THE DISTRIBUTION, BIOLOGY AND BEHAVIOUR OF MAJOR NATURAL ENEMIES OF *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) ON CASSAVA (*Manihot esculenta* Crantz) IN UGANDA

MICHAEL HILARY OTIM
BSc. Agric (Hons), MSc. Crop Science, MAK

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMNTS FOR THE AWARD OF THE DEGREE OF DOCTOR OF PHILOSOPHY OF MAKERERE UNIVERSITY

DEPARTMENT OF CROP SCIENCE
FACULTY OF AGRICULTURE

JULY 2007

DECLARATION

The work in this thesis is my own and has never been submitted to any other University

Signed..... Date..... July 25, 2007

Michael Hilary Otim

BSc. Agric (Hons), MSc. Crop Science

This thesis has been submitted with our approval as University supervisors

Signed ..... Date.....

Samuel Kyamanywa, PhD (Professor)
Department of Crop Science,
Makerere University, Uganda

Signed Date July 25, 2007

Dan Gerling, PhD (Professor)
Department of Zoology
Tel Aviv University, Israel

Signed..... Date.....

James Legg, PhD (Virologist / Vector Entomologist)
International Institute of Tropical Agriculture-Tanzania

DEDICATION

To my dear wife Dr. Betty Apica and Adrian Okot our son.

ACKNOWLEDGEMENT

My sincere appreciation goes to all those who in one way or another, contributed to my work or well-being. I am indebted to USAID's Collaborative Research Program (Grant # TA MOU-02 C22-005) for financing this study.

Sincere thanks go my University Supervisor, Professor Samuel Kyamanywa, for his guidance, supervision and management of the Project. Thanks to Ms. Jane Nyamburu, Mr. Mabonga, Mr. Stephen Kubalikenda and Ssalongo Lubega for the support they provided.

I would like to in a special way, express my appreciation to Dr. James Legg for his commitment in this work. Dr. Legg was involved in the preparation of the proposal, supervising my fieldwork and provision of workspace in his laboratory where I conducted most of my work. James gave constructive criticisms of this work and made it what it is. Lastly, I appreciate your timely intervention when I lacked transport for this work. God bless you.

My thanks go to colleagues of IITA Virology laboratory for their contribution to this work: Stephen Ecaat for lab-based work. It was not easy but you helped me up to the end. I thank Peter Asiimwe for his continuous help and cooperation. Geoffrey Okao-Okuja for allowing his field assistants help in times of demand. I sincerely thank Kabaalu Richard, Odongo James, Joseph Mubiru, Robert Obonyo, Michael Kiryewala and David Otim for all they did.

I am indebted to Professor Dan Gerling for the useful advice. I sincerely thank Prof. Gerling for the keen interest he had in this work; his practical input is immeasurable, let alone his personal assistance outside the project. His supervision gave me the inspiration that there is light at the end of the tunnel. Thanks to you and family for organizing social activities while I was at Tel

Aviv University. The friendly people in your laboratory (Eyal, Ronnie, Shlomit, Shunit and Yariv) made me feel at home. Thanks for their kindness, ideas and constructive suggestions. I am also indebted to Dr. Moshe Guershon for his guidance during the design of the experiments and initial data collection, and reading the draft thesis. Dr. Guershon also introduced me to The Observer Program 5.0® (Noldus, Information Technology) during my visit to Tel Aviv University.

Sincere thanks go to Thomas Odong for his assistance in data analysis, and Dr. Ansie Dippener for her assistance in identifying the spiders. Finally, I thank Mr. Patrick Kiwomya, an extension officer of Lyantonde sub-county, Robert Byaruhanga (a farmer) and Obedmoth Issa (field assistant) for their assistance, and all those whose names I have not mentioned. I am also indebted to the anonymous external examiner for the constructive suggestions.

TABLE OF CONTENTS

CHAPTER THREE

FIELD POPULATIONS OF *Bemisia tabaci* AND ITS NATURAL ENEMIES ON CASSAVA, CASSAVA COMPONENT CROPS AND WEEDS

CHAPTER FOUR

LIFEHISTORY OF *Eretmocerus mundus* AND *Encarsia sophia* on *Bemisia tabaci* ATTACKING CASSAVA

CHAPTER FIVE

THE SEARCHING AND OVIPOSITION BEHAVIOUR OF *Eretmocerus mundus* AND *Encarsia sophia* ON *Bemisia tabaci* ATTACKING CASSAVA

CHAPTER SIX

APPENDICES

LIST OF TABLES

LIST OF FIGURES

LIST OF PICTURES

ABSTRACT

The whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) is an important pest of cassava (*Manihot esculenta* Crantz) causing substantial yield losses due to transmission of cassava mosaic geminiviruses that cause cassava mosaic disease (CMD) and direct damage to CMD-resistant varieties. In this study, the population levels of *B. tabaci* and its natural enemies on cassava, cassava component crops and weeds, the life history of the principal parasitoids of *B. tabaci* and, the influence of cassava leaf pubescence on the searching and oviposition behaviour of the principal parasitoids of *B. tabaci* were investigated.

Bemisia tabaci and its natural enemies were most abundant on cassava than on cassava component crops and weeds. The parasitoid, *Eretmocerus mundus* Mercet was the most abundant followed by *Encarsia sophia* Girault and Dodd and an undescribed black-headed *Encarsia* (=*Encarsia* sp.). The incidence of parasitoids and parasitism differed significantly between locations and time of the year, being highest at Busukuma, followed by Bulisa and Lyantonde. Predators of *B. tabaci* recorded on cassava included: ants, predatory beetles (*Serangium* sp.), spiders, lacewings, hoverfly larvae and predatory bugs. Ants, predatory beetles and spiders were the most abundant at all the surveyed locations. No component crops or weeds harboured high populations of whitefly or its natural enemies. Nevertheless, fewer parasitoids were recorded from *Ipomea batatas*, *Commelina* sp., *Melhania* sp., *Bidens* sp., and *Euphorbia* sp.

Eretmocerus mundus emerged with more mature eggs and produced more offspring than *E. sophia*. *Encarsia sophia* on the other hand developed faster, lived longer, and had a higher intrinsic rate of increase, net reproductive rate and generation time compared to *E. mundus*. The females of *E. sophia* developed ca. two days earlier than their male counterparts.

The parasitoids exhibited a similar search pathway on the two varieties, but often stopped and groomed for a while upon encountering leaf hairs before resuming host searching. The observed frequencies of some behaviours deviated from what was expected. The duration of host assessment (antennation) was higher for both parasitoid species on the glabrous variety than on the hirsute clone. *Eretmocerus mundus* females probed, groomed and rested on the leaf for a longer duration on the glabrous variety than on the hirsute clone, whilst *E. sophia* host-fed and fed on liquids on the leaf for a longer duration on the glabrous variety.

Combining all the data together, it is evident that, although parasitoids cause up to 42% parasitism of *B. tabaci*, parasitoids by themselves were not effectively controlling *B. tabaci* on cassava. This is partly because no crops or weeds host high populations of whitefly and their natural enemies to enable earlier colonization of the crop by parasitoids and, the limitations posed by low reproductive rates of the parasitoids. Nevertheless, this study has demonstrated the importance of parasitoids in regulating *B. tabaci* populations and generated important information for comparison in case of importation or the need for augmentative biological control.

CHAPTER ONE

INTRODUCTION

1.1 Importance of cassava

Cassava is one of the most important staple food crops in the tropics. It is adapted to diverse environmental conditions and farming systems. It was ranked the seventh most important crop throughout the world, and provides primary source of carbohydrates for more than 200 million people including the poorest on the African continent (Hahn *et al.*, 1980). Besides serving as human food, cassava is also fed to animals. On average, fresh tubers contain 62% water, 20–25% starch, 1–2% protein, and 1-2% fibre, with traces of fats and minerals (Onwueme and Sinha, 1991). Cassava production requires less labour per calorie harvested than other staple food crops. Moreover, it allows a degree of flexibility in the timing of labour inputs in cases of labour shortage (Okali and Berry, 1985).

1.2 Cassava production constraints

Despite the importance of cassava, a number of factors, which include insect pests and diseases, weed infestation, poor agronomic practices, inadequate post harvest handling technology and poor marketing structures affect its production (Anon., 1994). Consequently, yields of the crop have remained consistently low (<10 t/ha) in farmers' fields, in comparison with 25 t/ha in experimental stations and a potential of 80 t/ha (Fauquet and Beachy, 1989). Among these challenges, the whitefly *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) is a serious insect pest of cassava in the tropics and sub-tropics (Oliveira et al., 2001). It transmits cassava mosaic geminiviruses (CMGs) that cause cassava mosaic disease (CMD), the principal constraint to cassava production in Africa (Bock and Woods, 1983). The disease is estimated to cause annual losses of between 12 and 23 million tonnes of cassava in Africa (Thresh *et al.*, 1997).

Besides virus transmission, high whitefly populations have been reported on some of the virus-resistant varieties released to control CMD and cause direct damage by feeding and, by reduction of photosynthesis due to leaf distortion (Plate 1.1c & d) and sooty mould growth on the honeydew (Legg *et al.*, 2003). Recently, Legg (unpublished) showed that direct damage might account for between 34 to 50% of the tuberous yield reduction depending on variety. This therefore highlights the need for a concerted effort to control CMD and the vector.

Plate 1.1. Effects of *B. tabaci* infestation (1.1a, on abaxial leaf surface) on cassava through disease transmission (1.1b) and leaf distortion and chlorosis (1.1c & d).

1.3 Control of CMD and *B. tabaci*

In order to control CMD and *B. tabaci*, an integrated pest management strategy is required (Hilje *et al.*, 2001). For CMD control, the methods are aimed at reducing the proportion of plants that become infected, delay infection to such a stage of crop growth that losses become unimportant or decrease severity of the damage sustained after infection has occurred (Thresh and Otim-Nape, 1994).

Host plant resistance (HPR) is considered the only long-term and sustainable way of CMD control in Africa (Seif, 1982; Thresh and Otim-Nape, 1994). Consequently, numerous CMD-resistant varieties have been bred, released and distributed to farmers in the affected regions of Uganda (Otim-Nape *et al.*, 1994; Thresh *et al.*, 1994; Otim-Nape *et al.*, 1999). Unfortunately, there are difficulties of logistics, cost of multiplication and dissemination, which make it impossible to avail the resistant varieties to all farmers. Apart from the problem of availability, recent studies have shown that the CMD-resistant varieties Nase 4 and Nase 12 are heavily attacked by the whitefly, damaging them by removal of sap and contaminating the crop with honeydew, which leads to the development of sooty moulds (Legg *et al.*, 2003). To alleviate this condition, research efforts are required to combine resistance to the viral disease and to *B. tabaci*, which will result in overall host plant resistance.

Phytosanitation, fertilizer application, intercropping, manipulating plant population, and varietal mixtures have also been investigated as possible CMD control measures. With respect to the use of virus-free planting materials, the provision of CMD–free materials of susceptible varieties are inappropriate and ineffective in controlling CMD under epidemic conditions (Thresh *et al.*, 1998). Roguing of infected cassava plants (< 6 months old) is not effective under farmers' condition, but good for official schemes for the selection and maintenance of CMD-free stocks

for release to farmers. These coupled with the fact that CMD spread is mainly between cassava fields and not from internal foci within a field makes roguing of limited usefulness (Beck, 1982; Fargette *et al.*, 1990; Otim-Nape, 1993).

High plant populations have been associated with low *B. tabaci* and CMD incidence (Fargette and Fauquet, 1988; Fargette *et al.*, 1990; Egabu *et al.*, 2002). One way of manipulating plant population is intercropping, the results of which are not consistent. For Instance, Fargette and Fauquet (1988) reported inconsistent results on the relationship between whitefly populations and disease incidence on cassava intercropped with maize, while Ekpe and Chinaka (2000) never found a significant difference in CMD severity in local cassava grown as an intercrop compared to that grown as a monocrop although yield increased with fertilizer application and cropping systems. Other authors have however, demonstrated reduced *B. tabaci* and CMD incidence in cassava intercropped with cowpea, maize and groundnuts than in monocrop (Ahohuendo & Sarkar, 1995; Fondong *et al.*, 2002; Oneka *et al.*, 2002) with increased yields in the intercrop than the monocrop (Oneka *et al.*, 2002). Gold (1994) found that intercropping cowpea with cassava reduced the numbers of *Aleurotrachelus socialis* Bondar and *Trialeurodes variabilis* Quaintance, their egg density per leaf, and increased cassava yield in South America. None of these studies dealt with the role of intercrops on the activity of the natural enemies of *B. tabaci.* Consequently, the importance of intercrops on whitefly activity and their natural enemies remains unknown.

Varietal mixtures have been found to reduce vector populations and the incidence of CMD especially on susceptible cassava varieties and resulted in higher yields, especially of the susceptible variety in the mixture than pure stands of the susceptible variety (Sserubombwe, 1998; Osiru *et al.*, 1999). The mixtures are however only applicable where susceptible varieties

are mixed with resistant ones (to both the virus and vector) and in areas of low disease spread (Sserubombwe, 1998). However, the use of virus-resistant varieties that are heavily attacked by *B. tabaci* such as Nase 4 may instead lead to the build up of *B. tabaci* populations and subsequent migration of these vectors to the susceptible variety and diluting the effect of the mixture.

Sseruwagi (1998) and Ekpe & Chinaka (2000) investigated fertilizer application. Ekpe & Chinaka (2000) never got a significant difference in the severity of CMD between fertilised and unfertilised cassava fields, while Sseruwagi (1998) reported increased *B. tabaci* populations on moderately susceptible and susceptible varieties than in the most susceptible variety after application of NPK fertiliser. Sseruwagi's results further demonstrated that CMD incidence increased on the resistant varieties following NPK application, while there was no effect of fertiliser application in the susceptible variety. Interestingly though, higher tuberous yields were attained on the resistant varieties which had increased CMD incidence after fertiliser application, and not in the susceptible variety. This therefore, means that the benefits of fertilization outweighed losses incurred from increased CMD incidence in resistant varieties but not in the susceptible varieties. From a practical point of view therefore, benefits from NPK application can only be achieved with healthy than with CMD-infected plants.

Sharaf (1986) reviewed the use of chemicals to suppress whitefly populations and their ability to reduce the incidence of the viral diseases they transmit. The review revealed that, although some chemicals controlled the whitefly, they did not necessarily control the virus diseases transmitted. For instance, aldicarb, carbaryl, bromophos, carbicron, chlorfenvinphos, dimeton, disulfoton, endosulfan, mevinphos, methyl parathion, phorate, phoxim, vamithodion, oxamyl and mephospholan effectively controlled *B. tabaci* on different crops, but only endosulfan,

mevinphos, mephospholan, phorate, oxamyl and dimethoate efficiently eliminated the spread of different virus diseases on various crops through the control of their vector, *B. tabaci* (Sharaf, 1986). On cassava, smallholders do not usually attempt to control cassava pest problems with pesticides because of limited access to such chemicals and because cassava is of low value per unit weight (Nweke, 1994).

For whitefly management, there have been very few deliberate breeding programs aimed at developing higher levels of resistance in cassava cultivars, and to combine resistance to viruses and whiteflies in the same genotype. The few efforts have investigated HPR to *A. socialis* in the Americas with the resultant development of several resistant varieties to *A. socialis* (Bellotti and Arias, 2001). For *B. tabaci* feeding on cassava in Africa, plans to combine resistance to the viral disease with that of the whitefly in cassava are still at an early stage (Bellotti and Arias, 2001). Given the increasing importance of the whitefly and, in light of the fact that no other control method is as effective as host plant resistance, there is a need to develop a balanced approach to CMD/vector management, which can combine the deployment of CMD/whitefly-resistant cultivars and alternative control methods, such as the use of *B. tabaci* natural enemies.

1.4 Problem statement and justification

Several parasitoid and predator species have been reported to attack *B. tabaci* on cassava in Africa (Robertson, 1985; Nyirenda *et al.*, 1993; Fishpool & Burban, 1994; Otim, 2002). However, there are no records on their impact, biology and behaviour on cassava, and on the *B. tabaci* biotype that attacks it. In Uganda, Legg (1995) reported that natural enemies, primarily parasitoids, commonly give rise to about 50% mortality. Recently, Otim (2002) conducted a study in Uganda that included a survey in five fields each in three locations conducted once every three months for a period of one year and recorded natural enemies on cassava only,

disregarding the natural vegetation and other crop plants. The results showed that up to 90% parasitism might occur, albeit rarely and when host populations are low. The study further showed that the patterns in the build-up in numbers of parasitoids followed a similar pattern to that of the whitefly host, while percent parasitism decreased with increase in nymph numbers. In order to understand better the driving forces that shape *B. tabaci* population fluctuations on cassava, it was necessary to conduct detailed studies on the factors that govern this pest in the field. These include existence and development on other host plants and the biological and behavioural characteristics of the pest and its natural enemies. In the present work, a more detailed study was undertaken to determine the factors influencing *B. tabaci* populations and give better insight into the possible causes of the present situation.

With an ultimate goal of designing sustainable management of *B. tabaci*, it is necessary to evaluate the potential and characteristics of natural enemies. The study of plant-natural enemy relationships, biology and behavioural characteristics is essential for understanding the role of the natural enemies in determining *B. tabaci* population levels. It can provide necessary information for understanding the factors that determine population levels and procedures for improving the natural enemy activity. The information obtained on life history parameters can also be used as a baseline for comparing with that of other known *B. tabaci* parasitoids, which could be likely candidates for importation to bolster the activity of the indigenous natural enemies and finally, it could help assess the cost and possible usefulness of augmentative biological control.

1.5 General Objective

The overall objective is to develop sustainable management of *B. tabaci* on cassava, which would also check the spread of CMD.

1.5.1 Specific objectives

i. To assess the population levels of *B. tabaci* and its natural enemies on cassava, crops grown in association with cassava and weeds within and outside cassava gardens.

i. To determine the development duration, reproductive capacity and longevity of the principal parasitoids of *B. tabaci* on cassava

i. To determine the influence of inherent plant factors on the searching and oviposition behaviour of the principal parasitoids of *B. tabaci*.

1.6 Hypotheses

i. There are differences in the abundance of *B. tabaci* and its natural enemies on cassava under different climatic conditions

ii. Whitefly and its natural enemies occur on crops intercropped with cassava, and on weeds in cassava fields

iii. There are differences in the biology of the principal parasitoids of *B. tabaci* on cassava

iv. There are differences in the searching and oviposition behaviour of the principal parasitoids of *B. tabaci* on different cassava varieties

CHAPTER TWO

LITERATURE REVIEW

2.1 Natural enemies of *Bemisia tabaci*

There have been many attempts to find efficient natural enemies of whitefly in different parts of the world (Gerling, 1986; Gerling, 1990; Gerling *et al.* 2001). The natural enemies reported to attack whitefly in these reviews are mainly predators and parasitoids.

2.1.1 Predators of whitefly

Gerling *et al.* (1986) listed six arthropod orders of predators attacking whitefly, although this was subsequently expanded to nine (Gerling *et al.*, 2001) with the majority being in the orders: Coleoptera, Hemiptera, Neuroptera, Mesostigmata and Araneae. In Malawi, Nyirenda *et al.* (1993) found *Scymnus* sp. (Coleoptera: Coccinellidae) and *Semidalis* sp. (Neuroptera: Coniopterygidae) as the main predators, while Robertson (1985) recorded phytoseiid mite, *Scolothrips* sp., coniopterygid and cecidomyiid larvae as predators of *B. tabaci* in Kenya. In Ivory Coast, Fishpool and Burban (1994) reported the occurrence of *Euseius* sp. Acari: Phytoseiidae), *Stethorus jejunus* Casey (Coleoptera: Coccinellidae), *Holoborus pallidicornis* Cameron (Staphylinidae), and *Scolothrips latipennis* Priesner.

The role of predators in *B. tabaci* control has not been investigated, partly because of the difficulty in assessing their impact on *B. tabaci* populations, especially in crops that harbour numerous predator and prey species. Additionally, the potential of many predator species in reducing the pest is only recognized following the establishment and outbreak of pest populations in new areas, where the predators do not occur or are in insufficient numbers to suppress pest populations (Gerling *et al.*, 2001). Consequently, the inventory of *B. tabaci* predators is continuously changing in terms of the number of included species and their utility as

biological control agents. In Uganda, there are no published reports of predators attacking *B. tabaci* on cassava. The paucity of information on the predators attacking whitefly therefore highlights the need to identify predators most commonly associated with whitefly and to study their impact.

2.1.2 Parasitoids of whitefly

Among the different categories of natural enemies attacking whitefly, parasitoids are the most successful (Gerling *et al.* 2001). Parasitoids of the genera *Encarsia, Eretmocerus* (both Chalcidoidea: Aphelinidae) (Gerling *et al.*, 1980) and *Amitus* (Proctotrupoidea: Platygasteridae) (Joyce *et al.*, 1999; Gerling *et al.*, 2001) are reported to be potentially efficient whitefly control agents, especially under greenhouse conditions, and have therefore received more attention than the other natural enemies. To date, there are more than 200 species of *Encarsia* described (Woolley and Heraty, 1998). Gerling *et al.* (2001) listed 34 *Encarsia* spp. and 14 *Eretmocerus* spp. that have so far been identified as parasitoids of *B. tabaci* in the field. These authors indicated that biological studies have only been conducted on eleven *Encarsia* spp. and eight *Eretmocerus* spp. *Amitus* spp. have been recorded from many whitefly species (Gerling *et al.*, 2001). One hyperparasitic species, *Signiphora aleyrodis* (Ashmead) (Hymenoptera: Signiphoridae) has also been described from *B. tabaci* (Schuster *et al.*, 1998; Viscarret *et al.*, 2000). Studies by Inayatullah and Ghani (1987) revealed the occurrence of *Eretmocerus mundus* (Mercet), *Eretmocerus corni* Haldeman, *Eretmocerus* sp., *Encarsia* sp. nr. *tricolor, Encarsia lutea* (Masi) (= *Prospaltella lutea*), and three *Encarsia* spp. (= *Prospaltella* spp.) on whitefly attacking cotton, eggplant, gardenia, aristolochia and lantana in Pakistan. Zaki *et al.* (2002) noted that *E. mundus* attacked whitefly on cotton and melon in Egypt, whilst Ryckwaert and Alauzet (2002) found *Eretmocerus tejanus* Rose & Zolnerowich on tomato, eggplant, cucurbits and

cabbage; *Encarsia luteola* (Howard) on cabbage, lettuce, sweetpepper, and euphorbia; *Encarsia nigricephala* Dozier on tomato, eggplant, and euphorbia; *Encarsia sophia* Girault and Dodd (*E. transvena*) on cabbage; *Amitus bennetti* Viggiani and Evans on eggplant and poinsettia; and *Signiphora* sp. on tomato, poinsettia and eggplant in Martinique. These results suggest the possible movement of parasitoids from one crop to another since the same species of parasitoids attack whitefly on more than one crop. Such a movement has already been observed in California when parasitoids moved from collard and sunflower and attacked whitefly in cotton and melon fields (Naranjo et al., 2001). In cassava fields, however, there are few records on parasitoids attacking *B. tabaci* and on whether crops grown in association with cassava and weeds in cassava fields harbour whitefly and their natural enemies. The only record is that of Ssemaganda *et al.* (2003) in which *E. mundus* and *E. sophia* were both found to attack *B. tabaci* on cassava and sweet potato. This study was therefore conducted to incorporate documentation of whitefly host plants (component intercrops and weeds) and associated parasitoids in cassava fields.

2.2 Factors influencing the efficacy of parasitoids

2.2.1 Climate

Seasonal extremes of temperature, rainfall, and humidity exert a direct influence on the survival of the whitefly and the parasitoid (van Driesche, 1993), with the influence of temperature being the most studied. High temperatures (25-35°C) were found to quicken the development of *Encarsia formosa* Gahan on poinsettia, *Eretmocerus* sp. on tomato and *Eretmocerus longipes* Compere on jasmine (Enkegaard, 1993; López and Botto, 1997; Sengonca and Liu, 1998) and increase the intrinsic rates of increase and net reproductive rate (Enkegaard, 1993) perhaps due to the reduced development time.

Temperatures between 25-30°C were also reported to increase the walking speed of *E. formosa* on gerbera (Sütterlin and van Lenteren, 1997), thereby increasing the chances for parasitoid-host encounters for successful parasitism. Similarly, Abd El-Kareim (1998) reported that high temperatures increased the searching rate of *E. lutea* (as *P. lutea*) on lantana, while that of *E. mundus* was reduced, leading to *E. lutea* and *E. mundus* populations maintaining higher rates of parasitism during the hot and cold seasons, respectively.

2.2.2 Biology of parasitoids

There are several reports on the biology of *E. mundus* and a few on *E. sophia* under laboratory conditions. The important characteristics of parasitoids studied include development duration, longevity, fecundity and fertility. The published data are, however, in disagreement with each other because of differences in experimental conditions (whitefly species, host plant species, confusion over taxonomic status of parasitoid species, temperature and relative humidity).

The development duration of *E. mundus* has been reported to range between 14 - 64 days (Gameel, 1969; Tawfik *et al.*, 1978; Sharaf & Batta, 1985 a &b; Kapadia & Puri, 1990; Jones & Greenberg, 1998; Gerling & Fried, 2000; De Barro *et al.*, 2000; Ardeh, 2004; Qiu *et al.*, 2004; Ghahari *et al.*, 2005). A range of 8.1-18.7 days was observed for *E. sophia* (Kapadia & Puri, 1990; Gerling, 1983; Antony *et al.*, 2003). For both parasitoid species, development duration is shorter at higher temperatures (Sharaf & Batta, 1985 b; Kapadia & Puri, 1990; Qiu *et al.*, 2004) and with increasing whitefly age (Antony *et al.*, 2003; Ghahari *et al.*, 2005). Similarly, development duration has been reported to decrease with increase in temperature for other aphelinids (López & Botto, 1997; Powell and Bellows, 1992) and is greatest when earlier instar nymphs are attacked (Williams, 1995).

Longevity of *E. mundus* has been studied on whitefly infesting cotton, tomato, gerbera and poinsettia and found to average from 10 - 28 days (Kapadia & Puri, 1990; Gerling & Fried, 2000; Qiu *et al.*, 2004; Ghahari *et al.*, 2005). The longevity of *E. sophia* was found to be 4.2 days on a poinsettia variety, "Annette Hegg Brilliant Diamond" and 5.4 days on "Lilo" (Heinz and Parella, 1994). For other aphelinids, longevity was affected by presence or absence of hosts and the prevailing temperatures. The longevities of *Eretmocerus* spp., *E. longipes* and *Amitus fuscipennis* MacGown and Nebeker were reported to be higher when the parasitoids were provided with hosts in comparison to situations where no hosts were available (López & Botto, 1997; Sengonca and Liu, 1998; De Vis *et al.*, 2002). These results further indicated that longevity decreases with increasing temperatures but the reasons for this are not known.

The reported fecundity and fertility of *E. mundus* varied with host plant species (Sharaf & Batta, 1985 b; Gerling & Fried, 2000; De Barro *et al.* 2000; Ardeh, 2004). Fecundity values of *E. mundus* ranged from 20 - 247 eggs per female (Sharaf & Batta, 1985 a & b; Gerling & Fried, 2000), whereas fertility varied between 19 - 138 females per female (De Barro *et al.* 2000; Ardeh, 2004; Ghahari *et al.*, 2005). There are, however, no records available on the fecundity of *E. sophia*. For other aphelinids, variable fecundity and fertility values have been reported. De Vis *et al.* (2002) reported fecundity of *A. fuscipennis* to be 338, 430 and 119 eggs per female at 15, 25, and 30 ^{0}C, respectively. López & Botto (1997) found fertility of an *Eretmocerus* sp. to be 130 females/female on *Trialeurodes vaporariorum* (Westwood); Williams (1995) reported 85 eggs/female for *Encarsia tricolor* Förster on cabbage, and Joyce *et al.* (1999) reported 78.8 females/female for *A. bennetti* on *Bemisia argentifolii* Bellows and Perring. Estimation of the reproductive potential of parasitoids based on number of eggs (fecundity) may give an overestimate because it does not take into account nymphal mortality. In contrast, fertility

estimation based on emerged progeny, leaving out pupae that have failed to emerge, may lead to an under estimation of the parasitoid's efficiency (De Vis *et al.*, 2002). It is therefore important to consider both emerged progeny and pupae that have failed to make it to adulthood. These differences notwithstanding, it is still apparent that parasitoid fecundity and fertility differ between parasitoid species. With respect to host feeding, *Encarsia* and *Eretmocerus* spp. feed on the haemolymph of whitefly in order to mature a full complement of eggs (Gerling, 1990), while *Amitus* spp. emerge with a full egg complement, which is laid in about 3 days (Joyce *et al.*, 1999) and does not therefore depend on host-feeding.

2.2.3 Behaviour of parasitoids

Differences in searching behaviour are also reported to be responsible for observed variations in parasitoid activity. For instance, Abd El-Kareim (1998) reported that *E. mundus* had a high searching rate, and exhibited a higher density dependent response to *B. tabaci* populations in comparison with *E. lutea*. Drost *et al.* (2000) compared the searching strategies of five parasitoid species of *B. argentifolii* on poinsettia and the results showed that *A. bennetti* and *Eretmocerus stauferri* had higher walking speeds before oviposition, whilst there were no significant differences in walking speed after oviposition. They also found that *A. bennetti* and *Eretmocerus eremicus* Rose and Zolnerowich performed area restricted searches after oviposition - an adaptation to hosts that are distributed in a clumped manner (Godfray, 1994). Based on walking speed alone, *A. bennetti* was expected to be the most efficient natural enemy of *B. argentifolii*, followed by *Eretmocerus* species and *E. formosa*. The actual relationship between walking speed and actual parasitism was not tested.

2.2.4 Host plant effects

Among the factors influencing parasitoid behaviour and parasitism is host plant morphology, especially leaf pubescence. This was reported to affect the searching efficiency of parasitoids by slowing or inhibiting their movements (Hua *et al.*, 1987; Gerling, 1990). van Lenteren *et al.* (1995) and van Roermund and van Lenteren, (1995) found that leaf hairs interfered with locomotion and parasitisation efficiency of *E. formosa* on cucumber and tomato, while McAuslane *et al.* (1995) found reduced parasitism of *B. argentifolii* by *Encarsia* and *Eretmocerus* spp. on soybean.

Greathead and Bennet (1981) in their review noted that parasitism rates varied with different vegetable species and other plants. Similarly, Headrick *et al.* (1996a) found varied parasitism levels on cotton (62%), melon (100%) and sweet potato (51%). The high parasitism on melon was because the hairs on melon leaves raised the nymphs and made it easier for *E. eremicus* to place its eggs under the nymphs, unlike on cotton and sweetpotato where nymphs lay flat on the leaf and therefore making it difficult to place the eggs under the nymphs. Gruenhagen and Perring (1999) found no parasitism of whitefly on velvetleaf (*Abutilon theophrasti*) leaves, both in the field and in the greenhouse, because parasitoids remained entrapped and were killed in glandular trichomes on the plant leaves. Rajam *et al.* (1969) reported different parasitism levels on cotton (16%), field beans (2.8%), brinjal (1.2%) and no parasitism on prickly chaff. The lack of parasitism on prickly chaff was associated with the dense hairs, which prevented the free movement of parasitoids. This demonstrates the need for plant breeders to be aware of the tritrophic interactions that may occur when new varieties are released. Thus, the strong need to study the influence of plant characteristics (leaf pubescence) on the searching and oviposition behaviour of parasitoids on cassava.

2.2.5 Host plant diversity

The extensive host range of *Bemisia* species means that there are large non-crop reservoir populations. These reservoirs may act as refugia, from which parasitoids migrate to nearby annual crops (Hoelmer, 1995). For instance, *Malva parviflora* was found to harbour whitefly and their parasitoids when cotton leaves were not present (Gerling, 1967), whilst field bindweed and sunflower supported *Eretmocerus* sp. nr *californicus* in the Imperial Valley although with lower levels of parasitism (Coudriet *et al.*, 1986). Although parasitoids are reported to occur on weeds near gardens, the movement of parasitoids from these habitats to nearby crops has received little attention. Naranjo (2001) reported that *Eretmocerus* spp. readily move from collard and sunflower grown as a refuge into cotton and melon fields, but the extent of parasitism was not reported. Under Ugandan conditions, however, there are no records on the host range of whitefly and the potential for these plant hosts to act as parasitoid refugia. This therefore highlights the need to document plants that could act as whitefly or parasitoid reservoirs.

Cropping techniques may be used to enhance the conservation of natural enemies (Dent, 1991). Mixed cropping/intercropping may be used to attract pests away from the primary crop and it may sufficiently change the environment to promote the activity of natural enemies (Dent, 1991). For instance, in a cotton/sesame intercrop, with sesame grown in row strips, *Heliothis* spp. and its natural enemy *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) were attracted away from cotton (Pair *et al.*, 1982). Although the crop environment may be changed in favour of the natural enemies by changes in cultural practices, limited work has been done on the influence of such practices on the activity of *B. tabaci* natural enemies in cassava fields. Recently, Ssemaganda *et al* (2003), found a proportionately higher number of parasitized nymphs on cassava grown in association with sweetpotato than in cassava alone. Although the latter finding

seems to give indications that sweet potato may act as a parasitoid refuge, the results are not conclusive, hence the need to conduct further studies to ascertain whether indeed parasitoids move (and in sufficient numbers) from sweetpotato to attack whitefly on cassava. The studies should be extended to cover other crops grown together with cassava, and the weeds commonly found in and around cassava crops.

2.3 Research gaps

From the above literature review, it is clear that previous research efforts concentrated on identity of the natural enemies (especially parasitoids) of *B. tabaci* on cassava. The major gaps that need immediate attention include: i) understanding the diversity of natural enemies under different cropping systems and climatic conditions, ii) the development time, longevity and fertility of the principal parasitoids of *B. tabaci* iii) the oviposition behaviour of these parasitoids on cassava of different leaf hair density. The gaps identified in this review were the basis of this thesis research work.

CHAPTER THREE

FIELD POPULATIONS OF *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) AND ITS NATURAL ENEMIES ON CASSAVA, CASSAVA COMPONENT CROPS AND WEEDS

3.0 Introduction

Bemisia tabaci is a vector of cassava mosaic geminiviruses (CMGs) that cause the widely distributed cassava mosaic disease (CMD) in Africa and the Indian sub-continent. To control the disease, virus resistant varieties of cassava have been developed, multiplied and disseminated to farmers (Otim-Nape *et al.*, 1999). Recently, however, high whitefly populations have been recorded on virus-resistant varieties in areas that had epidemics of CMD in East Africa. The high whitefly population may be responsible for up to 50% yield loss (Legg, unpublished). This has called for a holistic approach to the management of the disease and the vector. Integrating biological control of the vector in the overall management strategy of the disease is one aspect of the holistic approach.

Among the natural enemies, 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.*, 1993). 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 predators of *B. tabaci* reported, but biological studies are often limited to laboratory observations and qualitative field data (Gerling *et al.*, 2001), and it is only *Delphastus catalinae* and *Serangium parcesetosum*, *Macrolophus caliginosu*, *Chrysoperla carnea* and *C. rufilabris* whose biological control potential has been assessed (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* sp.), and *Encarsia* nr. *mineoi*, and the abundance of and parasitism by both *E. mundus* and *E. sophia* varied between locations, whilst *Encarsia* sp. 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* and its natural enemies. The study reported here assessed 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) determined whether crops grown in association with cassava and weeds in and around cassava fields harbour *B. tabaci* and its natural enemies.

3.1 Material and methods

The study was conducted in three districts of Uganda, which were chosen to follow up on a previous study that had a long sampling interval and never took into account the predators and other plants in and around cassava gardens. 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.

3.1.1 Study area description

The survey in Bulisa was conducted between 36 331870.05 to 36 337019.37 (Easting) and 0238520.41 to 0244448.27 (Northing). This area receives a bimodal pattern of rainfall, with peaks in May-June and August–November. The altitude in the area is about 700m.a.s.l. Temperatures average 25.8°C, while mean annual rainfall average 1116mm. Cassava in is intercropped in this sub-county with mainly maize and beans. In Busukuma, the survey was conducted between 36 451933 to 36 461599 (Easting) and 0056089 to 0221061 (Northing). Busukuma is at an average altitude of 1150m.a.s.l. and receives a bimodal pattern of rainfall, with peaks in March-April and September - November. Temperatures average 22°C and mean annual rainfall is 1250mm. Cassava-cropping system in Busukuma is diverse, involving one or more of these crops: banana, maize, coffee, and beans. In Lyantonde, the survey was conducted between 36 290327.78 to 36 298549.73 (Easting) and 9948683.94 to 9960162.32 (Northing). Lyantonde lies at an altitude of 1200m.a.sl and has bimodal pattern of rainfall. Cassava in Lyantonde is intercropped with beans, maize, eggplants, banana, groundnuts and potato.

3.1.2 Data collection

Each sub-county was visited once a month for twelve months (Table 3.1). In each sub-county, five fields of three to six months old cassava 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 (Legg, 1995). 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. *Bemisia tabaci* adults were counted from five top most expanded leaves of cassava. 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 healthy and parasitized *B. tabaci* nymphs, 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. From each cassava leaf, healthy and parasitized whitefly were counted under a stereomicroscope on three alternating leaflets. In total, eighteen cassava leaflets were observed per plant. *Encarsia sophia* parasitised nymphs appeared as black pupal cases with meconia symmetrically located on both sides posteriorly, while *E. mundus* appeared orange with a shiny pupal skin (with the pupae having red eyes). After the observations, leaflets were put in emergence bottles (Plate 3.1) 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, ten of each component crop or twenty weed plants 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 adults of *B. tabaci* 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.

Plate 3.1. Emergence bottle used for rearing out adult parasitoids

Table 3.1. 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

3.2 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 because they were not normally distributed (Mead *et al.*, 2003) and analysed using General treatment structure of Genstat Release 3.2 (Lawes Agricultural Trust – IACR-Rothamsted). 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 unparasitised 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. Data on *B. tabaci* numbers and parasitoid abundance where plotted against mean monthly rainfall, relative humidity and temperatures.

3.3 Results

3.3.1 The incidence of *B. tabaci* on cassava

The numbers of nymphs and adults of *B. tabaci* varied significantly ($p<0.001$) between locations, being highest in Busukuma (nymphs: 187.9 ± 16.4, mean ± SE, adults: 73.5 ± 0.8), followed by Bulisa (nymphs: 106.1 ± 6.7, adults: 11.4 ± 0.8) and least in Lyantonde (nymphs: 47.4 ± 3.0, adults: 7.7 ± 0.6).

Significant ($p<0.001$) variations occurred in the numbers of *B. tabaci* nymphs and adults between sampling dates at each location (Fig. 3.1). The numbers of adult *B. tabaci* peaked in December 2003, March 2004 and October 2004 at Bulisa, while there was a peak in March 2004 at both Busukuma and Lyantonde, and another in October 2004 at Lyantonde. At Bulisa, nymph numbers increased from November 2003, peaked in December 2003, 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.

The numbers of adult *B. tabaci* were highest at four months after planting in Busukuma, whilst there was a reduction with crop age at Bulisa and Lyantonde (Bulisa: $P<0.001$; coeff. = -0.7; SE = 0.1 and Lyantonde: $P = 0.036$; coeff. = -0.1; SE = 0.1, Fig. 3.2 a). The numbers of nymphs were highest at three, four-five and five months after planting at Bulisa, Busukuma and Lyantonde, respectively (Fig. 3.2 b). 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 ($P>0.05$).

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

Eretmocerus mundus, *E. sophia* and an undescribed *Encarsia* species (hereafter referred to as *Encarsia* sp.) were recovered from *B. tabaci* on cassava (Fig. 3.3). *Eretmocerus mundus* and *E. sophia* were present in all the locations throughout the year, while *Encarsia* sp. was rare at all locations. *Eretmocerus mundus* was the most abundant parasitoid species at all the locations, followed by *E. sophia* and *Encarsia* sp. *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* sp. 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* sp. on most sampling dates at all locations (Fig. 3.3).

The relationship between the abundance of parasitoids with crop age was not consistent across locations (Fig. 3.4). 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. 3.5). Peak parasitism occurred in March 2004 at all the locations, and again in June 2004 and July 2004 at Lyantonde and Busukuma, respectively (Fig. 3.5).

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. 3.6). 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.

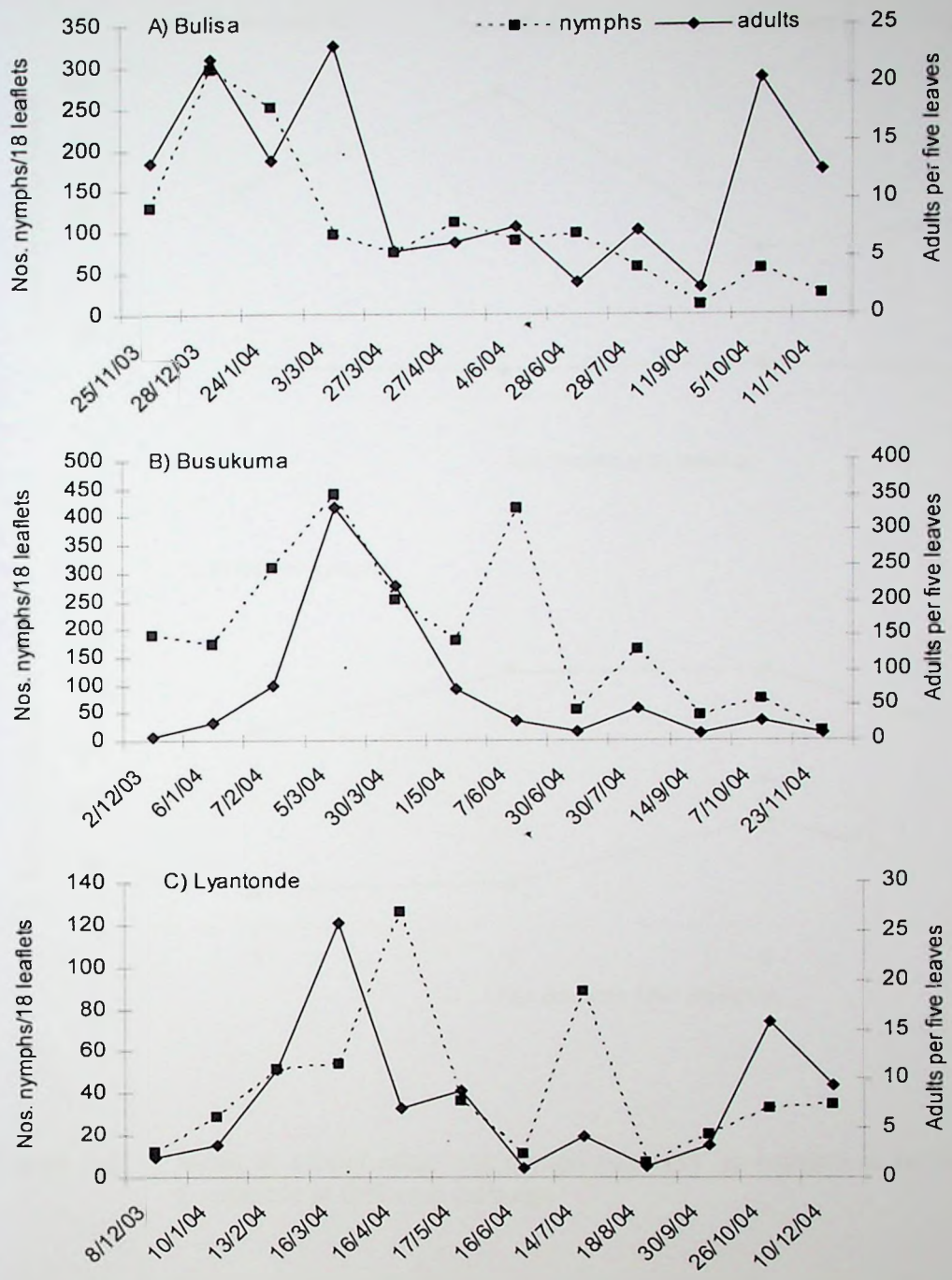

Figure 3.1: Mean *B. tabaci* nymph and adult numbers on cassava at Bulisa (A), Busukuma (B) and Lyantonde (C) from November 2003 to December 2004

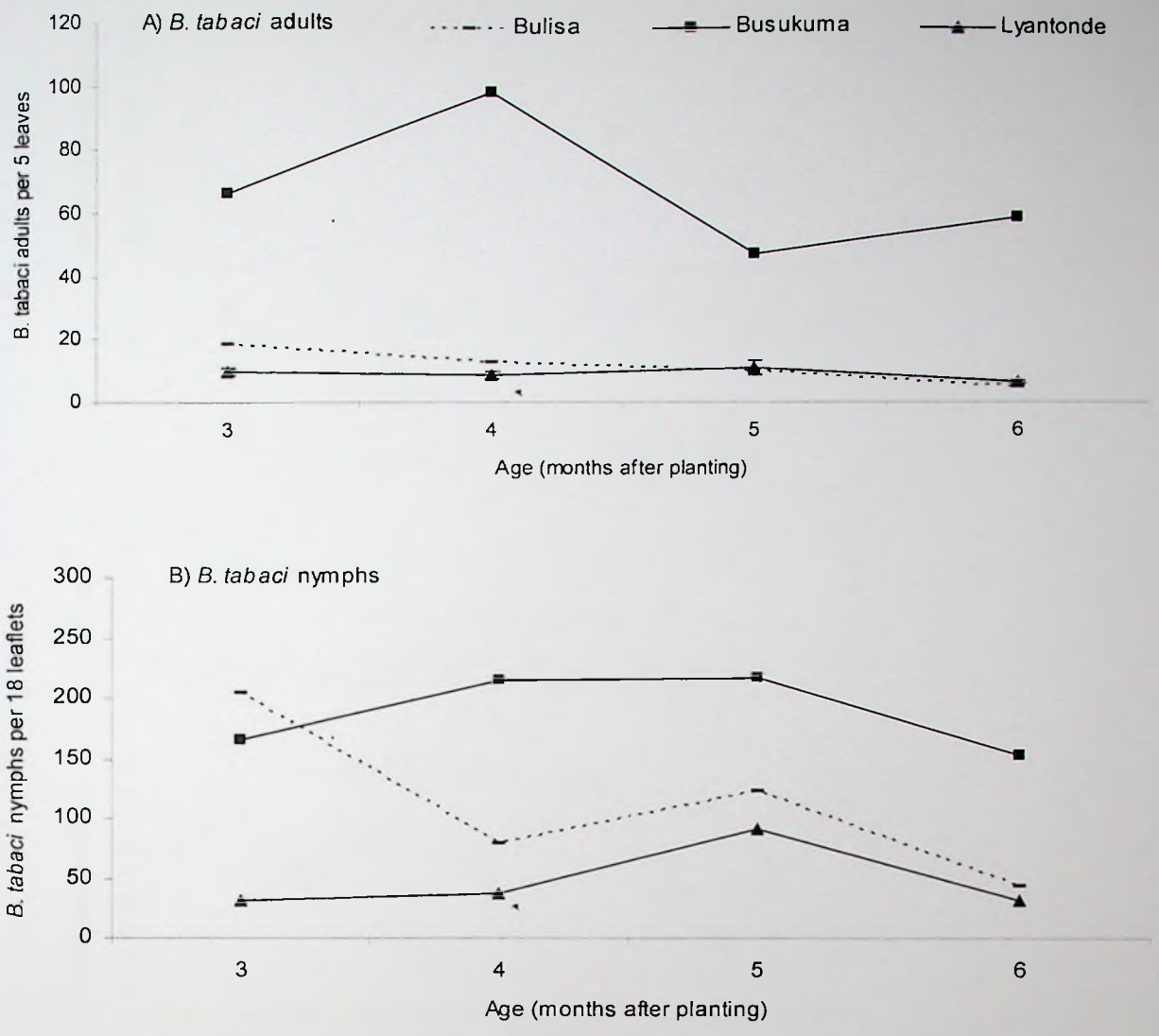

Figure 3.2: Mean *B. tabaci* adult and nymph numbers on cassava at Bulisa, Busukuma and Lyantonde at different crop age

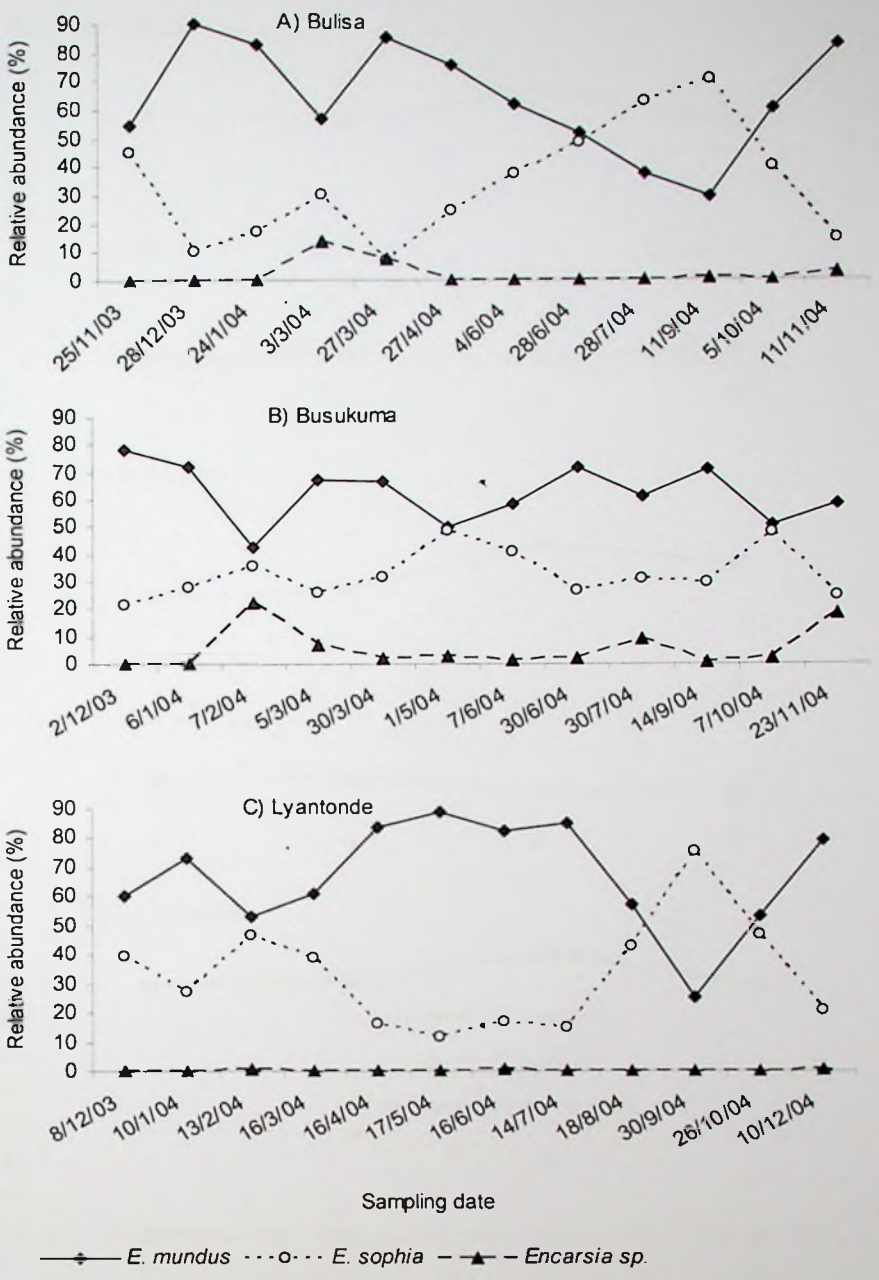

Figure 3.3. Species composition and abundance of *B. tabaci* parasitoids on cassava at Bulisa, Busukuma and Lyantonde from November 2003 to December 2004

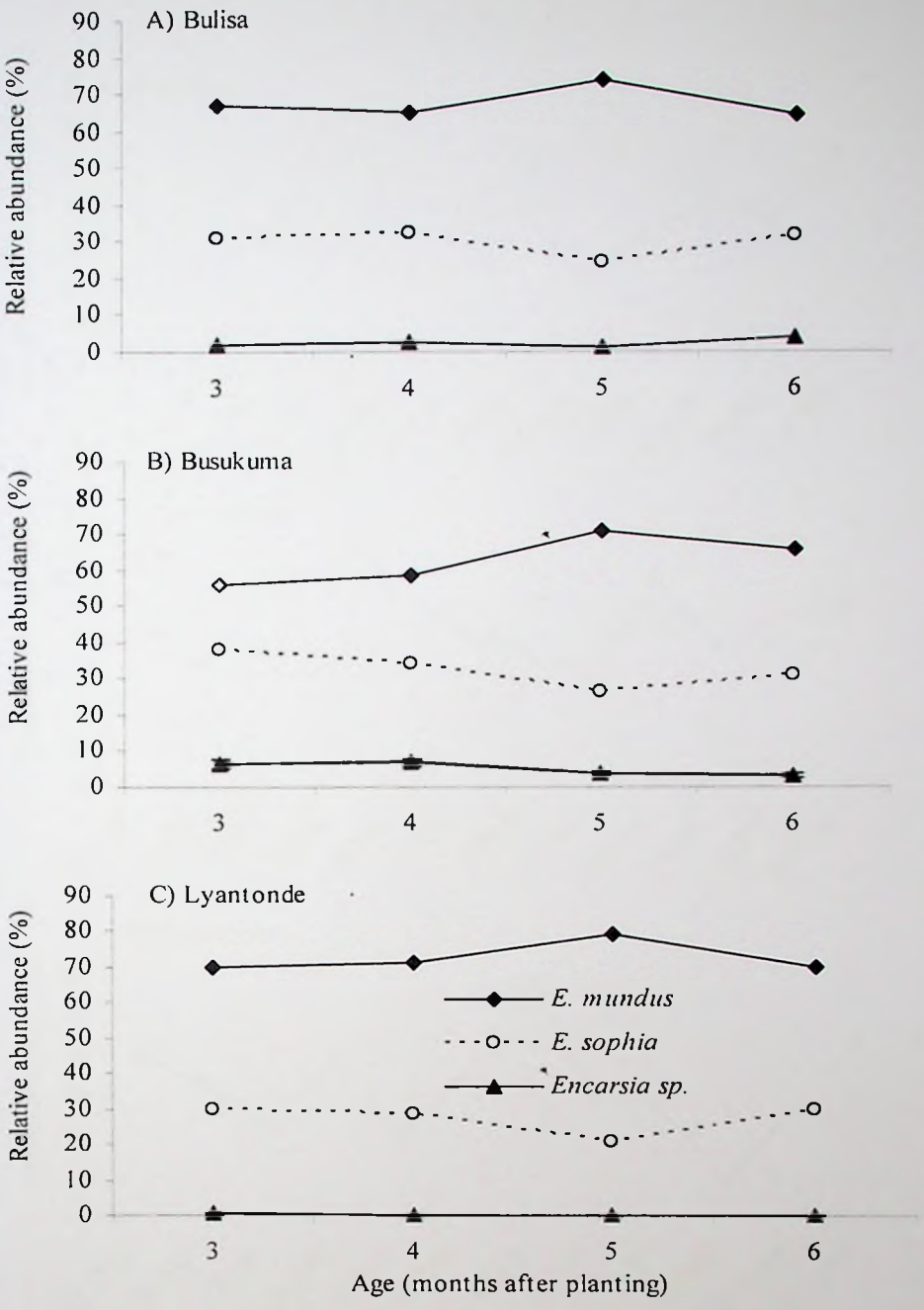

Figure 3.4. Species composition and abundance of *B. tabaci* parasitoids on cassava at Bulisa (A), Busukuma (B) and Lyantonde (C) at different crop ages

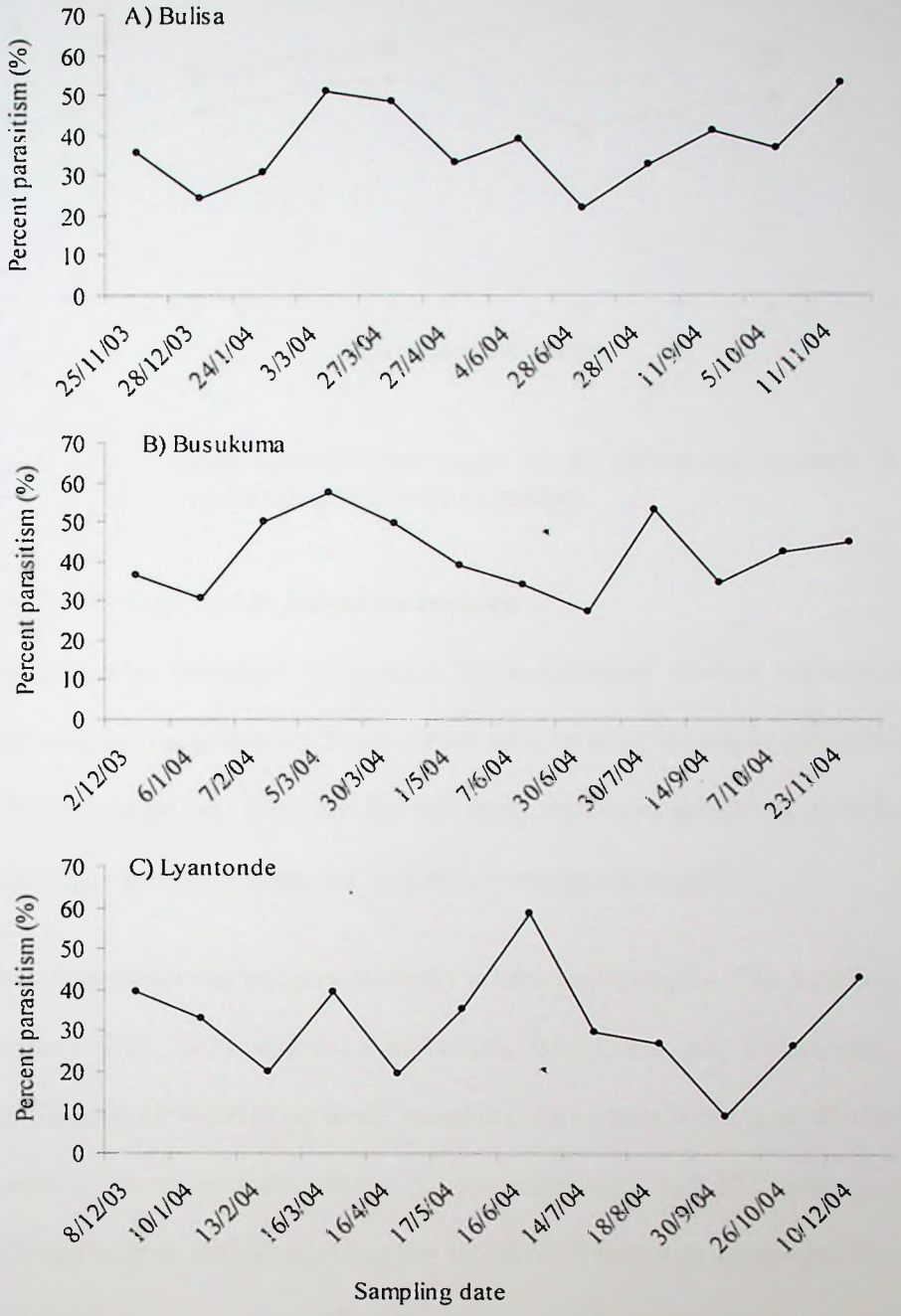

Figure 3.5. Mean percent parasitism of *B. tabaci* on cassava at Bulisa (A), Busukuma (B) and Lyantonde (C) from November 2003 to December 2004

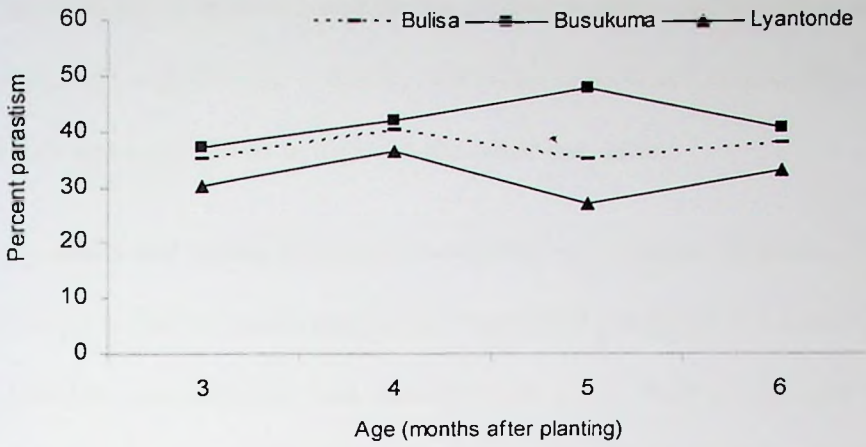

Figure 3.6. Mean percent parasitism of *B. tabaci* on cassava at Bulisa, Busukuma and Lyantonde at different crop ages

3.4 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 ants (Table 3.2). 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. 3.7), 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 *Serangium* sp. 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 *Serangium* sp. 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 3.2); *B. tabaci* was found trapped in 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. 3.6). 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. 3.7).

Table 3.2. Predators of *B. tabaci* sampled from cassava fields from November 2003 to December 2004

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

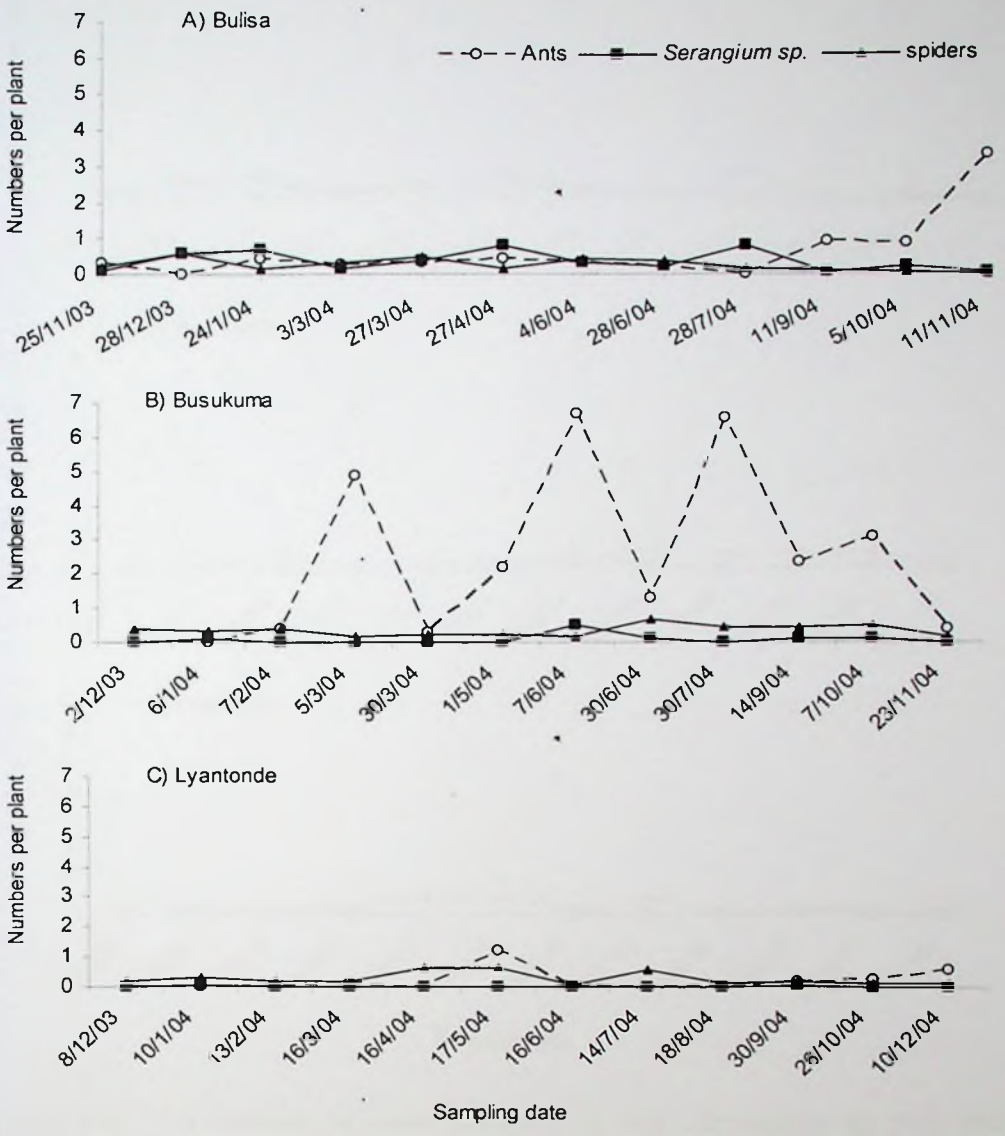

Figure 3.7. Mean numbers of ants, *Serangium* sp. and spiders at Bulisa (A), Busukuma (B) and Lyantonde (C) in cassava between November 2003 and December 2004

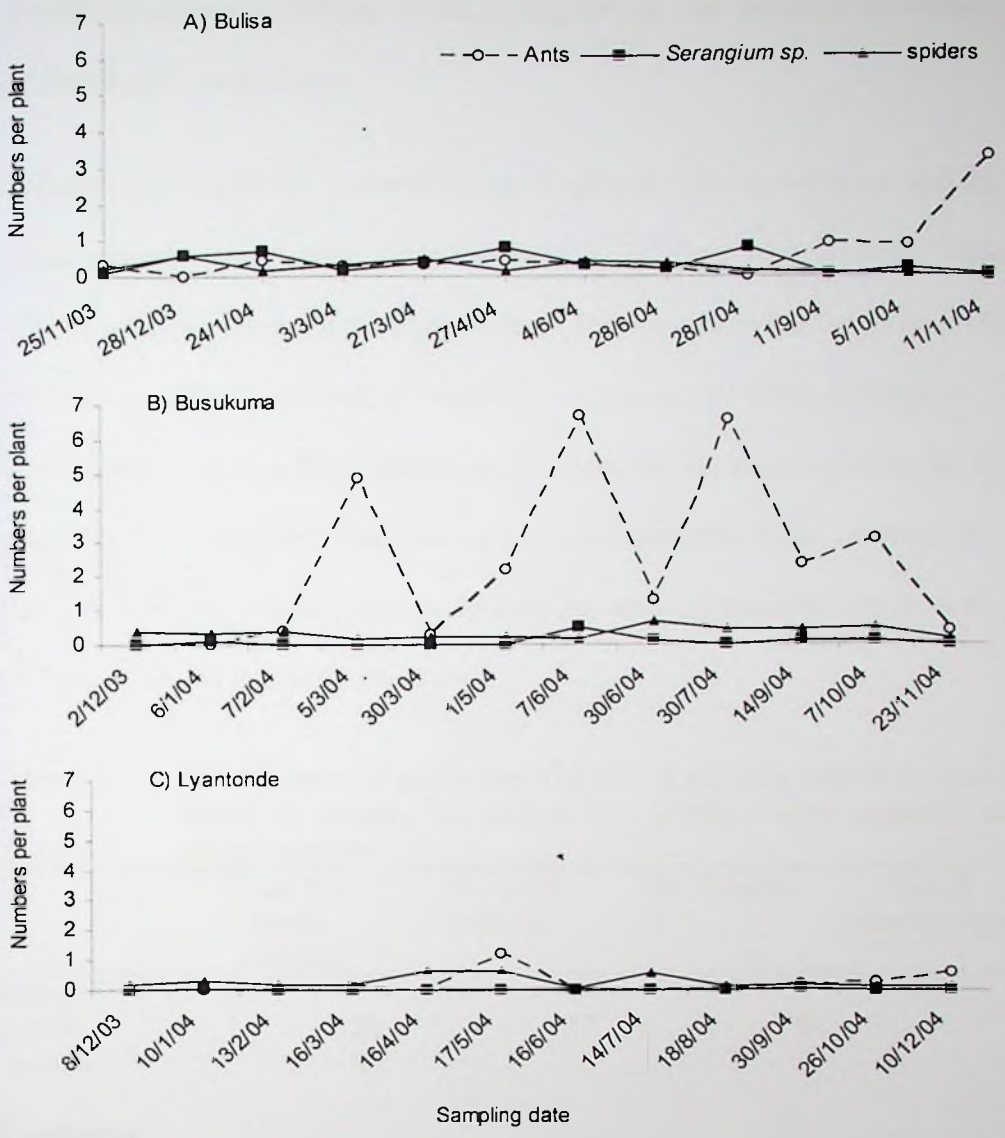

Figure 3.8. Variations in mean numbers of ants, *Serangium* sp. and spiders at Bulisa (A), Busukuma (B) and Lyantonde (C) in cassava at different crop ages

3.5 The incidence of whitefly and their natural enemies on crops grown in association with cassava and on weeds found in and around cassava gardens

Of the crosps grown in association with cassava, adult whiteflies were found on cowpea and cotton at Bulisa, beans and sweetpotato at Busukuma and Lyantonde (Table 3.3). 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.

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 recovered from whitefly on *Commelina* sp. and *Melhania* sp. at Bulisa, from *Bidens* sp., *Commelina* sp. and *Euphorbia* sp. at Busukuma, and on *Bidens* sp. at Lyantonde. *Encarsia sophia* was recovered from *Melhania* sp. at Bulisa. Spiders were recorded on *Bidens* sp. At Busukuma and Lyantonde, while ants were recorded on *Commelina* sp. At Bulisa (Table 3.4).

Table 3.3. The numbers of adults and nymphs of whitefly and their natural enemies on crops found in cassava gardens at the different sites 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

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

Table 3.4. Total number of whitefly adults and nymphs and their natural enemies on weeds found in and around cassava gardens at the different sites summed over all 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

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

3.7 Relationship between abundance of *B. tabaci* numbers and parasitoid abundance with weather parameters

The results revealed that *B. tabaci* numbers reduced with rainfall at both Bulisa and Busukuma (Figs. 3.9A-D), while there was no clear discernible effect of temperature on *B. tabaci* populations (Fig. 3.9E-H) although a lower number of *B. tabaci* was recorded when temperatures were highest at Bulisa (Fig. 3.9 E & G).

The abundance of *E. mundus* and *E. sophia* were highest at lower rainfall intensities at both Bulisa and Busukuma (Figs. 3.10A-D). There did not seem to be a marked effect of temperature on the abundance of *E. mundus* at Bulisa (Fig. 3.10E), but that of *E. sophia* was lowest at higher temperatures (Fig. 3.10H). At Busukuma, the abundance of both parasitoid species followed a similar pattern to that of variations in temperature (Fig. 3.10F & H).

Adult *B. tabaci* population were generally low at high relative humidity levels at both Bulisa and Busukuma (Fig. 3.11 A, B, E & F). The abundance of *E. mundus* had a positive relationship with relative humidity at Bulisa, while the converse was true for Busukuma. The abundance of *E. sophia* related negatively with relative humidity at Bulisa and Busukuma.

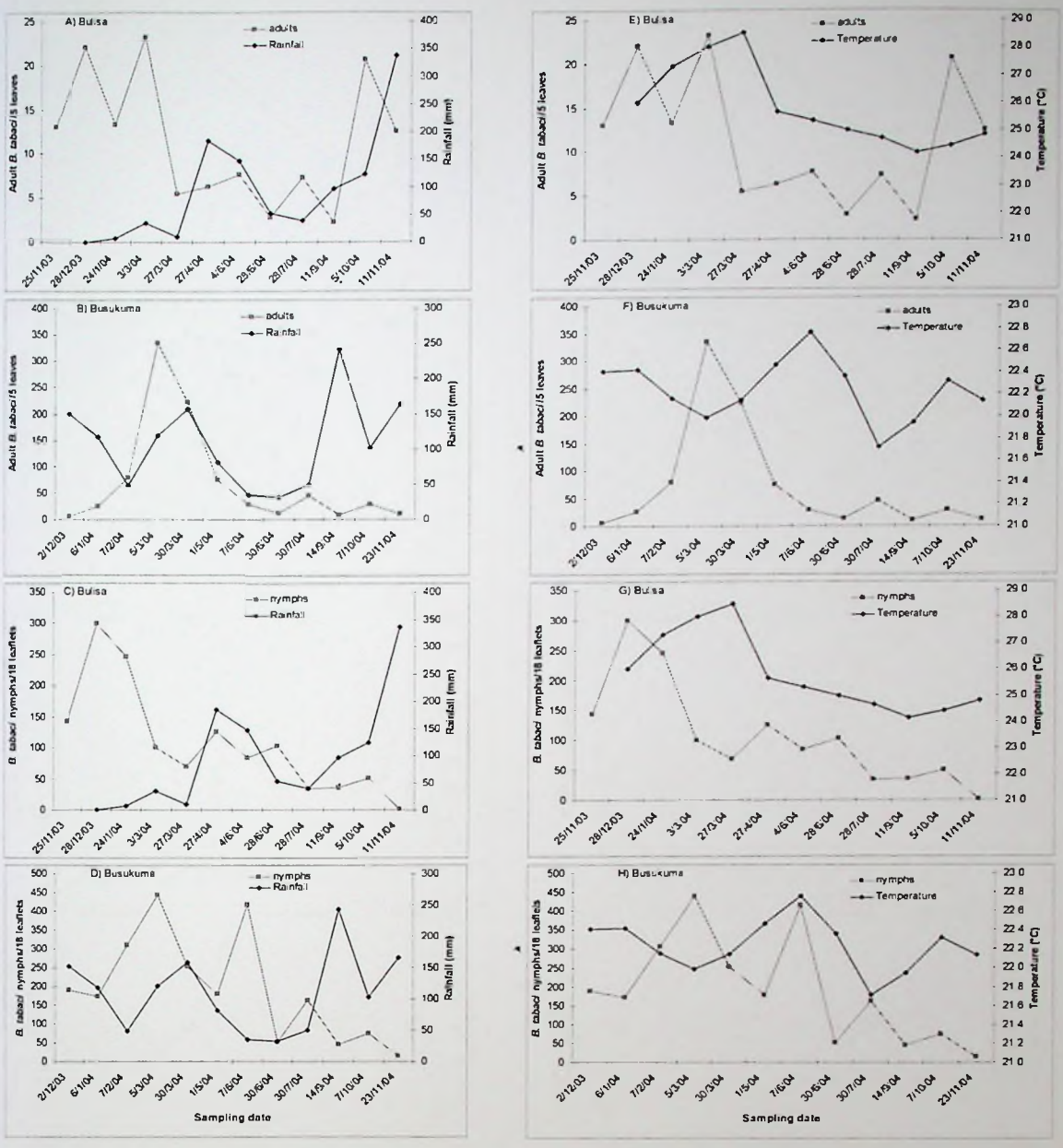

Figure 3.9. Variations in numbers of *B. tabaci* with rainfall (Left column) and temperature (right column) on cassava between November 2003 and December 2004

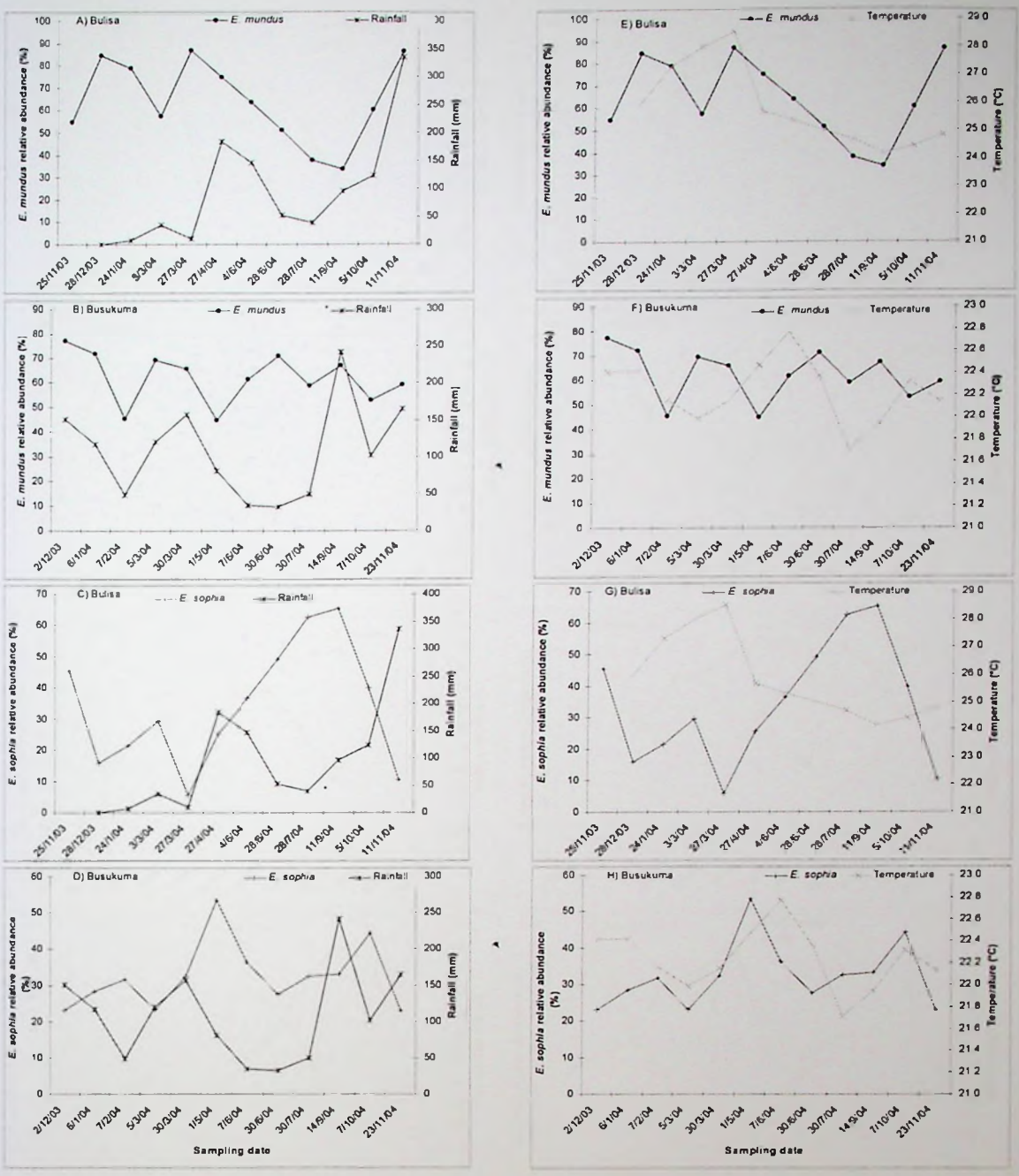

Figure 3.10. Variations in the abundance of major parasitoids *B. tabaci* on cassava with rainfall (Left column) and temperature (right column) between November 2003 and December 2004

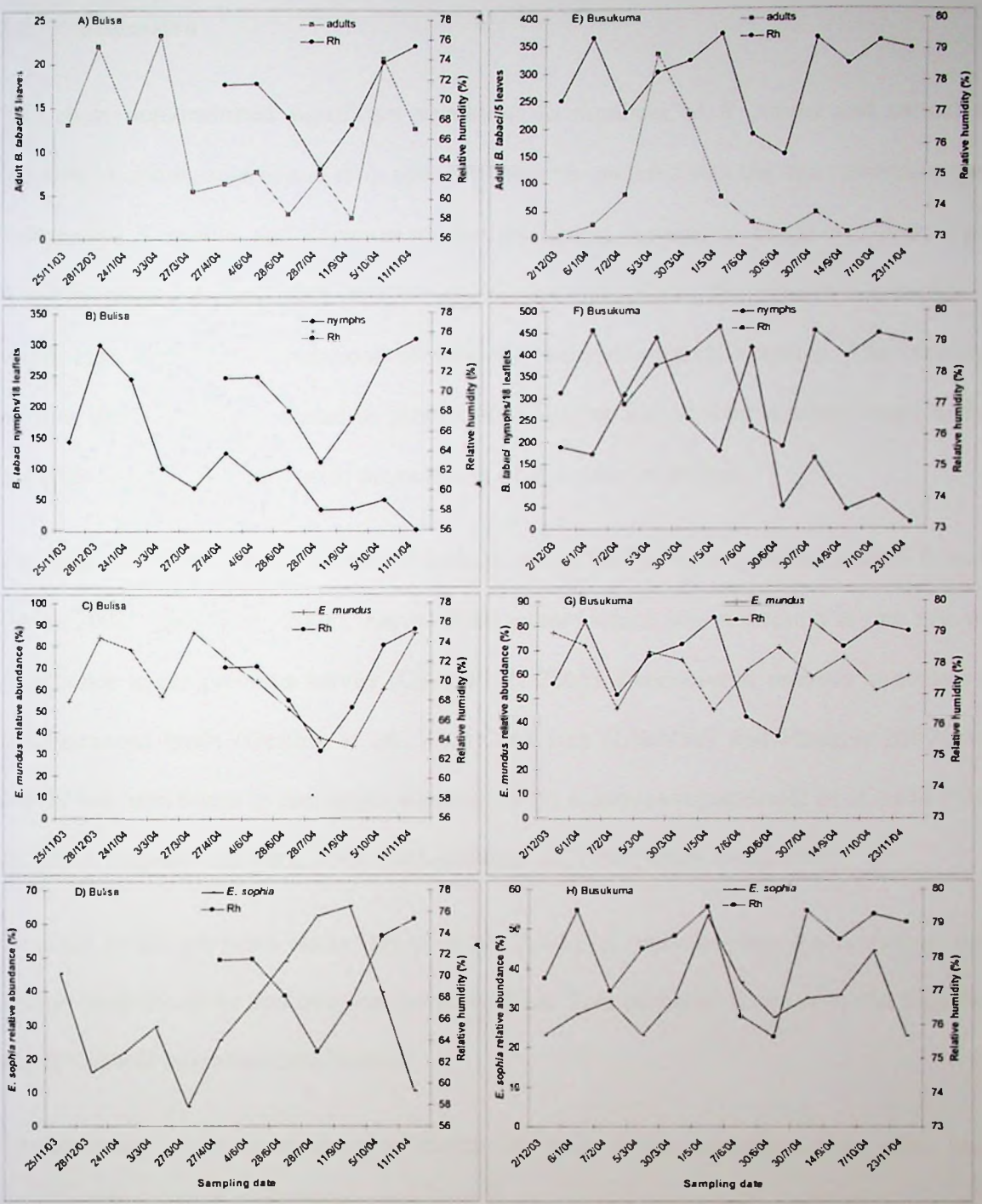

Figure 3.11. Variations in numbers of *B. tabaci* and abundance of major parasitoids with relative humidityin cassava between November 2003 and December 2004

3.8 Discussion

This study demonstrated significant variations in numbers of *B. tabaci* and natural enemies between locations, season and crop age. *Eretmocerus mundus* was the most abundant parasitoid, followed by *E. sophia*, and *Encarsia* sp. was the lowest in number. 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 relative humidity at Bulisa, whilst temperature and relative humidity related negatively with the numbers of *E. sophia* at Bulisa.

The three parasitoid species recovered from *B. tabaci* had previously been reported from Uganda (Otim, 2002; Otim *et al.*, 2005). *Encarsia* nr. *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; 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.

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, *Serangium* sp., 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., *S. jejunus*, *H.*

pallidicornis, and *S. 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, rainfall, 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 (Appendix 1) 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 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 (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 age at Bulisa followed a reduction in numbers of *B. tabaci* nymphs, whilst the increase in numbers of *Serangium* sp. with crop age

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 ages, except for ants at Busukuma (Figs. 3.7 & 3.8). These low numbers may demonstrate the limited 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, temperatures of 28°C did seem to lower *B. tabaci* populations at Bulisa. At Busukuma, peak *B. tabaci* populations did not necessarilty occur at lower or higher temperatures. Nevertheless, the conincidence of peak *B.*

tabaci population with peak temperature in June 2004 at Namulonge, might be because of the variety TME14 that was found to be heavily infested in one of the fields then. This demonstrates that temperatures within the studied range did not affect *B. tabaci* populations significantly. Higher temperatures however affected the abundance of *E. sophia* much more than *E. mundus,* suggesting that *E. mundus* is more heat tolerant than *E. Sophia.*

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). Thus, making assessment of the overall effect of rain difficult. This study however found found that *B. tabaci* numbers and parasitoid abundance were negatively affected by high rainfall and relative humidity, indicatuing that these two factors were more critical in shaping the pest and natural enemey populations. For clear information on the best temperatures for survival and reporoduction of the pest and natural enemies, assessment at varied levels of the climatic factors must be done under controlled conditions. This information can be important in population predictions.

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; 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, 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 cropping system (Appendix 2) 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. Even with properly designed experiements, there have been inconsistent results on the influence of intercrops on *B. tabaci* and CMD (Fargette & Fauquet, 1988; Ekpe & Chinaka, 2000). For instance, inconsistent results between the populations of the vector and disease

incidence, and similarity in severity levels between a susceptible cassava grown as an intercrop and cassava monocrop have been reported. Other authors have reported low *B. tabaci* populations and CMD incidence in cassava intercropped with cowpea, maize and groundnuts than in monocrop (Ahohuendo & Sarkar, 1995; Fondong *et al.*, 2002; Oneka *et al.*, 2002) and higher yields in the intercrop than the monocrop (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 monocrop (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.

The weed species found in and around sampled cassava fields did not support high numbers of whitefly and their natural enemies. 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 *B. tabaci* and its natural enemies are more abundant in cassava than on cassava component crops and weeds. *E. mundus* and *E. sophia* are the most abundant parasitoid species, where as ants, *Serangium* sp. and spiders are the most common predators. Thus, indicating 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.

Since the success of parasitoids depends on their biology and behaviour, the next two chapters therefore dealt with the study of biology and behaviour of the principal parasitoids, *E. mundus* and *E. sophia*. Work on the predators was done under a different study.

CHAPTER FOUR

LIFE HISTORY OF *Eretmocerus mundus* AND *Encarsia sophia* ON *Bemisia tabaci* attacking cassava

4.0 Introduction

The aphelinid parasitoids, *E. mundus* and *E. sophia* were the most abundant parasitoids of *B. tabaci* on cassava in the surveyed locations in Uganda with *E. sophia* being more abundant (Otim *et al.*, 2005). In the current study (chapter three), *E. mundus* was considerably more abundant than *E. sophia* in the same locations. 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.

4.1 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.

4.1.1 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. In order to initiate the colony, cassava plants of the variety, Nase 4 were grown in 1-litre buckets containing sterilized soil. When the plants reached 4-leaf stage, adult *B. tabaci* were introduced onto the plants. To obtain adults used in initiating the colony, nymphs were collected from cassava fields at National Crops Resources Research Institute, Namulonge (formerly Namulonge Agricultural and Animal Production Research Institute) in 2004 and held in emergence bottles as described in Chapter three. 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% RH (range, 25.3-91.7% RH)].

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

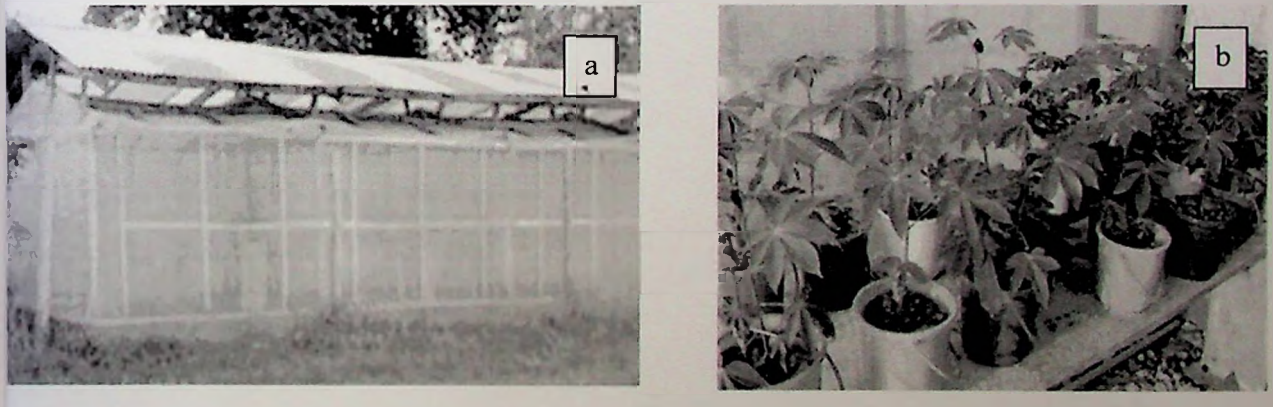

Plate 4.1. The screenhouse used for raising *B. tabaci* culture (a) and cassava plants grown in 1-litre buckets on a bench in the screenhouse (b)

4.2 Parasitoid life history

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

Twenty to thirty 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 (Plate 4.2). The experimental design was a completely randomised design. 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 time female parasitoids were introduced to *B. tabaci* infested leaflets to adult emergence.

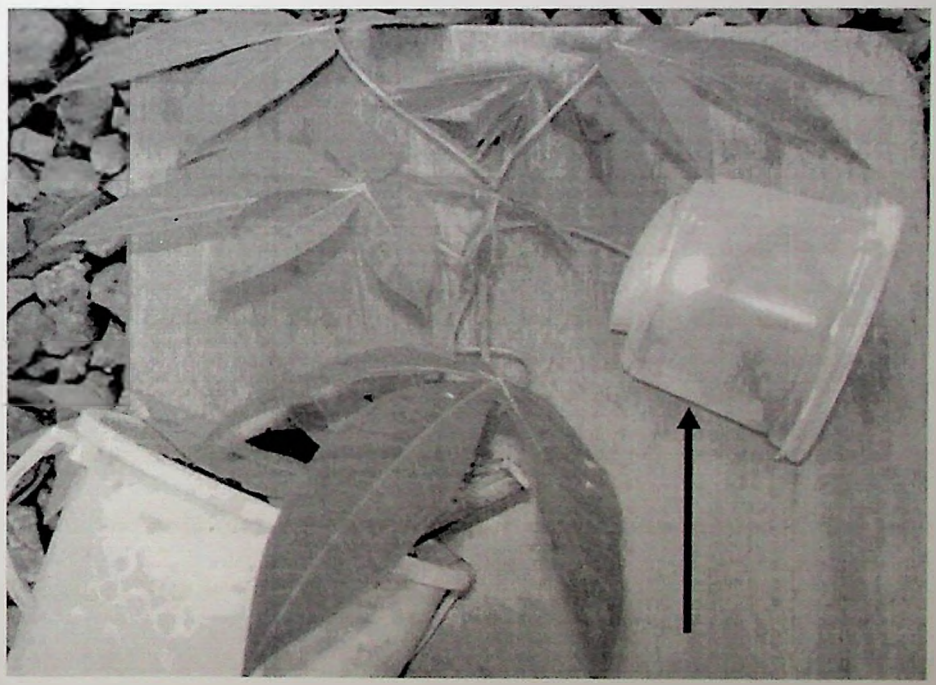

Plate 4.2. Leaf cage used for the development duration experiment

4.2.2 Longevity

Longevity refers to the period an organism lives. This was determined in the laboratory, under similar conditions as above. Parasitoids were maintained on two food sources, honey and *B. tabaci* nymphs. Where honey was used, 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) adult females of each parasitoid species were placed individually in each glass vial. Honey was renewed when necessary. The parasitoids' presence was 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.

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

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

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 cm long and 5 cm in diameter, fitted with a fine insect screen on one side and open on the other end. Upon release of the parasitoids, a whitefly infested cassava leaflet, containing a mixture of 50-60 second and third instar nymphs was inserted into the tube, and the tube opening was closed using a round piece of cut mattress foam (plate 4.3). The parasitoid couples were provided with new leaflets every day until the female died. If the parasitoids were found on the leaves during transfer, they were tapped off

onto glass before transferring the glass and parasitoids to another leaflet. If the male died within the first three days, another newly emerged 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 *petridishes* 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.

$$R_0 = \sum l_x . m_x$$

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

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

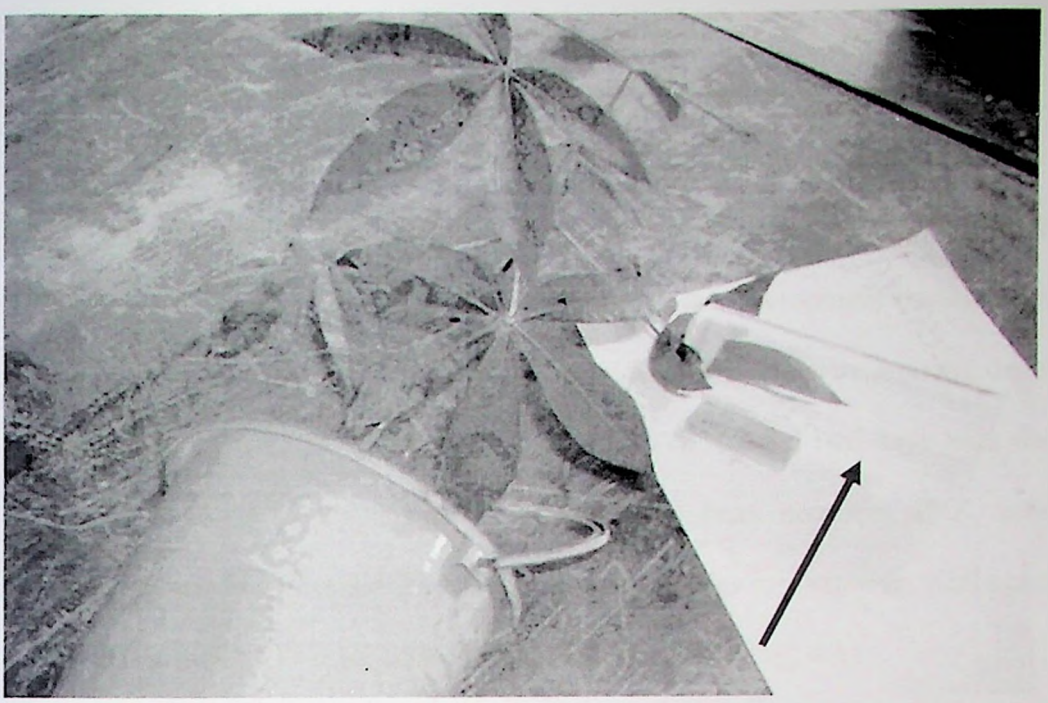

Plate 4.3. Glass tube used in the fertility experiment

4.3 Data analysis

Data on development duration and longevity met the assumptions of normality and homogeneity of variance and were not transformed. Data on fertility were square root transformed since they did not meet the assumptions. Longevity and fertility data were analysed using ANOVA, while development duration between species and sexes of species was analysed using T-test (Genstat Release 3.2, Lawes Agricultural Trust – IACR-Rothamsted). 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.

4.4 Results

4.4.1 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 4.1). *Eretmocerus mundus* developed two days earlier than *E. sophia* did. 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 (Fig. 4.1).

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

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

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

The initial egg count differed significantly (P<0.001) between species; *E. mundus* had an average of 35 ± 1.54 (mean ± SE) (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) in total progeny between species, and between female and male progeny of *E. mundus* (Table 4.2). *Encarsia sophia* however, produced

significantly (P = 0.012) more females than males (Table 4.2). Age-specific fertility was higher for *E. mundus* for the first 10 days, averaging *ca.* 2 daughters per female and gradually declining thereafter (Fig. 4.1 C). For *E. sophia*, the age specific fertility averaged one female per female per day and oscillated between one and two (Fig. 4.1 D).

A regression of fertility on female longevity showed that the longer the female lived, the more were the eggs laid (Fig. 4.1E &F)). On average, an ovipositing female *E. mundus* lived for 7 days (range, 2-12 d), whilst those that never laid lived for 3 days (range: 2–6 d). *Encarsia sophia* that laid lived for 13.8 d (range: 2-25), whilst those that never laid lived for 7.4 d (range: 2-25).

4.4.4 Demographic 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 (d) and 26.2 d for *E. mundus* and *E. sophia*, respectively and intrinsic rates of increase were 0.10 daughters per female per day for *E. mundus* and 0.11 daughters per female per day for *E. sophia*.

Table 4.1. Preimaginal development duration of *E. mundus* and *E. sophia* parasitizing *B. tabaci*

	Preimaginal development period, d			
	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	

Data within a column followed by same lower case letters are not statistically different (P> 0.05).

Table 4.2. 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	

Data within a column followed by same lower case letters are not statistically different (ANOVA; P> 0.05)

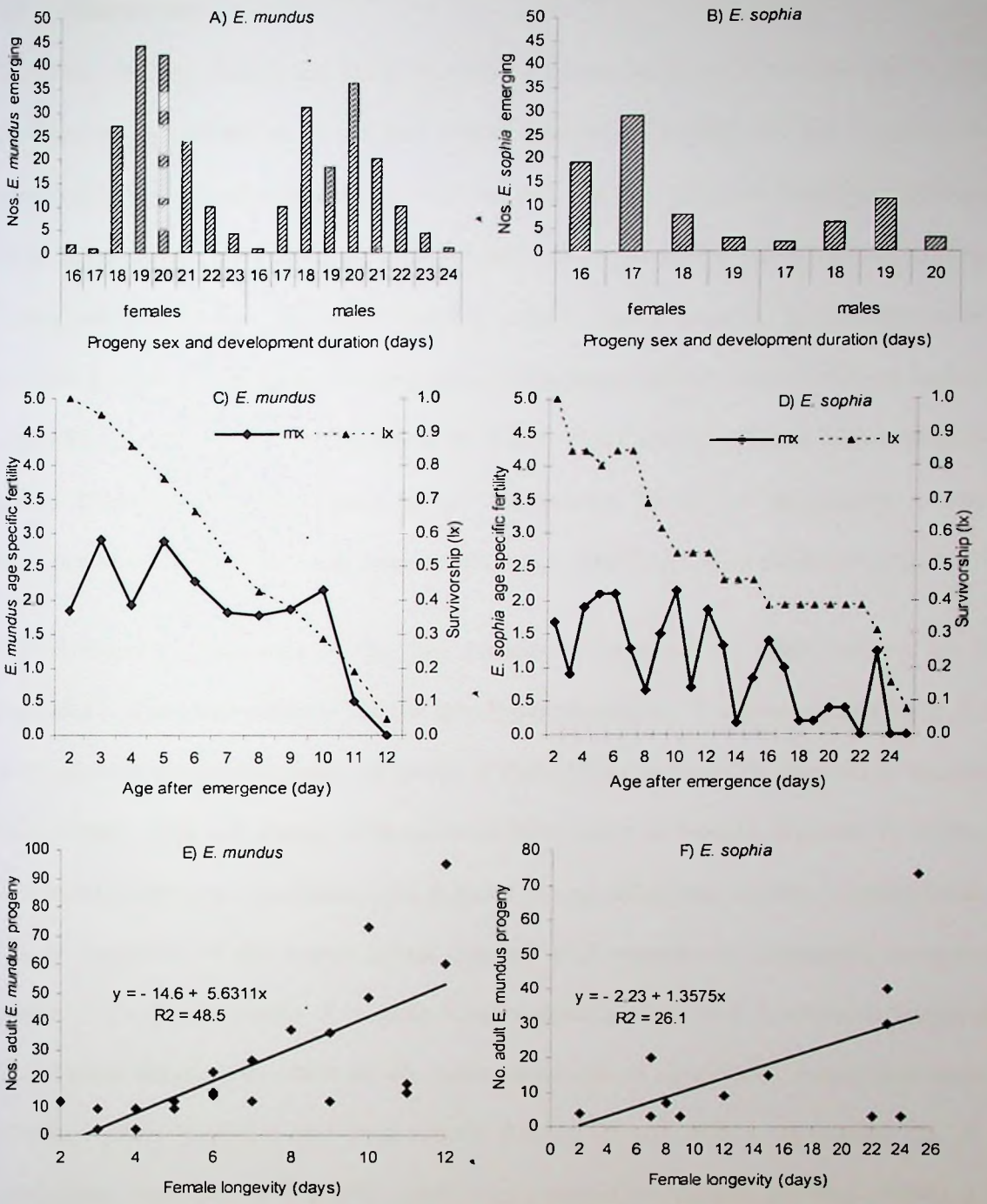

Figure 4.1. Variations in the development duration (top panel: A, *E. mundus*; B, *E. sophia*), age-specific fertility (mx) and survivorship of females (lx) during the fertility experiment (middle panel: C, *E. mundus*; D, *E. sophia*) and the relationship between numbers of progeny with female longevity (bottom panel: E, *E. mundus*; F, *E. sophia*) on *B. tabaci* attacking cassava

4.5 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 two days earlier than their females, moreover from hosts that were exposed to parasitoids for only 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 (Apendix 3, 4 & 5).

The development durations of the two parasitoids reported by other authors are listed in Appendix 3. The observation of shorter development duration *E. sophia* compared to *E. mundus* on *B. tabaci* was reported earlier (Kapadia & Puri, 1990) and may be because *E. mundus* has to mature many eggs and emerge with most of them ready to be laid, whereas *E. sophia* on the other hand is strongly synovigenic and matures its eggs after host feeding (Gerling *et al.*, 2001). This is supported by the higher initial eggload of *E. mundus* at emergence compared to *E. sophia*. In the present study, *E. sophia* females developed in 16.8 d, which is longer than the development duration reported for the same parasitoid on sowthistle, cotton and sweet potato (Gerling, 1983; Kapadia and Puri, 1990; Antony *et al.*, 2003) (Appendix 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 earlier development of male *E. sophia* compared with their female counter parts corroborate the findings of Antony *et al.* (2003) where the males developed in 11.3 – 15.1 d as opposed to the 12.1 – 14.6 days for the females. This may be a survival strategy to ensure that

males are available to fertilise females when they have just emerged in the otherwise strongly female-biased parasitoid species. 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 (Appendix 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. Legg's work was however not conducted under similar conditions to the present study and hence the need to evaluate the development of the parasitoids and *B. tabaci* under similar conditions.

The observations in the present study that male-producing eggs of *E. sophia* developed from healthy 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 Appendix 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 in both the presence and absence of hosts. Therefore, the reason for the similarity in the longevity of *E. mundus* in the presence and absence of 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 (Appendix 4). The longevity recorded for *E. sophia* in the current study is longer than the values reported by Heinz and Parella (1994) on two poinsettia varieties. This may be due to the use of plucked leaves in Heinz and Parella's work in contrast to the present work where new intact leaves were provided daily. 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 was 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 congener, *E. tricolor* on cabbage (85 eggs per female).

Many scenarios 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.*, 1996a & b; Ardeh, 2004). However, 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 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 (Appendix 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 = 0.10) are lower than the values for *E. sophia* (R_O = 15.1; T = 26.2; r_m = 0.11). 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 than values reported by Ardeh (2004) and Ghahari *et al.* (2005). The higher intrinsic rate of increase of *E. sophia* compared with that of *E. mundus* might partly be attributable to the greater longevity and 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 many more offspring than *E. sophia* produces. *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. Since differences in life history parameters are known to be associated with differences in searching and host selection behaviour of parasitoids, the next chapter examined the searching and oviposition behaviour of the two parasitoid species, *E. mundus* and *E. sophia* on two cassava varieties.

CHAPTER FIVE

THE SEARCHING AND OVIPOSITION BEHAVIOUR OF *Eretmocerus mundus* AND *Encarsia sophia* ATTACKING *Bemisia tabaci* ON CASSAVA

5.0 Introduction

Bemisia tabaci was found to be attacked by three aphelinid parasitoid species (chapter three). In declining order of abundance, these were *E. mundus E. sophia* and *Encarsia* sp. Parasitoid efficiency, as reflected in parasitism rates, is dependent, in part on foraging abilities. Parasitoids occur in a tritrophic environment in which the host plant in addition to the host insect have a profound effect on the parasitoids' behaviour and success (Price *et al.*, 1980). Thus, knowledge and understanding of the causes for a particular foraging behaviour are important in developing a successful biological control approach (Godfray, 1994). Since leaf hair density has been found to influence the searching behaviour of other *Encarsia* species (van Lenteren *et al.*, 1995), it was relevant to examine this parameter also in relation to our agroecosystem. Consequently, the influence of leaf pubescence on the searching and oviposition behaviour of the principal parasitoid species on cassava was studied.

5.1 Material and methods

5.1.1 Choice of plants used

The cassava genotypes used in this experiment were chosen because they support high whitefly populations. In addition, Nase 4 is glabrous (hairless), whilst the cassava clone, MM97/0245 is hirsute (hairy). Leaf hair characteristics were determined by counting the number of trichomes on the underside of 1 cm diameter (made using a number five cork borer) leaf discs under a stereoscopic microscope. The leaf discs were got from leaves of two months old cassava. Leaf

hair length was measured individually using a micrometer fitted in the microscope objective. A sample of 20 discs and 20 leaf hairs per disc was used. Leaf hair density was significantly higher ($P<0.001$) on the hirsute clone (average 88 ± 7.85 cm^{-2}, mean ± SE) (range, 13-163 cm^{-2}) than on the glabrous variety with no hairs at all. Similarly, the length of the leaf hairs averaged 3.3 ± 0.21 (2-4.9 mm) and was higher ($P<0.001$) on the hirsute clone.

5.1.2 Searching behaviour of *E. mundus* and *E. sophia* on cassava

The *B. tabaci* and parasitoids used in this experiment were obtained as described in chapter four. The searching behaviour of *E. mundus* and *E. sophia* was studied using approaches used by Headrick *et al.* (1995) in which parasitoids were allowed access to nymphs in a Petridish. In this study, however, direct visual observations were made unlike those of Headrick *et al.* (1995, 1996a & b) in which the females were videotaped and a built-in recorder on the tape was used to count the duration of events. The experimental arena consisted of cassava leaflets bearing 50-60 3rd instars nymphs, placed abaxial side up on moist filter paper in an 8.8 cm diameter *petridish*. The leaflets were held in position by a piece of masking tape. Single (0-24 hr old), naïve female parasitoids were picked from emergence bottles and placed individually on a leaflet in the *petridish*. The *petridish* was then placed under a binocular microscope. The experimental arena was illuminated using a fibre optic cold light source. Once exposed to the leaflet, the female had a choice of remaining to search, walking or flying away. The behaviours of each parasitoid were recorded using "The Observer®" computer software: (Program 5.0, Noldus Information Technology), for a maximum period of 1 hr, or until the parasitoid left the leaflet. In order to record the information on parasitoid activity on the computer, each behaviour was coded on the computer keyboard and the appropriate button was pressed when a paticular activity was initiated. The magnification was varied according to need, in order to clearly see what the

parasitoid was doing. The duration of the following behavioural elements were recorded: searching, host encounter, antennation, probing, host-feeding, feeding (on liquids on the leaf), standing (resting) on leaflet and host, and grooming. There were fifteen replicates for each species.

5.1.4 Data analysis

The females that left leaflets without searching searching were not included in the analysis. Behavioural data were entered into Microsoft Excel spreadsheets and collated for statistical analysis. Means were based on total frequencies of the behaviours summed over all trials for each parasitoid species on a variety or clone. Durations of the different behaviours were square root transformed and differences among mean durations were examined by ANOVA using Genstat Release 3.2 (Lawes Agricultural Trust- IACR-Rothamsted). Behavioural frequencies were used to create ethograms for the parasitoid species on the cassava variety or clone. The frequencies of behaviours were subjected to chi-square analysis for association between behaviours of the different parasitoids and cassava variety/clone. The percentage of time spent on different behaviours were used to create time budget graphs (Headrick *et al.*, 1995).

5.2 Results

5.2.1 Search Behaviour

When female parasitoids of either species were placed on whitefly-infested leaflets, most of them immediately began searching; six *E. mundus* females walked off the leaflets of the hirsute clone and two from the glabrous variety, while one *E. sophia* female left the leaflet of the hirsute clone, and five walked off the leaflets of the glabrous variety without searching. Searching females walked on the whitefly-infested leaflet, drumming with their antennae, i.e. alternately raising and lowering the tip of each flagellum to the substrate as they walked. A host encounter was recorded

when any part of the parasitoid's body met the whitefly nymph. Upon encountering a host, the females of *E. mundus* antennated it by drumming the lateral margins of the host while making clockwise and anti-clockwise movements (antennation). Such movements were rarely observed in *E. sophia*. On many occasions, the parasitoids stood still on the leaflet without performing any activity (standing on leaf) or stopped and fed on liquids on the leaf. Antennation was followed either by walking away from the host (antennal rejection) or by probing the host using the ovipositor. Probing involved a female positioning herself either perpendicular to the margin of the host (*E. mundus* females) or on top of the host (both parasitoids species) and contacting it with the basal portion of her abdomen. The ovipositor was then inserted either into the nymph through the vasiform orifice (*E. mundus*) or through the dorsal integument (*E. sophia*). Following probing, host-feeding was recorded and this typically involved feeding on the haemolymph from the injured part of the host. Host feeding was alternated with grooming, repeat probing, and then either feeding from the host or turning again for a new attempt to make a wound, or walking away. Occasionally, *E. mundus* females withdrew their ovipositor and drummed the dorsal part of the host with the hind legs. Feeding on liquids on the leaf was also recorded. The other behaviours that frequently occurred were grooming, which involved using the front legs to remove accumulated liquids from the antennae or using the hind legs to clean the wings and the metasoma; and standing still (resting) on the leaflet or host without performing any activity. Upon encounter with leaf hairs, the parasitoids, especially *E. mundus* females, stopped to groom before proceeding with the search.

5.2.2 Behavioural pathway

Ethograms for *E. mundus* and *E. sophia* females were developed from the recorded sequences. Frequencies are reported as a percent of the total number of times a particular behaviour was

recorded (Figs 5.1-5.4). The main behavioural pathway is shown from top to bottom on the left margin. The figures in the rectangles represent the total number of times a particular behaviour occurred. Arrows associated with the horizontal lines to the right of each main behavioural pathway components indicate the frequencies of the behaviours that followed or led to the behaviour on the left. Other sequences not associated with the main behavioural components account for the situations where the percentages do not add up to 100.

5.2.2.1 Behavioural pathway of *E. mundus*

When placed on leaflets of the hirsute clone, females of *E. mundus* began searching (Fig. 5.1) which was followed by resting on the leaflet, host encounters and feeding on liquids on the leaf, which represented 54%, 38% and 4% of the total search frequencies, respectively. Host encounters led to antennation 100% of the time and antennation led to probing 73% of the time. Antennation led to resumption of searching 10% of the time, grooming 3% of the time and, to resting on the host and feeding on liquids on the leaf, 1% each. Probing was followed by searching (39% of the time), antennation (22% of the time), grooming (20% of the time), drumming (18% of the time) and resting on the leaflet (1% of the time).

On the glabrous variety, searching by *E. mundus* females was followed by resting on the leaf 50% of the time and host encounters 47% of the time (Fig. 5.2). Host encounter was followed by antennation and resting on the leaflet 90% and 7% of the time, respectively. Antennation led to probing and searching for 61% and 7% of all antennations, respectively. The probed hosts were antennated 35% of the time, or the females resumed searching (23%), or drummed (11%). Antennation also led to grooming (2%) and resting on the leaf (1%), resting on host (2%) and feeding on liquids on the leaf (1%). Host-feeding followed probing 2% of the time and led to

antennation, grooming, searching and resting on the host 45, 31, 16 and 2% of the time, respectively.

5.2.2.2 Behavioural pathway of *E. sophia*

The females of *E. sophia* searching for hosts on the hirsute clone, rested 50% of the time, encountered hosts 26% of the time and fed on liquids on the leaf 19% of the time (Fig. 5.3). Host encounter was followed by antennation 96% of the time and the remaining 4% were divided between resting on the leaflet and on the host. Antennation led to one of five behaviours; probing 37% of the time, host-feeding 34% of the time, searching 15% of the time, grooming 7% of the time, resting on the host 5% of the time and feeding on liquids on the leaf 2% of the time. Probed hosts were either antennated 45% of the time, or probing was followed by grooming and searching, represented by 36 and 14% of all probes, respectively. Host-feeding followed probing for 2% of the time and led to probing 35% of the time, searching (20% of the time), grooming (20% of the time), antennation (15% of the time) and resting on the leaflet (2% of the time) and resting on the host (4% of the time). Host-feeding was also followed by feeding on liquids on the leaf 2% of the time.

Searching by *E. sophia* females on the leaflets of the glabrous variety led to resting on the leaf, host encounter and feeding on liquids on the leaf for 63, 25 and 6% of all searches, respectively (Fig. 5.4). The females antennated 82% of the encountered hosts, rested on the leaflet 8% of the time following host encounter or, groomed (3%), rested on host (5%) or host-fed (3%). Antennation led to probing 39% of the time, host-feeding 21% of all antennations, searching 14% of the time, resting on the leaflet 11% of the time, grooming and resting on host 7% of all antennations in each case. Antennation was also followed by feeding on liquids on the leaf 2% of

the time. The probed hosts were either reassessed 46% of the time, or probing was followed by grooming and searching, 31 and 23% of the time, respectively.

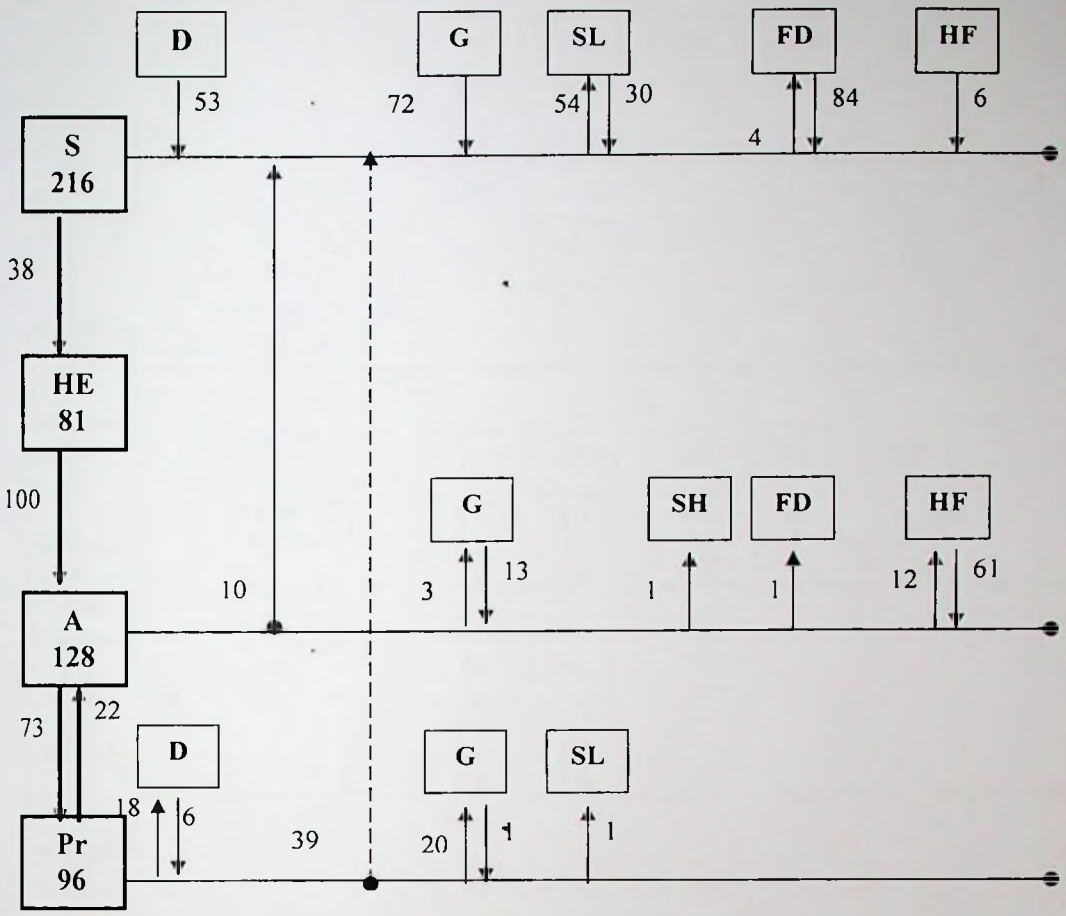

Figure 5.1. Ethogram for behaviours of *E. mundus* attacking *B. tabaci* on the hirsute cassava clone, MM97/0245. The main behavioural pathway begins at the top left, and moves down the left margin. The figures in the rectangles represent the total number of times a particular behaviour occurred. Arrows indicate subsequent behavioural events and the associated numbers indicate the percent frequency of each observation, summed over all trials. A-Antennation, D-drumming on host, FD-feeding liquids on the leaf, G-grooming, HE-Host encounter, HF-Host feeding, Pr-Probing, S-searching, SH-standing on host and SL-standing on leaf. Dotted lines are used for arrows that cross lines of the main behavioural events.

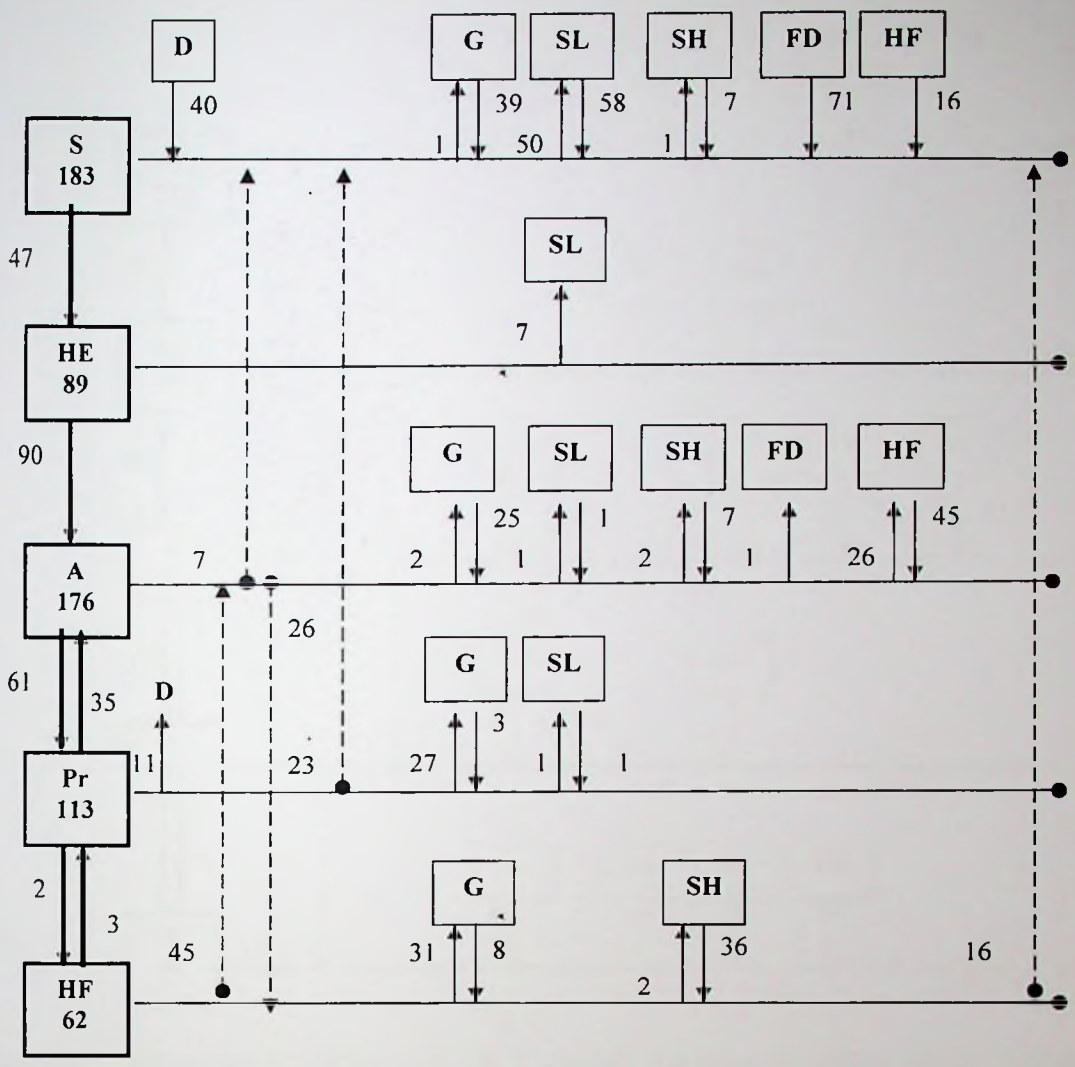

Figure 5.2. Ethogram for behaviours of *E. mundus* attacking *B. tabaci* on the glabrous variety, Nase 4. The main behavioural pathway begins at the top left, and moves down the left margin. The figures in the rectangles represent the total number of times a particular behaviour occurred. Arrows indicate subsequent behavioural events and the associated numbers indicate the percent frequency of each observation, summed over all trials. A-Antennation, D-drumming, FD-feeding on liquids on the leaf, G-grooming, HE-Host encounter, HF-Host feeding, Pr-Probing, S-searching, SH-standing on host and SL-standing on leaf. Dotted lines are used for arrows that cross lines of the main behavioural events.

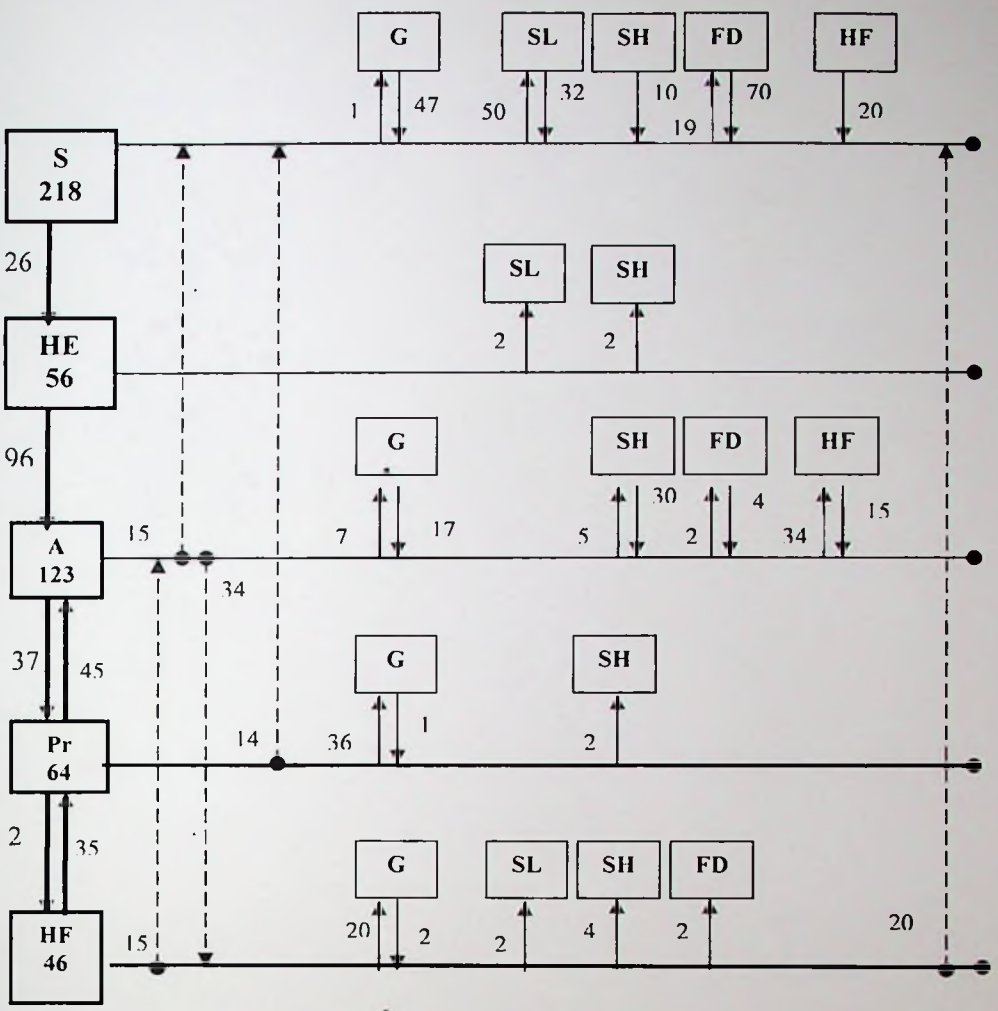

Figure 5.3. Ethogram for behaviours of *E. sophia* attacking *B. tabaci* on the hirsute clone, MM97/0245. The main behavioural pathway begins at the top left, and moves down the left margin. The figures in the rectangles represent the total number of times a particular behaviour occurred. Arrows indicate subsequent behavioural events and the associated numbers indicate the percent frequency of each observation, summed over all trials. A-Antennation, D-drumming, FD-feeding on liquids on the leaf, G-grooming, HE-Host encounter, HF-Host feeding, Pr-Probing, S-searching, SH-standing on host and SL-standing on leaf. Dotted lines are used for arrows that cross lines of the main behavioural events.

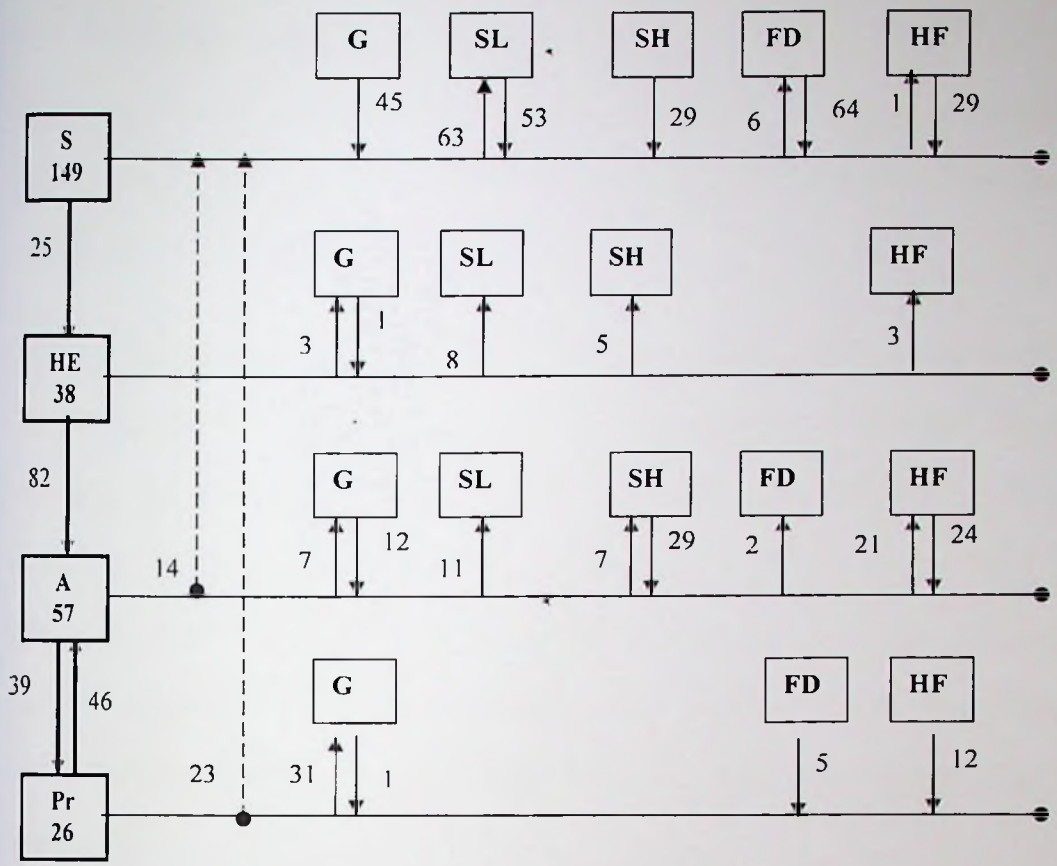

Figure 5.4. Ethogram for behaviours of *E. sophia* attacking *B. tabaci* on the glabrous variety, Nase 4. The main behavioural pathway begins at the top left, and moves down the left margin. The figures in the rectangles represent the total number of times a particular behaviour occurred. Arrows indicate subsequent behavioural events and the associated numbers indicate the percent frequency of each observation, summed over all trials. Antennation, D-drumming, FD-feeding on liquids on the leaf, G-grooming, HE-Host encounter, HF-Host feeding, Pr-Probing, S-searching, SH-standing on host and SL-standing on leaf. Dotted lines are used for arrows that cross lines of the main behavioural events.

5.2.3 Frequency and duration of events

In total, 826 and 881 behavioural events were recorded for *E. mundus* on the hirsute clone and glabrous variety, and 887 and 514 for *E. sophia* on the hirsute clone and glabrous variety, respectively.

The observed frequencies of antennation, grooming, probing, host-feeding, and resting on the host differed significantly ($P<0.05$) from what was expected; in all these behaviours (except grooming), the observed frequencies were less than expected on the hirsute clone and more than expected on the glabrous variety for *E. mundus* females. Whilst for *E. sophia*, the observed frequencies were more than expected on the hirsute clone and less than the expected on glabrous variety. The observed frequencies of searching, host encounters, feeding on liquids on the leaf and resting on the leaf did not differ significantly ($P>0.05$) from what was expected by chance (Table 5.1).

For *E. mundus,* the mean duration of antennation, probing, grooming and resting on the leaf was significantly ($P<0.05$) higher on the glabrous than on the hirsute clone, whilst the duration of searching, host-feeding, feeding on liquids on the leaf, and resting on the host did not differ significantly ($P>0.05$) between the variety and clone (Table 5.2).

For *E. sophia*, the mean duration of antennation, host-feeding, and feeding on liquids on the leaf was significantly higher on the glabrous than on the hirsute clone, whilst the duration of resting on the host was significantly longer on the hirsute clone than on the glabrous variety (Table 5.2). The duration of searching, probing, grooming and resting on the leaf did not differ significantly between the variety and clone.

Table 5.1. Frequencies of behaviours of *E. mundus* and *E. sophia* females on cassava

	E. mundus		*E. sophia*		
	Hirsute	Glabrous	Hirsute	Glabrous	Chi-values
Searching	216	183	218	149	2.16
Antennation	128	176	123	57	31.2***
Resting on the leaf	127	114	144	131	0.01
Grooming	107	108	142	67	14.44***
Probing	96	113	64	26	16.03***
Host encounter	81	89	56	38	3.45
Feeding on liquids on the leaf	31	7	74	22	0.32
Host-feeding	18	62	46	17	36.38***
Drumming	17	15			0.12
Resting on the host	5	14	20	7	10.25***

*** Denotes that the means were significant at 0.001 probability level

Table 5.2. Duration (in seconds) of behaviours of *E. mundus* and *E. sophia* females on cassava

	E. mundus		*E. sophia*	
	Mean ± SE		Mean ± SE	
Behaviour	Hirsute (826)	Glabrous (887)	Hirsute (889)	Glabrous (514)
Searching	12.5 ± 0.6a	11.0 ± 0.6a	13.9 ± 0.6a	14.4 ± 0.6a
Antennation	6.0 ± 0.4a	11.3 ± 0.7b	11.1 ± 0.6a	15.9 ± 1.4b
Resting on the leaf	6.9 ± 0.8a	22.3 ± 3.6b	31.8 ± 4.7a	30.7 ± 3.4a
Grooming	15.7 ± 2.0a	21.8 ± 1.9b	26.8 ± 1.6a	24.8 ± 1.7a
Probing	56.8 ± 4.6a	88.0 ± 7.2b	87.6 ± 7.1a	92.5 ± 12.7a
Feeding on leaf nectarines and water	25.4 ± 5.7a	48.2 ± 14.6a	47.8 ± 5.4a	85.2 ± 20.7b
Host-feeding	201.3 ± 131.7a	149.3 ± 24.4a	105.1 ± 15.2a	169.7 ± 27.2b
Drumming	10.0 ± 1.5a	10.7 ± 1.7a		
Resting on the host	17.0 ± 5.6a	3 3.3 ± 9.0a	41.0 ± 6.2b	17.5 ± 3.2a

Means in a row, for each parasitoid species, followed by the same letters are not significantly different. Figures in brackets associated with cassava genotypes are the numbers of times behaviours were performed on the different genotypes

5.2.4 Time budget of the different parasitoids

The time budget for each parasitoid species did not differ markedly between the variety and clone; *E. mundus* females spent most of their time probing and host feeding on the variety and clone (Fig. 5.5); these were followed by walking and grooming on the hirsute clone; searching, antennation, grooming and resting on the leaf on the glabrous variety. *Encarsia sophia* spent the greatest percentage of time probing on the hirsute clone, followed in decreasing order by host-feeding, resting on the leaf, grooming, feeding on liquids on the leaf, searching, antennation and resting on the host (Fig. 5.5). On the glabrous variety, *E. sophia* females spent most of the time resting on the leaf, followed by host-feeding, probing, searching, feeding on liquids on the leaf, grooming, antennation and resting on the host. When summed over variety and clone, *E. mundus* spent most of the time probing and host-feeding in contrast to *E. sophia*, which spent more time resting and feeding on liquids on the leaf (Fig. 5.6). There were similarities in the percent of time spent searching, antennating and grooming.

Figure 5.5. Time budgets of *E. mundus* and *E. sophia* attacking *B. tabaci* on cassava

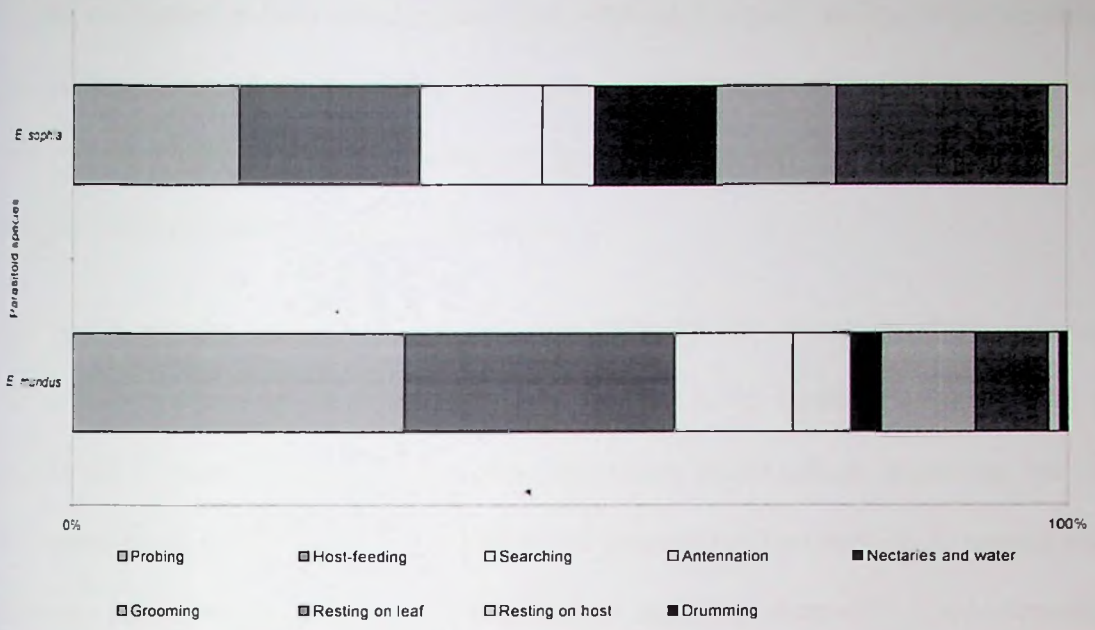

Figure 5.6. Time budgets of *E. mundus* and *E. sophia* attacking *B. tabaci* summed over cassava variety and clone

5.3 Discussion

There were similarities in the generalised behavioural pathway of *E. mundus* and *E. sophia* on the variety and clone. However, some variations occurred in the numbers of females remaining to search, the frequency and mean duration of behaviours and time budgets. Whereas 40% and 13% of *E. mundus* left the leaves of the hirsute clone and glabrous variety without encountering hosts, respectively, the corresponding percentages for *E. sophia* were 6.7% and 33%. *Eretmocerus mundus* antennated, rested on the leaf, groomed and probed for longer durations on the glabrous variety than on the hirsute clone, whilst *E. sophia* antennated, fed on liquids on the leaf, and host-fed for longer durations on the glabrous variety than on the hirsute clone. *Encarsia sophia*, however, spent a significantly longer time resting with legs on the host on the hirsute clone than on the glabrous variety. The percentage of time spent by *E. mundus* probing and host-

feeding was higher on both cassava genotypes, whereas *E. sophia* spent a large percentage of its time feeding on liquids on the leaf, grooming and standing still on the leaf. Antennal drumming that is reported to be peculiar to *Eretmocerus* species (Foltyn and Gerling, 1985; McAuslane and Nguyen, 1996) was also observed in this study.

The more *E. mundus* females that left the leaves of the hirsute clone than of the glabrous variety was probably because of the presence of leaf hairs. Similarly, Headrick *et al.* (1996a) observed that 70% of *E. eremicus* left the leaves of melon (a hairy plant) without searching, but concluded that parasitism in the field is more related to the propensity of parasitoids to remain and search hosts on a particular plant species. The reasons why higher numbers of *E. sophia* females left the leaves of the glabrous variety than those of the hirsute clone are not discernible, but may be due to differences in the characteristics of the varieties other than pubescence.

The females of *E. mundus* that remained searching, spent almost 80% of their time-budget searching, assessing hosts, probing and host-feeding on both cassava genotypes, whilst similar females of *E. sophia* spent much less time searching, assessing, probing and host-feeding when compared to *E. mundus* females and about 30 to 35% of the time resting and feeding on liquids on the leaf. This may explain why *E. sophia* females probed hosts less frequently when compared to *E. mundus*. A study on the initial egg load showed that *E. sophia* and *E. mundus* had an average of 3 and 35 mature eggs on emergence and this could have influenced the parasitoids' willingness to search. Thus, the readiness of *E. mundus* to search when released on leaves may be because it emerges with most of its eggs ready to be laid, whereas *E. sophia* emerges with few eggs, which might not cause a strong oviposition pressure like in *E. mundus*. Additionally, *E. sophia* is strongly synovigenic and must host-feed in order to lay (Gerling, 1990).

For the *E. mundus* females that remained searching on the hirsute clone, the observed frequencies of antennation, probing, host-feeding, grooming, and resting on the leaves were significantly lower than would be expected by chance and may be attributable to the influence of leaf hairs and the females that left the leaves without searching. Unlike for *E. mundus*, the observed frequencies of antennation, probing, host-feeding, grooming, and resting on the host were generally higher than expected for *E. sophia* on the hirsute clone. This may also be partly because six *E. sophia* females left the leaves without searching. It could also be possible that leaf hairs slowed down the parasitoids and stimulated them to search more. Although the movement of *E. mundus* females was interrupted by the presence of leaf hairs, they generally spent less time resting on the leaves of the hirsute clone. This might, in part, explain the high encounter rates for *E. mundus* on the hirsute clone than on the glabrous variety.

The searching and oviposition behavioural pathways of both parasitoid species were similar, except when the parasitoids encountered leaf hairs. Upon such encounters, females of both species stood for a while and groomed before resuming the search. *Eretmocerus mundus* appeared to be more affected than *E. sophia* because of the orientation of the antennae while searching; whereas *E. mundus* held the antennal club more or less vertically, the antennae of *E. sophia* were held in a more horizontal manner. This may have caused irritation in *E. mundus* than in *E. sophia*. The pathways described for *E. eremicus* on smooth sweetpotato, cotton and on hairy melon plants were similar (Headrick *et al.*, 1995; 1996a & b). The studies, however, indicated that trichomes on melon leaves affected the female's ability to recognize cues from host on melons as reflected in a longer duration of circling antennation on melon leaves. In the present study, the duration of antennation was significantly longer for both parasitoids species on the glabrous variety. Since there was no observable hindrance of leaf hairs on antennation, it

seems that honeydew from leaves of the glabrous variety interfered with the recognition of hosts, thereby making the period of host assessment longer on this variety.

Probing had the second longest duration of all host-handling activities. The mean duration of probing in the present study ranged between 56.8 to 92.5 s. The significantly longer duration of probing by *E. mundus* females on the glabrous variety than on the hirsute clone may be due to the difficulty in exserting the ovipositor between the nymph and the leaves of the glabrous variety than where nymphs are a bit raised such as that of the hirsute clone. Similarly, Headrick *et al.* (1996a & b) reported that hairs on melon leaves caused nymphs to be raised and made it easier for *E. eremicus* to exsert their ovipositors than on sweet potato and cotton where the nymphs lay flat on the leaves. The observed mean durations of probing in this study are close to the mean values of 89.1 and 74.2 s for initial and repeated probes reported for *E. eremicus* on melon (Headrick *et al.*, 1996b). For other parasitoid species, different values have been reported: 25.6 s for *A. bennetti* (Joyce *et al.*, 1999), 31.9 s (*A. fuscipennis*; Drost *et al.*, 1999) and 52.9 s (*A. fuscipennis*; Manzano *et al.*, 2002). These values are lower than the ones observed in this study and might be attributed to the ease of probing first instar nymphs preferred by *Amitus*. *Encarsia* spp. on the other hand prefer to probe third instar nymphs (Hunter and Kelly, 1998), which are more mature and difficult to puncture.

After probing, *E. mundus* females either abandoned their hosts, host-fed or oviposited after which they often drummed their hosts with the hind legs (Foltyn and Gerling, 1985; McAuslane and Nguyen (1996). Drumming was considered a host-marking activity (Foltyn and Gerling, 1985), but McAuslane and Nguyen (1996) found that eggs were laid under both hosts that were drummed and those that were not drummed. During the present study, oviposition under the

probed hosts were not assessed, but further studies are recommended to elucidate the role of drumming in *E. mundus*, and oviposition under probed hosts.

Host-feeding was longest while nearly all host haemolymph was consumed, resulting in a flat and a somewhat transparent appearance of the whitefly nymph. Host-feeding is considered a prerequisite for maturation of a full complement of eggs in synovigenic parasitoids like *Eretmocerus* and *Encarsia* spp. (Flanders 1935, Gerling, 1990).

It is not clear why the duration of resting on the leaf and grooming were longer for *E. mundus* on the glabrous variety and why the durations of feeding on liquids on the leaf, and host-feeding were longer for *E. sophia* on the glabrous variety. It may however be postulated that differences in duration of behaviours by different females may to some extent explain this observation.

Several authors have shown that host plant morphology affects the searching efficiency of parasitoids by slowing or inhibiting their movements (Hua *et al.*, 1987; Gerling, 1990) and reducing parasitization efficiency (McAuslane *et al.*, 1995; van Lenteren *et al.*; 1995; van Roermund and van Lenteren., 1995). In the present experiment, parasitism was not assessed in the laboratory, but plants of both the variety and clone were placed in one-litre buckets for natural infestation to occur and the results showed similarity in percent parasitism. This demonstrates that although there were differences between the variety and clone in the duration of some behaviours for both parasitoids species, percent parasitism is not affected.

One of the hairiest cassava clones was used and the results suggest that leaf hairs at the density investigated caused only minor changes in parasitoid behaviour. Since most cassava varieties are less hairy than the hirsute clone that was used, leaf pubescence in cassava seems to have an insignificant effect on parasitoids' ability to parasitise *B. tabaci*. This is supported by field data

nat show a similar level of parasitism between the variety and clone (Otim, unpublished). This rst report on the behaviour of parasitoids of *B. tabaci* on cassava has provided useful nformation in respect of possible effect of leaf hairiness on parasitoid behaviour and parasitism. has demonstrated that leaf hair affects *E. mundus*' readiness to search when on a hairy leaf, but lso make probing by *E. mundus* easier on the hirsute clone than on the glabrous one. onsequently, the females that remain spend most of their time in host searching and the effect f leaf hair may be neutralised by having raised nymphs that are easier to parasitize. For *E. ophia* however, it can be concluded that leaf hair did not influence its searching behaviour. imilar types of behavioural observations should also be conducted to examine the effect of ther variables such as leaf shape-broad versus narrow leaves and disease-CMD affected versus MD-free leaves.

CHAPTER SIX

0 GENERAL DISCUSSION AND CONCLUSIONS

he present study was conducted to: i) assess the levels of infestation of *B. tabaci* and its natural nemies on cassava, cassava component crops and weeds in and around cassava gardens; iii) etermine the development duration, longevity and fertility of the principal parasitoids of *B. baci* and; iv) determine the influence of leaf pubescence on the searching and oviposition ehaviour of the principal parasitoids of *B. tabaci*.

he survey demonstrated that *B. tabaci* and its natural enemies were more abundant on cassava ompared to cassava companion crops and weeds. *E. mundus* was more abundant than *E. sophia*, hich was in turn more abundant than *Encarsia* sp. Predators found were spiders, *Serangium* sp., ats, lacewings, *Orius* sp. and syrphid larvae. They also varied in number between locations and mes of the year. Furthermore, only low numbers of *B. tabaci* nymphs and their natural enemies ere found on sweet potato, *Melhania* sp. and *Commelina* sp. All other plant species that were xamined in and around cassava fields supported no or rare numbers of these insects.

he longevity and fertility of *E. mundus* and *E. sophia* when provided only honey were similar. owever, *E. sophia* developed faster, and lived longer than *E. mundus* when the two parasitoids ere provided *B. tabaci* nymphs, whilst *E. mundus* had more mature eggs on emergence than *E. ophia*. The study on the behaviour of the two parasitoids demonstrated that both *E. mundus* and *E. sophia* exhibited a similar search pathway, but *E. mundus* spent a bigger percentage of its time robing and host-feeding, while *E. sophia* on the other hand, spent much of its time standing on he leaf.

All the recorded parasitoid species and ants were more abundant at Busukuma than at the other two locations, whereas coccinellids were more abundant at Bulisa than in the other sites. The generally higher numbers of natural enemies at Busukuma and Bulisa compared with Lyantonde could be due to the higher populations of *B. tabaci* on cassava. This may have been brought about by extensive cassava growing throughout the year in these locations, thereby availing abundant supply of nutrition and hosts for the natural enemies. In Lyantonde, however, cassava growing is not continuous, resulting in few whiteflies and their natural enemies.

Although the *B. tabaci* on sweet potato and *Melhania* sp. have been demonstrated to be different biotypes that may not pose any threat to cassava, the same parasitoids that occurred on these plant species may move to *B. tabaci* on cassava as observed by Gerling (1990) on other plant species. Legg (1996) and Sseruwagi *et al.* (2005) however, demonstrated that the cassava biotype of *B. tabaci* is in a limited way capable of colonizing other host plants like cotton, sweet potato, okra, jatropha, eurphorbia and aspilia. Among these host plants, *B. tabaci* was recorded on sweet potato and euphorbia in the surveyed locations. Those on sweet potato were the sweet potato biotype, whereas the one on euphorbia appeared to be the cassava biotype. Whereas these results may suggest that no suitable alternative hosts for cassava-attacking *B. tabaci* parasitoids occur in the locations surveyed, migration of even small numbers might speed up the pattern of colonization of new crops. Therefore, additional efforts are needed to document the host range and population dynamics of the different whitefly biotypes on plants, their natural enemies, and their possible role as virus vectors. This would provide information for management of the crop and its environment and thus reducing the risks associated with whitefly and the associated viruses.

Although the cassava component crops did not seem to directly act as hosts of *B. tabaci*, intercrops are known to influence the host-seeking behaviour of the pest and may determine the severity of pest infestation (Hilje *et al.*, 2001) and several experiments on the role of intercrops in the dynamics of whitefly on cassava are known from literature (Fargette and Fauquet, 1988; Gold, 1994; Ahohuendo and Sarkar, 1995). Gold (1994) reported lower infestations of whiteflies (*Aleurotrachelus socialis* Bondar and *Trialeurodes variabilis* Quaintance) and other arthropod pests on cassava in Columbia when intercropped with cowpea and maize compared with sole cassava. In Ivory Coast and Benin, the incidence of CMD decreased in cassava intercropped with maize or cowpea (Fargette and Fauquet, 1988; Ahohuendo and Sarkar, 1995), suggesting that mixed cropping may decrease whitefly vector populations, vector movement and the spread of CMD. Thus, the presence of intercrops could have influenced the dynamics of *B. tabaci* and its natural enemies. This area requires research attention to give an overall picture of infestation levels under different cropping systems.

From the survey results, *E. mundus* is more abundant than *E. sophia*. This may be attributed to higher fecundity of *Eretmocerus* than *Encarsia* as reported by Gerling *et al.* (2001). Additionally, differential response of the two parasitoids to environmental conditions may also favour the competitive advantage of *E. mundus* over *E. sophia*. This is supported by the results of Kapadia & Puri (1990) and the current study, which showed a positive relationship between relative humidity and the abundance of *E. mundus* in the field. Although there was no significant difference between the total progeny *E. mundus* (ca. 27) and *E. sophia* (ca. 17), a difference of 1 parasitized *B. tabaci* nymphs per female *E. mundus* would result in a very big difference in parasitism when considered in space and time.

oretically, starting with one female parasitoid of each species and using the mula, $N_t = N_0 \exp^{rt}$; where N_t is the population at time t, N_0 is the initial population, and r the intrinsic rate of increase, we would end up with 34 *E. mundus* parasitized nymphs and 23 *sophia* parasitized nymphs in thirty days. The respective numbers would increase to 13,734 d 19,930 parasitized nymphs in ninety days. In 120 days, the numbers of *E. sophia* parasitized mphs (540,365) would be greater than the numbers of *E. mundus* parasitized nymphs 5,856). Although these results suggest that *E. sophia* can outnumber *E. mundus* with time, the pulation of both parasitoid species are continuously breeding and such chances are therefore ote unless other unknown factors come in to favour *E. sophia.*

spite the limited influence of leaf hairs on the numbers of *E. mundus* that remained to search the hirsute clone, results from the behavioural studies provide more evidence in support of the ll performance of *E. mundus* compared to *E. sophia*. This is reflected in the more hosts ountered and probed by *E. mundus* (Figs. 5.1 & 5.2) than by *E. sophia* (Fig. 5.3 & 5.4). Thus reasoning of Headrick *et al.* (1996 a) that the propensity of a parasitoid to remain and search the leaf is more related to field parasitism can be applied here. This may account for the her abundance of *E. mundus* in the field than *E. sophia*. The readiness of *E. mundus* to search lay its eggs within a short lifespan and the reluctance of *E. sophia* to search, but lay its eggs an extended period of time demonstrate different life history strategies typical of the two era (Gerling, 1990).

h the biology and behavioural study suggest that *E. mundus* may be a good candidate for trol of high numbers of *B. tabaci* early in the season, while *E. sophia* is a good candidate for trol of low *B. tabaci* populations. This in agreement with the argument of Hoelmer *et al.*

that *E. sophia* is useful in reducing low infestations because of its short development time effectiveness at low host densities.

high populations of *B. tabaci* on cassava early in the season make biological control difficult flected in levels of parasitism, averaging between 32 and 41%. As noted by Gerling (1996) biological control, even if only partially successful can contribute to the overall integrated agement strategy. Since the results indicate that parasitoids offer some level of control of *B.* *ci*, but are constrained due to low reproductive rate, it is important to find ways of enhancing level of parasitism of *B. tabaci* in the field. These should be geared at looking for ways of suraging the parasitoids through conservation, finding additional species that are capable of easing mortality of *B. tabaci* under our conditions, and developing cassava varieties less eptible to *B. tabaci* on which parasitoids will contribute to bringing the host under control.

s study has given insight and a revelation that: i) *E. mundus* and *E. sophia* are the most ndant parasitoids in the studied locations, whilst ants, spiders and coccinellids were the most mon predators; ii) *B. tabaci* and its natural enemies rarely occur on crops grown in ciation with cassava and weeds in around cassava fields at the locations studied; iii) there are erences in the biology of the two *B. tabaci* principal parasitoids; iv) there are some erences in the searching and oviposition behaviours of the two principal parasitoids of *B.* *ci* on cassava of different hair densities.

REFERENCES

El-Kareim, A.I. 1998. Searching rate and potential of some natural enemies as biocontrol agents against the cotton whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae). *Journal of Applied Entomology* 122, 487-492

Gbendo, B.C. & Sarkar, S. 1995. Partial control of the spread of African cassava mosaic virus in Benin by intercropping. *Journal of Plant Disease Protection* 102(3), 249-250

Howartha, H.G. & Birch, L.C. 1954. The distribution and abundance of animals. Chicago, USA: Chicago University, Chicago Press. pp: 782

Anonymous. 1994. *Cassava Growers' Guide*. National Agricultural Research Organization. Agricultural Communication Centre, Entebbe. 18pp

Gerling, B., Palaniswami, M.S. & Henneberry, T.J. 2003. *Encarsia transvena* (Hymenoptera: Aphelinidae) development on different *Bemisia tabaci* (Homoptera: Aleyrodidae) instars. *Environmental Entomology* 32(2), 584-591

Gerling, M.J. 2004. Whitefly control potential of *Eretmocerus* parasitoids with different reproductive modes. PhD Thesis, Wagenigen University. The Netherlands. 112pp

Legg, P., Ecat, J.S., Otim, M., Gerling, D., Kyamanywa, S. & Legg, J.P. 2006. In press. Life table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda. *Entomologia Experimentalis et Applicata.*

Nweke, B.D.A. 1982. Historical perspectives of cassava breeding in Africa. In: *Proceedings of a Workshop on Root Crops in Eastern Africa* 13-18, 23-27 November 1980, Kigali, Rwanda

Belloti, A.C. & Arias, B. 2001. Host plant resistance to whiteflies with emphasis on cassava as a case study. *Crop Protection* 20, 813-823

Bock, K.R. & Woods, R.D. 1983. African cassava mosaic virus disease. *Plant Disease* 67, 994-995

Coudriet, D.L., Meyerdirk, D.E., Prabhaker., N. & Kishaba, A.N. 1986. Bionomics of sweetpotato whitefly (Homoptera: Aleyrodidae) on weed hosts in the Imperial Valley, California. *Environmental Entomology* 15, 1179-1183

De barro, P.J., Hart, P.J. & Morton, R. 2000. The biology of two *Eretmocerus* spp. (Haldeman) and three *Encarsia* spp. Forster and their potential as biological control agents of *Bemisia tabaci* biotype B in Australia. *Entomologia Experimentalis et Applicata* 94, 93-102

De Vis, R.M.J., Fuentes, L.E. & van Lenteren, J.C. 2002. Life history of *Amitus fuscipennis* (Hymenoptera: Platygasteridae) as parasitoid of the greenhouse whitefly *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae) on tomato as a function of temperature. *Journal of Applied Entomology* 126, 24-33

Dengel, J. 1981. Untersuchegnen über das auftreten der imagines von *Bemisia tabaci* (Genn.) auf versschiedenen manioksorten. *Zeitschrift für Pflanzenkrakheiten und Pflanzenschutz* 88, 355-366

Dent, D. 1991. Insect Pest Management. CAB International, Wallington, Oxon OX108DE, UK. 604pp.

Driesche, R.G., van. 1993. Methods for the field colonization of new biological control agents. In: Steps in Classical Biological Control 67-86 (Eds Driesche, R.G. van & Bellows, T.S).

Thomas Say Publication in Entomology, Proceedings of the Entomological Society of America, Lanham, Maryland

Drost Y.C., Qiu Y.T., Posthuma Doodeman C.J.A.M. & van Lenteren J.C. 1999. Life history and oviposition behaviour of *Amitus bennetti*, a parasitoid of *Bemisia argentifolii*. *Entomologia Experimentalis et Applicata* 90, 83-189

Drost. Y.C., Qiu, Y.T., Posthuma-Doodeman, J.A.M. & van Lenteren, J.C. 2000. Comparison of searching strategies of five parasitoid species of *Bemisia argentifolii* Bellows and Perring (Homoptera: Aleyrodidae). *Journal of Applied Entomology* 124, 105-112

Egabu, J. 2002. The influence of plant population on the incidence, progress and severity of cassava mosaic disease in central Uganda. MSc. Thesis, Makerere University. 73pp

Egabu, J., Osiru, D.S.O., Adipala, E. & Thresh, J.M. 2002. The influence of plant population on the incidence, progress and severity of cassava mosaic disease in central Uganda. *Forum 5. Programme and Extended Abstracts. Fifth Regional Meeting of Forum on Agricultural Resource Husbandry* 171-173, 12-16 August 2002, Entebbe, Uganda

Ekpe, E.O. & Chinaka C.C. 2000. An assessment of cassava mosaic disease severity in cassava–maize mixture at different NPK levels. *African Crop Science Journal* 8(3), 311-316

Enkegaard, A. 1993. *Encarsia formosa* parasitizing the poinsettia strain of the cotton whitefly, *Bemisia tabaci,* on poinsettia: bionomics in relation to temperature. *Entomologia Experimentalis et Applicata* 69, 251-261

Fargette, D. & Fauquet, C. 1988. A preliminary study on the influence of intercropping maize and cassava on the spread of African cassava mosaic virus by whiteflies. *Aspects of Applied Biology* 17, 195–202

Fargette, D., Fauquet, C., Grenier, E. & Thresh, J.M. 1990. The spread of African cassava mosaic virus into and within fields. *Journal of Plant Phytopathology* 130, 289-302

Fauquet, C. & Beachy, R.N. 1989. Cassava viruses and genetic engineering. *International Cassava Trans Project*. Department of Biology, Washington University. St. Luis. 30pp

Fishpool, L.D.C. & Burban, C. 1994. *Bemisia tabaci*: the whitefly vector of African cassava mosaic geminiviruses. *Tropical Science* 34, 55-72

Flanders, S.E. 1935. An apparent correlation between the feeding habits of certain pteromalids and the condition of the ovarian follicles. *Annals of the Entomological Society of America* 28, 438–444

Foltyn, S. & Gerling, D. 1985. The parasitoids of the aleyrodid *Bemisia tabaci* in Israel: development, host preference and discrimination of the aphelinid wasp *Eretmocerus mundus*. *Entomologia Experimentalis et Applicata* 38, 255-260

Fondong, V.N., Thresh. J.M. & Zok, S. 2002. Spatial and temporal spread of cassava mosaic virus disease in cassava grown alone and when intercropped with maize and or cowpea. *Journal of Plant Pathology* 150, 365-374

Gameel, O.I. 1969. Studies of whitefly parasites *Encarsia lutea* Masi and *Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae). Reviews of Zoology and Botany in Africa, 79:65-77

Gerling, D & Rejouan, N. 2004. Age-related pupal defenses against congeneric internecine activity in *Encarsia* species. *Entomologia Experimentalis et Applicata* 110, 87-93

Gerling, D. & Fried, R. 2000. Biological studies with *Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae) in Israel. *OILB/SROP Bulletin* 23, 117-123

Gerling, D. 1967. Bionomics of the whitefly-parasite complex associated with cotton in Southern California (Homoptera: Aleyrodidae; Hymenoptera: Aphelinidae). *Annals of Entomological Society of America* 60, 1306-1321

Gerling, D. 1983. Observations of the biologies and interrelationships of parasites attacking the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) in Hawaii. *Proceedings of the Hawaiian Entomological Society* 24, 217-226

Gerling, D. 1986. Natural enemies of *Bemisia tabaci*. Biological characteristics and potential as biological control agents: A review. *Agriculture, Ecosystems and Environment* 17, 99-110

Gerling, D. 1990. Natural enemies of whitefly: predators and parasitoids. In *Whitefly: their bionomics, Pest Status and Management* 147-185. (Ed. D, Gerling), Intercept, Andover, Hants, UK

Gerling, D. 1996. Status of *Bemisia tabaci* in the Mediterranean countries: Opportunities for biological control. *Biological Control* 6, 11-12

Gerling, D., Alomar, O. & Arnó. J. 2001. Biological control of *Bemisia tabaci* using predators and parasitoids. *Crop Protection* 20, 779-799

Gerling, D., Horowitz, A.R. & Baumgartner, J. 1986. Autoecology of *Bemisia tabaci*. In: Proceedings of a Symposium on *Bemisia tabaci* – Ecology and Control; XVIIth International Congress of Entomology 17, 5-20, 19-23 August 1986, Hamburg, FRG. Agriculture, Ecosystems and Environment. Special Issue

Gerling, D., Motro, U. & Horowitz, R. 1980. Dynamics of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) attacking cotton in the coastal plain of Israel. *Bulletin of Entomological Research* 70, 213-219

Gerling, D., Rottenberg, O. & Bellows, T.S. 2004. Role of natural enemies and other factors in the dynamics of field populations of the whitefly *Siphonimus phillyreae* (Haliday) in introduced and native environments. *Biological control* 31, 199-209

Ghahari, H. & Hatami, B. 2000. Study of the natural enemies of whiteflies (Homoptera: Aleyrodidae) in Isfahan Province. *Journal of Entomological Society of Iran* 20, 1-24

Ghahari, H., Huang, J. & Wang, Z.H. 2005. Biology of a thelytokous biotype of *Eretmocerus mundus* (Hymenoptera: Aphelinidae) on *Bemisia tabaci* (Homoptera: Aleyrodidae)

Godfray, H.C.J. 1994. Parasitoids: Behavioral and Evolutionary Ecology. Princeton: Princeton University Press

Gold, C.S. 1994. The effects of cropping systems on cassava whiteflies in Colombia: Implications for control of African cassava mosaic virus disease. *African Crop Science Journal* 2(4), 423-436

Golding, F.D. 1936. Cassava mosaic in southern Nigeria. *Bulletin of the Department of Agriculture, Nigeria* 11, 1-10

Greathead, D.J. & Bennet, F.D. 1981. Possibilities for the use of biotic agents in the control of the whitefly, *Bemisia tabaci. Biocontrol News and Information* 2, 7-13

Gruenhagen, N.M. & Perring, T.M. 1999. Velvetleaf: A plant with adverse impacts on insect natural enemies. *Environmental Entomology* 28(5), 884-889

Hahn, S.K., Howland, A.K. & Terry, E.R. 1980. Correlated resistance of cassava mosaic and bacterial blight diseases. *Euphytica* 29, 305-311

Headrick, D.H., Bellows, T.S. & Perring, T.M. 1995. Behaviours of female *Eretmocerus* sp. nr. *californicus* (Hymenoptera: Aphelinidae) attacking *Bemisia argentifolii* (Homoptera: Aleyrodidae) on sweet potato. *Environmental Entomology* 24, 412–422

Headrick, D.H., Bellows, T.S. & Perring, T.M. 1996 a. Host-plant effects on the behaviour of *Eretmocerus* sp. nr. *californicus* raised from melon. *Entomophaga* 41(1), 15-26

Headrick, D.H., Bellows, T.S. Jr. & Perring, T.M. 1996 b. Behaviours of female *Eretmocerus* sp. nr. *californicus* (Hymenoptera: Aphelinidae) on cotton, *Gossypiun hirsutum* (Malvaceae) and Melon, *Cucumis melo* (Cucurbitaceae). *Biological Control* 6, 67-75

Heinz K.M. & Parrella, M.P. 1994: Poinsettia (*Euphorbia pulcherrima* Willd. Ex Koltz.) cultivar-mediated differences in performance of five natural enemies of *Bemisia argentifolii* Bellows and Perring, n.sp. (Homoptera: Aleyrodidae). *Biocontrol* 4, 305-318

Hilje, L., Costa, H.C. & Stansly, P.A. 2001. Cultural control for managing *Bemisia tabaci* and associated viral diseases. *Crop Protection* 20, 801-812

Hoddle, M.S. & van Driesche, R.G.W. 1999. Evaluation of inundative releases of *Eretmocerus eremicus* and *Encarsia formosa* Beltsville strain in commercial greenhouses for control of *Bemisia argentifolii* on poinsettia stock plants. *Journal of Economic Entomology* 92, 811-824

Hoelmer, K. A. 1995. Whitefly parasitoids: can they control field populations of *Bemisia*? In: *Bemisia* 1995: *Taxonomy, Biology, Damage, Control and Management* 451–476. (Eds Gerling, D., Mayer, R.T.), Intercept Ltd., Andover, Hants, UK

Hoelmer, K.A. 1996. Whitefly parasitoids: can they control field populations of *Bemisia*? In: Gerling, D., Mayer,R.T. (Eds.), *Bemisia* 1995: Taxonomy, Biology, Damage, Control and Management. Intercept Ltd., Andover, Hants, UK, pp. 451–476

Hoelmer, K.A., Osborne, L.S., Bennett, F.D. & Yokomi, R.K. 1994. Biological control of sweetpotato whitefly in Florida. In: Rosen, D., Bennett, F.D., Capinera, J.L. (Eds.), Pest Management in the Subtropics. Biological Control—a Florida Perspective. Intercept

Horowitz., A.R., Podoler, H. & Gerling, D. 1984. Life table analysis of the tobacco whitefly *Bemisia tabaci* (Gennadius) in cotton fields in Israel. *Acta Oecologia* 5, 221-233

Hua, L.Z., Lammes, F., Lenteren, J.C. van, Huisman, P.W.T., Vanvianen, A. & Deponti, O. M. B. 1987. The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). Influence of leaf structure on the searching activity of *Encarsia formosa*. *Journal of Applied Entomology* 104, 297-304

Hunter, M.A. & Kelly, S.E. 1998. Hyperparasitism by an exotic autoparasitoid: secondary host selections and the window of vulnerability of conspecific and native heterospecific. *Entomologia Experimentalis et Applicata* 89, 249-259

IITA, 1990. Cassava in tropical Africa. A reference manual: International Institute of Agriculture, Ibadan, Nigeria. 20pp

Inayatullah, C. & Ghani, M.A. 1987. Incidence of cotton whitefly and its natural enemies in Pakistan. *Pakistan Journal of Agricultural Research* 8(2), 179-183

Jones, W.A. & Greenberg, S.M. 1998. Suitability of *Bemisia argentifolii* (Homoptera: Aleyrodidae) instars for the parasitoid *Eretmocerus mundus* (Hymenoptera: Aphelinidae). *Environmental Entomology* 27, 1569-1573

Joyce, A.L., Bellows, T.L. & Headrick, H. 1999. Reproductive biology and search behaviour of *Amitus bennetti* (Hymenoptera: Platygasteridae), a parasitoid of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Environmental Entomology* 28(2), 282-289

Kajita, H., Samudra, I.M. & Naito, A. 1992. Parasitism of the tobacco whitefly *Bemisia tabaci* (Homoptera: Aleyrodidae), by *Encarsia transvena* (Timberlake) (Hymenoptera: Aphelinidae) in Indonesia. *Applied Entomology and Zoolology* 27, 468-470

Kapadia, M.N. & Puri, S.N. 1990. Development, relative proportions and emergence of *Encarsia transvena* (Timberlake) and *Eretmocerus mundus* Mercet, important parasitoids of *Bemisia tabaci* (Gennadius) *Entomon* 15(3), 235-239

Lawes Agricultural Trust, 1995. Genstat 5 Release 3.2. Rothamsted Experimental Station, AFRC Institute of Arable Crops Research, Harpenden, Hertfordshire AL5 2JQ, UK.

Legg, J. P. 1995. The ecology of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae), vector of African cassava mosaic geminivirus in Uganda. *Doctoral thesis*, University of Reading, UK. 183pp.

Legg, J.P. 1994. *Bemisia tabaci*: The whitely vector of cassava mosaic geminiviruses in Africa: An ecological perspective. *African Crop Science Journal* 2, 437-448

Legg, J.P., Mallowa, S. & Sseruwagi, P. 2003. First report of physical damage to cassava caused by the whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Sternorrhyncha: Aleyrodidae). *Book of Abstracts, 3rd International Bemisia Workshop. Barcelona 17-20 March, 2003*

gg. J.P. 1996. Host-associated strains within Uganda populations of the whitefly *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae). *Journal of Applied Entomology* 120, 523-527

nteren, J.C. van, Li, Z.H., Kamerman, J.W. & Rumei, X. 1995. The parasite-host relationship of *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae) XXVI. Leaf hairs reduce the capacity of *Encarsia* to control whitefly on cucumber. *Journal of Applied Entomology* 119, 553-559

euschner, K. 1978. Whiteflies: biology and transmission of African cassava mosaic disease. *Proceedings of the Cassava Protection Workshop* 51-58, 7-12 November 1977, CIAT, Cali, Columbia (Eds Brekelbaum, T., Bellotti, A. and Lozano, T.C).

imited, Andover, pp. 101–113

.ópez, S.N. & Botto, E.N. 1997. Biology of South American population of *Eretmocerus* sp. (Hymenoptera: Aphelinidae) attacking the greenhouse whitefly. *Biological Control* 9, 1-5

Manzano, M.R., Lenteren, J.C. van & Cardona, C. 2002. Searching behaviour of *Amitus fuscipennis*, a parasitoid of the greenhouse whitefly. *Journal of Applied Entomology* 126, 529-533

McAuslane, H.J. & Nguyen, R. 1996. Reproductive behaviour and biology of a thelytokous species of *Eretmocerus* (Hymenoptera: Aleyrodidae) parasitizing *Bemisia argentifolii*. *Annals of Entomological Society of America* 89, 686-693

McAuslane, H.J., Johnson, F.A., Colvin, D.L. & Sojack. B. 1995. Influence of foliar pubescence on incidence and parasitism of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on soybean and peanut. *Environmental Entomology* 24, 1135-1143

McAuslane, H.J., Johnson, F.A., Knauft, D.A. & Colvin, D.L. 1993. Seasonal abundance and within-plant distribution of parasitoids of *Bemisia tabaci* (Homoptera: Aleyrodidae) in peanuts. *Environmental Entomology* 22(5), 1043-1050

Mead, R., Curnow, R.N. & Hasted, A.M. 2003. Statistical methods in Agriculture and experimental biology. 3rd ed. Chapman and Hall/LRC. A CRC Company Press. 472pp

Naranjo, S.E. 2001. Conservation and evaluation of natural enemies in IPM systems for *Bemisia tabaci. Crop Protection* 20, 835-852.

Noldus Information Technology, 2003. Prefessonal Software for collection and analysis of observational data. Wageningen, The Netherlands

Nweke, F.I. 1994. Farm level practices relevant to cassava plant protection. *African Crop Science Journal* 2(4), 563–582

Nyirenda, G.K.C., Munthuli, D.C., Phiri, G.S.N., Sauti, R.F.N. & Gerling, D. 1993. Integrated pest management of *Bemisia* spp. whitefly in Malawi. *Report.* Makoka Research Station, Thondwe Malawi

Okali, C. & Berry, S. 1985. Alley farming in west Africa in comparative perspective. Boston University, African–American Issues Center. Working paper No. 11

Oliveira MRV, Henneberry TJ, Anderson PK, 2001. History, current status and collaborative research projects for *Bemisia tabaci. Crop Protection* 20, 709–723

Oneka. J., Osiru, D.S.O., Adipala, E. & Thresh. J.M. 2002. Influence of intercropping cassava with cowpea or maize on epidemiology of cassava mosaic disease (CMD) in central Uganda. *Book of Abstracts and List of participants.* Integrated Pest Management Conference for sub-Saharan Africa. P 89. 8-12 September 2002. Kampala, Uganda

Onwueme, I.C. & Sinha, T.D. 1991. Roots and Tuber Crops: Cassava (*Manihot esculenta* Crantz). In: *Field Crop Production in Tropical Africa* 233-266

Osiru, D.S.O., Sserubmbwe, W.S., Sseruwagi, P., Thresh, J.M. & Otim-Nape, G.W. 1999. Effects of cassava mosaic virus disease on the growth and yield of cassava (*Manihot esculenta* Crantz) – Some highlights from Makerere experiments. *African Crop Science Journal* 7, 511-522

Otim, M. 2002. The potential for the use of parasitoids in the biological control of the whitefly, *Bemisia tabaci,* vector of cassava mosaic geminiviruses. *MSc. Thesis*. Makerere University, Kampala, Uganda. 80pp

Otim, M., Legg, J., Kyamanywa, S., Polaszek, A. & Gerling, D. 2006. Population dynamics of *Bemisia tabaci* (Homoptera: Aleyrodidae) parasitoids on cassava mosaic disease resistant and susceptible varieties. *Biocontrol Science and Technology* 16(2), 205-214

Otim, M., Legg, J.P., Kyamanywa, S., Polaszek, A. & Gerling, D. 2005. Occurrence and activity of *Bemisia tabaci* parasitoids on cassava in different agro-ecologies in Uganda. *Biocontrol* 50, 87-95

Otim-Nape, G.W. 1993. Epidemiology of the African cassava mosaic geminivirus disease (ACMD) in Uganda. PhD Thesis, University of Reading, U.K. 252pp

Otim-Nape, G.W., Bua, A. & Baguma, Y. 1994. Accelerating the transfer of improved production technologies: controlling cassava mosaic virus disease epidemics in Uganda. *African Crop Science Journal* 2, 479-495

Otim-Nape, G.W., Ssemakula, G.N., Baguma, Y., Bua, A., ogwal, S. & van der Grift. 1999. Application for release of new cassava varieties. *Internal variety release report*. NARO, Namulonge, Uganda. 45pp

Pair, S.D., Laster, M.L. & Martin, D.F. 1982. Parasitoids of *Heliothis* spp. (Lepidoptera: Noctuidae) larvae in Mississippi associated with sesame interplanting in cotton, 1971-1974: implications of host-habitat interaction. *Environmental Entomology* 11, 509-512

Polaszek, A., Evans G.A. & Bennet, F.D. 1992. *Encarsia* parasitoids of *Bemisia tabaci* (Hymenoptera: Aphelinidae, Homoptera: Aleyrodidae); a preliminary guide to identification. *Bulletin of Entomological Research* 82, 375-392

Powell, D. A. & Bellows T. S. 1992. Development and reproduction of two populations of *Eretmocerus* species (Hymenoptera: Aphelinidae) on *Bemisia tabaci* (Hymenoptera: Aphelinidae). *Environmental Entomology* 21, 651-658

Price, P.W., Bouton, C.E., Gross, P., Mcpheron, B.A., Thompson, J.N. & Weis, A.E. 1980. Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecological systems* 11, 41-65

Qiu, Y.T., Lenteren, J.C. van, Drost, Y.C. & Posthuma Doodeman, C.J.A.M. 2004. Life history parameters of *Encarsia formosa*, *Eretmocerus eremicus* Rose & Zolnerowich and *Eretmocerus mundus,* aphelinid parasitoids of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *European Journal of Entomology* 101, 83-94

Rajam, B., Clement, P. & David, B.V. 1969. Influence of host plants on the parasitism of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) by *Encarsia* sp.

Robertson, I.A.D. 1985. Cassava/whitefly project. Part of Crop Virology Project R3177 at the Kenya Agricultural Research Institute. Final Report. Overseas Development Administration, London

Roermund, H.J.W. van & Lenteren, J.C. van. 1995. Residence times of the whitefly parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) on tomato leaflets. *Journal of Applied Entomology* 119, 465-471

Rose, M. & Debachi, P. 1992. Biological control of *ParaBemisia myricae* (Kuwana) (Homoptera: Aleyrodidae) in California. *Israel Journal of Entomology* 25-26, 73-95

Rose, M. & Zolnerowich, G. 1997. *Eretmocerus* Haldeman (Hymenoptera: Aphelinidae) in the United States, with descriptions of new species attacking *Bemisia tabaci* complex) (Homoptera: Aleyrodidae). *Proceedings of Entomological Society of Washington* 99(1), 1-27

Ryckwaert, P. & Alauzet, C. 2002. The natural enemies of *Bemisia argentifolii* in Martinique. *Biological Control* 47, 115-126

Schauff, M.E., Evans, G.A. & Heraty, J.M. 1996. A pictorial guide to the species of *Encarsia* (Hymenoptera: Aphelinidae) parasitic on whiteflies (Homoptera: Aleyrodidae) in North America. *Proceedings of Entomological Society of Washington* 98(1), 1-35

Schuster, D.J., Evans, G.A., Bennett, F.D., Stansly, P.A., Jansson, Leibee, R.K. & Webb, S.E. 1998. A survey of parasitoids of *Bemisia* spp. in Florida, the Caribbean, and Central and South America. *International Journal of Pest Management* 44, 255–260

Seif, A.A. 1982. Effect of cassava mosaic on yield of cassava. *Plant Diseases* 66, 661-662

Semaganda, R., Legg, J.P., Gerling, D., Kyamanywa, S. & Adipala, E. 2003. Augmenting the activity of *Bemisia tabaci* parasitoids on cassava by intercropping cassava with sweet potato. *Programme, Abstracts of papers and list of participants, 6th Biennial Conference of the African Crop Science Society* 127, 12-17 October, 2003, The Hilton Hotel Nairobi, Kenya

Sengonca, C. & Liu, B. 1998. Biological studies on *Eretmocerus longipes* Compere (Hymenoptera: Aphelinidae), a parasitoid of *Aleurotuberculatus takahashi* David et Subramaniam (Homoptera: Aleyrodidae) in the laboratory. *Journal of Applied Entomology* 122, 207-211

Sengonca, C., Uygen, N., Kersting, U. & Ulusoy, M. R. 1993. Successful colonisation of *Eretmocerus debachi* (Hymenoptera: Aphelinidae) in the Mediterranean citrus region of Turkey. *Entomophaga* 38, 383-390

Sharaf N. & Batta Y. 1985 a. Effect of some factors on the relationship between the whitefly *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) and the parasitoid *Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae) in Jordan. *Journal of Applied Entomology*. 99, 267-276

Sharaf N. & Batta, Y. 1985 b. Effect of temperature on life history of *Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae). *Agricultural Sciences*. 23, 214-219

Sharaf, N. 1986. Chemical Control of *Bemisia tabaci*. *Agriculture, Ecosystems and Environment* 17, 111–127

Sserubombwe, W.S. 1998. Progress of cassava mosaic virus disease (CMD) and its effects on growth and yield of four cassava varieties. MSc. Thesis. Makerere University, Kampala 185pp

Sseruwagi, P. 1998. Influence of NPK fertilizer on disease spread, growth and yield of cassava mosaic disease affected plants. MSc. Thesis. Makerere University, Kampala 103pp

Sseruwagi, P., Legg, J.P., MAruthi, M.N., Calvin, J., Rey, M.E.C. & Brown, J.K. 2005. Genetic diversity of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) populations and presence of the B biotype and a non-B biotype that can induce silverleaf symptoms in squash. *Annals of Applied Biology* 147, 252-265

Stansly, P.A., Schuster, D.J. & Liu, T.X. 1997. Apparent parasitism of *Bemisia argentifolii* (Homoptera: Aleyrodidae) by Aphelinidae (Hymenoptera) on vegetables crops and associated weeds in south Florida. *Biological Control* 9, 49-57

Storey, H.H. 1936. Virus diseases of East African Plants. VI– A Progress report on studies of the diseases of cassava. *East African Agricultural Journal* 2, 34-39

Sütterlin, S. & Lenteren, J.C. van. 1997. Influence of hairiness of *Gerbera jamesonii* on the searching efficiency of *Encarsia formosa*. *Biological Control* 9, 157-165

Swirski, E., Blumberg, D., Wysoki, M. & Iyhar, Y. 1988. Phenology and biological control of the Japanese berry whitefly, *ParaBemisia myricae* on citrus in Israel. *Proceedings of the 6th International Citrus Congress* Middle East, Tel Aviv, Israel 3, 1163-1168

Tawfik, M.F.S., Awadallh, K.T., Hafez, H. & Sarhan, A.A. 1978. Biology of the aphelinid parasite *Eretemocerus mundus* Mercet. *Bulletin on Entomological Society of Egypt* 62, 33-48

Thresh, J.M. & Otim-Nape, G.W. 1994. Strategies for controlling cassava mosaic geminiviruses. *Advances in Disease Vector Research* 10, 215-236

Thresh, J.M., Fishpool, L.D.C., Otim-Nape, G.W. & Fargette, D. 1994. African cassava mosaic disease: Underestimated and unsolved problem. *Tropical Science* 34, 3-14

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).

Thresh, J.M., Otim-Nape, G.W., Thankappan, M. & Muniyappa, V. 1998. The mosaic diseases of cassava in Africa and India caused by whitefly-borne geminiviruses. *Review of Plant Pathology* 77, 935-945

Viscarret, M.M., Botto, E.N. & Polaszek, A. 2000. Whitefly (Hemiptera: Aleyrodidae) of economic importance and their natural enemies (Hymenoptera: Aphelinidae, Signiphoridae) in Argentina. *Review of Chilean Entomology* 26, 5–11

Williams, T. 1995. The Biology of *Encarsia tricolor:* An autoparasitoid of whitefly. *Biological Control* 5, 209-217

Woolley, J.M & Herraty, J.M. 1998. *Encarsia* species of the World: a searchable database. http:\\ chalcidoids.tamu.edu/*Encarsia*/*Encarsia*.htm [a catalogue of about 313 species of *Encarsia* with information on types, distribution, and hosts]

Zaki, F.N., El-Shaaraway, M.F. & Farag, N.A. 2002. Populations of aphids, whiteflies and associated predators and parasites on different vegetables cultivated in plastic greenhouses. *Journal of Pest Science* 75,128-131

Appendix 1. Frequency of occurrence of cassava varieties at the study locations

Cassava variety	Bulisa	Busukuma	Lyantonde
Improved			
00057 (*Omongole*)	1	2	19
00067 (*Akena*)		1	
TMS 30572 (*Migyera*)	59		
TME 204 (*Mwido*)		8	
NASE 4 (SS4)			4
TME 14		23	
Local			
Bukalasa			2
Kwatamumpale			6
Mpologoma			3
Mweru		17	
Njule		7	
Unknown		2	23

NB: For the improved varieties, names in parentheses are names used by farmers.

Appendix 2. Frequency of appearance of cassava component crops, expressed as numbers of fields during the entire period of study

Component crops	Bulisa	Busukuma	Lyantonde
Banana		5	
Banana/coffee		2	
Beans		4	3
Coffee		2	
Cotton	2		
Eggplants			2
Greenpepper/coffee/vanilla		2	
Greengrams			1
Maize	32	9	12
Maize/banana		1	4
Maize/banana/beans		1	1
Maize/beans		6	2
Maize/beans/groundnuts			1
Maize/beans/greenpepper			1
Maize/cowpea	6		
Maize/groundnuts			1
Maize/potato			1
Maize/sweet Potato			1
Sole cassava	2	27	29
Sweet potato		1	1

Appendix 3. Preimaginal development duration (days) of *E. mundus* and *E. sophia* reported by other authors

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, respectively.

Appendix 4. Longevity of *E. mundus* and *E. sophia* reported by other authors

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

$^{thel\ \&\ ar}$ = Longevity of the thelytokous and arrhenotokous populations of *E. mundus*, respectively.

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

Reference	Host whitefly	Test plant	Fecundity/ Fertility	R_O	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

$^{thel\ \&\ ar}$ = Fecundity of the thelytokous and arrhenotokous populations of *E. mundus*, respectively.