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This contribution is dedicated
to the memory of Prof. Dan Gerling,
a scientist, a colleague and a friend

The incidence of *Bemisia tabaci* (Homoptera: Aleyrodidae) and its parasitoids on cassava and associated plants in Uganda

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ABSTRACT

Biotic and abiotic factors can influence the population dynamics of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae), a key pest of cassava and a vector of several viral diseases, and that of its parasitoids. To gain a better understanding of possible roles these factors, different crops/cropping systems and weeds play in determining *B. tabaci* population dynamics, cassava fields were surveyed monthly from November 2003 to December 2004 in Buliisa (Buliisa district), Busukuma (Wakiso district) and Lyantonde (Lyantonde district), Uganda. *Bemisia tabaci* and its parasitoids were more abundant on cassava than on both intercrops and weeds. *Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae) was the most abundant parasitoid species followed by *Encarsia sophia* Girault & Dodd (Hymenoptera: Aphelinidae). An undescribed *Encarsia* sp. was relatively rare. The level of parasitism on cassava was highest at Busukuma (41.7%), followed by Buliisa (37.2%) and Lyantonde (32.2%). The only companion crop that harboured *B. tabaci* nymphs was sweet potato with 22 nymphs from 20 plants and 68% parasitism. Similarly very low numbers of nymphs were observed on the following weeds: *Commelina benghalensis* (4 parasitized nymphs from 1340 plants), *Melhania* sp. (over 76 nymphs from 60 plants with about 60% parasitism), *Bidens pilosa* (2 parasitized nymphs from 1080 plants) and *Euphorbia* sp. (8 nymphs from 580 plants with 75% parasitism). This demonstrates that cassava companion crops and weeds in the surveyed locations are not major hosts of *B. tabaci.* For these two reasons, cassava is the only significant source of cassava-colonizing *B. tabaci*. Whitefly and disease control on cassava should therefore focus on an integrated management strategy, including breeding for resistance to both constraints, and enhancing natural enemies, in a manner that addresses specific agro-ecosystems.

KEYWORDS: Afrotropical, *Bemisia tabaci*, biological control, *Encarsia sophia*, *Eretmocerus mundus*, cassava, population dynamics.

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INTRODUCTION

Bemisia tabaci (Gennadius, 1889) (Homoptera: Aleyrodidae) is a vector of cassava mosaic geminiviruses (CMGs) that cause the widely distributed cassava mosaic disease (CMD) in Africa and the Indian sub-continent (Legg & Fauquet 2004; Patil & Fauquet 2009), leading to annual losses of 12–34 million tons of cassava in Africa (Thresh *et al.* 1997; Legg *et al.* 2006). To control CMD, virus-resistant varieties of cassava were developed, multiplied and disseminated to farmers (Otim-Nape *et al*. 1999). However, high whitefly populations have been recorded on these virus-resistant varieties in areas that had CMD outbursts in East Africa. This has resulted in the increased pest status of *B. tabaci* on cassava through direct and indirect damage by sap feeding and formation of sooty moulds. Consequently, tuberous yield reductions of up to 34–50% may result (Legg *et al*. 2003). *Bemisia tabaci* gained new prominence since cassava brown streak virus (CBSV), the causal agent of cassava brown streak disease (CBSD), had been shown to be transmitted by *B. tabaci* (Maruthi *et al*. 2005). This disease is particularly severe on some CMD-resistant varieties in Uganda (Alicai *et al*. 2007) and can lead to total crop failure. This demands an integrated control of the diseases and the vector, including integrating biological control of the vector in the overall management strategy.

There have been many attempts to find efficient natural enemies of *B. tabaci* in different parts of the world. Parasitoids have been more widely studied than predators and fungi as they are more easily monitored and have been successful in the control of whitefly infestations on other crops (Gerling *et al*. 2001). In Uganda, *B. tabaci* is attacked primarily by three aphelinid parasitoid species (Hymenoptera: Aphelinidae): *Eretmocerus mundus* Mercet, *Encarsia sophia* Girault & Dodd and an undescribed *Encarsia* sp. (Otim *et al*. 2005). Although the parasitoids do not seem to be effectively reducing *B. tabaci* populations early in the season (Otim *et al*. 2006), Legg (1995) and Asiimwe *et al* (2007) showed that the parasitoids *Encarsia* spp. and *Eretmocerus* sp. were instrumental in regulating *B. tabaci* populations and can cause up to 50% mortality of the pest. In order to enhance parasitism at this stage, it is important to understand factors that affect it, with a view to enhancing the positive factors whilst minimising the negative ones affecting the parasitoid performance.

Parasitism rates depend on the availability of food resources and suitable habitat that sustain the population of parasitoids. In these tripartite interactions, the herbivore-enemy relationship on one plant species can be influenced by the presence of associated plants or their herbivores (Price *et al*. 1980). Thus, increased diversity and improved stability in an ecosystem can be achieved by providing more refuge habitats for natural enemies as staging grounds for colonization (Stansly *et al*. 1997). This has already been demonstrated with *Eretmocerus* spp. moving from collard and sunflower grown as refuges into cotton and melon fields (Naranjo 2001). In Uganda, however, little has been published on host plants and their potential to act as whitefly and/or parasitoid refugia (Ssemaganda *et al*. 2003; Sseruwagi *et al*. 2006). Ssemaganda *et al.* (2003) found a proportionately higher number of parasitized nymphs on cassava intercropped with sweet potato than if grown in monoculture.

Thus, knowledge of parasitism levels on different crops is important as a prelude to developing a successful biological control approach. In our investigations, we assessed the abundance of *B. tabaci* and its parasitoids on cassava, crops grown in association with cassava and weeds in and around cassava fields. The specific objectives were: (1) to assess the level of infestation of cassava by *B. tabaci* and its parasitoids in selected districts of Uganda in different seasons and (2) to determine whether crops grown in association with cassava and weeds in and around cassava fields harbour *B. tabaci* and its parasitoids.

MATERIALS AND METHODS

Study settings

The study was conducted in three districts of Uganda. In each district, one sub-county (smaller administrative unit within a district) was selected for the survey; these were Buliisa, Lyantonde and Busukuma sub-counties in Buliisa (formerly part of Masindi district), Lyantonde (formerly part of Rakai district), and Wakiso districts, respectively. Each subcounty was visited once a month for twelve months. In each subcounty, five 3–6 months old cassava fields were sampled to assess the abundance of *B. tabaci* and its parasitoids; at this age cassava is most susceptible to whitefly infestation (Fishpool *et al.* 1995). With a few exceptions, different fields were visited on each occasion; records were taken on the exact age of the cassava crop, type of intercrop and infestation by *B. tabaci* and the associated parasitoids.

Ten cassava plants were examined per field. Six leaves were picked per plant, beginning with the top-most first red-eyed nymph-bearing leaf (Otim *et al.* 2005). Picked leaves were placed in a cool box and taken to the laboratory, where they were kept in paper bags at 4 °C until observations could be made. For each cassava leaf, a sub-sample was picked, comprising three alternate central leaflets. Each leaflet was examined for whitefly presence under a stereoscopic microscope and the number of healthy and parasitized fourth instar nymphs was recorded. Parasitoid pupae were identified as described by Otim *et al.* (2005), where *E. sophia* parasitised nymphs appeared as black pupal cases with black meconia symmetrically located on both sides posteriorly, while *E. mundus* appeared orange with a shiny pupal skin (with the pupae having red eyes). *Encarsia* sp. pupa appeared black towards the anterior of the nymph. In total, 18 cassava leaflets were observed per plant. After the observations, leaflets were put in emergence bottles and kept at room temperature to allow parasitoids to emerge. Emerged parasitoids were identified using guides by Polaszek *et al.* (1992), Schauff *et al.* (1996) and Rose & Zolnerowich (1997), and kept in 70 % ethanol. Samples were sent to the Tel Aviv University to confirm their identity, while voucher specimens were deposited at the National Crops Resources Research Institute, Namulonge (NaCRRI).

In order to assess infestation on crops grown in association with cassava and weeds within and around cassava fields, ten plants of each component crop or 20 weed plants were inspected for the presence of whitefly and associated natural enemies. For infestation on sweet potato 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 20 plants. Similarly, infestation on weeds was assessed by examining ten plants per garden, and ten plants outside the garden. Where infestations occurred, nymphs and natural enemies were counted and recorded from all the leaves of the selected plants. Weed plants that could not be identified in the field were picked and taken to the Makerere University Herbarium for identification. The data on weeds were summed for plants both within and outside cassava fields because of the low counts of whitefly and parasitoids. Whiteflies on *Melhania* were given to Dr P. Sseruwagi (National Crops Resources Research institute) for identification of their biotype. Data were also collected on relative humidity, temperature and rainfall in each location and were used to establish relationships between *B. tabaci* and its natural enemies, and the weather parameters.

Data analysis

Nymph and parasitoid counts on cassava were natural log transformed, and parasitism percentage values were transformed using the arcsine square root. These data were analysed using the unbalanced design of Analysis of Variance of Genstat 12.1 (VSN 2009). Data were transformed when the assumptions of normality and homogeneity of variance were not fulfilled (Mead *et al*. 2003). The treatment terms were subcounty, sampling date, cassava varieties and cropping systems, while the dependent variables were number of nymphs and parasitoids, and parasitism percentage. The total number of nymphs was calculated as a sum of parasitized and apparently healthy nymphs (hereafter referred to as nymphs). Parasitism rate was calculated as the proportion of parasitized nymphs to the total nymph count. This allowed for including all incidences of parasitism in the estimates since all known *B. tabaci* parasitoids emerge from the fourth instar nymphs and their developing stages are clearly visible through the transparent nymphal cases. All statistical interpretations are based on the transformed values of the different parameters. Data on whitefly and parasitoid infestation on component crops and weeds were not subjected to statistical analysis because of the rare occurrence of the insects on both weeds and crops intercropped with cassava. Weather data of the previous sampling dates were used for investigating the relationship with *B. tabaci* and parasitoid numbers, and parasitism percentage on the next sampling date.

RESULTS

Abundance of *B. tabaci* on cassava

The total number of *B. tabaci* nymphs (both healthy and parasitized) per 18 leaflets ranged from 0–1581 at Buliisa, 0–3375 in Busukuma and 0–693 in Lyantonde. Of the 600 plants examined in each location, 18% in Buliisa, 10% in

Busukuma and 29 % in Lyantonde had no nymphs at all, and these were generally found in fields with other cassava plants that were infested. However, most examined plants (51 % in Buliisa, 54 % in Busukuma and 59 % in Lyantonde) had nymph numbers ranging from 1–100 nymphs per 18 leaflets.

The mean number of nymphs varied significantly ($F_{2,177}$=11.45; P<0.001) between the locations; the highest figures occurred at Busukuma (192±42 nymphs per 18 leaflets; mean ± SE), followed by Buliisa (107±16.2 nymphs per 18 leaflets) and Lyantonde (41.74±6.8 nymphs per 18 leaflets).

Significant (P<0.001) variations occurred in the number of *B. tabaci* nymphs between sampling dates at all the locations: Buliisa ($F_{11,43}$=6.15), Busukuma ($F_{11,19}$= 3.36) and Lyantonde ($F_{11,19}$=3.79) (Fig. 1). At Buliisa, nymph numbers increased from November 2003, peaked the following month and declined thereafter. At Busukuma, there were two peaks of nymph numbers, in March and June 2004, and their abundance decreased to the lowest value in November 2004. At Lyantonde, there was a gradual increase in the number of nymphs from December 2003 to a peak in April 2004 and another peak in July 2004 (Fig. 1). The age of the cassava crop significantly affected the number of nymphs only at Buliisa ($F_{1,43}$=11.21; P<0.001). The were no significant influence of the age of cassava at Busukuma ($F_{1,19}$=0.18; P=0.673) and Lyantonde ($F_{1,19}$=0.2; P=0.204). The number of nymphs decreased with crop age at Buliisa, while the opposite was observed at Busukuma.

Abundance of parasitoids, and parasitism rate of *B. tabaci* on cassava

Eretmocerus mundus, *Encarsia sophia* and *Encarsia* sp. were recovered from *B. tabaci* on cassava. *Eretmocerus mundus* and *Encarsia 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 and on most sampling dates, followed by *E. sophia* and *Encarsia* sp. (Fig. 2). There was a significant difference in the abundance of *E. mundus*, *E. sophia* and *Encarsia* sp. between locations ($F_{2,177}$=8.96–18.08; P<0.001). The number of *E. mundus* averaged 16.8±2.65, 32.6±7.2 and 6.5±1.18 individuals per 18 leaflets at Buliisa, Busukuma and Lyantonde, respectively. The number of *E. sophia* averaged 4.9±0.7, 15.7±3.05 and 2±0.37 per 18 leaflets at Buliisa, Busukuma and Lyantonde, respectively. The number of *Encarsia* sp. was 4.0±1.56 per 18 leaflets at Busukuma, 0.6±0.29 at Buliisa and 0.02±0.007 at Lyantonde.

The relationship between the abundance of parasitoids with the age of the cassava crop was not consistent across locations. The number of *E. mundus* significantly decreased with the cassava crop age at Buliisa ($F_{1,43}$=5.92; P=0.019). There was no significant influence of the age of cassava on the number of nymphs at Busukuma ($F_{1,19}$=0.99; P=0.333) and Lyantonde ($F_{1,19}$=0.44; P=0.513). In the case of *E. sophia* abundance, the effect of the cassava crop age was negative at Buliisa ($F_{1,43}$=5.98; P=0.019) and not significant at both Busukuma ($F_{1,19}$=0; P=0.979) and Lyantonde ($F_{1,19}$=0.32; P=0.578). There was no significant effect of the cassava crop age on the abundance of *Encarsia* sp. at Buliisa ($F_{1,43}$=0.12; P=0.728) and Busukuma ($F_{1,19}$=1.84; P=0.191). However, there was a significant influence of the

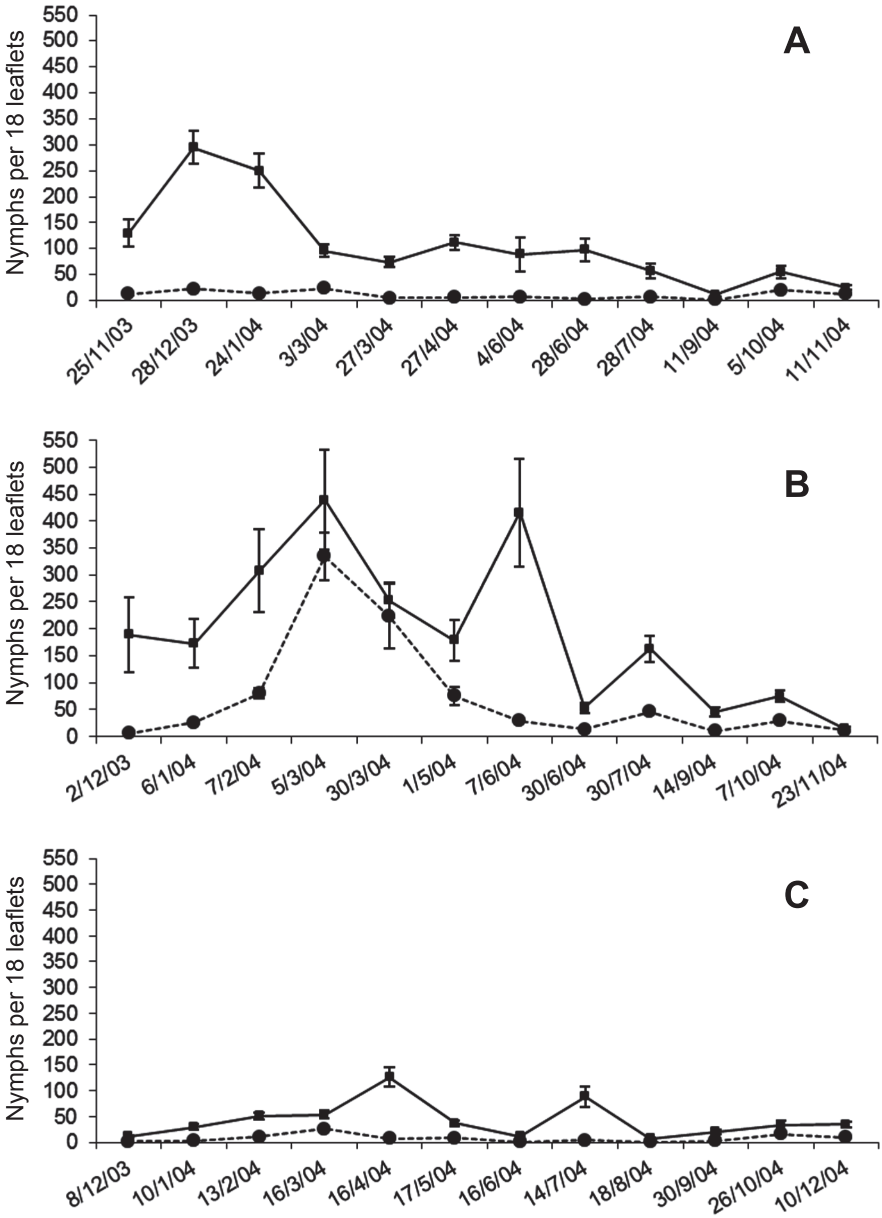

Fig. 1: Number of nymphs of *B. tabaci* (mean ± SE) on cassava at Buliisa (A), Busukuma (B) and Lyantonde (C) from November 2003 to December 2004.

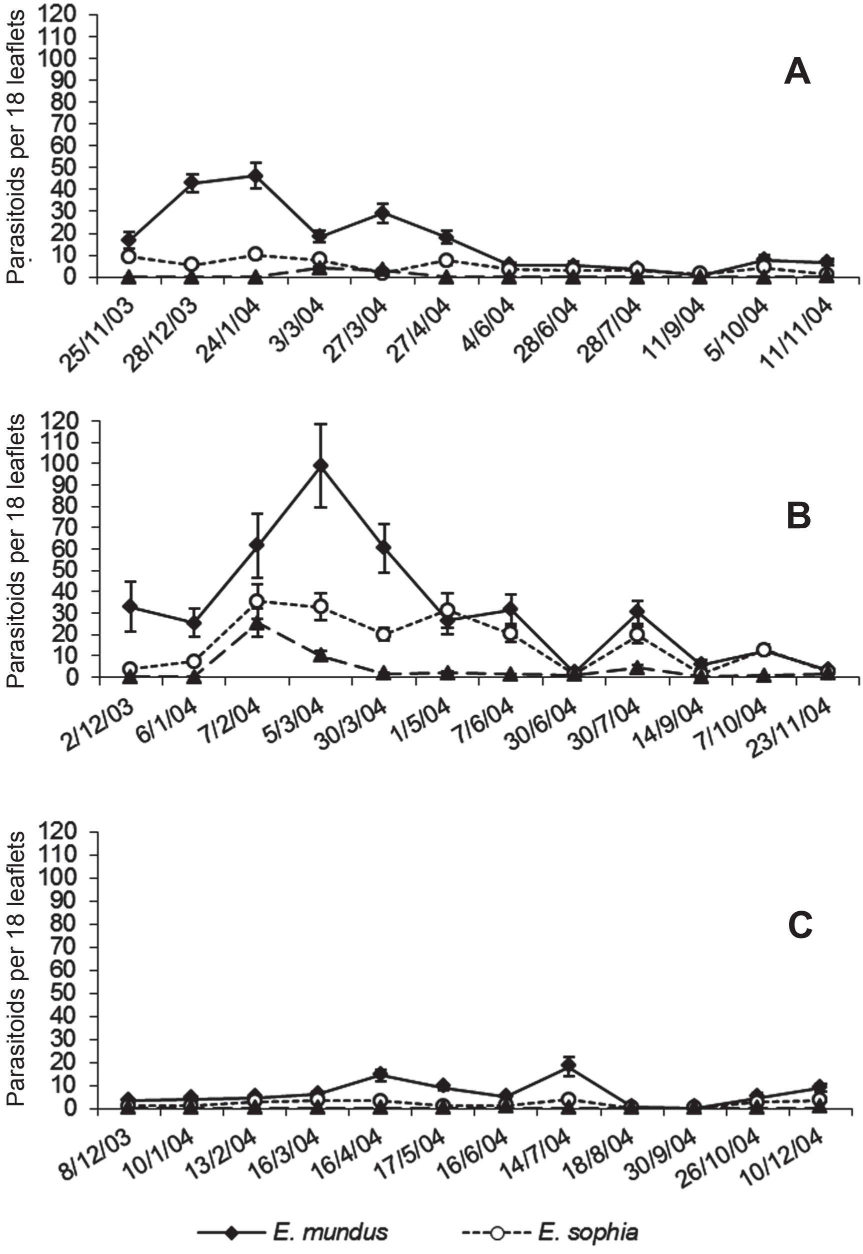

Fig. 2: Species composition and abundance of *B. tabaci* parasitoids on cassava (mean ± SE) at Buliisa (A), Busukuma (B) and Lyantonde (C) from November 2003 to December 2004.

age of the cassava crop on the abundance of *Encrasia* sp. at Lyantonde ($F_{1,19}$=9.19; P=0.007), where it reduced with age.

The abundance of *E. mundus* and *E. sophia* increased (following a similar pattern) with the total number of nymphs in all the study locations (Figs 1, 2). The regression between abundance of the parasitoids *E. mundus* and *E. sophia* against the total number of nymphs was significantly (p<0.001) positive in all locations (*E. mundus*: y=-0.581+0.713; R^2=79.4 at Buliisa; y=-1.017+0.825; R^2=81.4 at Busukuma and y=-0.128+0.524; R^2=69.2 at Lyantonde; *E. sophia*: y=-0.141+0.365; R^2=59.2 at Buliisa, y=-0.918+0.673; R^2=73.1 at Busukuma and y=-0.125+0.305; R^2=61.1 at Lyantonde). There was a negative relationship between the number of *Encarsia* sp. and the number of nymphs at Busukuma y=-0.518+0.288; R^2=28.2, whilst there was no significant (P>0.05) relationships at the other locations.

Parasitism rate ranged from 0–100% at all the locations. Both extremes of parasitism percentage were recorded at relatively low levels of *B. tabaci* infestation and were generally not restricted to specific fields. The lowest number of unparasitized nymphs was one per 18 leaflets at all the locations, while the highest numbers of unparasitized nymphs were 56, 289 and 126 per 18 leaflets at Buliisa, Busukuma and Lyantonde, respectively. The 100% parasitism rate was recorded in a minimum of one nymph per 18 leaflets, while the highest numbers of 100% parasitized nymphs per 18 leaflets were 25 at both Buliisa and Lyantonde, and 37 at Busukuma.

The highest mean parasitism was observed at Busukuma (41.7±1.21%), followed by Buliisa (37.1±1.074%) and Lyantonde (32.2±1.21%). There were significant variations in parasitism between sampling dates at Buliisa ($F_{11,43}$=2.04; P=0.049) and Busukuma ($F_{11,19}$=2.65; P=0.03), but not Lyantonde ($F_{11,19}$=2.09; P=0.110) (Fig. 3). Parasitism rate peaked in March 2004 at all the locations, and again in June 2004 and July 2004 at Lyantonde and Busukuma, respectively.

The age of the cassava crop did not have a significant effect on parasitism rate at all locations: Buliisa ($F_{1,43}$=0.13; P=0.725), Busukuma ($F_{1,19}$=2.58; P=0.125) and Lyantonde ($F_{1,19}$=2.09; P=0.110). Parasitism percentage weakly correlated with the total number of nymphs at Busukuma (y=36.7+3.27; p=0.015; R^2=8.3).

The incidence of *B. tabaci* and parasitoids on different varieties of cassava at different locations

Two cassava varieties were grown by farmers in Buliisa, with *Nase 2* constituting 98% of the surveyed fields and variety *TMS I92/00057* recorded in only one field (2%). Seven varieties were recorded in each of Busukuma and Lyantonde. The dominant varieties in Busukuma were *TME 14*, an introduced West African landrace that was found in 38% of the fields, followed by a local landrace, *Mweru* found in 28% of the fields. The other cassava varieties grown in Busukuma were *TME 204*, *Njule*, *TMS I92/0057*, an unknown variety and *TMS I92/0067*, recorded in 13%, 12%, 3%, 3% and 1.5% of the fields, respectively. The dominant varieties in Lyantonde were an unknown variety and *TMS I92/0057* recorded in about 38%

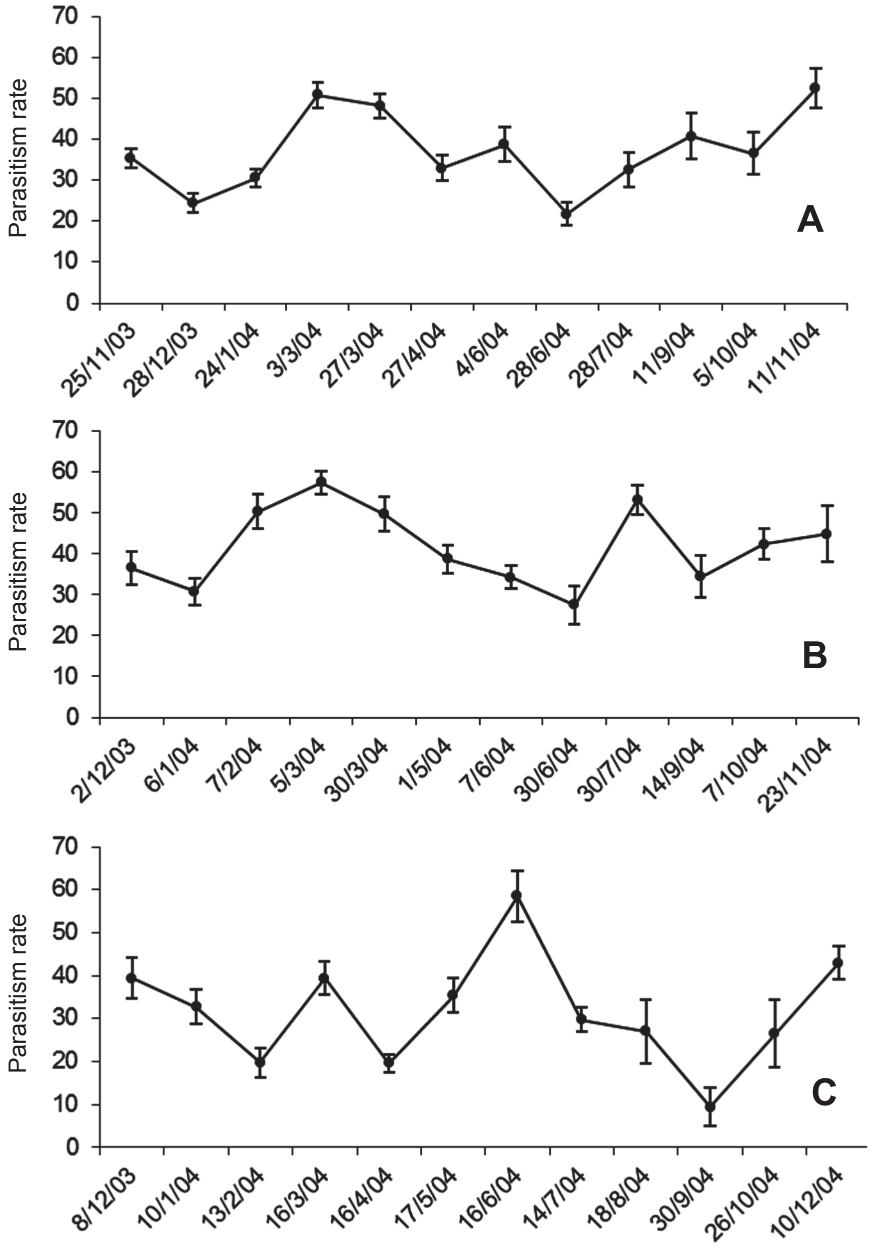

Fig. 3: Mean parasitism percentage (±SE) of *B. tabaci* on cassava at Buliisa (A), Busukuma (B) and Lyantonde (C) from November 2003 to December 2004.

Table 1. The number of adults and healthy nymphs of *B. tabaci* and their natural enemies (pupae) on crops found in cassava fields at the different sites summed for all plants and sampling dates.

Subcounty and component crop	Total number summed for all dates				
	Plants sampled	Adults	Nymphs	*E. mundus*	*E. sophia*
Buliisa					
Cotton	20	12	0	0	0
Cowpea	60	3	0	0	0
Busukuma					
Beans	110	56	0	0	0
Coffee	60	0	0	0	0
Sweet potato	10	1	0	0	0
Lyantonde					
Beans	80	15	0	0	0
Sweet potato	20	8	7	15	0

and 32 % of the fields, respectively. The other cassava varieties recorded in Lyantonde were *Nase 4*, *Weyambule, Mpologoma* and *Bukalasa* recorded in 7 %, 5 %, 5 %, and 3 % of the fields, respectively.

The abundance of whiteflies and their parasitoids on other plants in and around cassava fields

Of the crops grown in association with cassava, adult whiteflies were found on cowpea and cotton at Buliisa, and on beans and sweet potato at Busukuma and Lyantonde (Table 1). Healthy and parasitized whitefly nymphs were recorded only on sweet potato at Lyantonde. *Eretmocerus mundus* was the only parasitoid recovered from *B. tabaci* on sweet potato and accounted for 68 % of the parasitized nymphs (Table 1).

Among the weeds, *Ageratum conyzoides*, *Bidens pilosa*, *Commelina benghalensis*, *Euphorbia hirta*, *Lantana camara*, and *Melhania* sp. growing in and around cassava fields were found to be infested with whitefly adults (Table 2). The whitefly biotypes on weeds were not examined because of the low colonization (as reflected in numbers of healthy and parasitized nymphs), except those that occurred on *Melhania* sp. The *Melhania* whitefly belonged to the okra biotype of *B. tabaci*. The numbers of apparently healthy and parasitized nymphs were extremely low on all weeds species (Table 2). Very small numbers of nymphs were found on *C. benghalensis*, *B. pilosa* and *E. hirta* but almost all were parasitized by *E. mundus*.

Relationship between abundance of nymphs, parasitoids and parasitism rate with weather parameters

A regression of the numbers of nymphs and parasitoids, and parasitism percentage against relative humidity did not reveal any significant relationship at any location. A regression with rainfall revealed no significant effect on the number of

Table 2. Total number of adults and nymphs of *B. tabaci* and their parasitoids (pupae) on weeds found in and around cassava fields at the different sites summed for all plants and sampling dates.

Subcounty and plants	Total number summed for all dates				
	Plants sampled	Adults	Nymphs	*E. mundus*	*E. sophia*
Buliisa					
Commelina	620	16	0	2	0
Melhania sp.*	60	30	-	39*	7*
Bidens sp.	160	4	0	0	0
Busukuma					
Ageratum sp.	280	9	0	0	0
Bidens sp.	520	35	0	1	0
Commelina sp.	400	11	0	2	0
Euphorbia sp.	580	49	2	6	0
Lantana sp.	40	3	0	0	0
Lyantonde					
Bidens sp.	400	8	0	1	0
Commelina sp.	320	5	0	0	0

* The number of healthy and parasitized whiteflies could not be ascertained because leaves were entirely covered with sooty mould, and so parasitism was based on emerged whitefly and parasitoids.

E. mundus, *E. sophia*, number of nymphs or parasitism rate at Buliisa, nor for all parasitoid species, nymph numbers and parasitism percentage at Busukuma. The effect of rainfall on these factors was not investigated at Lyantonde because of few data points (4) collected on rainfall. Temperature (x) only had a significant positive relationship with the number of nymphs (Y) at Buliisa ($Y=-10.98+0.55x$; $P=0.027$; $R^2=37.2$) and Lyantonde ($Y=-6.85+0.39x$; $P=0.003$; $R^2=66.1$), and the number (N) of *E. mundus* ($N=1.05+0.069x$; $P=0.03$; $R^2=39.7$) and *E. sophia* ($N=1.86+0.03x$; $P=0.016$; $R^2=47.5$) at Lyantonde. There was no significant effect of temperature on the other parameters. The relationship between climatic parameters and abundance of *Encarsia* sp. was investigated only in Busukuma because they were present on more than five sampling dates in Busukuma, and on less than five sampling dates in Buliisa and Lyantonde.

DISCUSSION

There has been limited research on the host plants of *B. tabaci* in Uganda (Sseruwagi *et al.* 2006) and elsewhere in Africa (Gnankiné *et al.* 2013; Tocko-Marabena *et al.* 2017; Romba *et al.* 2018), and on the plants hosting parasitoids of *B. tabaci*. This study investigated the occurrence of *B. tabaci* and its parasitism on cassava and adjacently growing crops and weeds in order to understand better their dynamics as a key for successful pest management. The study has demonstrated that the whitefly and its parasitoids are primarily found on cassava, not weeds or other crops.

The presence of adult whiteflies and lack of eggs and nymphs on some crops grown together with cassava and weeds within and around cassava fields may be explained by the mobility of adult whiteflies rather than their readiness to develop on the examined plant species. This suggests whitefly-host-restriction as earlier reported (Legg 1996; Abdullahi *et al.* 2003). Nevertheless, Sseruwagi *et al*. (2006) reported *B. tabaci* cassava biotype infesting the non-cassava plant species, *Manihot glaziovii*, *Jatropha gossypiella*, *Aspilia africana* and *Abelmoschus esculentus* in Uganda. However, our results indicate that the level of infestation on non-cassava plants was low, and additionally that a majority of pests were parasitized, thus making them pose little risk to cassava cultivation. This is relevant for managing whitefly, CMD and CBSD because the apparent lack of or limited alternative hosts that serve as whitefly reservoirs would mean limited vector and virus movement to the cassava crop. This would result in a low infestation level, damage and virus dispersal, thereby protecting cassava from direct damage and the *B. tabaci* vectored viruses. Although this may be true, it is vital to assess a possible role of plants that are successfully colonized as likely alternative hosts and reservoir of *B. tabaci* vectored viruses.

Our results have also confirmed that parasitism plays a key role in regulating the population of this pest (Legg 1995; Asiimwe *et al*. 2007). Similar to the results of Otim *et al.* (2005), the key parasitoid species were *E. mundus* and *E. sophia*, both of which were recorded in all the study locations. The positive relationship between the abundance of these parasitoids and the total number of nymphs indicates a density dependent relationship, a quality that would result in the production of more parasitoids as the numbers of the host increase. A positive correlation between parasitoids and whitefly immatures has been noted by Romba *et al*. (2018) in West Africa.

The abundance of these parasitoids, their whitefly host and parasitism percentage varied between and within the studied locations. Possible reasons behind the differences may include climatic conditions, cassava cultivation intensity and the age of the crop.

The three locations studied differed in the cultivation practices and climatic factors, which appears to be reflected in the whitefly and parasitoid population dynamics. The observed differences included cultivars, intensity of cassava growing and cropping systems. Whereas only two cassava varieties were grown in Buliisa, seven cultivars (local and improved) were planted in the fields surveyed in both Busukuma and Lyantonde (Table 3). Moreover, four varieties (unknown, *TME 204*, *TME 14* and *Njule*) supported relatively higher *B. tabaci* populations (216–341 nymphs per 18 leaflets) in Busukuma compared to any variety at the other two locations. These four varieties were followed in *B. tabaci* infestation level only by *Nase 3*, commonest in Buliisa, with an average of 109 nymphs per 18 leaflets, and the *TME 14* variety with 76 nymphs per 18 leaflets. Such uneven levels of infestation among cultivars corroborate earlier studies by Otim *et al.* (2006),

Table 3. The mean incidence of parasitoids and parasitism of *B. tabaci* nymphs on different cassava varieties at Buliisa, Busukuma and Lyantonde.

Subcounty and cassava variety	Total nymphs			*E. mundus*			*E. sophia*			*Encarsia* sp.			Parasitism		
	Per 18 leaflets	SEM	CV	Per 18 leaflets	SEM	CV	Per 18 leaflets	SEM	CV	Per 18 leaflets	SEM	CV	%	SEM	CV
Buliisa															
Nase 2	108.8	16.43		16.9	2.7	122.9	4.9	0.7	110.7	0.6	0.297	369.8	37.3	2.143	43.7
I92/00057	41.3	0	0	13.7	13.7	0	2.0	2.0	0.0	0.8	0	0	51.9	0	0
Busukuma															
Variety 00067	2.2	0	0	0.3	0	0	0.2	0.0	0.0	0.0	0	0	64.2	0	0
Mweru	90.6	18.89	85.96	12.5	3.331	109.8	11.2	2.8	102.0	1.1	0.284	111.2	42.2	3.79	37
TME 204	293.2	176.5	170.3	57.1	38.25	189.5	21.4	9.1	120.3	5.1	1.809	100.6	42.7	7.068	46.79
Njule	259.6	154.6	157.5	57.5	27.43	126.1	27.5	15.4	148.1	19.1	12.25	169.6	46.3	5.096	29.14
I92/00057	85.6	29.8	49.23	15.5	5.1	46.53	7.8	5.2	94.0	1.5	1.5	141.4	53.9	3.997	10.5
TME 14	215.9	74.66	165.9	33.4	9.752	139.8	14.9	5.3	170.4	1.6	0.573	172.2	35.3	4.349	59.11
Unknown	341.0	295.2	122.4	42.3	28.35	94.89	13.3	2.8	29.4	3.8	3.8	141.4	43.0	29.08	95.54
Lyantonde															
Bukalasa	0.0	0	0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0	0
Kwatamumpale	36.1	23.36	158.7	11.6	6.593	139.4	2.2	1.2	136.2	0.0	0	0	41.5	9.211	54.33
Mpologoma	4.3	0.751	30.03	1.3	0.656	87.37	0.5	0.3	103.3	0.0	0	0	44.4	17.89	69.84
Nase 4	36.8	9.767	53.08	4.7	1.635	70.33	1.1	0.4	69.8	0.0	0	0	34.2	11.66	68.3
I92/00057	76.4	16.02	91.37	8.6	2.4	122.3	2.6	0.7	110.4	0.0	0	0	24.3	2.818	50.49
Unknown	28.2	6.319	107.4	5.5	1.443	126.9	2.3	0.7	151.1	0.0	0	0	34.4	4.371	49.21
Weyambule	8.9	7.417	144.9	4.0	3.504	151.7	0.5	0.3	121.8	0.0	0	0	54.0	2.236	7.17

Table 4. The mean incidence of parasitoids and parasitism of *B. tabaci* nymphs on cassava (per 18 leaflets) in different cropping systems at Buliisa, Busukuma and Lyantonde in 2003 and 2004.

Subcounty and intercrop	Total nymphs			*E. mundus*			*E. sophia*			*Encarsia* sp.			Parasitism		
	no.	SEM	CV	no.	SEM	CV	no.	SEM	CV	no.	SEM	CV	%	SEM	CV
Buliisa															
Cotton	26.4	0.2	1.1	8.1	2.0	34.3	1.0	0.1	14.1	0.4	0.1	20.2	54.9	1.4	3.6
Maize	129.5	24.8	108.1	18.8	3.9	117.6	4.7	0.9	107.3	0.2	0.1	347.1	34.3	2.7	44.3
Maize+cowpea	50.7	25.8	124.6	3.9	2.0	129.6	3.9	1.9	121.5	0.0	0.0	0.0	33.3	5.7	38.4
Sole cassava	97.9	25.7	117.5	18.3	4.7	113.5	5.8	1.4	109.8	1.5	0.8	255.3	42.2	4.0	42.5
Busukuma															
Banana	380.7	276.3	162.3	78.0	60.9	174.5	19.0	11.0	130.0	4.6	2.6	124.5	35.5	3.4	21.7
Banana+coffee	52.6	10.2	27.4	4.9	3.0	86.0	7.8	4.4	79.8	2.3	2.1	128.9	30.2	12.1	56.7
Beans	58.9	31.9	108.2	7.3	5.5	149.9	8.2	7.1	173.9	0.7	0.7	200.0	29.2	6.9	47.4
Coffee	43.2	2.6	8.5	11.2	2.7	34.1	9.3	1.3	19.1	5.0	2.6	73.5	52.6	19.5	52.5
Green pepper+ coffee+vanilla	833.0	722.0	122.6	56.5	54.4	136.2	28.7	28.6	140.9	1.7	1.7	141.4	29.5	8.7	41.7
Maize	50.2	18.3	109.6	7.5	7.5	139.8	4.9	2.5	152.9	0.2	0.2	226.8	32.9	6.3	57.4
Maize+banana	27.0	0.0	0.0	3.1	0.0	0.0	2.0	0.0	0.0	0.3	0.0	0.0	40.1	0.0	0.0
Maize+banana+beans	215.6	0.0	0.0	134.5	0.0	0.0	25.2	0.0	0.0	2.4	0.0	0.0	80.9	0.0	0.0
Maize+beans	180.3	76.1	103.4	28.5	14.1	121.2	21.0	15.9	185.1	2.0	1.1	140.6	44.1	8.5	47.0
Sole cassava	212.9	54.1	132.1	37.7	9.4	129.3	19.4	5.0	133.1	6.6	4.4	263.7	44.0	3.7	43.3
Sweet potato	2.2	0.0	0.0	0.3	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	64.2	0.0	0.0

Table 4. *(continued).*

Subcounty and intercrop	Total nymphs			*E. mundus*			*E. sophia*			*Encarsia* sp.			Parasitism		
	no.	SEM	CV	no.	SEM	CV	no.	SEM	CV	no.	SEM	CV	%	SEM	CV
Lyantonde															
Beans	64.8	14.9	39.9	10.7	6.5	105.4	0.1	0.1	114.6	0.1	0.1	114.6	25.6	13.9	94.2
Eggplants	27.1	4.4	23.0	5.5	0.4	10.3	0.0	0.0	0.0	0.0	0.0	0.0	45.8	7.8	24.1
Greengrams	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			
Maize	27.9	11.1	137.5	3.5	1.1	106.0	0.9	0.4	147.8	0.0	0.0	0.0	30.8	5.7	55.8
Maize+banana	31.7	11.1	137.5	7.3	2.8	76.1	1.3	0.6	99.5	0.0	0.0	0.0	40.0	6.4	27.6
Maize+banana+beans	23.7	0.0	0.0	11.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	50.9	0.0	0.0
Maize+beans	17.5	16.0	129.3	9.2	9.0	138.3	1.7	1.4	116.5	0.0	0.0	0.0	59.6	6.8	16.1
Maize+beans+ groundnuts	5.6	0.0	0.0	2.6	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	78.1	0.0	0.0
Maize+beans+ green pepper	1.4	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	58.3	0.0	0.0
Maize+groundnuts	235.8	0.0	0.0	33.8	0.0	0.0	5.3	0.0	0.0	0.0	0.0	0.0	20.1	0.0	0.0
Maize+potato	227.3	0.0	0.0	35.6	0.0	0.0	8.3	0.0	0.0	0.0	0.0	0.0	24.2	0.0	0.0
Maize+sweet potato	150.3	0.0	0.0	41.6	0.0	0.0	8.0	0.0	0.0	0.0	0.0	0.0	37.2	0.0	0.0
Sole cassava	37.6	7.7	110.2	4.3	1.1	137.7	2.0	0.6	154.2	0.0	0.0	299.6	27.2	3.3	58.8
Sweet potato	23.4	0.0	0.0	9.9	0.0	0.0	3.6	0.0	0.0	0.3	0.0	0.0	53.9	0.0	0.0

Alicai *et al.* (2007) and Omongo *et al*. (2012), who observed a similar pattern in infestation among cassava varieties.

Higher counts of *B. tabaci* in Busukuma and Buliisa compared to Lyantonde may also be partly explained by continuous cultivation of cassava throughout the year at the two former areas. Busukuma is a subcounty where the National Crops Resources Research Institute, Namulonge—housing the Root Crops Research Programme—is located. Thus, farmers in the surrounding communities are the first beneficiaries of promising/newly released cassava varieties and grow cassava to supply planting material that serve the rest of the country. As a result, cassava abundant all year round and the fields are not very far apart from each other. In Buliisa the locals depend on cassava as a major staple and prefer the *Nase 2* cultivar, which is perceived to make the best flour for cassava bread. In Lyantonde, cassava growing was on a lower scale and local varieties, which did not support heavy *B. tabaci* populations, predominated. Indeed, peaks *B. tabaci* nymphs in Busukuma and Lyantonde occurred due to a heavy load of *B. tabaci* in certain fields with widely promoted varieties. The two peaks at Busukuma coincided with high nymph populations on *TME 204* and *TME 14* during first and second peaks, respectively. In Lyantonde, the two *B. tabaci* peaks occurred due to high numbers of the whitefly on *TMS I92/0057*. In contrast, the outbreak of *B. tabaci* nymphs in Buliisa cannot be attributed to the varietal susceptibility, for only one cultivar predominated throughout the study period; this peak may be related to other ecological factors.

In addition to the cassava varieties, differences in cropping systems could have influenced the abundance of *B. tabaci* and its parasitoids (Table 4). Although there was no significant influence of cropping system on *B. tabaci* and parasitoid population in all locations, the population of *B. tabaci* and its parasitoids were higher than, lower than or at par with the population in the sole crop depending on the intercrop type in all the locations. This suggests that the intercrops may have direct or indirect effect on the *B. tabaci* population. There was high variability in infestation within the same cropping system, or among sole crops in different fields at the same location (Table 4), making it difficult to ascertain the level of influence during the survey. There is, therefore, a need for well-designed experiments to assess the impact of intercropping on *B. tabaci* and parasitoid populations and whether and how they can be integrated in vector and disease management.

Climatic factors, especially temperature and rainfall, may have direct and indirect influence on the population dynamics of the whitefly and its parasitoids, but their precise role is still an open field for investigation (Macfadyen *et al*., in press). A positive relationship was observed between temperature and number of nymphs at Buliisa and Lyantonde and the number of *E. mundus* and *E. sophia* at Lyantonde. We may attribute this to higher mean temperatures (28.8 °C and 27 °C) recorded at Buliisa and Lyantonde. These temperatures fall within ranges that are reported to be nearly optimal for the pest and its parasitoids (Gerling *et al*. 1986; López &

Botto 1997). In contrast, a lower mean temperature at Busukuma (22.4 °C) and the lack of correlation between temperature and *B. tabaci* and its parasitoids numbers appear to indicate that the cropping system has a more profound effect influencing their populations compared to temperature.

Our findings are consistent with those of Otim *et al.* (2005) and Macfadyen *et al.* (in press), who showed that *E. mundus* and *E. sophia* are most abundant parasitoid species with respect to *B. tabaci*. Our study has also revealed that no crop or weed plant plays a major role as an alternative host of *B. tabaci* in the surveyed locations. All the observations suggest that the main infestation source of cassava is whitefly migration from other cassava fields. Although crops like sweet potato and *Melhania* weed do harbour some parasitoids, their populations are not sufficient to impact the whiteflies dwelling on cassava. Movement of parasitoids early in the season is an important controlling activity that needs to be exploited by integrating it with other pest control methods. Therefore, major management considerations should focus on an integrated approach including introduction of new natural enemies and breeding cassava resistant to the vector and diseases. The lack of consistent influence of different variables on the number of *B. tabaci* and its parasitoids and the rate of parasitism clearly indicate the need to develop agro-ecosystem specific technologies based on sound ecological studies, as well as on solid knowledge of the host and parasitoid taxonomy and biology (Guastella *et al*. 2015; Otim *et al*. 2018; Sseruwagi *et al*. 2018).

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