohort based approach, daily direct observations were used to construct partial life tables for twelve generations of egg and nymph populations that were studied over a one year period. Mortality was categorized as due to dislodgement, predation, parasitism (for nymphs only), unknown death and inviability (for eggs only). Highest mean rates of mortality in the egg population was attributed to dislodgement with predation and inviability

following respectively while in the nymphs, highest mortality rates were attributed to dislodgement followed by parasitism, predation and least due to unknown death causes. Highest mean levels of mortality among the nymphal instars were observed in the fourth instars followed by first, second and third instars respectively. Generally high mean survival (52.5%) was observed in the egg generations while in the nymphs mean survival was low with only 5.78% making it to adulthood. Key factor analysis revealed that the major factor contributing to generational mortality in the eggs were unknown causes while in the nymphs major mortality was dues to parasitism. Highest irreplaceable mortality in both the egg and nymph generations was attributed to dislodgement. This was followed by predation for the eggs, while for the nymphs parasitism, predation and unknown death in declining order of importance followed dislodgement. Direct density dependence of mortality factors varied with stage of growth with inviability, unknown death, dislodgement and predation showing relationships with eggs, second, third and fourth instars respectively. Manipulative experiments revealed high rates of mortality due to dislodgement and minor levels of natural enemy induced mortality. There was higher egg survival in the manipulative experiments but little variation in nymph survival, with the open field study.

5.4 Developmental duration, host searching and oviposition behaviors of the main parasitoids of *B. tabaci* in Uganda, *Eretmocerus mundus* and *Encarsia sophia*.

A manuscript named "Development duration, longevity and fertility of *Eretmocerus mundus* Mercet, and *Encarsia sophia* Girault and Dodd on *Bemisia tabaci* attacking cassava" has been prepared and the draft is attached. The main findings are summarized in the following abstract:

Eretmocerus mundus Mercet and *Encarsia sophia* Girault and Dodd (all Hymenoptera: Aphelinidae) are the most abundant parasitoid species attacking *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) on cassava in Uganda. However, there are no studies of their life history parameters. This study therefore aimed at providing the first information on the development duration, longevity and fertility of these parasitoids on cassava, *Manihot esculenta* Crantz under laboratory conditions. The initial egg count on emergence averaged 35 ± 1.54 (mean ± SEM) and 3 ± 0.22 eggs per female for *E. mundus* and *E. sophia*, respectively. The egg-to-adult development duration of *E. mundus* was 19.6 ± 0.1 days and for *E. sophia* was 17.4 ± 0.1 days. There was no significant difference between the development duration of females (19.7 ± 0.1 days) and males (19.6 ± 0.1 days) of *E. mundus*, whilst the

females of *E. sophia* developed ca. two days earlier than their male counterparts. Mean longevity when provided with honey was 5.4 days for *E. mundus* and 6.6 days for *E. sophia*, whilst the corresponding values, when females were provided with hosts, averaged 5.5 days and 11.3 days, respectively. Average progeny production averaged 25.6 offspring for *E. mundus* and 16.5 for *E. sophia*. The net reproductive rate of *E. mundus* was 13.1 as opposed to 15.5 for *E. sophia*. The intrinsic rate of increase was 0.1 for *E. mundus* and 0.105 for *E. sophia*. Mean generation times were 24.9 and 26.2 days for *E. mundus* and *E. sophia*, respectively. The results suggest that *E. mundus* is the most suitable candidate for high *B. tabaci* population control, whilst *E. sophia* may be effective under low *B. tabaci* populations. The data collected may be of use in the future should parasitoids be imported for control of *B. tabaci* on cassava.

5.5 Biological studies (development duration, effect of leaf characteristics and prey consumption rate) of the coccinellid *Serangium* sp., a predator of *B. tabaci* on cassava, and its dynamics in relation to cassava varieties susceptibility to whitefly.

These studies were written up as manuscript entitled: Evaluation of *Serangium* n. sp. (coleoptera: coccinellidae), a predator of *Bemisia tabaci* (homoptera: aleyrodidae) on cassava', and accepted pending by the *Journal of Applied Entomology*. A copy is attached. The following is the abstract of the findings:

The potential of a new, previously unidentified *Serangium* species (Coleoptera: Coccinellidae) to control the high *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) populations on cassava was evaluated. Field and laboratory studies were carried out to determine the abundance and feeding capacity of this *Serangium* species feeding on *B. tabaci* on cassava. *Serangium* nymphs and adults were most abundant in cassava fields late in the season, rising sharply from 5 months after planting (MAP) to a peak at 7-8 MAP. Preimaginal development averaged 21.2 days and was longest in eggs and shortest in the L_1 instar. Mean total prey consumption of immature *Serangium* increased with stage of development, with the lowest consumption in the L_1 instar and highest in the L_4 instar. Mean daily consumption was lowest on the first day after hatching in the L_1 instar and rose to a peak on the 13th day after hatching in the L_4 instar. Each *Serangium* larva consumed a mean of over 1000 nymphs during its entire development. These results have demonstrated the potential of this *Serangium* species to control *B. tabaci* populations on cassava.

5.6 Examination of the whitefly and parasitoids dynamics under an intercropping regime of cassava and sweetpotato.

The experiment was set up in September 2004 and was completed in September 2005 at Namulonge Agricultural and Animal Production Research Institute (NAARI) and consisted of eight plots of cassava, intercropped with sweetpotato, and planted on different dates. It was set up in a randomized complete block design in four replications. Each replicate consisted of a single plot of sole cassava and sole sweetpotato and five plots of the intercrop. The intercrop plots were separated based on the time of planting of sweet potato, with the planting staggered at 0, 2, 4, 6 and 8 weeks before cassava. Within the plots, intra- and inter-row spacing was 1m, with the sweet potato planted on hilled ridges and the cassava planted in rows between the ridges. Between plot spacing was 1.5 m planted with sorghum to act as a barrier for whiteflies moving between plots. Weekly sampling began one month after planting the cassava and was continued up to harvest of each crop. Ten randomly selected plants each of cassava and sweet potato were sampled in both the sole and intercrops. Data was collected on number of 4th instar nymphs, parasitized nymphs and predated nymphs.

The results indicate that, in all cases, there is a high cost for the cassava plants to be intercropped as expressed in the lower yield of intercropped plots. There was also a reduction in number of whiteflies and their natural enemies in the intercropped plots compared to the sole cassava (Fig 1). Smallest reduction was observed in the intercrops where sweet potato was planted on the same date as the cassava. However, across all the planting dates, there were no significant differences in whitefly and parasitoid numbers between the sole and the intercrop, indicating that the intercrop was not able to increase parasitism on the cassava as had been hypothesized.

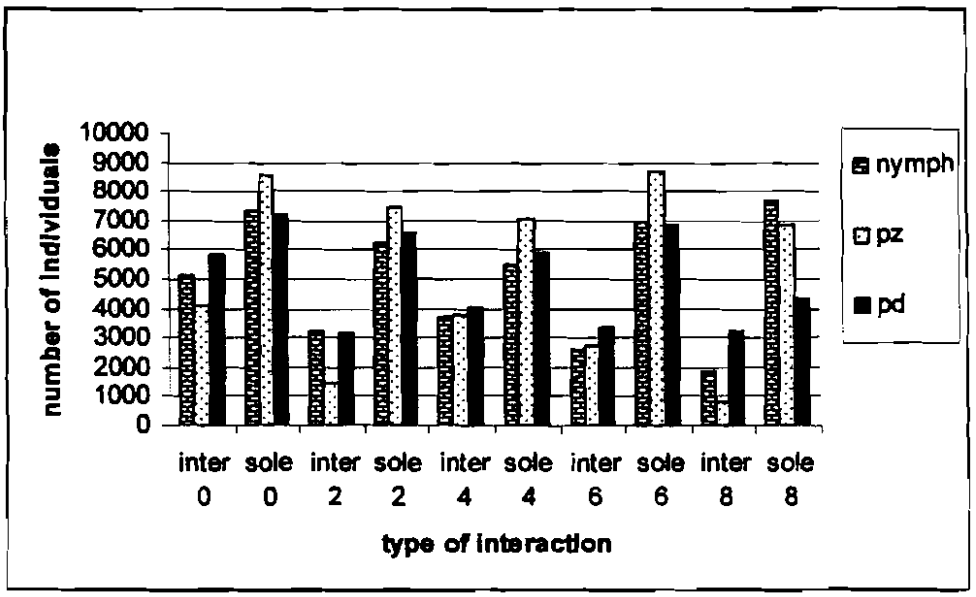

Fig 1. Overall results of the intercropping experiment showing total organisms registered in each of the experimental setups. Inter= interplanted sole = sole cassava pz = parasitoids and pd= predators. Numbers 0-8 refer to the interval between planting of sweet potatoes and cassava.

5.7 Plant-whitefly-parasitoid relationship studies.

These studies which were conducted in Israel, are reported here on a chronological basis since all constitute a continuous effort around the same topic.

First Year

a. Setup of plant and insects cultures

a.1. Plants: Importation, culture and establishment of cassava rearing from tissue culture and preliminary tests of infestation.

Plants of the varieties Ebwanateraka and SS4 (the latter being resistant to viral diseases and the former not) were imported as tissue cultures from Uganda in February 2003. They were hardened and planted in a secluded and closed greenhouse in Israel. Thereafter, and after having been tested and found free of diseases by the Plant Protection and Inspection Service in Israel, the plants were released and grown for experimental purposes.

Plants were kept in a greenhouse room and populated with numerous adults of *B. tabaci* from our culture that was reared on cabbage. This was done repeatedly for several months. Initially none of the whiteflies laid eggs on the cassava and usually lived for a few days only. Later, some oviposition was obtained on young cassava

foliage. Following this experience, we decided to try two alternative approaches. 1. to concentrate out efforts on working with sweet potatoes; and 2. to establish a culture of whiteflies on cassava by using cassava grown whiteflies for reinfestation of the same plants.

a.2. Insects: Development of *B. tabaci* on sweet potato

The purpose of the studies with sweet potatoes was to determine the suitability of the plants to serve as intercropping hosts for the cassava culture in Africa. The questions asked included: Are the plants themselves attractive to the parasitoids? Will parasitoids that have developed on sweetpotato-infesting whiteflies readily leave the plants so they can be used for banker plants in the intercropping with cassava? Are there any steps that we should take in order to have the parasitoids move more effectively from one plant species to the next? What levels of sweetpotato infestation do we need to obtain in order to make this system work effectively?

In order to study these parameters we first determined the developmental duration of the whiteflies on sweet potato; plants were grown in the greenhouse and kept in a temperature cabinet at 28$\pm$ 2°C . Their development was followed from oviposition to adult emergence and was found to range between about 20 to 27 days.

a.3. Additional topics: Importing the Ugandan parasitoids *Eretmocerus mundus*, *Encarsia sophia* and *Encarsia* n. sp. and predators.

Parasitoids were hand-carried to Israel and placed in quarantine on local cabbage plants infested with *B. tabaci*. In spite of the large numbers of parasitoids used and the repeated introduction of these onto the plants, we were unable to establish a culture of any of the parasitoid species upon the whiteflies. We obtained a small culture after one generation, but that also died out and no second generation was successfully established. Therefore, pending further introductions we decided to start working with the local *E. mundus* and *E. sophia*, which are akin those in Uganda (if not conspecific).

Predators were not imported since: 1. work on the existing insects was too intensive and 2. the *Conwenzia* sp. that we intended to import became a rare insect in Uganda. A final attempt to collect additional *Conwenzia* was made in the spring of 1996 but did not result in the establishment of a culture.

Second Year:

a. Attraction studies

Experiments included:

i. Attraction of *B. tabaci* to sweet potato vs. cassava (Ebwanatereka [=tereka])

ii. Attraction of *E. mundus* to sweet potato vs cassava (tereka) and to sweet potato vs. cssava (SS4).

Methods: A 4 arms olfactometer was used (with two arms closed). Each arm was connected to a vacuum pump and to three bottles. The first held water to retain humidity; the second held the tested leaf (sweet potato or cassava); and the third was used as a trap to catch the foraging wasp or the whitefly see diagram in (Vet....)

Results: More individuals of both *B. tabaci* and *E. mundus* were found on the Tereka variety of cassava than on the sweet potato (Fig. 2&3), whereas no difference was found in the numbers of *E. mundus* individuals using SS_4 and Tereka (Fig 4).

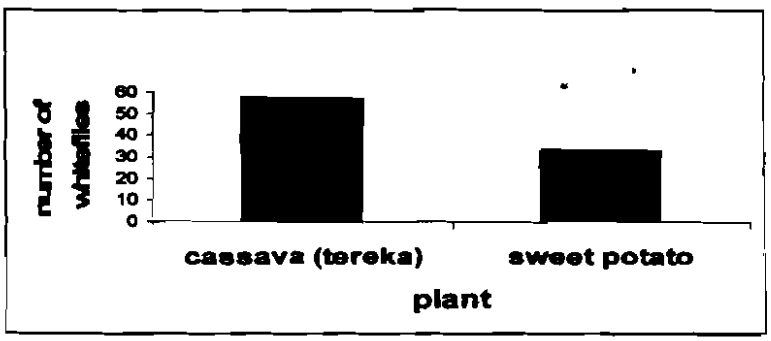

Figure 2: Number of *B. tabaci* attracted to cassava (tereka) vs. sweetpotato.

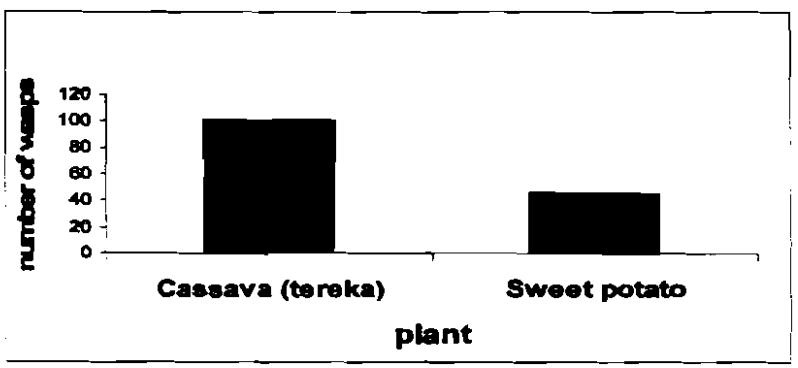

Figure 3: Number of *E. mundus* attracted to cassava (tereka) vs. sweetpotato.

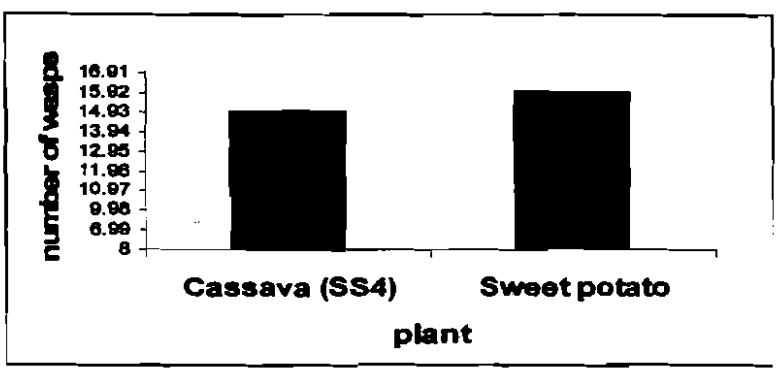

Figure 4: Number of *E. mundus* attracted to cassava (SS_4) vs. sweetpotato.

b. Landing preference of *B. tabaci* on cassava: tereka vs. SS_4

Methods: In order to determine which cassava variety (tereka vs SS4) is preferred for landing *by B. tabaci* adults, two leaves were each placed in a separate vial with water in a tall cylinder and ca. 200 *B. tabaci* adults were released into the top of the cylinder. The number of whitefly adults on each plant was at 10 minute intervals.

Results: As time progressed the number of *B. tabaci* slowly dropped until it had steadied after an hour. Fewer *B. tabaci* landed on the SS4 than on the tereka (fig. 5).

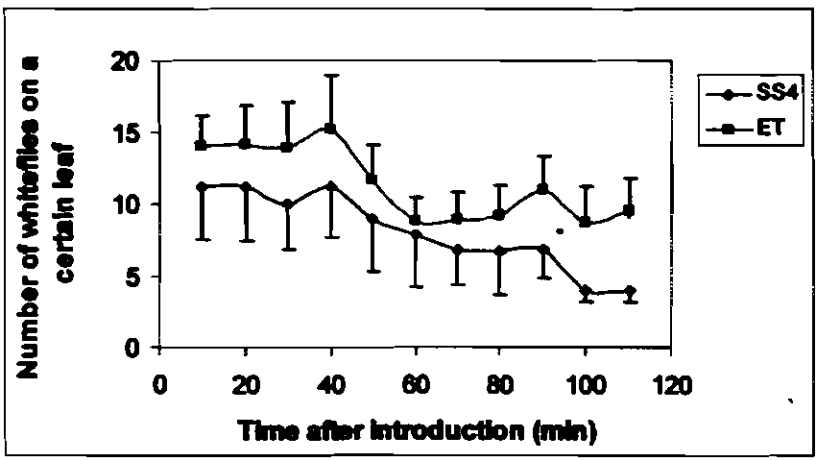

Figure 5: Number of *B. tabaci* landing on SS_4 vs. ET (tereka) leaves every 10 minutes for a period of two hours.

c. Oviposition preference of *B. tabaci* on sweet potato leaves of different ages

Methods: Leaves on a branch were classified by age as follows: the oldest, bottom leaf, was numbered 1 while the top, youngest leaf was marked 5 or 6 (according to the number of leaves per branch). All branches were kept in water and were exposed to whitefly adults for 48 hours, after which the adults were removed using an aspirator. Whitefly eggs and nymphs were counted every two-four days on each leaf.

Results: *B. tabaci* laid on leaves 4 and 5/6 from the bottom [i.e. the topmost and second leaves from the top, (Figure 6)].

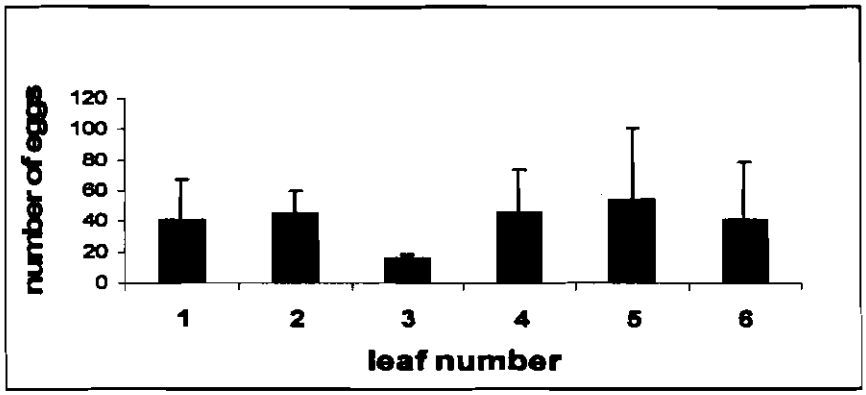

Figure 6: Number of eggs per leaf after 4 days of exposure to *B. tabaci* adults.

d. Developmental time of *B. tabaci* stages on sweet potato leaves of different ages.

Methods: Developmental time of the different *B. tabaci* stages on sweet potato leaves was examined by counting the numbers of each stage every two days. We checked and compared leaves of different ages on two populations of sweet potato: our field population, and a virus free population obtained from tissue culture through the courtesy of Rosh Hanikra Industries, Israel.

Results:

We found some differences in the oviposition patterns between the two sweet potato variants (figures 6 and 7). Differences in development duration and survival were found between the leaves of single branches (different leaf ages). However this difference was strongly heterogenous between branches which made their analysis difficult (figures 7 and 8).

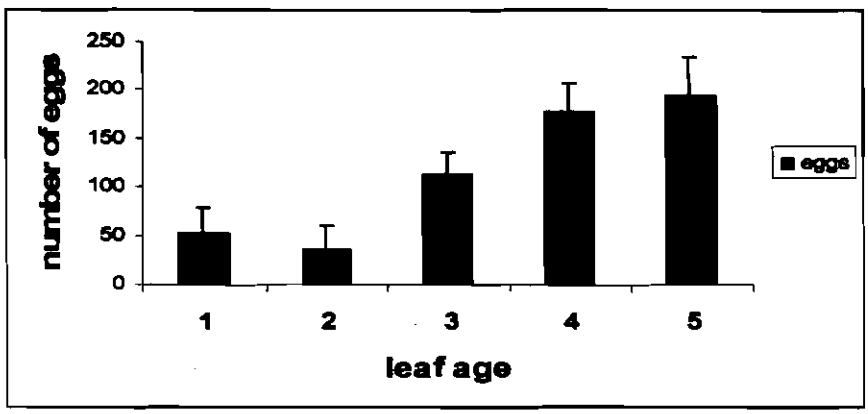

Figure 7: Number of eggs on virus-free leaves after 4 days of exposure to *B. tabaci* adults.

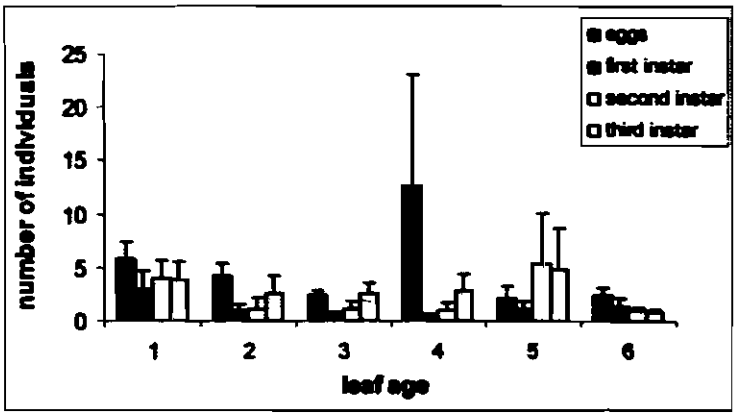

Figure 8: Number of different stages 8 days after oviposition by *B. tabaci* adults on sweet potatoes obtained from the field

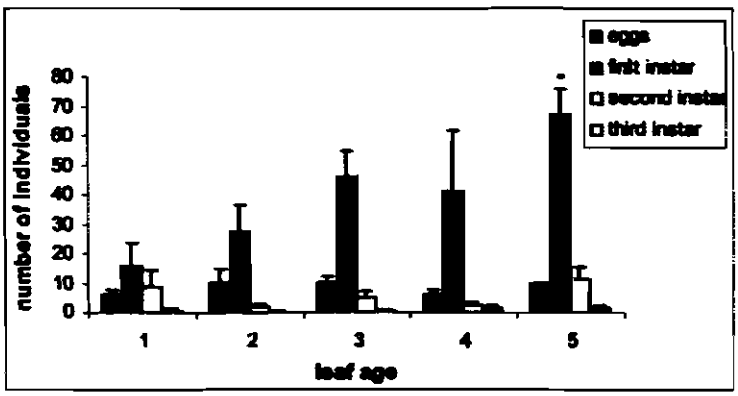

Figure 9: Number of different stages 8 days after oviposition by *B. tabaci* adults on sweet potatoes obtained from tissue cultures.

e. Oviposition preference as function of plant age (sweetpotato).

Methods: Sweetpotato plants of different ages, one month, 2 month and 2.5 month old, with the same numbers of leaves, were used in order to check the relation between oviposition of *B. tabaci* and plant age. The different plants were exposed to ca. 200 *B. tabaci* in closed cages.

Results: The number of eggs laid by *B. tabaci* was higher on the oldest plants (Fig. 10).

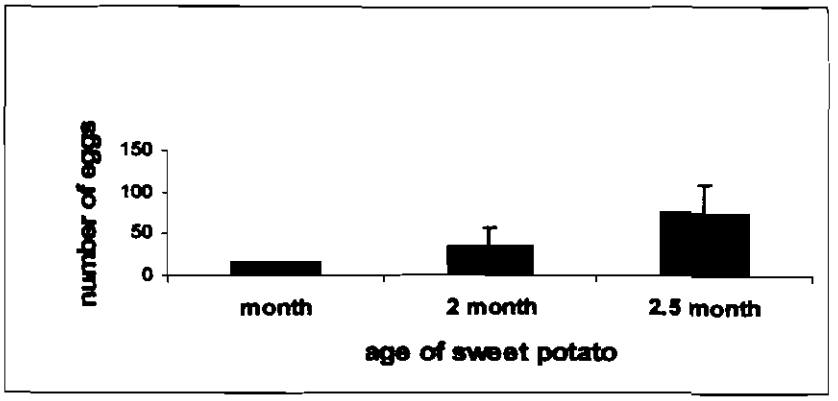

Figure 10: Number of eggs oviposited on sweet potato of different ages

Third Year:

a. Attraction studies

Following the previous year's results on attraction studies, we now added several new combinations in order to determine preference by the whitefly and the wasps.

Methods: See methodology on olfactometry described previously (second year).

Results: The following table summarizes all the results on the olfactory tests:

Organism	Odour source I	Odour source II	Results
B. tabaci	ET	SS4	N.S
	ET	Sweet potato	Attraction to ET
	SS4	Sweet potato	Attraction to s.p.
	ET	Infested ET	Attraction to ET
E. mundus	ET	SS4	Attraction to ET
	ET	Sweet potato	Attraction to ET
	SS4	Sweet potato	N.S
En. Sophia	ET	SS4	N.S
	SS4	Sweet potato	Attraction to S.p.
	ET	Sweet potato	Attraction to S.p.

ET=tereka; s.p. = sweet potato

b. Effectiveness of sweet potato as a banker plant for *E. sophia*.

In order to assess the effectiveness of sweet potato as a banker plant, the activity of the emerging parasitoids was checked at different distances from the source plant and under different conditions. Parameters tested included dispersal of adult from the source plants, and parasitism on plants at different distances without interference (masking by the closer plants) vs. with interference.

b.1. Dispersal of parasitoids from banker plants.

Methods: Sticky traps were located at different distances from the source plant and adult parasitoids were counted 3 days after their emergence.

Results: Although a higher number of adults was found on the trap located at 70 cm from the sweet potato, no significant difference was found between the traps (Fig. 11).

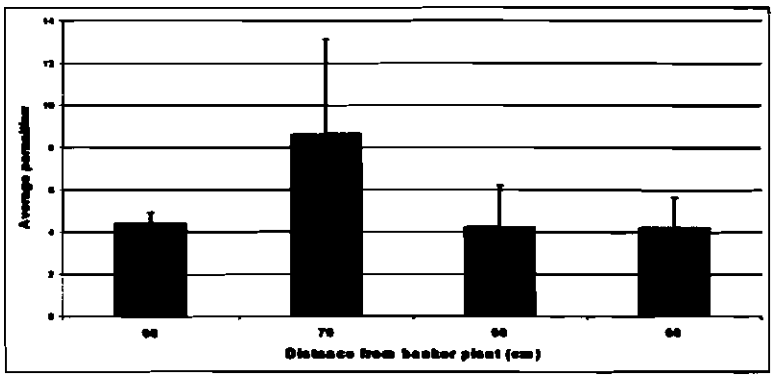

Figure 11: Adults of *E. sophia* caught on sticky traps at different distances from a source plant (average + SE, ANOVA, ns).

<u>b.2. Parasitism at different distances from source plant without masking by interfering plants</u>

Methods: Four target plants, infested with instar 2-4 *B. tabaci* nymphs (parasitization age), were located at different distances from a parasitized sweet potato source plant. The target plants were located at different angles from the plants to prevent their masking each other and enabling the parasitoids to have direct access to each at the different distances. Approx. 10 days later, the whitefly nymphs on the target plants were checked for signs of parasitization.

Results: Significantly different parasitism was found only between the tested extremes, 60 cm and 90 cm, being higher at the closer distance (Fig. 12).

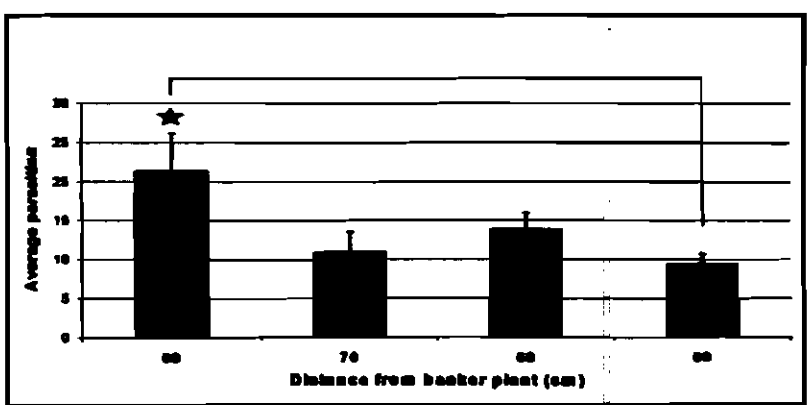

Figure 12: Number of whitefly pupae parasitized by *E. sophia* in target plants at different distances from source plant without masking interference (average + SE, ANOVA, *= significantly different)

c. Parasitism at different distances from source plant with masking interfering plants.

Methods: Three target plants were located consecutively at different distances from the source plant. Parasitism was assessed and compared between the three target plants. The plants were arranged so that the closer plants masked the more distant ones from the release source.

Results: A significant difference was found between the plants. The first plant in the target row was parasitized at a higher level than the two others (Fig. 13) indicating that masking the more distant plants may have an additional effect to that experienced by the more frequently parasitized plant seen in experiment a.2.

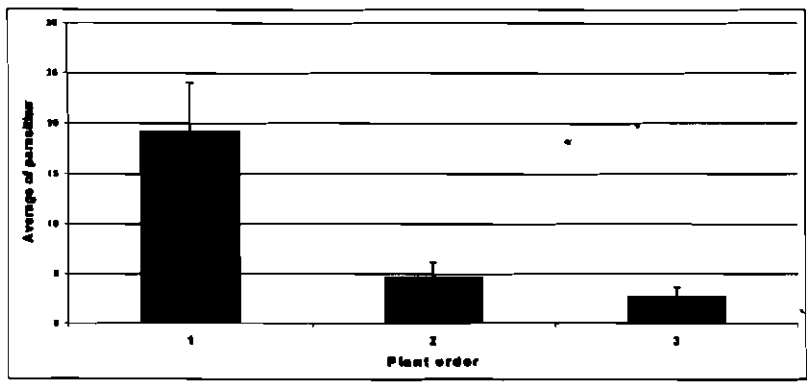

Figure 13: Number of whitefly pupae parasitized by *En. sophia* on target plants at different distances from source plant while experiencing interference (average + SE, ANOVA, $p<0.01$)

d. In order to assess the best combination of banker-target plant we tested the effects of two other plant characters on parasitization: leaf hairiness and host density. As known from the literature, these parameters may influence the optimal application of the biocontrol agent for both the banker and target plants.

<u>d.1 Influence of leaf hairiness on parasitism</u>

Methods: Eight cabbage plants, 4 glabrous and 4 artificially haired, were exposed to whitefly adults for oviposition. The artificial layer of hairs was produced on glabrous cabbage leaves by spreading finely cut lint fiber on the surface of the leaves using a delicate brush. After reaching third instar the plants were located around a sweet potato plant carrying parasitized nymphs in alternated positions. Numbers of parasitized nymphs in the different cabbage plants were counted.

Results: Parasitism was significantly higher on the non-hairy plants.

Figure 14: Number of whitefly pupae parasitized by *E. sophia* in target plants with different leave hairiness (average + SE, t-test, $p<0.01$)

d.2. Relation of host density to parasitism.

Methods: Sweet potato leaves infested with *B. tabaci* nymphs at different density levels (nymphs per leaf) were exposed to females of *Encarsia sophia* for 24 hrs. The number of parasitized nymphs reaching the pupae stage was counted. Following earlier studies by Gerling and Fried (1997) and Shimron et al 1992 we used low numbers of *B. tabaci* on the leaves in the knowledge that usually no numerical response is observed at high densities.

Results: no relationship was found between the host density value and the fraction of it that was parasitized (fluctuating around 40 ± 10% the regression line formula was $y=-0.0035x + 0.4134$; $R^2=0.0111$).

Discussion of the relationship studies:

Our goal was to use a series of laboratory and field methods in order to establish criteria that would help in assessing the suitability of plants as banker plants.

The laboratory methods were behavioral: measuring the relative attraction of the whiteflies and their parasitoids to infested and uninfested plants (both banker plants and cassava), assuming that the findings would also indicate the trends that occur in the field. Since we were not successful in rearing large numbers of the whitefly biotype which occurs in Israel on the cassava, we conducted our studies on sweet potatoes as a banker plant and cabbage as the main crop – the latter was chosen since, similar to cassava, it is a host to abundant whitefly populations.

Consequently, the laboratory results, which did indicate definite differences between the plants, (whether infested or not by the tested organisms), could not be used in the field, but did offer an appropriate test of the methodology that could be used for

determining plant suitability to the pest and its natural enemies, and therefore provide a suitable tool for plant breeders.

The tests also included examination of the oviposition pattern of the whiteflies on sweet potatoes and showed that *B. tabaci* laid the most eggs on the topmost and second leaves from the top. Moreover, different oviposition patterns were found on field and tissue culture reared sweetpotatoes. Although these findings are not of use in themselves, they do indicate that caution must be exercised when making generalizations about whitefly behavior.

Testing parasitism, we found, as expected, that the closer the plants were to the parasitoid source, the higher the percentage. However, it appears that two effects play a role here: the proximity to the source, and the masking of the more distant plants by the closer ones. Thus certain crop heights and planting patterns might be more beneficial or less so to parasitoid dispersal.

6. IMPACT RELEVANCE AND TECHNOLOGY TRANSFER

We interacted with Makerere University, undertaking the formal training of two students, Mr. Otim for his Ph.D. and Mr. Assimwe for his M.Sc. studies as well as the training of numerous technical workers. The studies in Uganda, all of which were carried out by local personnel, included learning the most up-to-date technology, involving behavioral and ecological field and laboratory studies. These and the courses taught voluntarily by Prof. Gerling at Makerere university all brought about an extensive transfer of knowledge and methodology pertaining to pest management in its most modern and sophisticated form. The results of these efforts can already be seen in the resent employment of Mr. Otim as an entomologist for the National Agricultural Research Organization in Uganda, and have also enabled Mr. Assimwe to apply for his Ph.D. studies. As mentioned in the 'future studies' section, the information and technologies gained in our research may form the basis for eventual new directions in plant-breeding processes, pending financial investment and experimentation with more cassava varieties and whitefly and enemy-related traits.

7. PROJECT ACTIVITIES/OUTPUTS

Scientific Meetings

Meeting	Venue	dates	participants	Papers presented
Sixth African Crop Science Society conference	Nairobi Kenya	12-17 October 2003	Otim, Legg	1,2
3rd international *Bemisia* workshop	Barcelona Spain	17-20 March 2003	Gerling, Legg, Otim	3,4,5
Second international whitefly workshop	Cavtat, Croatia	5-9 October 2004	Gerling, Legg, Asiimwe	6
Meeting of the Israel Entomological society	Bet Dagan Israel	Sept 2005	Gerling, Guershon, Sharon	7
Seventh African Crop Science Society conference	Entebbe Uganda	5-9 December 2005	Gerling, Legg, Otim, Asiimwe	8,9,10,11

1.Otim, M.H., Legg, J.P., Kyamanywa, S. and Gerling, D. (2003) Occurrence of parasitoids of *Bemisia tabaci* on cassava in Africa: A review. Abstract. Sixth African Crop Science Society conference. 12-17 October, Nairobi, Kenya

2.Semaganda, R., Legg, J. P., Gerling, D., Kyamanywa S. and Adipala, E. (2003). Augmenting the activity of *Bemisia tabaci* parasitoids on cassava by intercropping cassava with sweet potato. Abstract. Sixth African Crop Science Society conference. 12-17 October, Nairobi, Kenya

3. Legg, J.P., Otim, M., Owor, B., Ntawuruhunga, P., Ndyetabura, I., Obiero, H., Kyamanywa, S., Colvin, J., Gerling, D. 2003. Managing cassava mosaic geminiviruses and their *Bemisia tabaci* vector in Africa: current practice and future opportunities. 3rd International Bemisia Workshop, 17-20 March, Barcelona, Spain. Abstract. p131

4. Otim, M., Legg, J.P., Kyamanywa, S., Polaszek, A., Gerling, D. 2003. Potential for biological control of the whitefly, *Bemisia tabaci*, vector of cassava mosaic geminiviruses using parasitoids in Uganda. 3rd International Bemisia Workshop, 17-20 March, Barcelona, Spain. Abstract. p74.

5. Semaganda, R., Gerling, D., Legg, J.P., Kyamanywa, S., Adipala, E. 2003. Augmenting the activity of cassava whitefly parasitoids by intercropping cassava with sweet potato. 3rd International Bemisia Workshop, 17-20 March, Barcelona, Spain. Abstract. p39.

6. Asiimwe, P. Ecaat, J.S. Otim, M. Gerling, D. Guershon, M. Kyamanyawa, S. and Legg, J.P. 2004. Life table analysis of mortality factors affecting populations of *Bemisia tabaci* on a cassava mosaic disease resistant variety in Uganda. P.60 Proceedings, 2nd European whitefly symposium, Cavtat, Croatia

7. Olfactory responses of the parasitoid *Eretmocerus mundus* (Hymenoptera: Aphelinidae) and his host *Bemisia tabaci* to Cassava, SS_4 and Ebwenatereka variety and Sweet potato. Shirly Sharon, Moshe Guershon James Legg and Dan Gerling Annual Conference, Israel Entomological Society, Sept 2005.

8. The influence of foliar pubescence on the searching and oviposition behaviour of parasitoids of Bemisia tabaci (Gennadius) (Homoperta: Aleyrodidae) on different cassava Manihot esculenta Crantz Varieties Otim, M., Kyalo, G., Kyamanywa, S., Asiimwe, P., Legg, J.P., Guerhson, M. and Gerling, D. Seventh African Crop Science Society conference Kampala, Uganda 5-9 December 2005

9. Mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda Asiimwe, P., Ecaat, J.S., Otim, M., Gerling, D., Guershon, M., Kyamanywa, S. and Legg, J.P. Seventh African Crop Science Society conference Kampala, Uganda 5-9 December 2005 {received honorary citation- best student lecture).

10. Olfactory responses of the parasitoids *Eretmocerus mundus* and *Encarsia sophia* (Hymenoptera: Aphelinidae) and its host *Bemisia tabaci* to cassava and sweetpotato Sharon, S., Guershon, M., Gerling, D. and Legg, J.P. Seventh African Crop Science Society conference Kampala, Uganda 5-9 December 2005

11. Implications of Biological Sciences for Pest Management, Gerling, D. and Legg, J.P. Seventh African Crop Science Society conference Kampala, Uganda 5-9 December 2005; invited plenary lecture.

Publications:

Asiimwe, P., Ecaat, J. S., Otim, M., Gerling, D., Guershon, M., Kyamanywa, S. and Legg, J. P. Evaluation of *Serangium* n. sp. (coleoptera: coccinellidae), a predator of *Bemisia tabaci* (homoptera: aleyrodidae) on cassava. Journal of Applied Entomology: *in press*

Asiimwe, P., Ecaat, J. S., Otim, M., Gerling, D., Guershon, M., Kyamanywa, S. and Legg, J. P. Life table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda. Entomologia experimentalis et Applicata: *in press*

Travel and training of the directly involved personnel:

Trip #	Year	Traveler	Departure date	Return date	Comments
1	2003	Mr. Otim	22 May	5 Jun	Screenhouse management, sampling methods, The Observer, literature search, parasitoid dissection
2	2003	Dr. Guershon	28 Oct	04 Nov	Experimental designs and analysis, improving insect rearing in screenhouse, tutoring of 'The Observer', natural enemies survey, collection and import of parasitoids
3	2004	Prof. Gerling	28 Jan	02 Feb	Parasitoid dissection, experimental design and analysis, managerial issues
4	2004	Mr. Asiimwe	11 May	23 May	Training in laboratory and field rearing and sampling techniques, The observer, parasitoid dissection
5	2004	Prof. Gerling	20 Aug	27 Aug	Experimental design and analysis, guiding students and supervision
6	2004	Dr. Legg	13 Oct	14 Oct	Managerial issues, experimental design and supervision
7	2005	Prof. Gerling	11 Jan	28 Jan	Summarizing achievements, experimental planning, managerial issues, voluntary lectures to graduate students at Makerere University: behavioral ecology + parasitoids
8	2005	Prof. Gerling	6 Sept	19 Sept	Tutoring students, supervising experiments
9	2005	Prof. Gerling	2 Dec	13 Dec	African Crop Science conference, managerial isssues
10	2006	Prof. Gerling	10 Mar	26 Mar	Visit to Dr legg's new headquarters in Dar es Salaam. Voluntary lectures to graduate students at Makerere University: behavioral ecology + parasitoids
11	2006	Prof. Gerling	11 Sept	19 Sept	Preparation of final report, voluntary lectures to graduate students at Makerere University: journal club course

Comments on trip table:

1. The details of the trips funded by the CDR are given in the individual reports.
2. All trips involved detailed discussions of the administrative and scientific topics of the project as well as surveys of the situation and joint work with the students on their prospective projects.
3. The trip of March 2006 included a visit to James Legg in his new headquarters at IITA in Dar es Salaam.

Prof. Gerling and Dr. Guershon were personally engaged in training the technical personnel and students during each visit in Uganda. In addition, Prof Gerling volunteered to teach a course in behavioral ecology during March 2005 and 2006. He also taught a short practical lab course on parasitoid biology in March 2006 and a journal club discussion course in September 2006.

8. PROJECT PRODUCTIVITY

The original goal of using sweet potatoes as an intercrops by exploiting the fact that this plant crop harbors *B. tabaci* but is not severely damaged by it on the one hand, while harboring natural enemies that may help reduce the pest on cassava on the other, did not proved to be feasible on two account: 1. the very low whitefly populations on the sweet potatoes do not support enough enemies to make a difference in the cassava field; and 2. such intercropping has a negative effect on cassava, lowering the crop production of the latter (see results of the intercropping experiments above).

The present work nonetheless established at least two important findings: a. a detailed knowledge of the elements and interrelationships pertaining to the cassava whitefly situation in Uganda; and b. the suitability of observational methods for determining the detailed interrelationships between the plant, whitefly and natural enemies. These two findings may form the basis for further studies, both on the field conditions relating to cassava culture, and on ways of lowering their populations through plant and natural enemy manipulation in the future.

9. FUTURE WORK

Considering the findings listed under "project productivity", a proposal for a continuation of the CDR-financed effort was submitted, utilizing these findings for further development of healthy cassava plantings in East Africa. Due to the discontinuing of the CDR project, these were not materialized. The plans, which call for establishing criteria that will enable the cassava breeders to develop plants that are more suitable for natural enemy activity while being more unfavorable to whitefly development , can be adopted by any scientific entity.

10. LITERATURE CITED

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Legg, J.P. and Ogwal, S. 1998. Changes in the incidence of African cassava mosaic virus disease and the abundance of its whitefly vector along south-north transects in Uganda. *J. Appl. Entomol.* 122(4): 169-178.

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Thresh, J.M., Otim-Nape, G.W., Legg, J.P. & Fargette, D. 1997. African cassava mosaic disease: The magnitude of the problem? *African Journal of Root and Tuber Crops*. Special Issue: Contributions of Biotechnology to Cassava for Africa. In. *Proceedings of the Cassava Biotechnology Network, Third International Scientific Meeting* 13-19, 26-31 August, 1996, Kampala, Uganda (Eds Thro, A.M & Akoroda, M.O).

Vet L.E.M., vanLenteren J.C., Heymans M., Meelis E. 1983. An airflow olfactometer for measuring olfactory responses of hymnopterousparasitoids and other small insects. *Physiol. Entomol.* 8: 97-106.

Appendices

1. Draft of manuscript: Field populations of *Bemisia tabaci* and its natural enemies on cassava, cassava component crops and weeds.

2. Reprint (uncorrected proof): Life-table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda.

3. Draft of manuscript: Development duration, longevity and fertility of *Eretmocerus mundus* Mercet, and *Encarsia sophia* Girault and Dodd on *Bemisia tabaci* attacking cassava.

4. Reprint (uncorrected proof): Evaluation of *Serangium* n.sp. (Col., Coccinellidae), a predator of *Bemisia tabaci* (Hom., Aleyrodidae) on cassava.

Field populations of *B. tabaci* and its natural enemies on cassava, cassava component crops and weeds

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Abstract

Monthly visits were made from November 2003 to December 2004 to Bulisa (Masindi district), Busukuma (Wakiso district) and Lyantonde (Rakai district) to assess the level of infestation of whitefly and its natural enemies on cassava, crops intercropped with cassava, and weeds within and around cassava fields or crops. The results showed the occurrence of three parasitoid species; *Eretmocerus mundus*, *Encarsia sophia* and an undescribed black-headed species of *Encarsia* (all Hymenoptera: Aphelinidae) at all the locations. *Er. mundus* was the most abundant followed by *En. sophia*, and the relatively rare black-headed *Encarsia* in all the locations. Parasitism was highest at Busukuma (41.7%), followed by Bulisa (37.2 %) and Lyantonde (32.2 %). Parasitoids were also recorded from sweet potato, *Commelina* sp., *Melhania* sp., *Bidens* sp., and *Euphorbia* sp. Predators of *B. tabaci* recorded on cassava included: ants, predatory beetles, spiders, lacewings, hoverfly larvae and predatory bugs. No component crops or weeds harboured high populations of whitefly and its natural enemies. This paper discusses the implications of the findings on the management of *B. tabaci* on cassava.

Introduction: Among the natural enemies of whiteflies, aphelinid parasitoids have, for a long time, been used in the biological control of whiteflies in agricultural crops. For instance, *Eretmocerus debachi* Rose and Rosen has been used to control *Parabemisia myricae* (Kuwana) on citrus in California (Rose and Debach, 1992), in Israel (Swirski *et al.*, 1998) and in Turkey (Sengonca *et al.*, 1998). Similarly, *Encarsia inaron* (Walker) has been used to control *Siphoninus phillyreae* (Haliday) in the US (Gerling *et al.*, 2004), while *E. eremicus* Rose and Zolnerowich and *Eretmocerus mundus* Mercet are used to control whitefly in greenhouses (Rose and Zolnerowich, 1997; Hoddle and van Driesche, 1999).

There are numerous reported predators of *B. tabaci*, but these are often limited to laboratory observations and qualitative field data (for review see Gerling *et al.* (2001)). Moreover, biological control potential has only been examined with *Delphastus catalinae* and *Serangium parcesetosum* (Coccinellidae), *Macrolophus caliginosus* (Miridae), *Chrysoperla carnea* and *C. rufilabris* (Chrysopidae) (Gerling *et al.*, 2001).

For Africa, there are few reports on the natural enemies of *B. tabaci* on cassava, most of which give qualitative information (Robertson, 1985; Nyirenda *et al.*, 1993;

Fishpool and Burban, 1994; Legg, 1995; Otim, 2002; Otim *et al.*, 2005). Legg (1995) conducted life table studies in Uganda and found that natural enemies, primarily parasitoids of the genera *Encarsia* and *Eretmocerus*, cause about 50 % mortality of *B. tabaci* on cassava. Recently, a preliminary survey revealed the occurrence of four parasitoid species attacking *B. tabaci* on cassava: *Eretmocerus mundus* Mercet, *Encarsia sophia* Girault and Dodd, an undescribed black-headed *Encarsia* (=*Encarsia*?), and *Encarsia ?mineoi* and, that the abundance of and parasitism by both *E. mundus* and *E. sophia* varied between locations, whilst *Encarsia*? was rarely observed (Otim, 2002; Otim *et al.*, 2005). The above studies did not cover predators of *B. tabaci* and the possible alternate hosts of *B. tabaci*. The study reported here was therefore conducted to assess the abundance of *B. tabaci* and its natural enemies on cassava, crops grown in association with cassava and weeds in and around cassava crops or fields. The specific objectives were: to assess the level of infestation of cassava by *B. tabaci* and its natural enemies in selected districts of Uganda at different times of the year and ii) to determine whether crops grown in association with cassava and weeds in and around cassava fields harbour *B. tabaci* and its natural enemies.

Material and methods

The study was conducted in three districts of Uganda, in each district, one sub county was selected for the survey; these were Bulisa, Lyantonde and Busukuma sub-counties in Masindi, Rakai and Lyantonde districts, respectively. Each sub-county was visited once a month for twelve months, except when there was transport problem (Table1). In each sub-county, five cassava fields of three to six months old were sampled to assess the abundance of *B. tabaci* and its natural enemies (parasitoids and predators). The cassava age range of three to six months was chosen because that is when cassava is most susceptible to whitefly attack. From each field, records were taken on the age of the cassava crop, types of intercrops, their arrangement and ratio, infestation by *B. tabaci* and the associated natural enemies. For predator counts, ten cassava plants were randomly selected and inspected from top to bottom and the numbers of each potential predator of *B. tabaci* were recorded. Spiders were sent to Dr. A.S. Dippenaar-Schoeman of the biosystematics division of Plant Protection Research Institute, Republic of South Africa, while Coccinellids were sent to the United States Department of Agriculture for identification.

For parasitoids, the aforementioned plants were examined and six leaves per plant, beginning with the first red-eyed nymph-bearing leaf, were picked, put in a cool box, and taken to the laboratory. While in the laboratory, the leaves were kept in paper bags at 4 °C until observations could be made. For each cassava leaf, a sub-sample of three leaflets, which comprised the middle leaflet and next but one leaflets on either side of the middle leaflet, was picked. Each leaflet was examined for whitefly presence under a stereoscopic microscope and the numbers of healthy and parasitized fourth instar nymphs were recorded. In total, eighteen cassava leaflets were observed per plant. After the observations, leaflets were put in emergence bottles or cages and kept at room temperature to allow parasitoids to emerge. Emerged parasitoids were identified using identification guides (Polaszek *et al.*, 1992, Schauff, *et al.*, 1996 and Rose and Zolnerowich, 1997) and kept in 70% ethanol. Samples were sent to Tel Aviv University to confirm their identity, while voucher specimens were deposited at Namulonge Agricultural and Animal Production Research Institute.

In order to assess infestation on crops grown in association with cassava, and weeds within and around cassava fields, twenty of each component crop or weed were inspected for the presence of whitefly and associated natural enemies. For infestation on sweetpotato and coffee, two vines per hill or two accessible branches per tree were randomly selected for inspection. Infestation on bean, cotton and cowpea was assessed by examining all the leaves of the twenty plants. Similarly, infestation on weeds was performed by examining ten plants per garden, and an additional ten plants outside the garden. Where infestations occurred, nymphs and natural enemies were counted and recorded from all the leaves of the selected plants. Where the weed could not be identified, a weed plant was picked and taken to the Makerere University Herbarium for identification. The data on weeds were summed together for both within garden and outside-the-garden infestation. Data were also collected on relative humidity, temperature, and rainfall in the different locations and were used to examine the relationships between *B. tabaci* and its natural enemies with weather parameters.

Data analysis

The data on numbers of nymphs and predators on cassava were subjected to square root transformation, while that on percent parasitism and relative abundance were transformed using arcsine square root and analysed using General treatment structure of Genstat Release 3.2 (Lawes Agricultural Trust – IACR-Rothamsted). Data were

transformed when the assumptions of normality and homogeneity of variance were not fulfilled (Mead *et al.*, 2003). The treatment terms were sub-county and sampling dates, while the dependent variables were numbers of nymphs and predators, relative abundance of parasitoids and percent parasitism. Crop age and numbers of nymphs were used as covariates. Crop age was used as a covariate in the analysis of nymph numbers, whilst in the analysis of numbers of predators, relative abundance of parasitoids and percent parasitism, both crop age and numbers of nymphs were used as covariates. Where the covariates were significant, means were adjusted for covariates, whereas in cases where the covariate was not significant, unadjusted means are presented. Relative abundance was calculated for each parasitoid species based on the differentiated parasitoids, and expressed as a percentage of the total number of parasitoids of each species to the total number of differentiated parasitoids. Parasitism was estimated by expressing the number of parasitized nymphs as a proportion of total nymphs, which was calculated as a sum of parasitized and unparasitized nymphs. This method of estimating parasitism was used because it allows for a bigger number of samples to be handled within a short time, and it was hypothesized that by sampling fourth instars, most of the parasitized nymphs would have shown signs of parasitism. All statistical interpretations are based on the transformed values of the different parameters. Data on whitefly and natural enemy counts on component crops and weeds are presented as qualitative data because of the rare occurrences of the insects on both weeds, and crops intercropped with cassava.

Results

The incidence of *B. tabaci* on cassava

The numbers of nymphs of *B. tabaci* ranged from 0–1581, 0-3375, and 0–693 per 18 leaflets at Bulisa, Busukuma and Lyantonde, respectively. The mean numbers of nymphs varied significantly ($p<0.001$) between the locations; the highest numbers occurred at Busukuma (187.9 ± 16.4) nymphs per 18 leaflets), followed by Bulisa (106.1 ± 6.7) and Lyantonde (47.4 ± 3.0).

Significant ($p<0.001$) variations occurred in the numbers of *B. tabaci* nymphs between sampling dates at all the locations (Fig. 1); At Bulisa, nymph numbers increased from November 2003 and peaked in December 2004 and gradually declined thereafter. At Busukuma, there were two peaks of nymph numbers; in March and June 2004 then they gradually reduced up to the lowest value in November 2004. At

Lyantonde, there was a gradual increase in numbers of nymphs from December 2003 to a peak in April 2004 and another peak in July 2004 (Fig. 1).

The numbers of nymphs were highest at three, four-five and five months after planting at Bulisa, Busukuma and Lyantonde, respectively (Fig. 2). Numbers of nymphs reduced with crop age at Bulisa ($P<0.001$; coeff. = -1.99; SE = 0.2), whilst there was no relationship between the two at Busukuma and Lyantonde.

Abundance of parasitoids, and parasitism of *B. tabaci*

Eretmocerus mundus, *E. sophia* and an undescribed *Encarsia* sp. (hereafter referred to as *Encarsia*?) were recovered from *B. tabaci* on cassava (Fig. 3). *Eretmocerus mundus* and *E. sophia* were present in all the locations throughout the year, while *Encarsia*? was rare at all locations. *Eretmocerus mundus* was the most abundant parasitoid species at all the locations, followed by *E. sophia* and *Encarsia*? and lastly *Encarsia*?. *Eretmocerus mundus* represented 68.2 ± 1.4 %, 61.8 ± 1.3 % and 72 ± 1.6 % of the total parasitoids at Bulisa, Busukuma and Lyantonde, respectively. The abundance values for *E. sophia* were 29.5 ± 1.4 %, 32.8 ± 1.2 % and 27.8 ± 1.6 % at Bulisa, Busukuma and Lyantonde, respectively. *Encarsia*? accounted for 2.4 ± 0.4 %, 5.4 ± 0.5 % and 0.2 ± 0.1 % of the parasitoids at Bulisa, Busukuma and Lyantonde, respectively. Overall, *E. mundus* was more abundant than *E. sophia*, which was in turn more abundant than *Encarsia*? on most sampling dates at all locations (Fig. 3). There was an inverse relationship between the abundance of *E. mundus* and *E. sophia* in all locations.

The relationship between the abundance of parasitoids with crop phenology was not consistent across locations (Fig. 4). Whereas there was no significant relationship between abundance of *E. mundus* and crop age at both Bulisa and Lyantonde, a positive linear relationship was observed between its abundance and crop age at Busukuma ($P = 0.005$; coeff. = 3.3; SE = 1.16).

The abundance of *E. mundus* increased with increase in nymph numbers at Bulisa ($P<0.001$; coeff. = 0.83; SE = 0.2), while the converse was observed at Lyantonde ($P = 0.018$; coeff. = -0.53; SE = 0.2) and there was no relationship between the abundance of *E. mundus* and numbers of nymphs at Busukuma. The relationship between the abundance of *E. sophia* and crop age was significant only at Busukuma, where the abundance of *E. sophia* decreased with crop age ($P = 0.005$; coeff. = 3.3; SE = 1.2).

Parasitism ranged from 0 - 100 % at all the locations, and varied significantly ($p<0.001$) between locations; the highest mean parasitism was observed at Busukuma (41.7 ± 1.2 %), followed by Bulisa (37.2 ± 1.1 %) and lowest at Lyantonde (32.2 ± 1.3 %). There were significant variations in parasitism between sampling dates at all locations (Fig. 5). Peak parasitism occurred in March 2004 at all the locations, and again in June 2004 and July 2004 at Lyantonde and Busukuma, respectively (Fig. 5). Covariate analysis did not reveal any significant relationship between percent parasitism and crop age at Bulisa and Lyantonde. At Busukuma, percent parasitism increased with increase in crop age ($P = 0.011$; coeff. = 2.9; SE = 1.14) (Fig. 6). A negative relationship was found between percent parasitism and numbers of nymphs at Bulisa ($P < 0.001$; coeff. = -0.67; SE = 0.143), but none at both Busukuma and Lyantonde.

Predators of *B. tabaci* on cassava

The predators recorded in cassava fields included: beetles (*Serangium* sp.), dusty and green lacewing larvae, predatory bugs (*Orius* sp.), spiders, syrphids and sugar ants (Table 2). Ants, spiders and *Serangium* sp. were by far the most common predators found in cassava fields, whilst lacewings, predatory bugs and syrphids were rarely recorded.

Ants were observed to carry whitefly adults and nymphs. The numbers of ants per plant ranged between 0-29, 0-73 and 0-15 at Bulisa, Busukuma and Lyantonde, respectively, and varied significantly ($P<0.001$) between locations. More ants were recorded at Busukuma (2.3 ± 0.3 per plant), followed by Bulisa (0.6 ± 0.1 per plant) and least at Lyantonde (0.2 ± 0.1 per plant). The numbers of ants varied significantly ($P <0.001$) between sampling dates at all the locations (Fig. 7), but reduced significantly with crop age at Bulisa ($P = 0.05$; coeff. = -0.025; SE = 0.023) and not in the other locations.

The numbers of ants was positively related to the numbers of *B. tabaci* nymphs at Bulisa ($P = 0.04$; coeff. = 0.009; SE = 0.004), whilst no significant relationship existed between the numbers of ants and numbers of nymphs at the other two sites.

Both adults and larvae of *Serangium* sp. fed on *B. tabaci* nymphs. The numbers of *Serangium* sp. observed at the locations ranged between 0-20 per plant, 0-11 and 0-4 at Bulisa, Busukuma and Lyantonde, respectively, and averaged 0.4 ± 0.1, 0.09 ± 0.03 and 0.01 ± 0.01 per plant in the respective locations. The numbers of *Serangium* sp.

varied significantly between sampling dates at Bulisa (P <0.001) and Busukuma (P = 0.021) and not at Lyantonde (P > 0.05) (Fig. 3.7).

There was a negative relationship between the numbers of predatory beetles and crop age at Bulisa (P = 0.011; coeff. = -0.006; SE = 0.02), a positive one at Busukuma (P = 0.021; coeff. = 0.018; SE = 0.001) and none at Lyantonde (P > 0.05). A covariate analysis on the relationship between the numbers of predatory beetles and numbers of nymphs revealed positive relationship at both Bulisa (P <0.001; coeff. = 0.017; SE = 0.003) and Busukuma (P <0.001; coeff. = 0.004; SE = 0.001) and no relationship at Lyantonde (P > 0.05).

Spiders observed were either web spinners or hunters belonging to twelve species in six families (Table 2); *B. tabaci* was found trapped spider webs, while in a few cases hunters were observed carrying *B. tabaci* adults and nymphs in their mouths. The numbers of spiders per plant ranged between 0-3, 0-16 and 0-7 at Bulisa, Busukuma and Lyantonde, respectively. They averaged 0.3 spiders/plant at each location (p= 0.220) and their numbers varied significantly (P = 0.001) between sampling dates only in Bulisa and Lyantonde but not at Busukuma (Fig. 6). Further, the analysis did not reveal any significant relationship between the numbers of spiders with crop age or numbers of nymphs at all the locations (Fig. 7).

<u>The incidence of whitefly and their natural enemies on crops grown in association with cassava</u>

Of the crops grown in association with cassava, adult whiteflies were found on cowpea and cotton at Bulisa, beans and sweetpotato at Busukuma and Lyantonde (Table 3). Healthy and parasitized nymphs of whitefly were only recorded on sweet potato at Lyantonde. Ants were recorded on cowpea at Bulisa, whilst *Serangium* sp. was recorded on cotton and coffee at Bulisa and Busukuma, respectively.

<u>The incidence of whiteflies and their natural enemies on weeds found in and around cassava gardens at the different sites</u>

Ageratum sp., *Bidens* sp., *Commelina* sp., *Euphorbia* sp., *Lantana* sp., and *Melhania* sp. growing in and around cassava plots were found to be infested with whitefly adults (Table 3, 4). The whitefly biotypes were not examined except for the one on *Melhania* sp., which belonged to the okra biotype. The parasitoid, *E. mundus* was reared from whitefly on *Commelina* sp. and *Melhania* sp. at Bulisa, from *Bidens* sp., *Commelina*

sp. and *Euphorbia* sp. at Busukuma, and one pupa was recorded on *Bidens* sp. at Lyantonde. *Encarsia sophia* was reared from *Melhania* sp. at Bulisa.

Relationship between abundance of nymphs and parasitoid numbers, and percent parasitism with weather parameters

When the numbers of nymphs, abundance of parasitoids and parasitism (%) were regressed against average temperature (°C), relative humidity (%) and rainfall (mm), the abundance of *E. mundus* related positively with relative humidity at Bulisa (a= -156.6; b= 3.1; P= 0.023; R= 61), while the abundance of *E. sophia* related negatively with temperature and relative humidity at the same location (temperature: a= 227; b= -72; P= 0.039; R= 46.1; relative humidity: (a= 271.4; b= -3.2; P= 0.017; R = 65.5). The abundance of *Encarsia*? was however, positively related with temperature. There was no relationship between percent parasitism with temperature, relative humidity and rainfall at Bulisa and Lyantonde. At Busukuma, however, parasitism was negatively related with temperature (a= 422; b= -16.7; P= 0.04; R= 29.4).

Discussion

This study has demonstrated that *E. mundus* was more abundant, followed by *E. sophia*, and *Encarsia*? was the lowest in number. There were significant variations in numbers of *B. tabaci* and natural enemies between locations, season and crop age. The most common predators found in cassava gardens were ants, *Serangium* sp. and spiders. No cassava component crops or weeds harboured high populations of whitefly and their natural enemies. The numbers of *E. mundus* were positively related to temperature at Bulisa, whilst rainfall related negatively with the numbers of *E. sophia* at Lyantonde.

The three parasitoid species recovered from *B. tabaci* had previously been reported from Uganda (Otim, 2002; Otim *et al*., 2005). *Encarsia* ?*mineoi* which was not found is rare and was only found once in the previous survey (Otim *et al*., 2005). *Eretmocerus mundus* is common to the Mediterranean basin (Gerling *et al*., 2001) and Iran (Ghahhari and Hatami, 2000), while *E. sophia* has been found in numerous countries to be a dominant parasitoid of *B. tabaci* (Kajita *et al*., 1992; Kapadia and Puri, 1990; McAuslane *et al*., 1993; Stansly *et al*., 1997; Otim *et al*., 2005). Contrary to the previous study (Otim *et al*., 2005); *E. mundus* was the dominant parasitoid species in all locations and on most sampling dates. This probably arises

from the high fecundity and favourable environmental factors. However, the inverse relationship between the abundance of *E. mundus* and *E. sophia* may be attributable to some form on interspecific competition.

The inventory of predators observed during this study differs somewhat from other reports on cassava. Whereas the predators observed in this study were ants, spiders, predatory beetles, lacewings, predatory bugs and syrphid larvae, studies in other African countries revealed other predators. For instance, *Scymnus* sp. and *Semidalis* sp. were reported on cassava in Malawi, *Scolothrips* sp., coniopterygid and cecidomyiid larvae in Kenya, and *Euseius* sp., *Stethorus jejunus*, *Holoborus pallidicornis*, and *Scolothrips latipennis* in Ivory Coast (Robertson, 1985; Nyirenda *et al.* 1993; Fishpool and Burban, 1994). However, when compared to the list of predators reviewed by Gerling *et al.* (2001), most of the families of spiders recorded in this study were reported, except the families of Miturgidae, Nesticidae and Oxyopidae.

Variations in whitefly numbers have been attributed to seasonal fluctuations in parasitoid numbers, relative humidity, temperature, host abundance and host plant factors (Hoelmer, 1995, 1996), clearly demonstrating that many factors are important in determining the population dynamics of whitefly.

The high numbers of *B. tabaci* at Busukuma may be attributable to the continuous cultivation of cassava throughout the year, coupled with presence of improved varieties (TME 14 and TME 204) that support heavy populations of *B. tabaci*. At Bulisa, only one cassava variety (Nase 3), which supports a relatively low *B. tabaci* population is widely grown. Unlike at Busukuma and Bulisa where cassava growing is continuous throughout the year, cassava growing in Lyantonde is seasonal, and local varieties that do not support heavy *B. tabaci* populations predominate. This may explain the low *B. tabaci* whitefly population there.

The high numbers of *B. tabaci* nymphs between three-five months after planting might be attributable to a vigorous growth of cassava at this stage providing young, protein-rich leaves suitable for feeding and oviposition; similar results were noted by other workers (Legg, 1994; Sserubombwe, 1998; Egabu, 2002). Reductions following peak *B. tabaci* populations, mainly beyond five month after planting are attributed to the ageing of cassava when most assimilates are diverted for tuberous root formation than canopy development (IITA, 1990).

The decrease in numbers of ants and *Serangium* sp. with crop phenology at Bulisa followed a reduction in numbers of *B. tabaci* nymphs, whilst the increase in numbers of predatory beetles with crop phenology at Busukuma followed an increase in numbers of *B. tabaci* nymphs. The implication therefore is that these two predators respond positively to the abundance of their hosts. However, the numbers of these predators were generally low, averaging less than one per plant on most sampling dates and different crop phonologies, except for ants at Busukuma (Figs. 7 & 8). These low numbers may demonstrate the limited role and the difficulty in assessing the role of predators in determining field populations of *B. tabaci*. Since predators are usually mobile and may have alternative food sources, it is difficult to relate them directly to the numbers of *B. tabaci* available. However, Naranjo (2001) discussed different methods that can be used to assess the role of predators in suppressing *B. tabaci* populations, which include among others, immunological methods and life table construction. During the current study, information was gathered on the predators but not their impact, but cohort-based life table studies by Asiimwe *et al.* (2006) revealed parasitism in fourth instars to be key mortality factor on the nymphs when compared with predation. This may suggest that *B. tabaci* is a less preferred host of the predators.

Weather also affects *B. tabaci*, with temperature and relative humidity being the most important factors influencing whitefly populations in cotton fields in Israel (Horowitz *et al.*, 1984). On cassava, higher temperatures of about 30- 33 °C were reported to encourage faster development of whiteflies, but with a marked reduction beyond 33 °C (Storey, 1936; Leuschner, 1978; Dengel, 1981; Gold, 1994). Similarly, Kapadia and Puri (1990) and Sharaf and Batta (1985 b) found that the development duration of *E. mundus* and *E. sophia* was shorter at higher temperatures (25 & 28.9 °C) than at lower temperatures (14 & 19 °C), implying more generations per unit time at higher temperatures. During the current study, there was no relationship between the abundance of *E. mundus* and temperature, abundance was positively related with relative humidity at Bulisa, suggesting that humidity affected the abundance of *E. mundus*.

Although Golding (1936) reported reduced populations of *B. tabaci* after heavy rain showers, Leuschner (1978) and Dengel (1981) reported high populations during the rainy season, while Legg (1994) did not find any relationship between *B. tabaci* populations and rainfall. The observation of Golding (1936) may be attributed to the

direct mortality of *B. tabaci* when it is raining. Contrastingly, rains also increase the growth rate of plants, thereby increasing the amount of vegetative material that favour *B. tabaci* colonization. This may lead to population build up during the rainy season as observed by Leuschner (1978) and Dengel (1981). This makes assessment of the overall effect of rain difficult. This study however found no relationship between parasitism and the abundance of parasitoids with rainfall.

The positive relationship between percent parasitism and crop age at Bulisa may have been due to a gradual build up of parasitism as the plants grows older. This is consistent with the findings of Otim *et al.* (2006) and attributable to the fact that *B. tabaci* and its parasitoids migrate from neighbouring fields and build higher populations with time. The observed decrease in percent parasitism with increase in nymph numbers is consistent with previous findings (Gerling *et al.*, 1980; Gerling, 1996; Otim *et al.*, 2005, 2006); it indicates negative density dependence and is the main cause for the parasitoids' inadequacy as controlling factors at the earlier stages of cassava growth allowing for the build-up of high *B. tabaci* numbers. Nevertheless, the high parasitism levels at low host densities would imply that parasitoids could complement other control measures that reduce *B. tabaci* populations, such as the use of *B. tabaci* resistant varieties.

The present study further revealed that neither crops nor weeds growing in association with cassava support high populations of whitefly. Moreover, while adult whiteflies were found on some crops grown together with cassava (Table 3.3), nymphs and parasitoids were only recorded on sweetpotato, a factor that might be due to the adult whiteflies' mobility rather than their readiness to develop on the examined plant species. *Bemisia tabaci* growing on sweetpotato belongs to the sweetpotato biotype, which does not reproduce and/or survive on cassava (Legg, 1995; 1996). The *E. mundus* found on sweetpotato may move and parasitize the *B. tabaci* growing on cassava and vice versa. Looking from the perspective that cassava is heavily attacked, the numbers of parasitoids recorded on sweet potato may not be sufficient to impact on the whiteflies growing on cassava. Nevertheless, intercrops may play other roles in determining the population dynamics of *B. tabaci* such as interfering with the host seeking behaviour of *B. tabaci* and its natural enemies, and provide nectar sources for the natural enemies. Since there was a high variability in the plot sizes, density and spacing of crops and date of planting of component crops, it was not possible to relate *B. tabaci* and its natural enemy populations to the presence of a particular crop. There

have been inconsistent results on the influence of intercrops on *B. tabaci* and CMD (Fargette & Fauquet, 1988; Ekpe & Chinaka, 2000). For instance, Fargette and Fauquet (1988) reported inconsistent results between the populations of the vector and disease incidence, while Ekpe and Chinaka (2000) noted similar severity levels between a susceptible cassava grown as an intercrop and sole. Other authors have reported low *B. tabaci* populations and CMD incidence in cassava intercropped with cowpea, maize and groundnuts than in sole crop (Ahohuendo & Sarkar, 1995; Fondong *et al.*, 2002; Oneka *et al.*, 2002) and higher yields in the intercrop than the sole crop (Oneka *et al.*, 2002). Similarly, the numbers of *Aleurotrachelus socialis* Bondar and *Trialeurodes variabilis* Quaintance and their egg density per leaf decreased in intercropped cassava than in sole crop (Gold, 1994). These results show the complexity in assessing and making generalisations about the role of intercrops in determining *B. tabaci* populations and disease severity.

As said, also the weed species found in and around sampled cassava fields did not support high numbers of whitefly and their natural enemies (Table 3.4). Sseruwagi *et al.* (2005) recorded the Ug_1 strain of the cassava *B. tabaci* biotype from five non-cassava plant species, all from the Euphorbiaceae (*Manihot graziovii*, *Jatropha gossypiella*, *Euphorbia heterophylla*, *Aspilia africana* and *Abelmoschus esculentus*), suggesting that Ug_1 is not restricted to cassava, and is likely to have alternate hosts when cassava is not available. This also poses a threat of acquisition and transmission of different whitefly transmitted viruses.

In conclusion, this study has demonstrated that *E. mundus* and *E. sophia* are the most abundant parasitoid species, where as ants, *Serangium* sp. and spiders are the most common predators. The study has also revealed that no crop or weed plant plays a major role as an alternative host of *B. tabaci* in the locations surveyed. All the observations suggest that the main infestation source of cassava is whitefly movement from other cassava fields.

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1 Table 1. The sampling dates at the different locations

	Location		
Visits	**Bulisa**	**Busukuma**	**Lyantonde**
1	25/11/2003	2/12/2003	8/12/2003
2	28/12/2003	6/1/2004	10/1/2004
3	24/1/2004	7/2/2004	13/2/2004
4	3/2/2004	5/3/2004	16/3/2004
5	27/3/2004	30/3/2004	16/4/2004
6	27/4/2004	1/5/2004	17/5/2004
7	4/6/2004	7/6/2004	16/6/2004
8	28/6/2004	30/6/2004	14/7/2004
9	28/7/2004	30/7/200 4	18/8/2004
10	11/9/2004	14/9/2004	30/9/2004
11	5/10/2004	7/10/2004	26/10/2004
12	17/11/2004	23/11/2004	10/12/2004

2

1 Table 2. Predators of *B. tabaci* sampled from cassava fields at the different locations

2 (November 2003 to December 2004)

3

Order	Family	Genus +Species	Group
Insect orders			
Hymenoptera	Formicidae		Ants
Coleoptera	Coccinnelidae	*Serangium* sp.	Predatory beetles
Hemiptera	Anthocoridae	*Orius* sp.	Predatory bugs
Diptera	Syrphidae		Syrphid larvae
Neuroptera	Chrysopidae	*Chrysoperla* sp.	Greenlace bug
Spiders			
Araneae	Oxyopidae	*Oxypes* sp.	Wanderer
		Peucetia sp.	Wanderer
	Thomisidae	*Oxytate argenteoculata*	Wanderer
		Misumenops rubrodecoratus	Wanderer
	Miturgidae	*Cheiracanthium* sp.	Wanderer
	Nestidae	*Nesticella* spp.	Web dweller
	Theriidae	*Tidarren* sp.	Web dweller
		Chrysso pulcherrima	Web dweller
		Theridion sp.	Web dweller
	Araneidae	*Neoscona* sp.	Web dweller
		Araneus apricus	Web dweller
	Linyphiidae	*Ostearius melanopygius*	Web dweller

4

1 Table 3. The numbers of adults and nymphs of whitefly and their natural
2 enemies on crops found in cassava gardens at the different sites
3 summed over all plants and sampling dates

	Total No. plants sampled	No. adult whitefly	No. nymphs	No. *E. mundus* pupae	Predators
Bulisa					
Cotton	20	12	0	0	2 (SE)
Cowpea	60	3	0	0	6 (A)
Busukuma					
Beans	110	56	0	0	0
Coffee	60	0	0	0	6 (SE)
Sweet potato	10	1	0	0	0
Lyantonde					
Beans	80	15	0	0	0
Sweet potato	20	8	7	15	0

4 A = ants, and SE = *Serangium* sp.
5

1 Table 4. Total number of whitefly adults and nymphs and their natural enemies
2 on weeds found in and around cassava gardens at the different sites summed over all
3 plants and sampling dates

	Total No. of plants sampled	Adult whitefly	Nymphs	*E. mundus* pupae	*E. sophia*	Predators
Bulisa						
Commelina	620	16	0	2	0	3 (A)
Melhania sp. *	60	30		39	7	0
Bidens sp.	160	4	0	0	0	4 (SP)
Busukuma						
Ageratum sp.	280	9	0	0	0	0
Bidens sp.	520	35	0	1	0	0
Commelina sp.	400	11	0	2	0	2 (SP)
Euphorbia sp.	580	49	2	6	0	0
Lantana sp.	40	3	0	0	0	0
Lyantonde						
Bidens sp.	400	8	0	1	0	7 (SP)
Commelina sp.	320	5	0	0	0	0

4 * Whitefly and parasitoids were reared from infested leaves since leaves were entirely
5 covered with sooty mould. A = ants, and SP = spiders

Figure 1: Mean *B. tabaci* nymph numbers (± SE) on cassava at Bulisa (A), Busukuma (B) and Lyantonde (C) from November 2003 to December 2004

Figure 2: Mean *B. tabaci* nymph numbers (± SE) on cassava at Bulisa (—), Busukuma (■) and Lyantonde (▲) at different crop phenologies

Figure 3: Species composition and abundance of *B. tabaci* parasitoids on cassava (mean ± SE) at Bulisa (A), Busukuma (B) and Lyantonde (C) from November 2003 to December 2004

Figure 4: Species composition and abundance of *B. tabaci* parasitoids on cassava (mean ± SE) at Bulisa (A), Busukuma (B) and Lyantonde (C) at different crop phenologies

Figure 5: Mean percent parasitism (± SE) of *B. tabaci* on cassava at Bulisa (A), Busukuma (B) and Lyantonde (C) from November 2003 to December 2004

Figure 6: Mean percent parasitism (± SE) of *B. tabaci* on cassava at Bulisa (—), Busukuma (■) and Lyantonde (▲) at different crop phonologies

Figure 7: Mean numbers (SE) of ants, *Serangium* sp. and spiders at Bulisa (A), Busukuma (B) and Lyantonde (C) in cassava between November 2003 and December 2004

Figure 8: Variations in mean numbers (± SE) of ants, *Serangium* sp. and spiders at Bulisa (A), Busukuma (B) and Lyantonde (C) in cassava at different crop phenologies

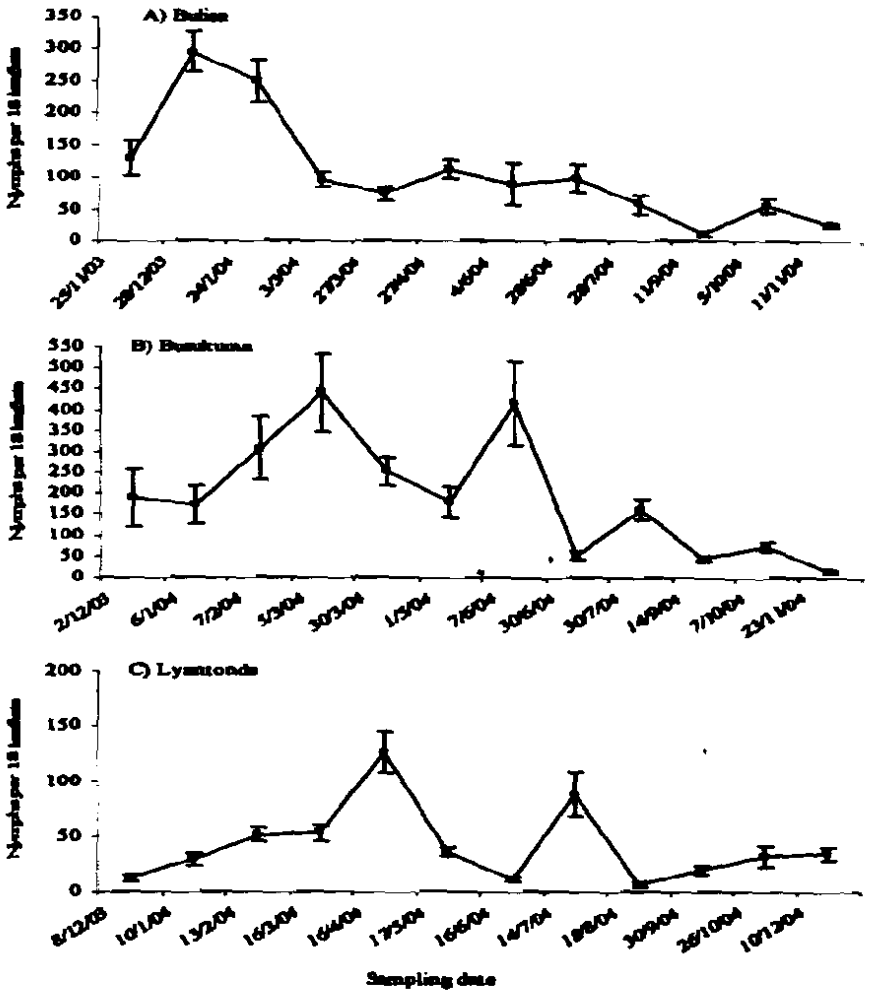
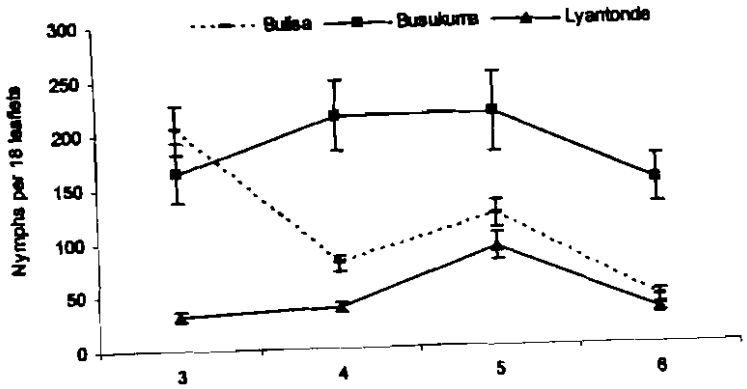

A) Bulion
B) Bunukuma
C) Lymtonda
Nymphs per 18 leaflets
Sampling date

Figure 1:

1


Bulisa
Busukuma
Lyantonde
Nymphs per 18 leaflets
300
250
200
150
100
50
0
3
4
5
6

2

3 Figure 2:

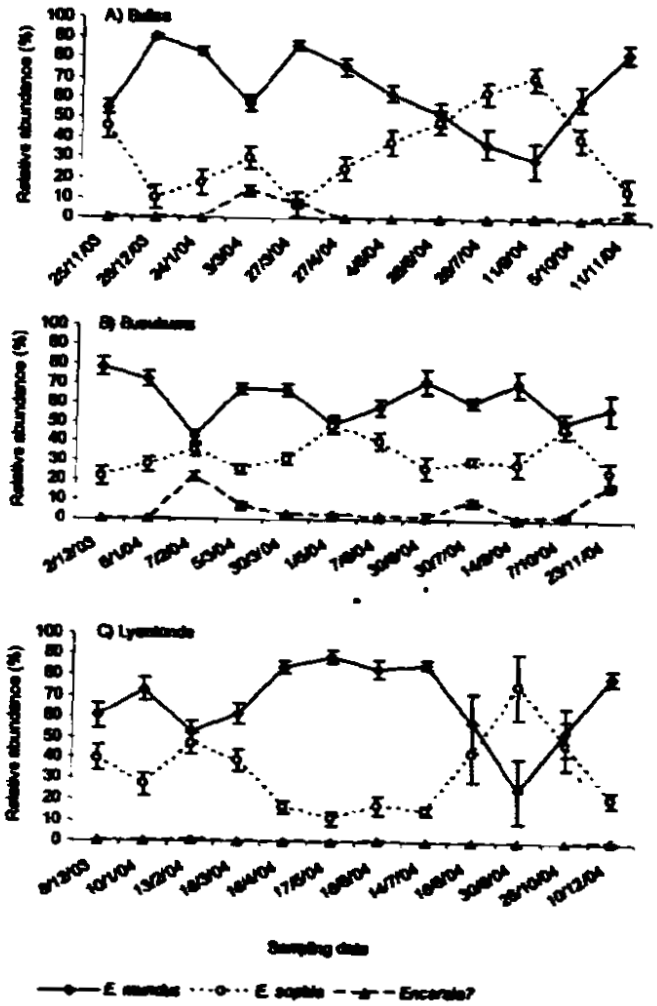

A) Bulbs
B) Rhizomes
C) Lymphoids
Relative abundance (%)
Sampling date
E. mandas
E. sapida
Encarsia?

Figure 3.

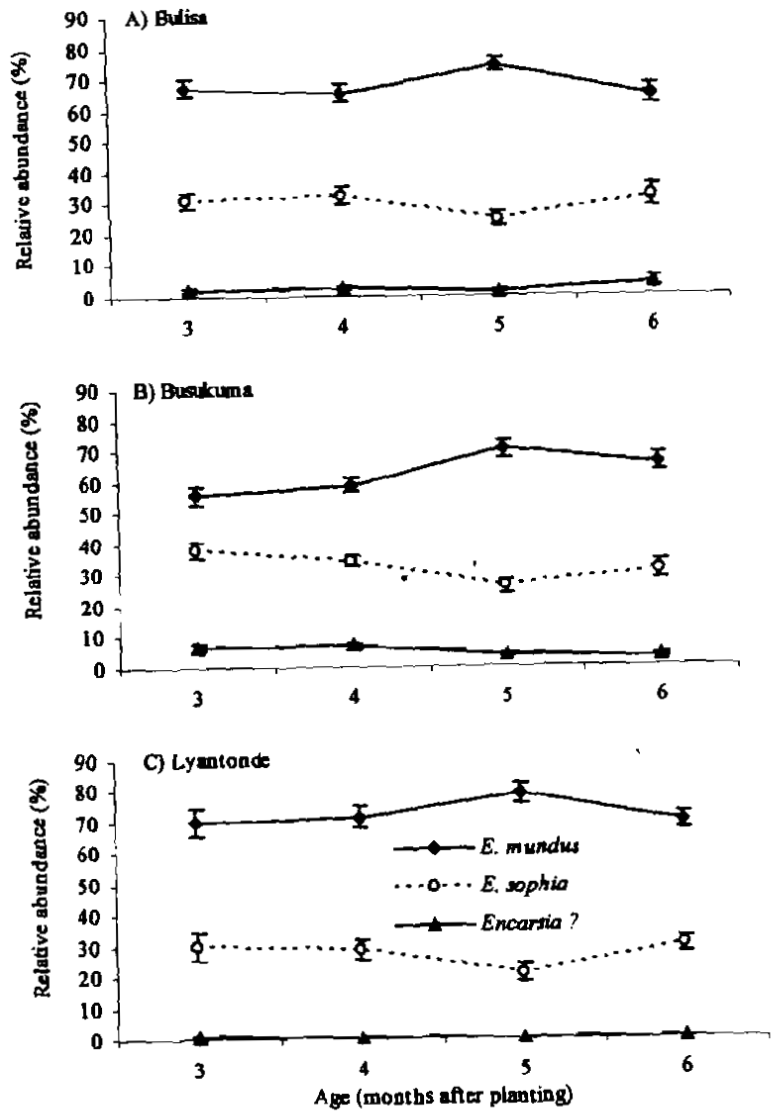

A) Bulisa
B) Busukuma
C) Lyantonde
Relative abundance (%)
90
80
70
60
50
40
30
20
10
0
3
4
5
6
E. mundus
E. sophia
Encarsia ?
Age (months after planting)

Figure 4.

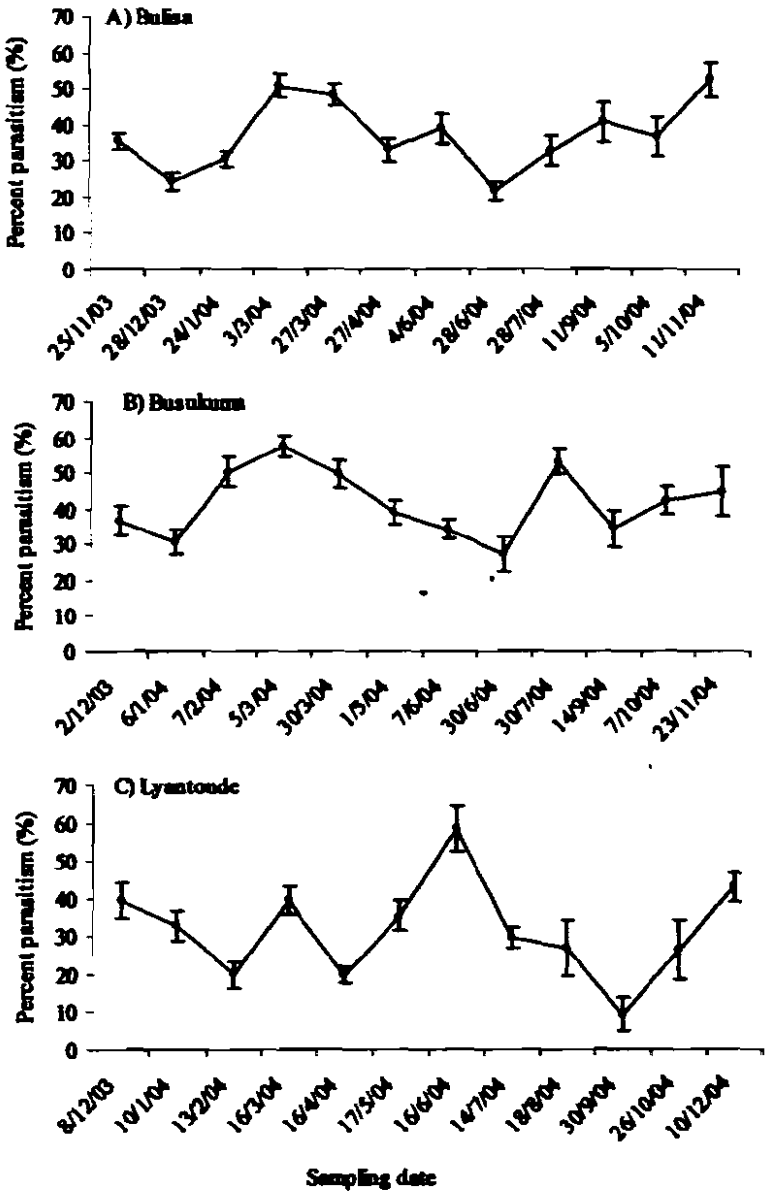

A) Bulisa
B) Busukuma
C) Lyantonde
Percent parasitism (%)
0
10
20
30
40
50
60
70
25/11/03
28/12/03
24/1/04
3/3/04
27/3/04
27/4/04
4/6/04
28/6/04
28/7/04
11/9/04
5/10/04
11/11/04
2/12/03
6/1/04
7/2/04
5/3/04
30/3/04
1/5/04
7/6/04
30/6/04
30/7/04
14/9/04
7/10/04
23/11/04
8/12/03
10/1/04
13/2/04
16/3/04
16/4/04
17/5/04
16/6/04
14/7/04
18/8/04
30/9/04
26/10/04
10/12/04
Sampling date

Figure 5.

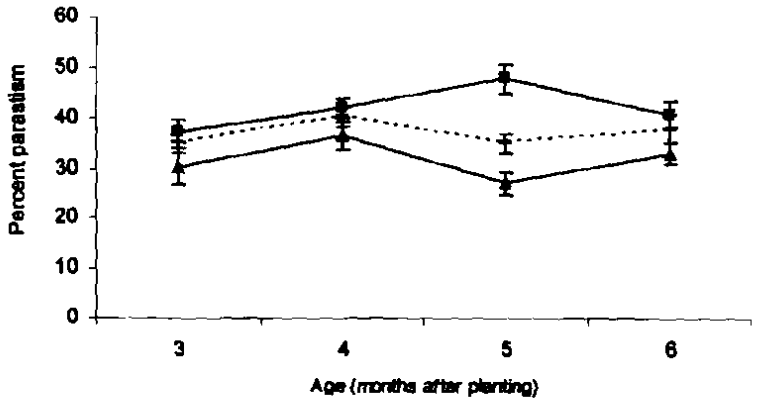

60
50
40
30
20
10
0
Percent parasitism
3
4
5
6
Age (months after planting)

Figure 6.

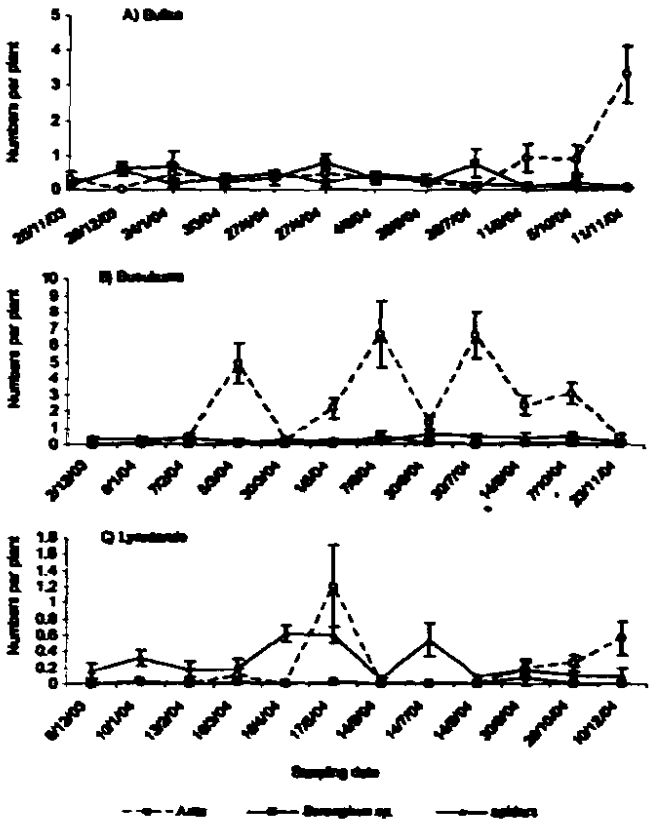


Figure 7. Mean numbers (SE) of ants, *Serangium* sp. and spiders at Bulisa (A), Busukuma (B) and Lyantonde (C) in cassava between November 2003 and December 2004

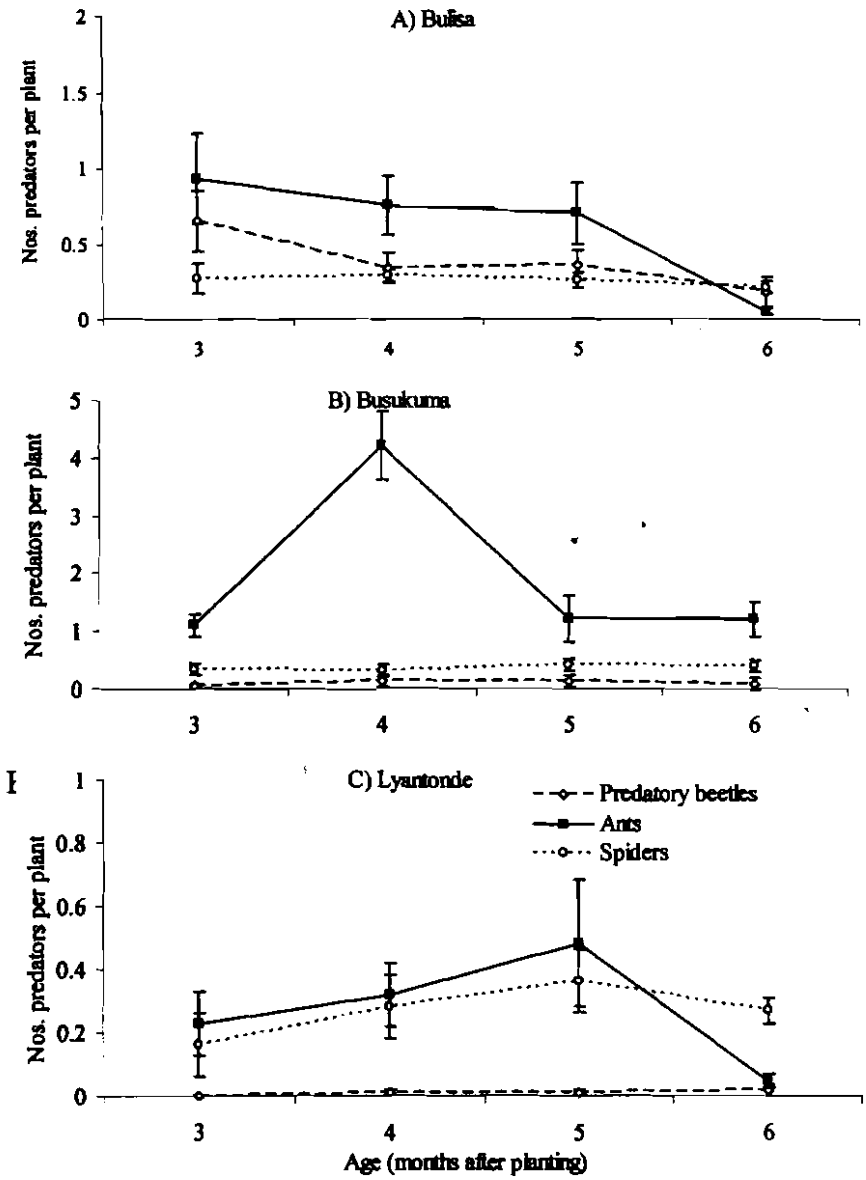

A) Bulisa
B) Busukuma
C) Lyantonde
Nos. predators per plant
Predatory beetles
Ants
Spiders
Age (months after planting)

Figure 8.

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Life-table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda

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Key words: Homoptera, Aleyrodidae, marginal mortality, irreplaceable mortality, key factor analysis, dislodgement, parasitism, predation, pest control

Abstract

A study was set up to determine the sources and rates of mortality of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) on field-grown cassava in Uganda. Using a cohort-based approach, daily direct observations were used to construct partial life tables for 12 generations of egg and nymph populations which were studied over a 1-year period. Mortality was categorized as dislodgement, predation, parasitism (for nymphs only), unknown death, and inviability (for eggs only). The highest mean rate of marginal mortality across all stages was attributed to parasitism, with dislodgement and predation following, respectively. Across all factors, the highest mean rate of marginal mortality was observed in the fourth instar followed by the eggs, first-, second-, and third-instars, respectively. Key factor analysis revealed that dislodgement was the major mortality factor contributing to generational mortality in eggs while for nymphs, parasitism in the fourth instar was the main driving force behind the observed generational mortality. Highest irreplaceable mortality in both the egg and nymph stages was attributed to dislodgement followed by parasitism and predation, and least was due to unknown death. Across stages, highest irreplaceable mortality rates were observed in the eggs and the fourth-instar nymphs. The other stages had relatively low rates of irreplaceable mortality. Rain-protection experiments revealed no significant differences in marginal mortality rates when compared to the open field situation.

Introduction

Bemisia tabaci (Gennadius) (Homoptera: Aleyrodidae) is a key pest of both field and greenhouse crops in many parts of the world. It causes both direct and indirect damage through feeding on plant sap. Direct feeding damage is shown by leaf chlorosis, a mottled appearance, reduction in plant vigour, general plant stunting, and induction of various phytotoxic disorders in several plants (Brown & Bird, 1992). Indirect damage is mainly through transmission of plant viruses, and to a lesser extent through encouraging development of sooty mould (Bedford et al., 1994; Schuster et al., 1996). Transmission of plant viruses in many tropical and subtropical countries represents the most economically important role of this pest (Basu, 1995). At least seven genera of whitefly-transmitted viruses have so far been described, of which the most economically important are the begomoviruses (Cohen, 1990; Brown & Bird, 1992). In Uganda, cassava is the main host of this pest, where it is the vector of cassava mosaic geminiviruses (CMGs) (Geminiviridae; genus: *Begomovirus*) that cause cassava mosaic disease (CMD). An epidemic of a unusually severe form of the disease spread throughout northern and central Uganda during the 1990s (Otim-Nape et al., 1997). More recently this epidemic has spread further into neighboring countries in East and Central Africa (Legg, 1999).

Several control options have been developed for CMD, the most important of which has been the use of CMD-resistant varieties. These varieties have been widely effective in controlling the CMD epidemic in Uganda (Otim-Nape et al., 1994; Thresh et al., 1994; Anon, 1999; Legg et al., 1999), but have recently been shown to support high *B. tabaci* populations (JP Legg, unpubl.). This poses a

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threat to the future effectiveness of CMD control because of the ability of these whiteflies to migrate and spread CMGs to susceptible varieties grown nearby and the increased likelihood of the appearance of more virulent virus strains through new virus–vector interactions.

Many of the biological characteristics of *B. tabaci* such as multivoltinism, high reproductive rate, broad host range, ability to migrate great distances, and vectoring of plant viruses have increased the difficulty of developing sustainable management options for this pest (Gerling & Mayer, 1996). Outbreaks of large *B. tabaci* populations have raised the need to obtain information as to their possible causes and cures. Despite major advances having been made in understanding the biology and behaviour of *B. tabaci* and in developing pest-management systems, there is a need to develop a better understanding of the factors affecting *B. tabaci* population dynamics on cassava. One approach is to develop age-specific/cohort-based life tables of *B. tabaci* under field conditions. These involve studying the population dynamics of a known number of individuals of the same developmental stage and using this information to determine the relevance and importance of the different mortality factors affecting the pest. Life tables have previously been used to study population dynamics of many insects, especially pests and their natural enemies (Carey, 1989; Cornell & Hawkins, 1995; Hawkins et al., 1999; Naranjo & Ellsworth, 2005). The current study therefore aims to use a comparable approach to determine the mortality factors affecting immature *B. tabaci* populations on CMD-resistant cassava in the field. This will provide essential background information for developing effective management options to control the current super-abundant *B. tabaci* populations on CMD-resistant varieties.

Materials and methods

Study site and plants used

The experiments were set up at Namulonge Agricultural and Animal Production Research Institute, Kampala, Uganda. The CMD-resistant variety, Nase 4 (Ssemakula et al., 1997), was planted in two fields in August and November 2003. Each field measured 14 × 9 m, and consisted of 150 plants planted in rows 1 m apart. The study was carried out over 6 months in each field, which represented half of the normal growing period of cassava.

Cohort establishment

Ten plants were randomly chosen from each field and monthly cohorts of both eggs and nymphs were established separately. Cohorts of eggs were selected from naturally established populations on the underside of the top-most expanded plant leaf. Eggs used were freshly laid and these were identified by their creamy white colour and location on the youngest leaves at the top of the plant. The leaves were turned over and a ×10 hand lens was used to locate the eggs. Using a nontoxic fine marker, a circle was drawn around each selected egg. All other eggs on the leaf were removed by gently rubbing them off the underside of the leaf with the edge of a soft paper. This ensured that every leaf chosen only remained with a specific number of eggs, all of which had been marked. A single leaf was used per plant and 10–20 eggs were marked depending on the populations on the plant at the time of marking. A small numbered tag was tied around the petiole of the leaf bearing the marked eggs.

Settled first-instar nymphs were identified and marked on separate leaves and plants. The leaves and nymphs were marked using the same procedure as above. Settled first-instar nymphs were identified by their translucent colour, small size, and characteristic ovoid shape. Marked nymphs were revisited after 1 h to ensure that they had settled. Any nymph that had crawled out of the circle was replaced by marking another one. A minimum of 30 nymphs were marked per plant for 10 plants, to give a total of 300 nymphs per cohort. The precise number per plant varied depending on the season and stage of growth of the plant but always approximated 30. All cohorts in each plot were established on the same day, and were marked between 09:00 and 11:00 hours. The cohorts were established monthly for 6 months, in each of the plots.

Determination of mortality factors

After cohorts had been established, each marked egg and nymph was observed daily using a ×10 hand lens. Each nymph was observed for 30 days unless it died or disappeared. This time period was sufficient to allow for both adult whitefly and parasitoid emergence. For the eggs, each was observed for a total of 15 days, substantially in excess of the previously reported average egg hatching period of 11 days for *B. tabaci* on cassava (Legg, 1995). Based on the establishment of separate cohorts of eggs and nymphs, mortality in the crawler stage is missed and thus is not accounted for in this study.

Each day, the instar and state of each nymph were recorded and categorized as alive, missing, dead, predated, or parasitized. A nymph was categorized as 'alive' based on its size, shape, and the symmetrical position of mycetomes; predation observed was mainly due to sucking, leaving the nymphs empty and translucent or, in some cases, partially empty, while parasitism was distinguished by the displacement of mycetomes or presence of parasitoid larvae in the third or pupae within the fourth-instar nymphs. A sample of 25 parasitized nymphs was collected and, basing on the methods

of Otim et al. (2005), were identified. Nymphs that were missing were assumed to have been displaced or eaten. The stage of missing was determined based on its appearance on the previous day. To maintain uniformity in determining causes of mortality, only three people carried out all field observations throughout the duration of the experiment.

The daily counts disclosed the continuous disappearance of marked individuals, either eggs or nymphs. The presence of these individuals had been accounted for on 1 day and they were absent without leaving a trace on the next. Naranjo & Ellsworth (2005) noted this phenomenon as 'dislodgement', a term subsequently adopted as a distinct mortality source in this experiment.

A parallel study conducted on the same fields to catalogue the predators of *B. tabaci* was done. All insects in the field were collected and fed on *B. tabaci* eggs and nymphs in the laboratory, and those found to be predators were sent to the US Department of Agriculture insect museum and identified (Asiimwe, 2006). A study to monitor the activity of these predators was carried out on the same fields. During this time, 24-h checks done at 3-h intervals over a 1-month period were carried out (Asiimwe, 2006).

Rain-protection experiments

Following the observation that heavy rains were able to dislodge whitefly nymphs from the leaves (Naranjo & Ellsworth, 2005), an experiment to determine the contribution of rain and direct wind was carried out on the same plots. Two plants were selected per field and protected from rain and wind by placing large umbrellas, covering the entire canopy of the plants. Two monthly cohorts, each consisting of 25 eggs and 50 nymphs, were marked on each plant. Each individual egg and nymph was followed for 15 and 30 days, respectively, or until it hatched, emerged or disappeared. During this time, the umbrellas were removed before each observation and replaced immediately after data collection.

Data analysis

Determination of mortality rates. The methods proposed by Buonaccorsi & Elkinton (1990), Elkinton et al. (1992), and Naranjo & Ellsworth (2005) were used to determine age-specific marginal rates of mortality for each factor based on observed (apparent) rates of mortality. The marginal rate estimates the level of mortality arising from a single factor assuming that factor was the only one operating at the time. A mortality factor may be obscured by another factor because these factors operate in a contemporaneous fashion with no obvious sequence of events. Dislodgement is the only factor for which the apparent rate of mortality is equal to the marginal rate because it can not be obscured by any other factor. The general equation for determining marginal rate of mortality was derived from Naranjo & Ellsworth (2005) and it is:

$$M_A = d_A/(1 - d_B),$$

where M_A is the marginal rate of mortality for factor A, d_A is the apparent (observed) rate of mortality from factor A while d_B is the sum of apparent mortalities from all other relevant contemporaneous factors. The apparent rates of mortality needed to estimate marginal rates of mortality for each factor within each stage are outlined in Table 1.

Irreplaceable mortality. Following the methods of Carey (1989) and Naranjo & Ellsworth (2005), irreplaceable mortality was calculated for each mortality factor and each developmental stage. Irreplaceable mortality is that portion of total generational mortality that would not occur if a given mortality factor was eliminated (Southwood, 1978; Naranjo & Ellsworth, 2005). The general equation for its determination is:

$$I_C = [D - (1 - M_A)(1 - M_B)], \text{ and}$$

$$D = [1 - (1 - M_A)(1 - M_B)(1 - M_C)],$$

where M_A is the marginal mortality for factor or stage A, B, or C. I_C is the irreplaceable mortality for factor or stage C and excludes marginal mortality of the factor or stage of interest (which in this case is C).

Key-factor analysis. Data were transformed to natural logarithms for key-factor analysis. The method of Varley &

Table 1 Matrix for determining marginal rates of mortality of *Bemisia tabaci* from apparent rates of relevant competing contemporaneous factors, based on the methods of Naranjo & Ellsworth (2005)

Marginal rate (M_A)	Apparent rate (d_A)	Other apparent rates (d_B)	Stage
Inviability	Inviability	Predation + dislodgement	Egg
Parasitism	Parasitism	Predation + dislodgement	Third and fourth instars
Predation	Predation	Dislodgement	Egg and all nymph stages
Unknown	Unknown	Predation + dislodgement	Egg and all nymph stages

Gradwell (1960) was used to calculate individual sources of mortality (k) and therefore total mortality (K) for each generation, where k = log number before mortality minus log number after mortality, and represents a proportion of the number dying due to the observed mortality factor. The method of Podoler & Rogers (1975) was then used to quantitatively evaluate key factors by regressing individual k-values on total K. This method identifies the key factor as that associated with the largest regression coefficient (slope). The method of Smith (1973) was then used to determine the relative importance of all factors by sequentially eliminating each key factor based on the regression coefficient until all but the final two factors were eliminated. Partial life tables were then constructed using the above values.

Results

Mortality experiments

Sources and levels of mortality. Partial life tables were developed for all 12 generations of eggs and nymphs separately with considerable variation in marginal mortality rates for each factor across all the generations ($P<0.001$, $n = 12$). The highest mean rates of marginal mortality across all stages were associated with parasitism (0.30 ± 0.127) (mean ± SE), followed by dislodgement (0.29 ± 0.039), predation (0.17 ± 0.020), inviable eggs (0.04 ± 0.009), and unknown death being the least (0.03 ± 0.009). Holm-Sidak pairwise comparisons (Hochberg & Tamhane, 1987) revealed significant differences between dislodgement and the other mortality factors affecting the egg population ($P<0.001$, $n = 3$) but no significant difference was observed between mortality due to predation and that due to inviability (Table 2).

Table 2 One-way analysis of variance of marginal rates of *Bemisia tabaci* egg and nymph mortalities across 12 generations on cassava in Uganda

Sources of mortality	Eggs (P values)	Nymphs (P values)
All sources	0.001	0.001
Dislodgement vs. inviable	0.001	–
Predation vs. inviable	0.121	–
Dislodgement vs. predation	0.001	0.133
Dislodgement vs. unknown death	–	0.001
Parasitism vs. unknown death	–	0.001
Predation vs. unknown death	–	0.001
Dislodgement vs. parasitism	–	0.444
Parasitism vs. predation	–	0.452

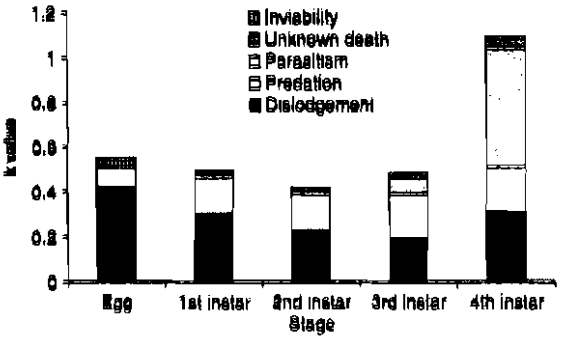

Figure 1 Mean levels of mortality factors within each immature *Bemisia tabaci* stage expressed as k values, across all generations on cassava in Uganda.

Pooled over all developmental stages, the highest marginal mortality rate was observed in the fourth instars (0.27 ± 0.101) followed by the eggs (0.18 ± 0.119), first (0.16 ± 0.079) and second instar (0.14 ± 0.062), with the least in the third instar (0.12 ± 0.045). Across generations, the highest levels of mortality were associated with parasitism, dislodgement, and unknown factors (Figure 1). There were no significant differences ($P = 0.340$, $n = 12$) in marginal rates of mortality across generations. Pooled over all instars, there was significant variation in the rates of marginal mortality acting on the nymph population ($P<0.001$, $n = 4$) and pairwise comparison (Holm-Sidak) revealed significant differences ($P<0.001$, $n = 4$) between all mortality factors except between predation and dislodgement, dislodgement and parasitism, and parasitism and predation (Table 2). Basing on the methods of Otim et al. (2005), parasitism was mainly due to *Encarsia sophia* (Girault and Dodd) and *Eretmocerus mundus* (Mercet), which are the most commonly occurring *B. tabaci* parasitoids in Uganda (Otim et al., 2005). A parallel study (Asiimwe, 2006) showed that predation was mainly due to *Serangium* spec. nov. (Coleoptera: Coccinellidae). Pooled over all instars, highest levels of dislodgement were observed on the first 3 days of the instar, with the numbers gradually rising until they peaked on the third day of a new instar (Figure 2).

Key-factor analysis. Using the methods of Smith (1973) and Podoler & Rogers (1975), multiple regressions were performed to determine the key factor for each stage. This was carried out for all mortality factors in each stage. Results revealed dislodgement as the major factor contributing to overall mortality in the egg populations ($P<0.001$, $R^2 = 0.66$). No other factor was found to significantly contribute to generational mortality in the egg populations. In the

Figure 2 Mean (± SE) rates of dislodgement of *Bemisia tabaci* instars pooled over all generations and all instars on cassava in Uganda.

nymph populations, parasitism in the fourth instar was most closely associated with overall generational mortality ($P<0.001$, $R^2 = 0.74$). On removal of this mortality factor, predation in the second instar was the most important factor ($P = 0.003$, $R^2 = 0.61$). No factor was found to significantly contribute to overall generational mortality in either the first or third instars (Table 3).

Across all developmental stages, highest rates of irreplaceable mortality were associated with dislodgement (0.13 ± 0.022), parasitism (0.07 ± 0.017), predation (0.06 ± 0.011), and unknown death (0.01 ± 0.003). No irreplaceable mortality was associated with egg inviability. Pooled over all developmental stages, the highest rates of irreplaceable mortality were associated with the egg stage (0.19 ± 0.025), followed by the fourth instars (0.17 ± 0.025), first instar (0.04 ± 0.008), third instar (0.04 ± 0.008), and second instar (0.03 ± 0.004) in declining order of importance.

Rain-protection experiments

There were no significant differences ($P = 0.25$, $n = 5$) in rates of marginal mortality between the rain protected and the open field experiments though generally lower rates were observed under the rain protection with dislodgement accounting for 0.17 (± 0.024), predation for 0.13 (± 0.031), and parasitism for 0.11 (± 0.005). Egg inviability and unknown death in nymphs were not observed in this experiment. The levels of natural enemy mortality varied between the experiments with predation occurring at a higher rate than parasitism in the rain-protected experiment, while the reverse was true in the open field experiment.

Discussion

The study showed that egg mortality was due to dislodgement, predation, and inviability. Sources of nymph mortality were dislodgement, predation, parasitism, and unknown death. This is consistent with findings in most of the previous studies, which also reveal natural enemies and weather-related factors as the major sources of mortality. The rates of mortality from this study are largely consistent with previous studies showing highest mortality due to dislodgement followed by natural enemies in both the egg and nymph populations. The main source of natural enemy induced mortality was parasitism in the nymphs, which accounted for the highest levels of mortality observed in the fourth instar. These two factors, dislodgement and parasitism, were also consistently associated with highest irreplaceable mortalities indicating their importance to overall immature *B. tabaci* mortality.

In previous studies, dislodgement has largely been associated with the combined effect of wind, rain, and chewing predators. Studies by Khalifa & El-Khidir (1964) in Sudan revealed a dramatic decline in *B. tabaci* populations

Table 3 Key-factor analysis of mortality factors affecting *Bemisia tabaci* populations over 12 generations on cassava in Uganda, based on the methods of Smith (1973) and Podoler & Rogers (1975)

	Step			
Stage/factor	1	2	3	4
Egg				
Predation	0.606			
Dislodgement	**0.879**			
Inviable	1.77			
First instar				
Predation	2.342			
Dislodgement	−0.466	−0.536	−0.326	
Unknown death	−9.892	1.250		
Second instar				
Predation	12.346			
Dislodgement	4.948	2.576		
Unknown death	8.362	2.465	2.208	
Third instar				
Predation	2.321	3.038	2.642	
Dislodgement	3.503			
Unknown death	0.982	1.036	1.776	0.643
Parasitism	2.277	4.303		
Fourth instar				
Predation	2.109			
Dislodgement	0.092	−0.591	−0.041	−1.741
Unknown death	0.369	1.635		
Parasitism	1.014			

Values represent the slope of individual k values on total K. At each subsequent step, the factor with the highest slope was eliminated to determine the relative contribution of each factor to generational mortality. The factor in bold was found to significantly ($P<0.001$, $n = 12$) contribute to total K and is therefore the key factor in the stage indicated.

following heavy rains. Similarly, Avidov & Harpaz (1969) revealed delays in outbreaks of *B. tabaci* populations in the Jordan valley following low relative humidities caused by Khamsims (hot and dry winds). Results from our manipulative experiments, in which the plants were protected from heavy rain, resulted in dislodgement rates that were not significantly different from those of unprotected plants. Considering the otherwise favourable climatic field conditions in our plots, and given that the experimental area does not experience high winds or large variations in relative humidity, we ruled out the effect of weather as a major whitefly dislodging factor. Whitefly dislodgement by chewing insects was also considered. Considering that *Serangium* spec. nov. kills its host by sucking out its contents and leaving the corpse on the leaf, only sugar ants were chewing predators capable of removing whitefly nymphs from the leaf. Observations of sugar ant activity on the leaf (Asiimwe, 2006) showed that they rarely fed on *B. tabaci* nymphs, preferring to feed on honeydew. This coupled with the fact that they were only occasionally seen in the fields, yet dislodgement was consistently high in most generations rules them out as a major cause of the observed dislodgement. Thus, it appears that dislodgement is related to life history and/or physiological factors. As shown in Figure 2, most of the dislodgement occurred on the third day of each instar, indicating a possible failure of the newly formed nymph to reinsert its stylets into the phloem of the leaf after moulting as shown by Walker & Perring (1994). In addition, studies by Jiang et al. (2001) on whitefly host resistance suggested that resistance is correlated with epidermal and/or mesophyll features that inhibit whiteflies from reaching phloem sieve elements explaining that the plant develops a defence mechanism whereby on reinsertion of the mouth parts, the nymph finds the plant sap unsuitable and thus starves and drops off after a few days. This could have been the case in our study.

Our study revealed that parasitism in the fourth instar is the most important factor driving nymphal mortality, while dislodgement is the key factor determining egg mortality. The relatively high irreplaceable mortality from parasitism, coupled with parasitism being the key mortality factor, points to its importance in reducing the nymph populations. This differs from previous similar studies on *B. tabaci* where Horowitz et al. (1984) found mortality due to disappearance in the first instar to be the key factor, and the most recent study by Naranjo & Ellsworth (2005), which found predation in the fourth instar as the major factor. These studies, however, were conducted using cotton as the host plant. The differences observed in this study could be due to the different microenvironment provided by cassava. A bushy year-round semiperennial such as cassava might provide a more favourable environment for the more specialist natural enemies such as parasitoids. The differences may have also occurred due to ecosystem variations between Uganda and Arizona, where their study was carried out. In Uganda, cassava is grown on small plots, which are never completely free of whiteflies and given that the cassava growth cycle is 1 year, the whiteflies are present all year round although the highest populations are observed at 3–4 months after planting. On harvesting the cassava, the whiteflies migrate to new cassava plants as there are no good alternative hosts for the cassava whitefly. This is in contrast with the Arizona system, where cotton has a spring and summer growth cycle (March–September), followed by a cool fall and winter during which no whitefly and parasitoid development occurs. On harvesting the cotton, the whiteflies move to other host plants where they develop until a new cotton crop is planted. Sucking predators, though observed in relatively high numbers, contributed much less to mortality compared to dislodgement and parasitism in both the eggs and nymphs. This could have been due to the fact that there was only one prominent sucking predator species, *Serangium* spec. nov. This contrasts with the cotton system described by Naranjo & Ellsworth (2005) where up to three species were found to contribute significantly to predation.

Results of this study serve to corroborate results of a similar study by Legg (1995), which found parasitism in the fourth instar and dislodgement in the eggs as the key factors. The study by Legg (1995) was carried out in a pre-CMD-epidemic situation while this study was carried out in the current post-epidemic situation. The similarity in results shows the absence of major differences in major factors causing *B. tabaci* mortality in pre- and post-epidemic situations.

The cohort-based system coupled with the daily observation of each individual in the cohort was able to give us comprehensive measurements on the rates of mortality affecting this pest. The combination of dislodgement and natural enemies causes most of the mortality observed on cassava in the field. Because parasitism is the key late stage source of mortality, enhancing the overall effect of parasitism is the most effective way of increasing overall generational mortality. Studies by Morris (1957) revealed that adding mortality to a factor that is already occurring at high levels will have a greater effect in reducing generational survival than adding it to a low level factor. In our case, addition of mortality to fourth instars and in particular to parasitism and dislodgement at this stage will bring about adequate control or even reduction of this pest on cassava. Therefore, efforts aimed at conserving and/or enhancing the levels of parasitism at this stage should be adopted for cassava. A good option in this case would be to

promote development of cassava varieties that support fewer *B. tabaci* numbers but encourage survival and oviposition of the native parasitoid species in Uganda and for this, future studies will need to concentrate on finding local land races or developing new varieties that discourage the pest while encouraging the parasitoids. An additional option for enhancing mortality could be the introduction, after careful climate matching and other suitability studies, of exotic parasitoids to complement the native species.

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Development duration, longevity and fertility of *Eretmocerus mundus* Mercet, and *Encarsia sophia* Girault and Dodd on *Bemisia tabaci* attacking cassava

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Abstract

Eretmocerus mundus Mercet and *Encarsia sophia* Girault and Dodd (all Hymenoptera: Aphelinidae) are the most abundant parasitoid species attacking *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) on cassava in Uganda. However, there are no studies of their life history parameters. This study therefore aimed at providing the first information on the development duration, longevity and fertility of these parasitoids on cassava, *Manihot esculenta* Crantz under laboratory conditions. The initial egg count on emergence averaged 35 ± 1.54 (mean ± SEM) and 3 ± 0.22 eggs per female for *E. mundus* and *E. sophia*, respectively. The egg-to-adult development duration of *E. mundus* was 19.6 ± 0.1 days and for *E. sophia* was 17.4 ± 0.1 days. There was no significant difference between the development duration of females (19.7 ± 0.1 days) and males (19.6 ± 0.1 days) of *E. mundus*, whilst the females of *E. sophia* developed ca. two days earlier than their male counterparts. Mean longevity when provided honey was 5.4 days for *E. mundus* and 6.6 days for *E. sophia*, whilst the corresponding values, when females were provided hosts, averaged 5.5 days and 11.3 days, respectively. Average progeny production averaged 25.6 offspring for *E. mundus* and 16.5 for *E. sophia*. The net reproductive rate of *E. mundus* was 13.1 as opposed to 15.5 for *E. sophia*. The intrinsic rate of increase was 0.1 for *E. mundus* and 0.105 for *E. sophia*. Mean generation times were 24.9 and 26.2 days for *E. mundus* and *E. sophia*, respectively. The results suggest that *E. mundus* is the most suitable candidate for high *B. tabaci* population control, whilst *E. sophia* may be effective under low *B. tabaci* populations. The data collected may be of use in future in case parasitoids are to be imported for control of *B. tabaci* on cassava.

Key words: Aleyrodidae, Aphelinidae, Generation time, Homoptera, Hymenoptera, Intrinsic rate of increase, *Manihot esculenta*, Net reproductive rate

Introduction

Whiteflies attack vegetable, ornamental, and agronomic crops throughout the world, and have caused enormous damage to many crops during the past century (Gerling, 1990; Gerling and Mayer, 1996). The whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) transmits cassava mosaic geminiviruses (CMGs) that cause cassava mosaic disease (CMD) (Bock and Woods, 1983), estimated to cause annual losses of between 12 and 18 million tonnes of cassava in Africa (Thresh *et al.*, 1997). Besides virus transmission, high whitefly populations are associated with mould on leaves, petioles and stems, reduction of leaf size, distortion of leaf shape, mottled chlorosis and general stunting (Legg *et al.*, 2003). In order to manage *B. tabaci* and the disease, the four cornerstones of integrated pest management (IPM) (host plant resistance, biological control, cultural control and chemical control) can be employed (Hilje *et al.*, 2001). To date, however, control of the disease has mainly relied on host plant resistance, without direct attempts to control the vector. Recent research in Uganda has focused on identifying the principal parasitoids of *B. tabaci* on cassava and understanding their population dynamics (Otim *et al.*, 2005; Otim *et al.*, 2006). The aphelinid parasitoids, *Eretmocerus mundus* Mercet and *Encarsia sophia* Girault and Dodd (Hymenoptera: Aphelinidae) were the most abundant parasitoids of *Bemisia tabaci* on cassava in Uganda with *E. sophia* being more abundant. In a follow up study however, (Otim, unpublished) has demonstrated that *E. mundus* was considerably more abundant than *E. sophia* in the same locations. Moreover, these two parasitoid species do not offer adequate control for their *B. tabaci* hosts (Otim, 2002). This study was therefore initiated to investigate the life history parameters of the two parasitoids, specifically the development duration, longevity and fertility of these species. This would help 1) to gain an understanding of the extent to which life history parameters influence abundance of

the parasitoids in the field, and 2) to compare the probabilities that other parasitoids, with different life histories might be used for improving biological control of *B. tabaci* in Uganda. Specifically, the study aimed at determining the development duration, longevity and fertility of *E. mundus* and *E. sophia* attacking *B. tabaci* on cassava.

Materials and methods

The experiments were conducted in a laboratory at Makerere University Agricultural Research Institute, Kabanyolo (MUARIK) (ca. 18 km North of Kampala at latitude of about 0° 28' N, longitude 32° 37' W). The area is about 1200 metres above sea level and receives a mean annual rainfall of 1270 mm in a bimodal pattern, with peaks in April/May in the first season and October/November in the second season. The maximum temperatures rarely exceed 30°C, while the minimum do not fall below 15°C.

Culture of *B. tabaci* and source of the parasitoids

The *B. tabaci* used in the study were obtained from colonies raised in a screenhouse at MUARIK. Cassava plants of the variety, Nase 4 were grown in 1-litre buckets containing sterilized soil. When the plants reached 4-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 Namulonge Agricultural and Animal Production Research Institute in 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 [22.8 ± 5.4 °C (range, 15.6 – 34 °C) and 64 ± 20.2 % r.h (range, 25.3-91.7 % r.h).

The parasitoids used for this study were reared from parasitized nymphs collected from the same fields as the *B. tabaci* nymphs. The parasitoids were collected a few days before observations and the parasitized nymphs were placed in emergence bottles.

Parasitoid life history

Development duration of *E. mundus* and *E. sophia*

20-30 females of *E. mundus* and *E. sophia* (0-24 hrs old) were caged on leaves of five plants bearing 100-200 third/fourth instar nymphs of *B. tabaci* each, in a screenhouse under fluctuating climatic conditions. The parasitoid females were removed after 24 hours, and the whitefly were held under similar conditions in the laboratory until the parasitoids pupated. The mean laboratory conditions were: Temperature 24.4 (°C) (range, 19.8-30.3); Relative humidity 65.5 % (range, 24.7-87.1). Upon parasitoid pupation, the leaves containing pupae were removed from the plant, put in petri-dishes and monitored daily for subsequent emergence. The numbers and sex of the emerging parasitoids were determined daily. Development duration was calculated from the period between parasitoid female introductions to adult emergence.

Longevity

Longevity was determined in the laboratory, under similar conditions to the above, for parasitoids maintained on two food sources, honey and *B. tabaci* nymphs. For the honey experiment, the inside of glass vials of size, 7.8 cm in length and 2.3 cm in diameter were streaked with honey and newly emerged (<24 hrs old) female adults of each parasitoid species were placed individually in each glass vial. Honey was renewed when necessary, the parasitoids' presence monitored daily until death and their longevity recorded. For longevity when exposed to nymphs, the survival duration of parasitoids used in the fertility experiment was used.

Initial egg load and fertility of *E. mundus* and *E. sophia*

In order to determine the initial egg load on emergence, 50 females of each of the two parasitoid species were dissected shortly after emergence (< 24 hours old) and the number of mature eggs counted.

The fertility of *E. mundus* and *E. sophia* was studied in the laboratory under similar conditions to that of the development duration. Parasitoid pupae of either species were collected from the field and kept under laboratory conditions in emergence bottles. A newly emerged female (0 – 24 hrs old) was confined with a conspecific male in a gelatine capsule for 24 hrs. Thereafter, each couple was transferred into an open glass tube (15 X 5 cm) with a fine insect screen on one side and open on the other end. Upon release of the parasitoids, an infested cassava leaflet was inserted into the tube, and the tube opening was closed using a round piece of foam. The couples were provided with new leaflets every day until the female died. If the male died within the first three days, another male was introduced into the glass tube. The leaves were thereafter monitored until parasitoid pupation. Upon pupation, leaflets containing pupae were picked and placed in petri dishes and the dishes monitored for adult parasitoid emergence. The number and sex of the parasitoids were determined daily until no more emergences took place. Parasitoid pupae that failed to produce adults were included in the calculation of total fertility. Based on the data on development duration, longevity, survival and fertility, age-specific fertility (m_x), intrinsic rates of increase (r_m), net reproductive rates (R_o) and generation time (T) were calculated. Age-specific fertility of the adult females (m_x) was expressed as the mean number of female progeny produced by a female of age x per day, whilst, intrinsic rates of increase, net reproductive rates, and generation time were calculated according to Andrewartha and Birch (1954) as follows.

$$R_0 = \sum l_x . m_x$$

$$T = \left(\sum x . l_x . m_x\right)\left(\sum l_x . m_x\right)^{-1}$$

$$r_m = (\ln R_0) . T^{-1}$$

Data analysis

Data on longevity and fertility were subjected to ANOVA, while development duration between species and sexes of species was analysed using T-statistics (Genstat Discovery Edition). In calculating progeny numbers, only ovipositing females were considered. Data on age specific fertility (mean number of female progeny per ovipositing female) were plotted against the age of females, and a regression analysis was performed to test the relationship between numbers of adult progeny and longevity for each parasitoid species.

Results

Development duration of *E. mundus* and *E. sophia*

There was a significant difference between the development duration of the two parasitoid species (t_{364} = 14.7; P<0.001) and between the females and males of *E. sophia* (t_{19} = -9.17; P<0.001), whilst there was no significant difference in development duration between the sexes of *E. mundus* (t_{254} = 10.54; P = 0.578) (Table 1). *Encarsia sophia* developed two days earlier than *Eretmocerus mundus*. The males of *E. sophia* developed two days later than their females from hosts exposed to females for only 24 hours. Peak numbers of *E. mundus* parasitoids emerging occurred at 19 d and 20 d for females and males respectively, while peak emergence of *E. sophia* occurred at 17 d for females and 19 d for males (Figure 1A & B).

Longevity of *E. mundus* and *E. sophia*

Mean longevity did not vary significantly ($p > 0.05$) between females of both species when provided with honey; longevity averaged 5.5 ± 0.45 days (mean ± SEM) (range, 2-13) for *E. mundus* and 6.6 ± 0.57 days (range, 1 – 11) for *E. sophia*. Longevity was however significantly ($P<0.001$) higher for *E. sophia* (11.3 ± 1.94 days; range, 1–25) than *E. mundus* (5.5 ± 0.57 days; range, 1 – 12) when hosts were provided.

Initial egg load and fertility of *E. mundus* and *E. sophia*

Upon emergence, the initial egg count differed significantly ($P<0.001$) between species; *E. mundus* had an average of 35 ± 1.54 (n = 50, range, 2-54) mature eggs per female, while *E. sophia* had an average of 3 ± 0.22 (n = 50, range, 0 – 7) eggs per female.

There were no significant differences ($P > 0.432$) between the total progeny across species, and between female and male progeny of *E. mundus*. *Encarsia sophia* however, produced significantly ($P = 0.012$) more females that males (Table 2). Age-specific fertility was higher for *E. mundus* for the first 10 days, averaging *ca.* 2 daughters per female and gradually declined thereafter (Figure 1C). For *E. sophia,* age-specific fertility ranged For *E. sophia* the m_x averaged one female per female per day and oscillated between one and two (Figure 1 D).

A regression of fertility on female longevity showed that the longer the female lived, the more were the eggs laid (Figure 1 E & F). On average, an ovipositing female *E. mundus*, lived for 7 days (range, 2-12 days), whilst those that never laid lived for 3 days (range, 2–6 days). *Encarsia sophia* that laid lived for 13.8 days (range, 2-25), whilst those that never laid lived for 7.4 days (range, 2-25).

Life table parameters of *E. mundus* and *E. sophia*

The net reproductive rates (R_O) were 13.1 and 15.5 daughters per female per generation for *E. mundus* and *E. sophia*, respectively. Generation time was 24.9 days and 26.2 days for *E. mundus* and *E. sophia*, respectively and intrinsic rates of increase were 0.1 daughters per female per day for *E. mundus* and 0.105 daughters per female per day for *E. sophia*.

Discussion

The study showed differences in development duration between *E. mundus* and *E. sophia*, and the females and males of *E. sophia*, initial eggload at emergence and longevity when the parasitoids were provided hosts. The two parasitoid species however lived for a similar duration when fed on honey. *Eretmocerus mundus* had more eggs and lived for shorter period than *E. sophia*, whist *E. sophia* developed two days earlier than *E. mundus*. It was also observed that males of *E. sophia* developed from hosts that were exposed to parasitoids for a period of 24 hrs. There is no published information on the life history of parasitoids attacking *B. tabaci* on cassava. However, the present results can be compared with those on the same species attacking whitefly on other plants (Tables 3, 4 & 5).

The development durations of the two parasitoids reported by other authors are listed in Table 3. The observation of shorter development duration *E. sophia* compared to *E. mundus* on *B. tabaci* were reported earlier (Kapadia & Puri, 1990). In the present study, *E. sophia* females developed in 16.8 d, which is longer than the development duration reported for the same parasitoid species on sowthistle, cotton and sweet potato (Gerling, 1983; Kapadia and Puri, 1990; Antony *et al.*, 2003) (Table 3). A longer development duration (18.7 d) of *E. sophia* was reported by Kapadia and Puri (1990) at 21.1 °C and 53.3 % RH. The development duration of *E. mundus* (19.6 d) is within the range reported by De Barro *et al.* (2000). Gameel (1969) and Sharaf and Batta (1985

b) reported longer development durations of *E. mundus* of 30 d at 29.5 °C and, 44 d at 14 °C. Similarly, Qiu *et al.* (2004) reported longer development durations of *E. mundus*; 64 d at 15 °C and 29.1 d at 20 °C. In contrast, shorter durations of development were reported for *E. mundus* by other authors depending on temperature, *E. mundus* strain and host stage attacked (Table 3). The development duration of both parasitoid species are lower than the 33.3 days reported for *B. tabaci* on cassava (Legg, 1995), which means the parasitoids are capable of multiplying at a faster rate than their host. Nevertheless, longevity and fertility also affect the performance of parasitoids in the field.

The observations in the present study that male-producing eggs of *E. sophia* developed from nymphs exposed to females for only 24 hours seems to be inconsistent with the autoparasitic habit of that insect, which required that male-producing eggs be deposited when female larvae are already in the host, thus enabling the autoparasitic life mode (Gerling, 1983; Hunter and Kelly, 1998). Gerling and Rejouan (2004) observed that eggs laid two days after female producing eggs were laid produced males. The present results seem to suggest that male eggs can be laid the same day as their female counter parts.

The longevities of the two parasitoids reported by other authors are listed in Table 4. Longevity of *E. mundus* when provided with nymphs was similar to those provided with honey, while *E. sophia* lived for a longer period when provided hosts than when honey was available (11.3 d vs. 6.6 d). Contrary to the present observation, Qiu *et al.* (2004) and Ghahari *et al.* (2005) observed a shorter longevity of *E. mundus* in the presence than in absence of hosts. They attributed the differences in the presence and absence of hosts to the effect of transferring parasitoids to fresh hosts and loss in quality of leaf disks, respectively. In the present study, fresh and intact leaves were provided daily and so leaf quality might not have influenced parasitoid longevity. Yet again

the effect of transfer might have been minimal since the parasitoids were tapped off the leaf onto the glass and they were moved with the glass. Powell and Bellows (1992) observed longer longevity of *E. eremicus* on cotton in the presence of hosts than in their absence and attributed it to a better nutritional quality of the honeydew secreted by the host nymphs. This argument may be true but does not answer the question why *E. mundus* lived for a similar duration both in the presence and absence of hosts. Therefore, the reasons for the similarity in the longevity of *E. mundus* in the presence and absence of hosts, and longer longevity of *E. sophia* when provided hosts seems to also be due to inherent factors that affect their biology.

The mean longevity of *E. mundus* with access to hosts (5.5 d) in the present experiment corresponds to the 6.1 d at 10 °C, but is lower than the 3.1 d at 23 °C found by Tawfik *et al.* (1978) on cotton. All the other authors, however, reported higher longevity values than the one got in the current study (Table 4). Longevity of *E. sophia* reported in this study is longer than the 4.2 d and 5.4 d reported by Heinz and Parella (1994) on two poinsettia varieties. The possible reason could be due to provision of plucked leaves during their study as opposed to the provision of intact leaves in the present study. It could also be due to difference in test plant characteristics and populations of the parasitoids used. There are no reports on the longevity of *E. sophia* to compare with the current observations. Since longevity is positively related to efficiency (Godfray, 1994), it is important to increase the longevity of the parasitoids.

Mean fertility in the present study was measured as the number of progeny that emerged plus those that reached pupal stage. In most studies however, the numbers of eggs laid were used to measure the reproductive potential of the parasitoids. Powell and Bellows (1992) argued that measurements based on egg counts do no take into account mortality before adult emergence and may therefore lead to over representation of the reproductive potential. The mean fertility of *E.*

mundus and *E. sophia* in the present study were 25.6 and 16.5 progeny per female, respectively. The fertility of *E. mundus* in this study is close to the fecundity values reported by Sharaf and Batta (1985 b) (20 eggs per female at 14 °C; 27.4 eggs per female at 25 °C) and by Ardeh (2004) on gerbera (19 and 26.8 eggs per female for the thelytokous and arrhenotokous populations of *E. mundus*, respectively). Similarly, Ardeh (2004) reported a fecundity value of 28.6 eggs per female for the thelytokous population of *E. mundus* on poinsettia. The fertility of *E. mundus* in this study falls within the mean fertility range reported by Powell and Bellows (1992) for an unknown *Eretmocerus* sp., which ranged from 20 to 47 progeny per female depending on source of the *Eretmocerus*, and host plant used. Reports on the fecundity and fertility of *E. sophia* are not available, but the value got falls way below the reported fecundity of a congeneric, E. tricolour on cabbage (85 eggs per female).

There are many scenarios that could explain the differences between fecundity and fertility values. The numbers of eggs laid per female vary depending on host plant influence (Heinz & Parella, 1994; De Barro *et al.*, 2000; Ardeh, 2004), experimental procedure and conditions. In order to oviposit, *E. mundus* females stand beside their host and locate a suitable position between the nymph and the leaf surface where they can lay their eggs (Gerling, 1990). Therefore, a host plant with smooth leaves like gerbera, where the margin of the nymph is flat on the leaf surface, results in difficulties during oviposition for the females (Headrick *et al.*, 1996 a & b; Ardeh, 2004), whereas hairy plants like poinsettia, tomato and melon make placement of the eggs under the nymph easier since the nymph does not rest flat on the leaf surface (De Barro *et al.*, 2000; Ardeh, 2004). In addition, length and density of leaf hairs can interfere with the movement of the parasitoids and reduce parasitism (van Lenteren *et al.*, 1995; De Barro *et al.*, 2000). While it is evident that host plant species affects fecundity and fertility of parasitoids,

experimental procedures could also have contributed to the differences between published results and the present study. For instance, De Barro *et al.* (2000) and Ghahari *et al.* (2005) studied the parasitoids over a ten day period, while Ardeh (2004) and the present one assessed the numbers of progeny per female until the female died. Furthermore, as noted by Sharaf and Batta (1985 b), the fecundity of *E. mundus* increased with increase in temperature (Table 5). Cassava (a glabrous variety) was the only host plant used in the current study and no other host plant was suitable for fecundity studies because attempts to rear this specific *B. tabaci* biotype on cotton and sweet potato did not succeed. Since survival was positively related to progeny production, improvement of the survival of the parasitoids could enhance *B. tabaci* control on cassava.

The demographic parameters calculated for *E. mundus* (R_O = 13.1; T_C = 24.9; r_m = 0.1) are lower than the values for *E. sophia* (R_O = 15.1; T = 26.2; r_m = 0.105). The net reproductive rate of *E. mundus* in the current study compares with that reported for the arrhenotokous population of *E. mundus* on gerbera (Ardeh, 2004), but lower values were reported by Ardeh (2004) and Ghahari *et al.* (2005). The higher intrinsic rate of increase of *E. sophia* compared with that of *E. mundus* may partly be attributable to the greater longevity and highly female biased sex ratio (ca. 99 % female *E. sophia* progeny compared to ca. 59 % female *E. mundus* progeny in the entire experiment). The intrinsic rate of increase of *E. mundus* is lower than the values reported for the different populations of *E. mundus* on the various plants (Ardeh, 2004). This is expected because of differences in populations of *E. mundus* used, host plants and use of numbers of eggs laid for calculating r_m. For comparison between *B. tabaci* and its parasitoids on cassava, there is a need to gather information on the development duration, longevity and fertility of *B. tabaci*.

From the life history parameters, it is evident that *E. mundus* may be a good candidate to reduce high populations of *B. tabaci* since it lives for a short time (5.5 days) and produces a little more

offspring than *E. sophia*. *Encarsia sophia* on the other hand would be good under low *B. tabaci* populations because it lives for a longer period (ca. 11 days) and produces few eggs per day. The data collected may be of use in future in case parasitoids are to be imported for control of *B. tabaci* on cassava.

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1 Table 1. Preimaginal development duration of *E. mundus* and *E. sophia* parasitizing *B. tabaci*

	Preimaginal development period (days)			
	sex	N	Mean ± SE	Range
E. mundus	♀♀	154	19.7 ± 0.11 a	16-23
	♂♂	131	19.6 ± 0.14 a	16-24
	df		254	
	t		0.56	
	P		0.578	
E. Sophia	♀♀	59	16.8 ± 0.10 a	16-19
	♂♂	22	18.7 ± 0.18 b	17-20
	df		79	
	t		-9.17	
	P		P<0.001	
Grand mean				
E. mundus		285	19.6 ± 0.09 b	16-24
E. Sophia		81	17.4 ± 0.13 a	16-20
	df		14.7	
	t		164	
	P		<0.001	

2 Data with a column followed by same lower case letters are not statistically different
3 (ANOVA; P> 0.05).
4
5
6
7

1 Table 2. Adult female fertility of *E. mundus* and *E. sophia* attacking *B. tabaci* on cassava

	Adult life time fertility (adult progeny)		
	Sex	Mean ± SE	Range
E. mundus (n = 21)	♀♀	13.1 ± 2.9 a	1-49
	♂♂	10.1 ± 2.5 a	0-46
P-value		0.432	
E. sophia (n = 13)	♀♀	15.5 ± 5.6 b	1-72
	♂♂	0.2 ± 0.0 a	0-2
P-value		0.012	
Grand mean			
E. mundus		25.6 ± 5.4 a	2.95
E. Sophia		16.5 ± 5.7 a	3-73
P-value		0.272	

2 Data with a column followed by same lower case letters are not statistically different (ANOVA; P> 0.05)
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4
5
6

Table 3. Preimaginal development duration of *E. mundus* and *E. sophia* reported in literature

Reference	Host whitefly	Test plant	Development time (days)	Temperature,°C
			E. mundus	
Present study	*B. tabaci*	Cassava	19.8	24.4 °C
Gameel, 1969		Cotton	30	29.5 °C
Tawfik *et al.*, 1978	*B. argentifolii*	Sweet potato	17.9	29.8 °C
Sharaf & Batta, 1985 b	*B. tabaci*	tomato	44	14 °C
		tomato	16	25 °C
Kapadia & Puri, 1990	*B. tabaci*	Cotton	17.1	21.4 °C
		cotton	16.7	19.4 °C
		cotton	15.9	21.1 °C
Jones & Greenberg, 1998	*B. argentifolii*	sweetpotato	15.4	26 °C
De Barro *et al.*, 2000	*B. argentifolii*	Cotton rockmelon tomato soybean hibiscus	19-22 (not specified for crops)	18 °C – 30 °C
Ardeh, 2004		gerbera	15.4[thel]	26 °C
		tomato	16.1[thel]	
		poinsettia	15.6[thel]	
		gerbera	15.3[ar]	
		tomato	15.2[ar]	
		poinsettia	15.6[ar]	
Qiu *et al.*, 2004	*B. argentifolii*	poinsettia	64	15 °C
		poinsettia	29.1	20 ° C
		poinsettia	17.1	25 C
		poinsettia	14	32 °C
Ghahari *et al.*, 2005	*B. tabaci*	Cotton	18.7 (N1)	25 °C
		cotton	15.9 (N2)	
		cotton	16.4 (N3)	
			E. sophia	
Present study	*B. tabaci*	Cassava	18	24.4 °C
Gerling, 1983	*T. vaporariorum*	sowthistle	15	24-26 °C
Kapadia & Puri, 1990	*B. tabaci*	Cotton	8.1	28.9 °C
		cotton	10.6	21.4 °C
		cotton	14.3	19.4 °C
		cotton	18.7	21.1 °C
Antony *et al.*, 2003	*B. tabaci*	sweetpotato	11.3-15.1	25–30 °C

[thel] & [ar] = Development duration of the thelytokous and arrhenotokous populations of *E. mundus*, respectively. N1, N2 & N3 = first, second and third nymphal instars, respectrively.

1 Table 4 Longevity of *E. mundus* and *E. sophia* reported in literature

Reference	Host whitefly	Test plant	Longevity (days)	Temperature, °C
			E. mundus	
Present study	*B. tabaci*	Cassava	5.5	24.4 °C
Tawfik *et al.*, 1978	*B. argentifolii*	Cotton	6.1	10 °C
		cotton	3.2	23 °C
Tawfik *et al.*, 1978	*B. tabaci*	Tomato	7.6	18 °C
		Tomato	10.5	30 °C
Sharaf & Batta, 1985 b	*B. tabaci*	Tomato	11.3	14 °C
		tomato	9.1	25 °C
Qiu *et al.*, 2004	*B. argentifolii*	Poinsettia	14.4	15 °C
		poinsettia	11.3	20 °C
		poinsettia	12.4	25 °C
Ghahari *et al.*, 2005	*B. tabaci*	Cotton	7.6	25 °C
Ardeh, 2004		Gerbera	8.4[thel]	26 °C
		tomato	9.2[thel]	
		poinsettia	7.6[thel]	
		gerbera	9.2[ar]	
		tomato	11[ar]	
		poinsettia	8.0[ar]	
			E. sophia	
Present study	*B. tabaci*	Cassava	11.3	24.4 °C
Heinz and Parella (1994)	*B. tabaci*	Poinsettia A	4.2	
Heinz and Parella (1994)	*B. tabaci*	Poinsettia B	5.4	

2 [thel & ar] = Longevity of the thelytokous and arrhenotokous populations of *E. mundus*, respectively.

3 A = cultivar "Annette Hegg Brilliant Diamond, B = cultivar, "Lilo"

1 Table 5. Fecundity/fertility of *E. mundus* and *E. sophia* reported by other authors

2

Reference	Host whitefly	Test plant	Fecundity/ Fertility	R_0	r_m	Temperature, °C
			E. mundus			
Present study	*B. tabaci*	Cassava	25.6	13.1	0.1	24.4 °C
Tawfik *et al.*, 1978	*B. tabaci*	sweet potato	14.5			18 °C
	B. argentifolii	sweet potato	48			20 °C
Sharaf & Batta, 1985 b	*B. tabaci*	Tomato	20			14 °C
		Tomato	27.4			25 °C
De Barro *et al.*, 2000	*B. argentifolii*	Cotton	97.8			18 °C–30 °C
		rockmelon	138.3			
		tomato	107.8			
		soybean	96			
		hibiscus	105.3			
Ardeh, 2004		Gerbera	19[thel]	17	0.17	26 °C
		tomato	54.6[thel]	51	0.23	
		poinsettia	28.6[thel]	26	0.20	
		gerbera	26.8[ar]	12	0.15	
		tomato	117.5[ar]	55	0.23	
		poinsettia	49.4[ar]	23	0.19	
Qiu *et al.*, 2004	*B. argentifolii*	Poinsettia	10.7			15 °C
		poinsettia	43.4			20 °C
		poinsettia	42.5			25 °C
Ghahari *et al.*, 2005	*B. tabaci*	Cotton		81.7		25 °C
			E. sophia			
Present study	*B. tabaci*	Cassava	16.5	15.5	0.105	24.4 °C
Antony *et al.*, 2003	*B. tabaci*	Sweetpotato				25–30 °C

3 [thel & ar] = Fecundity of the thelytokous and arrhenotokous populations of *E. mundus*, respectively.

1 Figure 1. Variations in the development duration (days) of *E. mundus* (A) and *E. sophia* (B),
2 age-specific fertility (m_x) and survivorship of females (l_x) during the fertility
3 experiment (middle panel: C, *E. mundus*; D, *E. sophiai*) and the relationship between
4 numbers of progeny with female longevity (bottom panel: E, *mundus*; F, *E. sophia*)
5 on *B. tabaci* attacking cassava

6

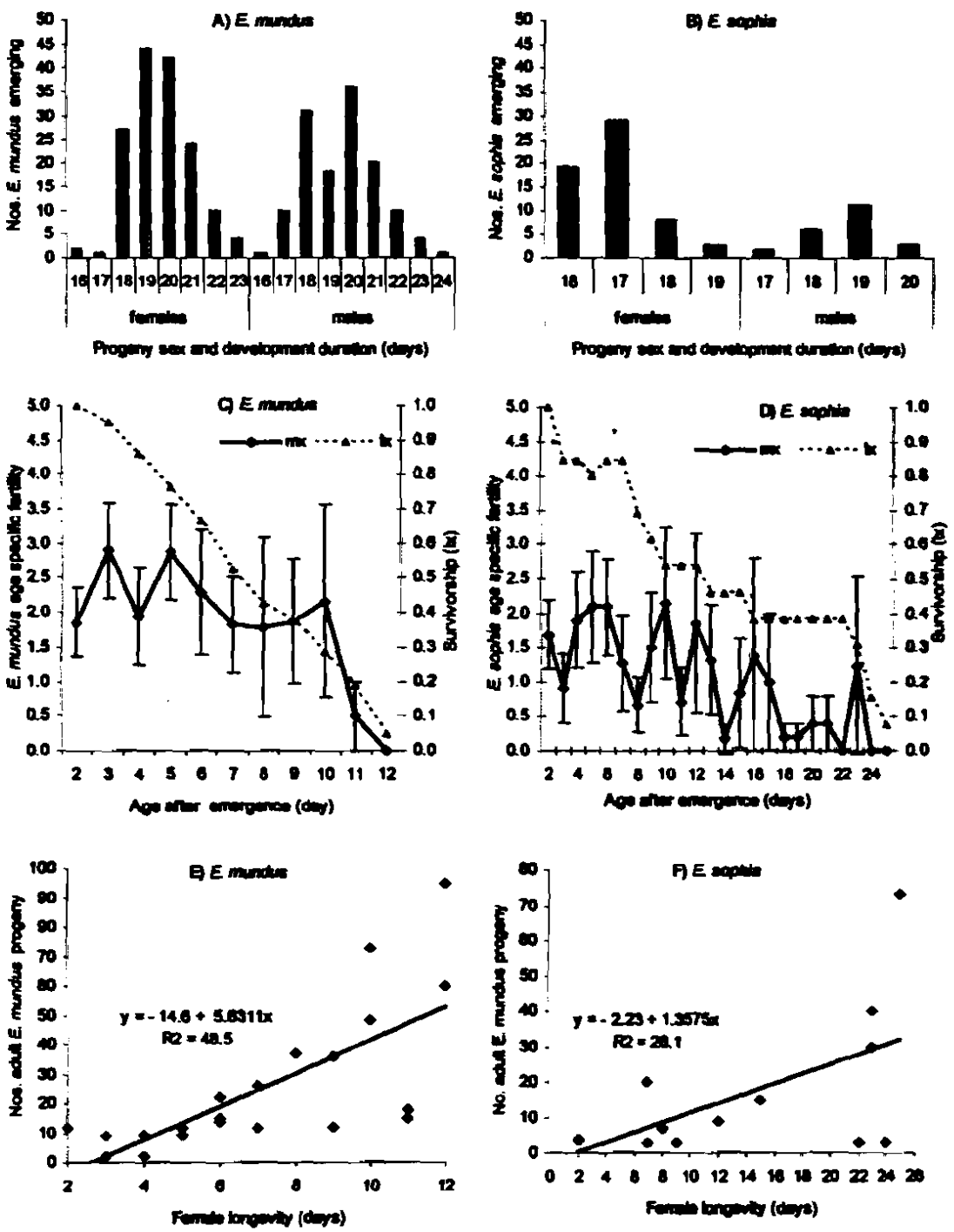
A) E. mundus
Nos. E. mundus emerging
females
males
Progeny sex and development duration (days)
B) E. sophie
Nos. E. sophie emerging
females
males
Progeny sex and development duration (days)
C) E. mundus
mx
lx
E. mundus age specific fertility
Survivorship (lx)
Age after emergence (day)
D) E. sophie
mx
lx
E. sophie age specific fertility
Survivorship (lx)
Age after emergence (days)
E) E. mundus
y = - 14.6 + 5.6311x
R2 = 48.5
No. adult E. mundus progeny
Female longevity (days)
F) E. sophie
y = - 2.23 + 1.3575x
R2 = 28.1
No. adult E. mundus progeny
Female longevity (days)

Figure 1

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Evaluation of *Serangium* n. sp. (Col., Coccinellidae), a predator of *Bemisia tabaci* (Hom., Aleyrodidae) on cassava

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Abstract The potential of a new, previously unidentified *Serangium* species (Col., Coccinellidae) to control the high *Bemisia tabaci* (Gennadius) (Hom., Aleyrodidae) populations on cassava was evaluated. Field and laboratory studies were carried out to determine the abundance and feeding capacity of this *Serangium* species feeding on *B. tabaci* on cassava. *Serangium* nymphs and adults were most abundant in cassava fields late in the season, rising sharply from 5 months after planting (MAP) to a peak at 7–8 MAP. Pre-imaginal development averaged 21.2 days and was longest in eggs and shortest in the L_1 instar. Mean total prey consumption of immature *Serangium* increased with the stage of development with the lowest consumption in the L_1 instar and highest in the L_4 instar. Mean daily consumption was lowest on the first day after hatching in the L_1 instar and rose to a peak on the 13th day after hatching in the L_4 instar. Each *Serangium* larva consumed a mean of over 1000 nymphs during its entire development. These results have demonstrated the potential of this *Serangium* species to control *B. tabaci* populations on cassava.

Key words: biological control, pre-imaginal development, prey abundance, prey consumption

1 Introduction

Bemisia tabaci (Gennadius) (Hom., Aleyrodidae) is a widely distributed pest species colonizing many agricultural systems including greenhouses in both the tropics and subtropics (Oliveira et al. 2001). It is a major vector of viral plant diseases especially begomoviruses (Brown and Bird 1992), and in Africa, it transmits cassava mosaic geminiviruses, which cause cassava mosaic disease (CMD) (Bock and Woods 1983). This disease has resulted in devastating yield losses throughout cassava growing regions in Eastern and Central Africa with losses in Uganda estimated at several millions of US dollars at the height of the epidemic during the early 1990s (Legg and Ogwal 1998; Otim-Nape et al. 2000). The development of virus resistant cassava varieties resulted in alleviation of the CMD-caused damage. However, feeding of *B. tabaci* also results in direct damage, which is shown by leaf chlorosis, a mottled appearance, reduction in plant vigour, general plant stunting and induction of phytotoxic disorders (Bedford et al. 1994). In addition, *B. tabaci* also causes indirect damage through production of honeydew that results in growth of sooty mould on leaves, petioles and stems. The new virus resistant varieties are often very susceptible to both direct and indirect whitefly damage, which may result in crop reduction of up to 50% (Legg et al. 2003). This has led to a need to develop and integrated approach to the management of this pest, and predators are being explored as an option. Recent studies (Otim 2006) have identified a new species of *Serangium* (Col., Coccinellidae) consistently occurring wherever cassava is grown in Uganda.

Serangium spp. are widely distributed in the world and are known to be useful predators of many whitefly species. The most commonly studied *Serangium* species is *Serangium parcesetosum* Sicard. It has been recorded feeding on *B. tabaci* on cotton (Kapadia and Puri 1992) and *Aleurolobus barodensis* Mask (Shah et al. 1986). It has also been successfully used against the citrus whitefly, *Dialeurodes citri* Ashmead (Yigit 1992a,b; Uygun et al. 1997; Yigit et al. 2003) and the silverleaf whitefly, *Bemisia argentifolii* (= *B. tabaci*) (Legaspi et al. 1996, 2001; Ellis et al. 2001). Several studies to determine the biology of *S. parcesetosum* feeding on different whitefly species have been conducted. Timofeyeva and Nhuan (1979) determined its development, mortality and fecundity when feeding on *D. citri* on citrus at 20–23°C, Kapadia and Puri (1992) determined its biology with *B. tabaci* on eggplant and cotton at 23.7°C and Patel et al. (1996) studied its development and longevity with *A. barodensis* on

sugarcane at 27°C. Studies on prey consumption by Legaspi et al. (1996) showed that both larvae and adults of *S. parcesetosum* are voracious feeders of immature whiteflies capable of consuming up to 400 nymphs in a 24-h period. They also found the cumulative lifetime predation rate to be about 5000 nymphs per adult beetle. These studies, therefore, document the potential for use of *Serangium* spp. for controlling whiteflies.

Although it has been shown that all of the known coccinellids belonging to the tribe Seranginii are obligate predators of whiteflies (Gordon 1985), there is no documented evidence of their ability to feed on *B. tabaci* populations on cassava and therefore aid in controlling the super-abundant populations on CMD-resistant varieties. Also, nothing is known about their abundance relative to age of the plant in cassava fields. This study therefore aimed at determining the abundance, development duration and consumption rates of *Serangium* n. sp. (here after referred to as *Serangium*) on cassava in Uganda.

2 Materials and Methods

2.1 Field studies

A field experiment was set up at National Crops Resources Research Institute (NACRRI), Namulonge to determine the variation in *Serangium* populations with age of the cassava plant. The field measured 10 m by 10 m with cassava plants spaced at 1-m intervals. The experiment was planted in August 2003, which coincided with the end of the short rains. The time of planting was chosen based on the usual cassava-planting season in Uganda, where farmers take advantage of the drought resistant nature of the crop by planting during the short rainy season and allowing the crop to go through most of its growth period during the dry season.

At 3 months after planting (MAP), 10 plants were randomly selected from the trial plot. Each plant was then observed from the top to bottom including all leaves (both the top and underside), petioles and the stem. A count of all *Serangium* larvae and adults was made. Data were collected once a week for a period of 6 months, i.e. from 3–8 MAP which is the active growth period of cassava and also the period when *B. tabaci* populations are highest on cassava (Fishpool et al. 1995). Each plant was sampled once and was only sampled again when all the plants in a particular trial had been sampled. This gave an average of two samplings per plant over the 6-month trial period, with a 10-week interval for each plant between samplings.

The field counts were compared statistically by using regression analysis (SIGMASTAT 3.0) to determine relationship between *Serangium* abundance and age of the crop.

2.2 Laboratory studies

Adult *Serangium* were collected daily from already established cassava fields at the National Crops Research Institute, Namulonge, by using an aspirator and were immediately transferred to the laboratory. All collections were performed in the morning hours between 9 AM and 11 AM. Leaves containing all whitefly nymph developmental stages were excised from whole plants in the field and transferred to the laboratory. Female *Serangium* were placed on the leaves and allowed to feed and oviposit on the leaf for 24 h. Following oviposition, the females were removed from the Petri dish and the eggs were allowed to hatch.

Each newly emerged first instar larva was placed in a single Petri dish containing a fresh leaf with all nymphal stages of *B. tabaci* except the pharate adults, as preliminary observations revealed a tendency of the larvae to avoid these stages. The leaf was placed on a filter paper at the bottom of the Petri dish, which was punctured with five small holes at the top to allow ventilation. The sides were sealed with parafilm to hold the lid and base of the Petri dish together, and to prevent escape of the predators. The number of healthy nymphs prior to introducing the larva was counted. The first and second larval instar predators were provided with > 200 nymphs each, while the third and fourth instars had > 400 nymphs. At 24-h intervals, the Petri dishes were checked to determine the number of nymphs consumed. The stage of the larva was also recorded and a new larval instar was determined based on the presence of an exo-skeleton in the Petri dish. Using a fine brush, the predator larva was moved to a new leaf containing prey and the old leaf was discarded. Glabrous leaves were used to allow free movement of the predators as they oviposited and foraged for prey. A total of 15 larvae of both sexes were monitored from hatching time to adulthood. No adults were used for the consumption studies because preliminary observations indicated a tendency for the adults to walk on the lid, probably looking for an exit point, and avoid the leaf containing prey, when placed in a Petri dish.

The number of prey consumed daily was determined by counting the number of predated nymphs, which appeared translucent and flat with all or most of the haemolymph sucked out. The temperature during the entire study was monitored by using a wall thermometer and was 25 ± 2°C, a 12L:12D photoperiod and ambient relative humidity. The data obtained were subjected to ANOVA by using SIGMASTAT 3.0. Holm-sidak multiple (Hochberg and Tamhane, 1987) comparisons were done to compare prey consumption between instars.

3 Results

3.1 *Serangium* abundance

Serangium larvae were generally more abundant than adults although both stages showed the same pattern in population build-up throughout the sampling period. Very low numbers (< 5) of both stages were observed during the first three sampling months (3–5 MAP). There was a sharp increase in numbers of *Serangium* larvae from 5 to 7 MAP, before declining at 8 MAP. *Serangium* adults increased from 5 MAP peaking at 8 MAP (fig. 1). Regression analyses showed significant differences between *Serangium* larvae ($P = 0.034$, $R^2 = 0.71$) and adults ($P = 0.011$, $R^2 = 0.83$), with age of the plant.

3.2 Development duration

Pre-imaginal development time ranged 18–27 days with a mean of 21.2 days from egg to adult. Mean within stage duration was highest in eggs (4.2 ± 0.09 days) (mean ± SE) and lowest in the L_1 instar (2.3 ± 0.11 days). There was little variation in mean development time among L_2, L_3 and L_4 instars

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sugarcane at 27°C. Studies on prey consumption by Legaspi et al. (1996) showed that both larvae and adults of *S. parcesetosum* are voracious feeders of immature whiteflies capable of consuming up to 400 nymphs in a 24-h period. They also found the cumulative lifetime predation rate to be about 5000 nymphs per adult beetle. These studies, therefore, document the potential for use of *Serangium* spp. for controlling whiteflies.

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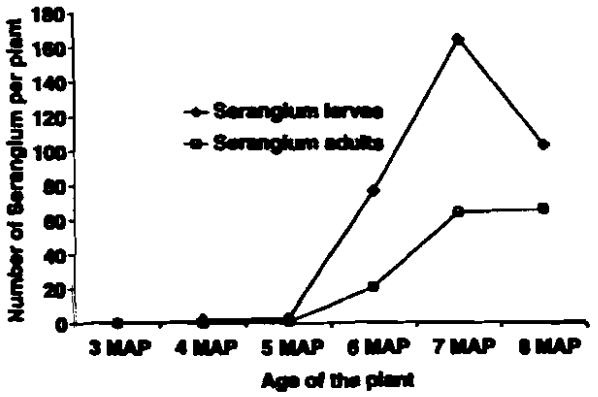

Fig. 1. Variation in populations of Serangium larvae and adults with age of cassava in Uganda

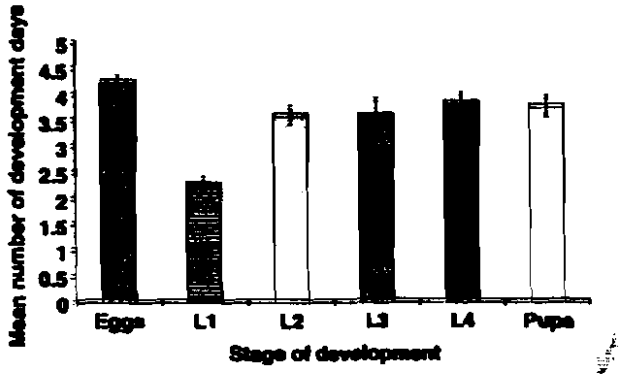

Fig. 2. Mean development time of immature stages of Serangium by feeding Bemisia tabaci nymphs as prey on cassava in Uganda at 25 ± 2°C

with L_2 instars taking 3.6 ± 0.15 days, L_3 instar took 3.6 ± 0.30 days, L_4 instar took 3.8 ± 0.17 days, and the pupa took 3.8 ± 0.18 days (fig. 2). There were significant differences in mean number of development days across the stages ($P < 0.001$, $n = 90$), although no differences were observed within the stages.

3.3 Prey consumption

The mean total prey consumption by the separate larval instars of *Serangium* feeding on *B. tabaci* nymphs increased with stage of larval development with the least, L_1 instar consuming 51.4 ± 4.68 nymphs and the highest L_4 instar consuming 551.3 ± 52.88 nymphs (fig. 3). In total, *Serangium* larvae consumed a mean of 1055.1 nymphs. Holm-sidak multiple pairwise comparisons revealed significant differences ($P < 0.001$, $n = 60$) in total numbers of *B. tabaci* nymphs consumed between larval instars except between L_2 and L_3, however no significant differences were found in total prey consumed within larval instars.

The mean daily consumption of nymphs was lowest on the first day after hatching in the L_1 instar 25.6 ± 8.19 nymphs, but rose to a peak of 233.3 ± 29.19 nymphs on the 13th day after hatching, in the L_4 instar. There was a sharp increase in number of nymphs consumed on the second day, rising to a mean of 132.9 from 25.6 on the first day after hatching (fig. 4).

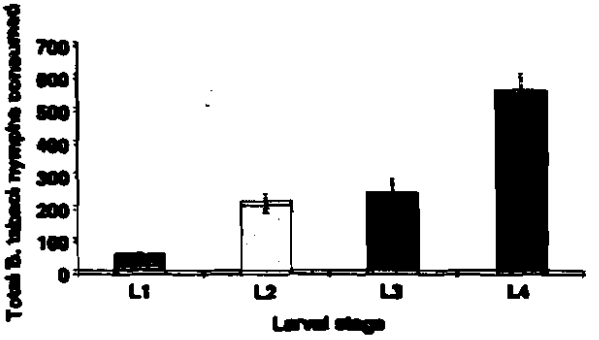

Fig. 3. Mean total prey consumption by Serangium larval instars feeding on Bemisia tabaci nymphs on cassava leaves at 25 ± 2°C

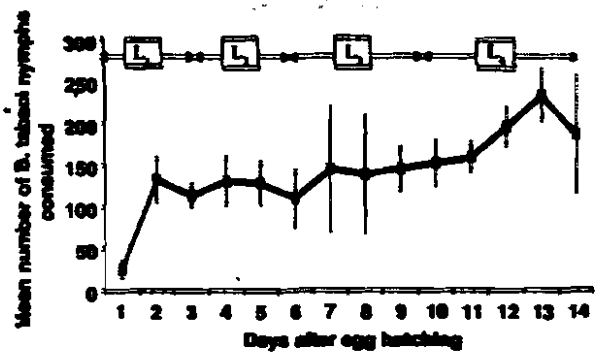

Fig. 4. Variation in mean number of prey consumed by Serangium on different days after hatching, when fed on Bemisia tabaci nymphs on cassava leaves at 25 ± 2°C

4 Discussion

The study showed that *Serangium* is present in cassava fields and is able to prey on immature *B. tabaci*. In the field, *Serangium* numbers are generally low in the early part of the season and only become abundant later in the season. This is in contrast to their prey where studies by Legg (1995) showed that *B. tabaci* populations on cassava are abundant in the early part of the season with highest nymph and adult numbers at 4–6 MAP. This indicates that there is a delayed response of the predator to the presence and abundance of its prey. At 7 MAP when *Serangium* populations are highest, the *B. tabaci* population is only beginning to decline but is still relatively high; therefore, the peak *Serangium* numbers observed in this study corresponded with a relatively high number of their prey. The 2-month delay between the peaks in *B. tabaci* and *Serangium* populations is probably due to a combination of prey density and suitable canopy, preferring plants that are older and with denser canopy than the young ones.

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The ability of a natural enemy to oviposit successfully and develop on the host plant on which its prey lives is one of the major factors in determining its ability to successfully control the pest. The preimaginal development period was studied and showed that the egg stage had the longest mean development period, which is similar to studies on development of other *Serangium* species. Vatanesever et al. (2003) found that mean development of eggs of *Serangium montazerii* Fursch was 5.5 days on both cotton and egg plant. This hatching period was, however, slightly higher than the 4.2 days observed in our study and could have been due to differences in the predator species, nature of the host plant and prey species. The overall mean developmental period of the *Serangium* on cassava was also much shorter (21.2 days) compared with other species carried out by using whiteflies on cotton (28.8 days) and eggplant (28 days) at similar temperatures (Yigit 1992b; Vatanesever et al. 2003). The development period of *Serangium* on cassava is much shorter than that of its prey, *B. tabaci*, in Uganda which was found to be 33.3 days at similar temperatures in the same location (Legg 1995). This is a favorable attribute of *Serangium* as a predator of *B. tabaci*. However, additional factors such as fecundity, survival rates, adult longevity and prey consumption have an important bearing on the predator–prey balance and may limit its usefulness.

The mean total prey consumption by the larvae increased with their developmental maturity, with much less numbers consumed by L_1 instars compared with the L_4 instars. These results are comparable with those of Sengonca et al. (2005) on *S. parcesetosum* where similar consumption trends were reported albeit with slightly higher numbers, with the L_1 instar consuming up to 78.9 nymphs and the L_4 instar consuming 675.9 nymphs, although at 30°C. Studies on total prey consumption have revealed widely variable results. Kapadia and Puri (1992) found that *S. parcesetosum* larvae consumed a mean total of 89.2 nymphs of *B. tabaci* on cotton and 105.7 nymphs on eggplant at 27 ± 2°C. Also, Patel et al. (1996) reported that *S. parcesetosum* consumed a mean total of 671 nymphs of *A. barodensis* on sugarcane at 27 ± 1°C.

However, Sengonca et al. (2005) found that *S. parcesetosum* consumed up to 1119.1 nymphs, at 30°C, during its entire larval development on cotton. This is similar to results from this study which showed total consumption of 1055.1 nymphs, at 25 ± 2°C. The mean daily prey consumption of nymphs also increased with number of days after hatching. The lowest numbers were observed on the first day after hatching, peaking on the 13th day after egg hatch. These results are similar to the study by Sengonca et al. (2005) which found that the mean daily consumption of nymphs was up to 22.7 nymphs on the first day after hatching and increased to a peak of 161 nymphs on the 20th day after hatching, in the L_4 instar.

This study indicated that *Serangium* is abundant at a time when its prey is still in high numbers. This together with its shorter development duration compared with the prey and its ability to oviposit successfully and feed on the sessile stage of its otherwise mobile prey, make *Serangium* a promising agent for biological control. The study also provided new information in understanding the biology of this predator on cassava. Successful biological control of a pest depends on the ability of the natural enemy to destroy a sufficient level of the pest to keep its density from increasing. In an agro-ecosystem, the prey population will never be constant and will always fluctuate in response to many factors, the ability of the predator to adapt to such fluctuations in prey availability is important if it is to be considered as an efficient natural enemy. Studies by Legg et al. (2003) showed that the cassava variety Nase 4 supported up to 100 *B. tabaci* adults per leaf at 4–5 MAP, therefore *Serangium*, though abundant at relatively the same time as its prey, still does not occur in sufficiently high numbers to control the ever increasing *B. tabaci* populations on cassava. Effective use of these predators as control agents would aim at having them in high numbers at 2–4 MAP when their prey populations is still low and only beginning to build-up. Therefore, timing of introduction and/or augmentation should aim at having high numbers of the most voracious stage, L_4 instar, at 2–4 MAP.

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