

**EFFECT OF CASSAVA GENOTYPE AND ENVIRONMENT ON POPULATION
CHANGE AND FITNESS OF THE WHITEFLY, *Bemisia tabaci* (Hemiptera: Aleyrodidae)**

BY

KASIFA KATONO

BSc. Agric (MAK), MSc. Crop Science (MAK)

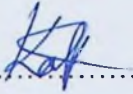
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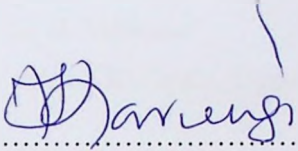
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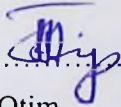
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Assoc. Prof. Jeninah Karungi

Makerere University

Date.....20/7/2023.....

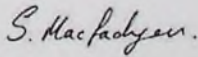
Signed 

Dr. Michael Hilary Otim

National Agricultural Research Organisation

Date19/7/2023.....

Signed



Dr. Sarina Macfadyen

Australian Centre for International Agricultural Research

Date ...18/07/2023

DOCTORAL COMMITTEE

Dr. Michael H. Otim

National Agricultural Research Organisation, Uganda.

Assoc. Prof. Jeninah Karungi

Makerere University (Mak), Kampala, Uganda.

Assoc. Prof. Herbert Talwana

Makerere University (Mak), Kampala, Uganda.

Assoc. Prof. Settumba B. Mukasa

Makerere University (Mak), Kampala, Uganda.

Dr. Christopher A. Omongo

National Agricultural Research Organisation, Uganda.

Dr. Mildred Ochwo Ssemakula

Makerere University (Mak), Kampala, Uganda.

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PUBLICATIONS DECLARATION

The articles below were drafted from the different chapters of the thesis.

Chapter Three of the Thesis:

Katono, K., Macfadyen, S., Omongo, C. A., Odong, T. L., Colvin, J., Karungi, J., and Otim, M. H. (2021). Influence of cassava morphological traits and environmental conditions on field populations of *Bemisia tabaci*. *Insects*, 12: 604. <https://doi.org/10.3390/insects12070604>

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DEDICATION

To God, the Almighty for His unending grace, mercy and strength.

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ABSTRACT

The whitefly pest complex *Bemisia tabaci* (Gennadius, 1889) is one of the most devastating agricultural pests globally. Over the past two decades, increased abundance of *B. tabaci* populations throughout the cassava-growing regions of East and Central Africa has been reported. The recent outbreak of large *B. tabaci* populations intensifies its significance as a direct pest of cassava and also increases the prevalence of *B. tabaci* transmitted diseases. However, there are no practical *B. tabaci* management options available for smallholder farmers in the region. This is largely because previous research efforts focused on the development of virus disease resistant cassava genotypes with no special emphasis on the vector. The main aim of this study therefore was to understand the factors that influence *B. tabaci* population dynamics and fitness.

To investigate the effect of cassava morphological traits, temperature, rainfall and relative humidity (RH) on the abundance of *B. tabaci*, five cassava genotypes (Alado alado, Njule Red, NAROCASS 1, NASE 14 and NASE 3) with varying levels of resistance to *B. tabaci* vectored diseases and *B. tabaci* infestation were planted in three Ugandan agro-ecological zones in 2016 and 2017 in a randomized complete block design. Results have shown that *B. tabaci* Sub-Saharan Africa 1 (SSA1) was the species on cassava in Uganda. The tallest genotype Alado alado supported the lowest number of *B. tabaci* adults. In areas with high *B. tabaci* prevalence, leaf area, leaf lobe width and leaf lobe number exhibited significant positive effects ($p < 0.001$) on *B. tabaci* adult count across locations. Positive effects of relative humidity, and negative effects of temperature and rainfall, on *B. tabaci* adult and nymph counts were observed in 2016 and 2017, hence the low populations in the North Eastern Savanna grassland. Temperatures of 28–30 °C, rainfall of 30–150 mm and RH of 55–70% and deployment of cassava genotypes of short stature with large leaf area and lobe width were significantly associated with increased *B. tabaci* populations.

A controlled study to evaluate the development duration, survival, and population parameters for *B. tabaci* was conducted at five constant temperatures (16, 20, 24, 28 and 32 °C) on three cassava genotypes (Alado alado, NAROCASS 1 and NASE 14) in a randomized complete block design in the laboratory. High temperatures significantly reduced development time of all stages and female longevity across all genotypes; the total life cycle was 63.8 days at 16 °C and 17.9 days at 32 °C on NAROCASS 1. However, there was no significant effect of temperature on development times

for all nymph instars except the third instar stage at 28 °C and 32 °C. Survival of each growth stage and for the entire life cycle, and fecundity increased with temperature, with highest values recorded at 32 °C. However, survival at 28 °C and 32 °C was remarkably similar. For all genotypes, the intrinsic rate of increase (r_m), finite rate of increase (λ) and net reproductive rate (R_0) increased with temperature, while mean generation time (T) reduced with temperature. At 32 °C, r_m , R_0 , λ and T were 0.2, 48.7, 1.2 and 22.6 days respectively, compared to 0.01, 1.9, 1.0 and 71.2 days at 16 °C on Alado alado. Therefore, the ideal development temperature for *B. tabaci* SSA1 was determined to be 32 °C. This study thus predicts possible expansion of *B. tabaci* populations in parts of the world with a hot and humid climatic condition.

Cohort-based life tables were constructed to determine the sources and rates of mortality of *B. tabaci* field populations in Uganda. Monthly cohorts (10 in total) were established separately for eggs and nymphs on two cassava genotypes (Alado alado and NAROCASS 1) in a randomized complete block design. Results revealed that disappearance followed by parasitism were the key mortality factors influencing *B. tabaci* populations in the field. This study has also shown that the highest mortality occurred during the third nymphal stage (55% on Alado alado), and only 12% of nymphs reached the adult stage. Therefore, management interventions that focus on enhancing the levels of disappearance and parasitism may lead to desirable *B. tabaci* population suppression. Cassava genotype had no effect on *B. tabaci* mortality.

Efficacy studies for the two common *B. tabaci* parasitoids: *Encarsia sophia* Girault and Dodd and *Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae) at five *B. tabaci* SSA1 host densities (10, 40, 60, 100 and 140) on three cassava genotypes (Alado alado, NAROCASS 1 and NASE 14) were conducted in the greenhouse. The results have shown that host density and parasitoid species ($p < 0.001$) and the genotype by parasitoid species interactions ($p < 0.001$ to $p < 0.05$) had significant effects on host feeding and parasitism of *B. tabaci* SSA1. The parasitic and host feeding capacity of both *E. mundus* and *E. sophia* was highly density dependent with levels of nymph death increasing with host density; *E. mundus* parasitised 1.5 and 40.2 nymphs at host density of 10 and 140 nymphs, respectively. At all host densities, *E. sophia* killed more host by feeding while *E. mundus* parasitized more hosts. However, *E. mundus* caused more total nymph death than *E. sophia* at all host densities. At a host density of 100 nymphs, *E. mundus* killed 38.9 nymphs

compared to the 22.4 nymphs killed by *E. sophia*. Thus, *E. mundus* is a more effective biological control agent. Thus, augmentative release of these hymenopteran parasitoids in areas with high *B. tabaci* populations would offer impressive pest population suppression. Further, it was observed that interaction of cassava genotype with parasitoid species improved bio-control efficiency. Glabrous cassava genotypes used in this study enhanced parasitoid effectiveness.

This is the first study in Uganda to investigate factors driving the *B. tabaci* population explosion on cassava, the findings will critically contribute to design of effective strategies for the management of this global pest for African farmers.

CHAPTER ONE

GENERAL INTRODUCTION

1.1. Origin and Importance of Cassava

Cassava (*Manihot esculenta*, Crantz), also known as *manioc*, *yucca* or *tapioca* is a woody perennial plant in the Euphorbiaceae family (Hillocks *et al.*, 2002). Cassava is native to South America (Olsen and Schaal, 1999; Allem, 2002), and is currently grown throughout the tropical and subtropical regions (Shackelford *et al.*, 2018), including Uganda where it was introduced in the 19th century (Langlands, 1972; Hillocks, 2002).

Cassava is the sixth most important food crop worldwide after wheat, rice, maize, potato, and barley (Saranraj *et al.*, 2019), and is cultivated for both food and industrial use (FAO, 2013). The crop is a staple food for over 500 million people in the tropical and subtropical regions of the world (Adenle *et al.*, 2012; Buyinza and Kitinoja, 2018). The significance of cassava stems from its value as a war and famine reserve crop, in addition to its resilience to climate change and the ability of its tuberous roots to remain in the soil for up to three years without deterioration (De Tafur *et al.*, 1997; Nweke, 2005; Jarvis *et al.*, 2012; Saranraj *et al.*, 2019). Furthermore, cassava is a cash crop as well as an industrial crop (Nweke, 2005; de Vries *et al.*, 2010; FAO, 2013; Saranraj *et al.*, 2019).

Global cassava production was 314 million tonnes in 2021, with 203 million tonnes (65%) produced in Africa (FAOSTAT, 2023). Nigeria is the largest producer of cassava worldwide while Uganda is the 23rd globally in terms of production, and the 9th in terms of area cultivated (FAOSTAT, 2023). In Uganda, cassava is among the 12 strategic crops for transforming the country's agricultural sector from a predominantly peasant to commercial and industrial production (Kato and Bendana, 2018). About 75% of small-holder farmers in Central, Eastern, North-Western and Northern regions of the country grow cassava (USAID, 2010; Kato and Bendana, 2018; UBOS, 2020), and its production comes fourth after sugar cane, cooking banana and maize (FAO, 2020). Cassava serves as a food crop, an industrial raw material, and a source of income for Uganda's population, particularly in rural areas (Odongo and Etany, 2018; Moi, 2020). In 2018, the sale of cassava stem cuttings alone generated 7.2 billion Uganda shillings (UBOS, 2020) making it a good source of income for resource poor farmers.

1.2. Constraints to Cassava Production

Production of cassava is marred by a host of both biotic and abiotic challenges, including pests, diseases, infertile soils, poor agronomic practices, limited access to good quality planting materials and weed infestation (Hillocks, 2002; Akinagbe, 2010; Bull *et al.*, 2011; Kuye, 2015; Kintché *et al.*, 2017). Because of these constraints, production in Uganda has been declining over the last 15 years (Appendix 1). For instance, annual cassava production dropped from 5.6 million tonnes in 2005 to 2.7 million tonnes in 2018, and the lowest production of 2.3 million tonnes was reported in 2017 (Appendix 1).

Pests and diseases are the major causes of cassava production losses in Africa, with yield losses of over 50% reported (IITA, 1990; Hillocks, 2002; FAO, 2015). Two major devastating viral diseases; cassava mosaic disease (CMD) and cassava brown streak disease (CBSD) (Legg *et al.*, 2014a, b; Kato and Bendana, 2018), negatively affect cassava yields and production in Africa. However, whereas CMD previously caused yield losses of up to 50% (Legg *et al.*, 2006), the disease has been managed through breeding and deployment of high yielding CMD-resistant cassava genotypes (Thresh *et al.*, 1994; Otim-Nape *et al.*, 2000). On the other hand, CBSD still causes high yield losses of 70–100% in susceptible cassava genotypes (Hillocks and Thresh, 2000) through reduced photosynthesis and presence of brown corky necrotic patches in the root and radial root constrictions which occur under severe infections (Alicai *et al.*, 2007). CBSD is recognized as one of the most serious threats to world food security (Pennisi, 2010), as it is widespread because of the absence of cassava genotypes with high levels of CBSD resistance (Abaca *et al.*, 2013; Tomlinson *et al.*, 2018). Fortunately, current genotypes such as NASE 14 and NAROCASS 1 that have moderate resistance to CBSD are available to farmers in Uganda (Kawuki *et al.*, 2016).

Both CMD and CBSD are transmitted by members of cryptic species complex of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) (Colvin *et al.*, 2004; Maruthi *et al.*, 2005; Boykin *et al.*, 2013; Legg *et al.*, 2014a), and through planting and sharing of infected cuttings by farmers. In addition, *B. tabaci* species cause direct feeding damage through sucking of phloem sap, and indirect feeding damage through the excretion of honey dew which results in the development of black sooty molds on leaf surfaces that reduce the photosynthetic ability of affected cassava plants (Polston *et al.*, 2014).

1.2.1. Management of *Bemisia tabaci* and Associated Viral Diseases

Since the early 1990s, very high populations of *B. tabaci* have been reported throughout the cassava growing regions of East and Central Africa (Colvin *et al.*, 2004; Legg, *et al.*, 2014b). In Uganda, this unprecedented increase in *B. tabaci* populations has enhanced its status as a direct crop pest (FAO, 2015). The dramatic increase in *B. tabaci* populations has also led to increased prevalence of CMD and CBSD (Legg *et al.*, 2011; Ally *et al.*, 2019) that has caused estimated annual losses of over US\$1 billion (Legg *et al.*, 2014b).

The *B. tabaci* species complex are majorly controlled by use of insecticides, especially in high value crops such as cotton and vegetables (Horowitz *et al.*, 2011; Legg *et al.*, 2014b). However, this has resulted in development of insecticide resistance and disruption of natural enemies (Takahashi *et al.*, 2008; Horowitz *et al.*, 2011), making chemical control a non-sustainable approach. Additionally, other control methods such as host plant resistance, biological control and cultural control have also been explored (Legg *et al.*, 2014b).

For low value subsistence crops like cassava grown by peasant farmers, pesticides are not only inaccessible but are too expensive, thus leaving small-holder farmers without practical management options (Neuenschwander, 2004; Guastella *et al.*, 2015). Even host plant resistance that would offer low-cost, practical, long-term solutions to *B. tabaci* problems on cassava (Bellotti and Arias, 2001) has not been exploited largely because earlier research efforts focused on developing virus disease-resistant cassava genotypes (Horowitz *et al.*, 2011; Legg *et al.*, 2014b; Kawuki *et al.*, 2016). Indeed, in Uganda, there has been success in the development of high yielding CMD resistant and CBSD tolerant cassava genotypes (Kawuki *et al.*, 2016). Nevertheless, further efforts must be geared to developing simpler, sustainable and easily accessible approaches to pest and disease management on cassava.

1.3. Problem Statement

Whereas several disease resistant and high yielding cassava genotypes were developed and disseminated to manage CMD in Uganda (Otim-Nape *et al.*, 2000; Adriko *et al.*, 2011), many of these genotypes support much higher populations of *B. tabaci* than local genotypes (Otim *et al.*, 2006; Omongo *et al.*, 2012). This has led to increased status of *B. tabaci* as a direct pest and vector of the Cassava Brown Streak Viruses which cause CBSD (Alicai *et al.*, 2007; 2016). The factors responsible for variations in *B. tabaci* populations among cassava genotypes are however not clearly known.

Whereas morphological traits influence insect populations (Shah *et al.*, 2015; Khalil *et al.*, 2015), it is not known whether particular cassava genotypes have traits that promote the ability of *B. tabaci* to survive and reproduce in a given environment, or that render natural enemies ineffective. Previous studies have shown that parasitism was a major mortality factor of *B. tabaci* (Asiimwe *et al.*, 2007a) but cassava genotype had no effect on percent parasitism (Otim *et al.*, 2006). At the time of those studies, *B. tabaci* was considered as a single species and CMD was the major constraint to cassava production. Current evidence, however, shows that *B. tabaci* is a species complex (Dinsdale *et al.*, 2010; Jiu *et al.*, 2017) while many of the CMD resistant cassava genotypes have succumbed to CBSD (Alicai *et al.*, 2007; Katono *et al.*, 2015) and have since been replaced with CBSD tolerant genotypes (Kawuki *et al.*, 2016). There is therefore need to conduct in-depth studies to evaluate any relationships between the traits of cassava genotypes currently grown, the dynamics of the prevalence of *B. tabaci* species, and the efficacy of parasitoids in controlling *B. tabaci*.

Although several abiotic factors, such as temperature, rainfall and relative humidity (RH), are known to have impact on *B. tabaci* populations (Naranjo and Ellsworth, 2005; Macfadyen *et al.*, 2018), their roles in influencing *B. tabaci* populations on different crops is contradictory, with both positive and negative effects reported (Robertson, 1987; Sseruwagi *et al.*, 2004; Pandey *et al.*, 2008; Sharma *et al.*, 2013). In Uganda, effects of environmental factors on *B. tabaci* populations on cassava are still undocumented, even when *B. tabaci* species continue to devastate cassava production in the entire country. There has also been a spike in *B. tabaci* populations with the widespread adoption of CMD resistant genotypes, which raises the question as to whether these resistant genotypes are interacting with the environment in favour of *B. tabaci* population increases or not. Considering the above, there is need for ecological studies to elucidate probable roles of the environment, cassava genotypes, natural enemies and interactions between these factors in influencing *B. tabaci* reproduction, survival and population dynamics.

1.4. Justification of the Study

Ecological studies will generate knowledge on how environmental factors, cassava genotypes and their interaction affect *B. tabaci* population change. This will aid the development and implementation of durable management strategies, such as choosing the most suitable cassava genotypes for a particular agro-ecological zone, and guide development of lasting strategies to manage cassava-virus disease pandemics, ensure improved cassava production, and address

possible future famines. Information obtained from studies on the effect of plant morphological traits on *B. tabaci* population dynamics may also assist breeders to identify possible sources of host-plant resistance to *B. tabaci* that can be incorporated into cassava breeding programs thereby checking *B. tabaci* outbreaks.

Understanding the timing, distribution and significance of specific mortality factors affecting immature *B. tabaci* populations will also provide critical information that can be used in the prediction of future pest outbreaks, and to develop effective management options for this global pest. Additionally, insight knowledge on parasitoid responses to varying *B. tabaci* host densities is key in evaluation of the ability of a parasitoid to regulate pest populations, which will guide deployment of augmentative biological control strategies in the different *B. tabaci* population zones in Uganda.

1.5. Objectives of the Study

The overall objective of this study was to contribute to the effective management of *B. tabaci* by generating knowledge on the factors influencing *B. tabaci* population dynamics and fitness.

The specific objectives were:

1. To determine the effect of morphological traits of cassava genotypes and environmental factors on *B. tabaci* population dynamics in three contrasting ecological regions of Uganda.
2. To determine the effects of temperature on the rate of development, reproduction and longevity of the predominant *B. tabaci* species on selected cassava genotypes.
3. To determine the impact of specific mortality factors acting on *B. tabaci* populations on selected cassava genotypes under field conditions.
4. To determine the effect of cassava genotype and *B. tabaci* host density on effectiveness of selected parasitoids.

1.6. Study Hypotheses

The following framework hypotheses were tested in this study:

1. Increase in values of morphological traits; leaf area, plant height, leaf area index of cassava genotypes enhances *B. tabaci* population abundance.
2. Increase in temperature, rainfall and relative humidity have positive effects on *B. tabaci* field population dynamics.

3. Increase in temperature enhances the rate of development, reproduction and longevity of *B. tabaci* (SSA1 species) on selected cassava genotypes.
4. Different mortality factors; disappearance, parasitism, predation cause varying levels of death on *B. tabaci* populations.
5. Different parasitoids have distinct levels of efficacy in the management of *B. tabaci* at varying host densities on selected cassava genotypes.

CHAPTER TWO

LITERATURE REVIEW

2.1. Origin, Distribution and Diversity of *Bemisia tabaci* (Hemiptera: Aleyrodidae)

Bemisia tabaci (Gennadius) is thought to be of Indian origin (Fishpool and Burban, 1994), and was dispersed to America and Africa by man (Mound and Halsey, 1978). *Bemisia tabaci* is distributed in all continents where crops are grown (Oliveira *et al.*, 2001), and is widely distributed in Uganda (Mugerwa *et al.*, 2012; Alicai *et al.*, 2019).

Previously considered a single, highly polyphagous species, *B. tabaci* is now known to be a complex of morphologically indistinguishable cryptic species (Dinsdale *et al.*, 2010; De Barro *et al.*, 2011). To date, over 34 *B. tabaci* cryptic species have been reported (Boykin *et al.*, 2012; 2013; Jiu *et al.*, 2017). Of these, five putative species; sub-Saharan Africa 1 to 5 (SSA1 to SSA5) colonise cassava in sub-Saharan Africa (Boykin *et al.*, 2007; Mugerwa *et al.*, 2012; Legg *et al.*, 2014a). Due to challenges of morphological identification, and the relatively new molecular tools, identity of *B. tabaci* species mentioned in earlier studies was often not clarified. As such, the ecological, biological and life-history parameters summarised below apply to the generic *Bemisia tabaci* pest species complex and may need to be refined as more species-specific information emerge.

2.2. Life History of *B. tabaci*

Bemisia tabaci has six life stages: egg, four nymphal instars and adult (Kedar *et al.*, 2014; Gangwar and Gangwar, 2018). The insect has arrhenotokous parthenogenetic reproduction where virgin females produce only males and mated females produce both males and females (Byrne and Bellows, 1991; McAuslane, 2002).

Eggs of *B. tabaci* are laid either singly or in circular groups of up to 40 eggs on the underside of leaves (Kedar *et al.*, 2014; Gangwar and Gangwar, 2018). The pear-shaped freshly laid eggs have a yellowish-white colour (Kedar *et al.*, 2014), and are about 0.2 mm long (Gangwar and Gangwar, 2018). Eggs hatch into 1st instar nymphs within 5-9 days depending on temperature, during which time they change to a dark brown colour before the nymphs hatch (McAuslane, 2002; Gangwar and Gangwar, 2018).

The first instar nymphs (crawler), the only mobile immature stage of *B. tabaci* are oval and whitish-yellow and have three pairs of well-developed legs and antennae (McAuslane, 2002; Simmons, 2002; Kedar *et al.*, 2014). The crawler moves for about 20 minutes (Simmons, 2002) to 120 minutes (2 hours) from the site of hatching in search of a suitable feeding location on the lower surface of the leaf, after which it becomes sessile throughout the remaining nymphal instar stages (Naranjo, 2007; Kedar *et al.*, 2014). Crawlers molt into second instar nymphs within two to three days (Gangwar and Gangwar, 2018).

The second, third and fourth nymphal instars have atrophied legs and antennae with small eyes (McAuslane, 2002), and are oval and flat in shape (Kedar *et al.*, 2014). The fourth instar nymph (pupa) is flat with an irregular oval shape, visible red eyes (Gangwar and Gangwar, 2018), and distinct legs and antennae (Byrne and Bellows, 1991). Nymphs range from 0.3 mm (crawler) to 0.662 mm (fourth instar) in length (McAuslane, 2002; Islam and Ren, 2007) and all nymphal stages have two yellow mycetomes on the abdomen (McAuslane, 2002). The second and third nymphal instars each last about two to three days, while the pupa lasts for five to six days (McAuslane, 2002).

Adult *B. tabaci* emerge through a 'T'-shaped rupture in the puparium (Kedar *et al.*, 2014), and are approximately 1 mm long with light yellow bodies and white wings that are covered with a waxy powder (Gangwar and Gangwar, 2018). Adult females have pale yellow broader abdomen with an ovipositor, while adult males have narrow abdomen with a pair of claspers and are generally smaller in size than females (Kedar *et al.*, 2014).

2.3. *Bemisia tabaci* Host Range and Damage on Cassava

To date, *B. tabaci* species are known to colonise over 500 host plant species (Berlinger, 1986; Navas-Castillo *et al.*, 2011; Dinsdale *et al.*, 2010), including crops such as cassava, cotton, beans and tomato (Mound and Halsey, 1978; Legg *et al.*, 2002; Gelman *et al.*, 2007; Dinsdale *et al.*, 2010).

2.3.1. *Bemisia tabaci* Damage on Cassava

Bemisia tabaci is one of the most important agricultural and economic pests worldwide (Oliveira *et al.*, 2001; Kanakala and Ghanim, 2019), and has been listed among the worst 100 invasive species since 2000 (Lowe *et al.*, 2000; GISD, 2020). *Bemisia tabaci* is known to cause

three types of damage: direct feeding damage, contamination with honeydew, and transmission of disease causing viruses to a wide range of host plant species, cassava inclusive (Byrne and Bellows, 1991; Jones, 2003; Navas-Castillo *et al.*, 2011; Polston *et al.*, 2014).

2.3.1.1. Direct feeding damage

Both adults and nymphs of *B. tabaci* cause direct feeding damage through sucking of sap from plant leaves (Chandel *et al.*, 2012; Polston *et al.*, 2014). This results in chlorotic mottling on the upper leaves of the plants, leaf deformation and stunting of affected host plants (Berlinger, 1986; Legg *et al.*, 2004; Mau and Kessing, 2007). Heavy infestations result in reduced plant vigor and plant death may occur (OEPP/EPPO, 2004; Mau and Kessing, 2007). Yield losses of 50 to 79% have been recorded in susceptible cassava genotypes (Legg *et al.*, 2004; Belloti *et al.*, 2012; Gangwar and Gangwar, 2018). For communities that consume cassava leaves as vegetable (Achidi *et al.*, 2005; Umuhozariho *et al.*, 2011), physical damage also causes quality reduction of harvested leaves (OEPP/EPPO, 2004; Mau and Kessing, 2007).

2.3.1.2. Contamination with honeydew

Bemisia tabaci excrete honeydew onto the surfaces of lower leaves and fruits which encourages the growth of sooty molds (Berlinger, 1986; Davidson *et al.*, 1994; Legg *et al.*, 2004; Polston *et al.*, 2014). Growth of sooty molds interferes with photosynthesis, leading to reduced growth, phytosanitary yield reductions of up to 49%, and reduction in quality and commercial value of crops produce (Berlinger, 1986; Rao *et al.*, 1989; Polston *et al.*, 2014).

2.3.1.3. Transmission and impact of plant viruses on cassava

Cassava mosaic begomoviruses (CMBs) and cassava brown streak ipomoviruses (CBSIs), the causative agents of cassava mosaic disease (CMD) and cassava brown streak disease (CBSD), respectively, are among the key viruses transmitted by *B. tabaci* (Legg *et al.*, 2011). These two diseases are among the biggest threats to food security in Africa (Pennisi, 2010; Legg, *et al.*, 2014a); as they cause yield losses of over 70% (Hillocks *et al.*, 2001; Legg *et al.*, 2011) and estimated annual losses of over US\$1 billion (Legg *et al.*, 2014b; IITA, 2014). Virus transmission therefore represents the greatest impact of *B. tabaci* on crops (Polston *et al.*, 2014; Gangwar and Gangwar, 2018).

In Uganda during the CMD pandemic in the 1990s, Sub-Saharan Africa 2 (SSA2) species of *B. tabaci* was predominant while SSA1 species was reported at or a head of the CMD epidemic front (Legg *et al.*, 2002). In this era of high CBSD prevalence, SSA1 was reported on the increase in Tanzania and Uganda, especially in areas with high CBSD incidence of over 30% (Tajebe *et al.*, 2014; Okao-Okuja, 2017), yet a subsequent study by Ally *et al.* (2019) recorded no SSA2 prevalence. Therefore, because high populations of *B. tabaci* complex is associated with the occurrence of severe CMD and CBSD pandemics (Alicai *et al.*, 2007; Legg *et al.*, 2011; 2014a; Ally *et al.*, 2019), there is need for species specific studies to help develop comprehensive management strategies to minimise *B. tabaci* population build-up while also reducing the spread and impacts of the viral diseases.

2.4. Factors that Influence *B. tabaci* Populations on Crops

Several biotic and abiotic factors such as natural enemies, host plant effects, and weather elements are known to act on *B. tabaci* populations (Naranjo and Ellsworth, 2005; Leite *et al.*, 2006; Macfadyen *et al.*, 2018). These factors operate to reduce or to promote *B. tabaci* numbers.

2.4.1. Host Plant Characteristics

Plant resistance to *B. tabaci* has often been expressed in different crop genotypes through antibiosis, antixenosis or tolerance (Painter, 1951; Berlinger, 1986; Sulistyo and Inayati, 2016; Horas *et al.*, 2018). Abundance of *B. tabaci* is reported to vary significantly among different plant species (Nava-Camberos *et al.*, 2001; Shah and Liu, 2013; Otim *et al.*, 2018a) and crop genotypes (Sippell *et al.*, 1987; Omongo *et al.*, 2012; Hasanuzzaman *et al.*, 2016; Baldin *et al.*, 2017). These variations are reportedly mediated by plant morphological characteristics and biochemical profiles (Shah *et al.*, 2015), although in most cases they are attributed to host plant non-preference (antixenosis) for oviposition or feeding, or to tolerance resistance mechanisms (Bellotti and Arias, 2001). Indeed, morphological traits such as trichome density, leaf shape, leaf area and plant height are known to influence *B. tabaci* populations on different crop genotypes (Gallun and Khush, 1980; Berlinger, 1986; Sippell *et al.*, 1987; Khalil *et al.*, 2015; Tian *et al.*, 2020), although their effects are sometimes contradictory (Walker and Natwick, 2006).

Among different cotton and soybean genotypes, low trichome density was reported to confer resistance to *B. tabaci* (Sippell *et al.*, 1987; Baldin *et al.*, 2017), while tomato genotypes with high density of glandular type IV trichomes were associated with resistance (Rakha and Hanson, 2017). Cotton lines with okra/super okra type leaf shapes were also found to be resistant to *B. tabaci* (Sippell *et al.*, 1987). In eggplant, *B. tabaci* populations were positively associated with high trichome density and length, and leaf lamina thickness (Hasanuzzaman *et al.*, 2016). The effect of plant height on *B. tabaci* numbers is similarly inconsistent. While Lambert *et al.* (1995) reported that plant height had no effect on *B. tabaci* infestation levels on soybean, a positive effect was reported by Khalil *et al.* (2015).

Whereas various studies show that many physical traits affect *B. tabaci* populations, for cassava in Uganda characterization of *B. tabaci* resistance has often only been done with regard to colonization preference of the different genotypes. Differences in *B. tabaci* infestation levels have been observed among different genotypes of cassava (Ariyo *et al.*, 2005), with improved genotypes supporting higher populations of the pest, i.e. those that are bred for resistance to CMD (Otim *et al.*, 2006; Omongo *et al.*, 2012). The underlying reasons for *B. tabaci* preference of CMD resistant cassava genotypes are not well understood.

There have been no attempts to understand the role of plant morphological traits in influencing *B. tabaci* population dynamics on cassava in Uganda, the pest thus continues to colonise large areas of the crop while spreading CBSD. There is need therefore, to define morphological traits that are driving *B. tabaci* population changes on the different cassava genotypes in the country. This will help to identify sources of resistance in cassava that can be incorporated in breeding programs to aid development of *B. tabaci* resistant cassava genotypes that will help curb the escalating occurrence of *B. tabaci* transmitted viral diseases (CBSD and CMD) that cause enormous yield and economic losses in cassava.

2.4.2. Environmental Factors

Abiotic environmental factors, notably temperature, relative humidity (RH) and rainfall, are known to be key determinants of insect population dynamics, including of *B. tabaci* (Birch, 1957; Horowitz, 1986; Palumbo, 2010; Savopoulou-Soultani *et al.*, 2012; Zeshan *et al.*, 2015). Variations in these factors affect the levels of infestation, survival and losses caused by *B. tabaci* in crops (Bhatt *et al.*, 2018; Macfadyen *et al.*, 2020).

2.4.2.1. Temperature

Spatial and temporal variations in temperature influence populations and distribution of ectothermic species through direct or indirect effects (Wallner, 1987; Huey and Kingsolver, 1993; Dillon *et al.*, 2009; Damos and Savopoulou-Soultani, 2012; War *et al.*, 2016). High temperatures are known to reduce insect development time, increase survival and fecundity and accelerate insect multiplication (Bonato *et al.*, 2007; Nava-Camberos *et al.*, 2001; Ezeakacha and Yee, 2019; Li *et al.*, 2020). Temperature also indirectly influences *B. tabaci* population size through its effects on host plant suitability for insect infestation, especially variations in host plant morphological and biochemical defenses and nutritional quality (White, 1984; Sharma and Dhillon, 2020). For example, high temperatures induce stress in plants resulting in increased concentrations of soluble nitrogen in sap thereby providing better food hosts for egg laying females and newly hatched nymphs, and resultant high fecundity and enhanced survival (White, 1984). For *B. tabaci* populations on different crops, however, effects of temperature are contradictory. While some researchers reported positive effects of temperature on *B. tabaci* population change (Alicai *et al.*, 1999; Sharma *et al.*, 2013; 2017), negative effects were reported by others (Anjali *et al.*, 2012; Jha and Kumar, 2017; Bhatt *et al.*, 2018).

Climate Change is known to have remarkable effects on incidences and intensity of pest populations (Dhaliwal *et al.*, 2010; Sharma, 2014). With anticipated increase in pest pressure in agricultural systems with increased global temperatures due the high sensitivity of insect physiology to changes in temperature (Yamamura and Kiritani, 1998; DeLucia *et al.*, 2008; Kroschel *et al.*, 2014; Skendžić *et al.*, 2021), understanding thermal responses of the predominant *B. tabaci* species in Uganda with regard to survival, longevity, fecundity, viability and development time in a cassava system is critical.

2.4.2.2. Rainfall

Rainfall influences *B. tabaci* populations by washing away *B. tabaci* adults and nymphs from the leaves of infested plants (Anzola and Lastra, 1985; Alicai *et al.*, 1999; Leite *et al.*, 2005; Sharma *et al.*, 2013), and by influencing expression of plant morphological traits (Aina *et al.*, 2007; Podleśny and Podleśna, 2011) which in turn influence *B. tabaci* population abundance. High amounts of rainfall enhance rapid vegetative growth in many plant species which produce large succulent leaves preferred by *B. tabaci*, hence promoting their population growth and explosion (Young, 1979; Wallner, 1987; Fishpool *et al.*, 1987; Anjali *et al.*, 2012).

2.4.2.3. Relative humidity

Being cold blooded, insects are sensitive to desiccation, and atmospheric humidity plays a critical role in their development by regulating water loss (Palumbo, 2010; Masika *et al.*, 2017). Although high humidity is expected to positively impact insect populations (Masika *et al.*, 2017), contradicting effects of humidity have been reported for *B. tabaci*. Whereas Anjali *et al.* (2012), Jha and Kumar (2017) and Pathania *et al.* (2020) reported positive effects of relative humidity on *B. tabaci* population change, negative effects were reported by Sharma *et al.* (2013; 2017) and Bhatt *et al.* (2018).

In summary, climatic factors are known to indirectly affect *B. tabaci* populations by altering host-plant quality especially under extreme conditions (Sharaf, 1982; Bauerfeind and Fischer, 2013). For example, high temperatures coupled with low rainfall have been associated with poor vegetative growth (Podlešný and Podlešná, 2011) yet *B. tabaci* is known to have preference for unstressed crops with large succulent leaves (Fishpool *et al.*, 1987). Given the inconsistent nature of the relationship between environmental factors and *B. tabaci* population dynamics in different environments, Therefore, there is need to extensively assess the effects of temperature, RH and rainfall on *B. tabaci* population changes to determine optimal conditions that support population growth on cassava in Uganda, particularly with regard to the *B. tabaci* species prevalent in the country.

2.4.3. Natural Enemies of *B. tabaci*

Bemisia tabaci is attacked by a large and diverse array of predators, parasitoids (Gerling *et al.*, 2001; Naranjo and Ellsworth, 2005; Arnó *et al.*, 2010) and entomopathogenic fungi (Mascarin *et al.*, 2013; Bugti *et al.*, 2018) that are found in various agro-ecologies globally (Gerling *et al.*, 2001; Simmons and Abd-Rabou, 2011). In Uganda, predators and parasitoids are of paramount importance in *B. tabaci* management given their widespread occurrence (Otim *et al.*, 2006; Asiimwe *et al.*, 2007a)

2.4.3.1. Predators

Over 150 arthropod species belonging to nine Orders are known as predators of *B. tabaci* (Gerling *et al.*, 2001; Arnó *et al.*, 2010). Both chewing and sucking predators are known to cause significant mortality of immature *B. tabaci* through dislodgement (here after referred to as disappearance) and predation in different host plant crops (Naranjo, 2001; Naranjo and

Ellsworth, 2005; Karut and Naranjo, 2009; Naranjo *et al.*, 2009; Naranjo *et al.*, 2010) including cassava (Asiimwe *et al.*, 2007a). Majority of the predators found on cassava in Uganda belong to the Orders: Coleoptera, Hemiptera, Neuroptera and Diptera (Otim, 2007). Coccinellids of the genus *Serangium* are widely distributed in the world and have demonstrated high levels of control of *B. tabaci* (Asiimwe *et al.*, 2007b; Al-zyoud, 2012). With the current shift in cassava genotypes available to farmers due to the CBSD pandemic and the existence of *B. tabaci* species complex, understanding the magnitude of death caused by predation on the predominant *B. tabaci* species in Uganda in a cassava system is critical.

2.4.3.2. Parasitoids

Worldwide, over 70 parasitoid species are known to attack *B. tabaci* (Gerling *et al.*, 2001, Arnó *et al.*, 2010). All parasitoids of *B. tabaci* are exclusive to the Order Hymenoptera in the Aphelinidae family, with species in the genera *Encarsia* and *Eretmocerus* being the most prevalent (Gerling, 1990; Ryckewaert and Alauzet, 2002). Reports on the role of parasitism on population regulation of *B. tabaci* are varied (Naranjo *et al.*, 2009). Some researchers have shown that parasitism was a major cause of mortality of immature *B. tabaci* (Asiimwe *et al.*, 2007a; Karut and Naranjo, 2009; Asiimwe *et al.*, 2016), while others consider parasitism to be a minor mortality factor (Naranjo and Ellsworth, 1999; 2005). These variations in parasitism levels have been associated with climate, season and host-plants (Simmons *et al.*, 2002; Ryckewaert and Alauzet, 2002; Otim *et al.*, 2005; 2018a). Effects of plant genotype on parasitism have also been reported by Li Zhao *et al.* (1987) who observed higher parasitism rates of *Encarsia formosa* on *Trialeurodes vaporariorum* on moderately hairy cucumber genotypes. On the other hand, Otim *et al.* (2008) observed that leaf hairiness had no effect on parasitism on cassava in Uganda.

In Uganda, Otim *et al.* (2005) reported differences in parasitism rates on *B. tabaci* in cassava in different agro-ecologies which were also differing in cassava genotypes planted. At the time of the study by Otim *et al.* (2008), CMD resistant genotypes such as NASE 4 had been widely adopted and *B. tabaci* was considered as a single species. In the CBSD pandemic, however, these genotypes succumbed to disease and were replaced with CBSD tolerant genotypes such as NASE 14 and NAROCASS 1 (Kawuki *et al.*, 2016), and *B. tabaci* is currently recognized as a species complex (Dinsdale *et al.*, 2010; Jiu *et al.*, 2017). The impacts of these new cassava genotypes on *B. tabaci* complex and natural enemy activity are unknown and studies are required to elucidate them.

In Uganda *B. tabaci* is mainly attacked by the parasitoids *Eretmocerus mundus*, *Encarsia sophia*, with higher parasitism observed when higher *B. tabaci* nymphal populations occur (Otim *et al.*, 2005; 2006; 2018a). The biological control efficiency of a parasitoid is a function of both host feeding and parasitism (Zang *et al.*, 2011), which are both influenced by host density (Lin *et al.*, 2018). For parasitoids, host feeding is important because, in addition to killing insect hosts, it provides nutrients for egg maturation and maintenance of female longevity (Chan and Godfray, 1993; Heimpel and Collier, 1996; Giron *et al.*, 2004) which in turn increase the reproductive potential and fitness of the parasitoid (Yang *et al.*, 2012).

For *B. tabaci* species complex in the Ugandan agricultural systems, information on the biological control efficacy of the two major parasitoids is lacking, yet parasitism is a key *B. tabaci* nymphal mortality factor (Asiimwe *et al.*, 2007a). This therefore called for detailed studies on the effect of varying *B. tabaci* host densities on host feeding and parasitism on cassava to help guide implementation of biological control through use of parasitoids in the country.

2.4.3.3. Entomopathogenic fungi

Entomopathogenic fungi (EPF) are microorganisms that are known to cause disease to *B. tabaci* (Qiu *et al.*, 2013; Zhang *et al.*, 2017; Dara, 2017), and over 20 species are effectively used against *B. tabaci* (Mascarin *et al.*, 2013; Bugti *et al.*, 2018; Sain *et al.*, 2019). Entomopathogenic fungi directly infect insects through the cuticle and are known to kill all the developmental stages of *B. tabaci*. Second instar nymphs are reportedly the most susceptible (Khan *et al.*, 2012; Mascarin *et al.*, 2013; Sani *et al.*, 2020), and pathogens such as *Aschersonia aleyrodis* cause 50 to 99% mortality in nymphs and adults of *B. tabaci* (Zhang *et al.*, 2017; Prayogo and Bayu, 2020).

Remarkable success in the control of *B. tabaci* using EPF in the greenhouse has been reported, and many commercial microbial insecticide formulations are available on the market and are commonly used as spray or dip applications (Al-Deghairi, 2008; Gul *et al.*, 2014; Perring *et al.*, 2018). However, the use of EPF has not been explored in smallholder cassava farming systems in Africa; hence not assessed in this study.

From the literature review, several key issues emerged that called for urgent research to help develop approaches to sustainably manage current *B. tabaci* problem in cassava production systems in Uganda. These included: (i) need to identify the *B. tabaci* species that are prevalent in Uganda; (ii) characterization of morphological traits of selected cassava genotypes in relation to *B. tabaci* infestation levels; (iii) understanding the influence of environmental conditions on *B. tabaci* population changes in cassava fields; (iv) understanding the effects of temperature on reproduction, survival and general fitness of the principal *B. tabaci* species on different cassava genotypes; (v) understanding the magnitude of mortality inflicted on the *B. tabaci* species complex by natural enemies and other factors in cassava fields; and (vi) elucidating the effectiveness of major parasitoids under different *B. tabaci* population densities on cassava. These constituted the studies reported in this thesis.

CHAPTER THREE

INFLUENCE OF CASSAVA MORPHOLOGICAL TRAITS AND ENVIRONMENTAL CONDITIONS ON FIELD POPULATIONS OF *Bemisia tabaci*

3.1. INTRODUCTION

Bemisia tabaci (Hemiptera: Aleyrodidae) is among the most devastating insect pests of agricultural crops worldwide (Oliveira *et al.*, 2001), and comprises a complex of 36 species that have a wide host plant range (Dinsdale *et al.*, 2010; Boykin *et al.*, 2013). Previous outbreaks of CMD led to the development and deployment of several CMD-resistant genotypes with no emphasis on the vector. Unfortunately, these genotypes appear to support very high *B. tabaci* populations (Omongo *et al.*, 2012), and it is not known whether these genotypes have morphological traits that enhance *B. tabaci* development.

It is clear that there is an increased status of *B. tabaci* as both a direct pest of cassava and a vector of CMD and CBSD (Alicai *et al.*, 2007). *Bemisia tabaci* has been reported in most agro-ecological zones (AEZs) of Uganda in varying densities (Katono *et al.*, 2015; Wamani *et al.*, 2016). Reported effects of climatic factors on *B. tabaci* population size are variable and so far inconclusive (Omongo, 2003; Otim, 2007). Indeed, previously high populations occurred in the Lake Victoria Crescent (LVC), which is a hot and humid environment. Yet relatively high populations have recently been reported in other AEZs, such as the North Eastern Savanna grassland which is a hot and dry environment. Noteworthy is the fact that the two AEZs are characterized by widespread adoption of disease-resistant cassava genotypes.

It is not known whether these genotypes are interacting with the environment to favor *B. tabaci* population increases in certain AEZs. Given the above facts, it became important to establish how the environmental factors, cassava genotypes and their interactions affect *B. tabaci* field populations. This knowledge will aid design of effective and sustainable management strategies, as well as guide future development and use of new cassava genotypes. This study was therefore undertaken to determine how morphological traits of cassava genotypes and changes in temperature, rainfall and RH influence *B. tabaci* population dynamics in three contrasting agro-ecological regions of Uganda.

3.2. MATERIALS AND METHODS

3.2.1. Field Experimental Setup

The study was conducted in March 2016 and March 2017. The 2016 study was established in two districts of Uganda: Wakiso (at National Crops Resources Research Institute (NaCRRI), Namulonge) and Lira (at Ngetta Zonal Agricultural Research and Development Institute (Ngetta ZARDI)). Wakiso is in the Lake Victoria Crescent (LVC) at 1200 m above sea level (masl) and a bi-modal rainfall pattern with an average annual rainfall of 1423 mm. Lira is in the North Eastern Savanna grassland at 1080 masl, and has uni-modal rainfall pattern with an average annual rainfall of 1341 mm. The 2017 study was established in the same AEZs as 2016 with addition of Kamuli district (Nakakabala village, Mbulamuti Sub County). It lies in the Kyoga plains at 1100 masl, and has bi-modal rainfall pattern with an average annual rainfall of 1447 mm.

These locations were chosen based on the pattern of *B. tabaci* population pressure – Wakiso, Kamuli and Lira have historically experienced high, moderate and low populations, respectively (Katono *et al.*, 2015; Wamani *et al.*, 2016). Although Wakiso was initially thought to support high *B. tabaci* populations, very low numbers were observed in 2016 hence the addition of Kamuli in 2017 which had high populations in 2016 (Omongo, C. A., personal communication, 18th October, 2016).

3.2.2. Cassava Genotypes Used

Five cassava genotypes with known responses to *B. tabaci* infestations and *B. tabaci*-transmitted diseases were used: Njule red and Alado alado are local genotypes that are tolerant to *B. tabaci* infestations but are susceptible to CBSD and CMD, and NAROCASS 1 is an improved genotype that is susceptible to *B. tabaci* infestations, but are resistant to CMD and tolerant to CBSD), while NASE 14 and NASE 3 are improved genotypes that are moderately tolerant to *B. tabaci* infestations but are resistant to CMD and tolerant to CBSD) (Omongo, C. A., personal communication, 2nd March, 2015; Kawuki *et al.*, 2016). Apparently CBSD/CMD-free planting materials selected based on visual inspection in areas with no or very low CBSD prevalence (Apac and Lira) (Katono, 2014; Alicai *et al.*, 2019) were planted at each of the three sites. Source and pedigree information for the improved cassava genotypes is provided in Appendix 2.

3.2.3. Experimental Layout

At all locations, the experiment was laid out in a randomized complete block design with the five genotypes as treatments in four replicate plots. The plots measured 9 m by 9 m at a plant spacing of 1 m by 1 m, with an alley of 2 m left between blocks. A total of 100 plants were grown per plot. Weeds were controlled manually by hand hoeing monthly for the first five months. The experiments were kept under natural pest infestations.

3.2.4. Data Collection

In 2016 at Wakiso, data were recorded monthly from 2 to 8 months after planting (MAP) on 10 randomly selected cassava plants per genotype (due to poor germination, the plant population was low, hence only 10 plants were sampled). In Lira data were collected monthly from 4–8 MAP on 15 randomly selected plants per plot. In 2017, data were recorded from 2 to 6 MAP in Wakiso and 2 to 7 MAP in Lira and Kamuli on 15 randomly selected plants per plot. Data collection covered *B. tabaci* counts, plant morphological characteristics and environmental parameters. Due to logistical challenges, data for some sample dates in Lira and Kamuli were missing.

3.2.4.1. *Bemisia tabaci* counts

Numbers of *B. tabaci* adults on each genotype were counted on the underside of the top five fully-expanded leaves of the tallest shoot on 15 randomly selected plants per plot between 07:00 and 11:00 h. In 2016 at Wakiso, *B. tabaci* adult counts were made on 10 randomly selected plants per plot. To obtain *B. tabaci* nymph count, the 15th leaf from the top, which hosts the highest number of 3rd and 4th instar nymphs was picked from each selected plant. All leaves per plot were kept in zip-lock bags by plots and taken to the Entomology laboratory where 3rd and 4th instar nymphs, including parasitized nymphs on each leaf were counted using a stereo-microscope.

Samples of *B. tabaci* adults were collected from the three experimental sites for genetic analysis using mtCOI partial gene as described in Appendix 3 to confirm the species present at each.

3.2.4.2. Plant morphological characteristics

Leaf lobe length of the central leaf lobe, leaf lobe width (cm) measured as the widest point of the central leaf lobe, and leaf width (cm) and petiole length (cm) of the fifth fully-expanded leaf were measured using a 30 cm ruler. Plant height (cm) of the tallest shoots were measured

using a 5-meter tape measure while stem girth (cm) of the same shoots were measured using vernier calipers (cm) (Plate 3.1 A and B). Leaf lobe number was the number of lobes of the fifth fully-expanded leaf. In 2017, leaf area (cm²) was measured using an LI-3100C Area Meter (LI-COR Inc., Lincoln, NE, USA) and leaf area index (LAI) measured using an AccuPAR Linear PAR/LAI Ceptometer (Decagon Devices Inc., Pullman, WA, USA) in the field (Plate 3.1 C and D). In 2016, the leaf area meter and the ceptometer were unavailable so leaf area was calculated as a product of leaf length and leaf width, and LAI was calculated using the mathematical formula for calculating the area of a circle (πr^2) for overall plant canopy ground area.

3.2.4.3. Environmental parameters

Temperature and relative humidity (RH) were recorded using a HOBO Pro v2 logger (Onset Computer Corporation) placed on one cassava plant at the center of the experiment at the trial site in each AEZ, and rainfall data were accessed from a weather station near the study site. The daily readings recorded at 15:00 h for rainfall, temperature and RH were used to calculate the total monthly rainfall and average monthly temperature and RH values, with a month being from one sample date to the next.

3.2.5. Data Analysis

All data for *B. tabaci* counts and plant morphological traits were analyzed using R statistical software (R Core Team, 2017). All data were tested for normality and where skewness occurred, data were subjected to the Box Cox procedure (Venables and Ripley, 2002) to determine the most appropriate transformation based on the lambda value. The data were then subjected to mixed model ANOVA (Kuznetsova *et al.*, 2016) for genotype, location and crop age (MAP) effects with replicate plots as a random effect nested within location. Where significant differences were obtained between treatments, were separated using the Least Significant Difference (LSD) test at 5% probability level (Felipe de Mendiburu, 2017).

Scatter plots with lines of best fit (Wickham, 2009) were used to visualize the relationship between *B. tabaci* adult counts and the different morphological traits in the different locations for each year. Based on the visualization of the scatter plots for all locations each year, regression analysis was performed separately for each location. Subset regression (Thomas Lumley based on Fortran code by Alan Miller, 2017) based on values of Schwartz' Bayesian

Information Criterion (BIC) was used to select the best multiple regression model for each location per year. Multiple linear regression (Wickham, 2017) was run for the effect of plant morphological characteristics on *B. tabaci* adult numbers using the multiple linear regression model:

$$Y_i = B_0 + B_1X_1 + B_2X_2 + B_3X_3 + \dots + B_kX_k + \epsilon_i$$

where: Y_i = i^{th} response variable, B_0 is the intercept, B_1 is the regression coefficient for factor X_1 , B_k is the regression coefficient for the X_k^{th} factor and ϵ_i is the error term.

Pearson's correlation analysis was performed to determine the strength and the direction of the relationship between weather parameters with *B. tabaci* adult and nymph counts (Revelle, 2017). Data for each location in each year with all cassava genotypes pooled together was analysed separately.

The combined *B. tabaci* count data, morphological traits data and climate data were then subjected to principal component analysis (PCA) (Vincent, 2011) to understand the interactive effect of cassava genotype and environment on *B. tabaci* population size. PCA was performed separately for each year.

3.3. RESULTS

3.3.1. Temporal Changes in *Bemisia tabaci* Adult and Nymph Population on Five Cassava Genotypes in Three Locations.

All main effects (location, genotype and crop age), two-ways and three-way interactions had significant ($p < 0.001$; Appendix 4) effects on *B. tabaci* adult and nymph counts in both 2016 and 2017. In 2016 in Lira, *B. tabaci* adult populations decreased steadily to reach negligible numbers at six MAP for all genotypes except NASE 14 that had minimum numbers at seven MAP (Figure 3.1). In Wakiso, fluctuations were observed in *B. tabaci* adult populations. Numbers were relatively high at two and three MAP followed by a decline to reach minimum numbers at five MAP for all cassava genotypes. Thereafter, *B. tabaci* adult populations slightly increased to reach a second peak at seven MAP followed by a drop in the population at eight MAP for all cassava genotypes except NASE 14 whose populations reached the highest number of 10.8 adults per plant at eight MAP (Figure 3.1). Fluctuations were also observed for *B. tabaci* nymph population in all locations in 2016 (Figure 3.2). In 2017, *B. tabaci* adult and nymph populations in all locations followed similar trends as the nymph populations in 2016 (Figures 3.3 and 3.4).

In 2016, higher *B. tabaci* adult populations were observed in Wakiso than in Lira for all crop growth stages among all cassava genotypes (Figure 3.1). However, nymph populations were higher in Lira at four and five MAP in all cassava genotypes (Figure 3.2; Appendix 5). In 2017, the highest *B. tabaci* adult and nymph populations among different genotypes were recorded in Kamuli (Figures 3.3 and 3.4). Mean nymph count on Alado alado at two MAP was 532.9 in Kamuli followed by 60.3 in Wakiso and 15.9 in Lira (Figure 3.4). Consistently, high mean *B. tabaci* adult and nymph populations were observed on NASE 14 and low numbers on Alado alado in Lira in 2016 (Figures 3.1 and 3.2) and across all locations in 2017 (Figures 3.3 and 3.4). Surprisingly in Wakiso, Alado alado had remarkably high mean *B. tabaci* adult population at 2 and 3 MAP in 2016 (Figure 3.1).

Also *B. tabaci* adult and nymph populations varied significantly ($p < 0.001$) with year, and lower populations observed were in 2016 than in 2017 (Appendix 5). In Wakiso, mean nymph count on NAROCASS 1 at three MAP was 7.5 times lower in 2016 than in 2017 (Figures 3.3 and 3.4).

3.3.2. Status of Cassava Plant Morphological Characteristics among Genotypes in Different Environments and their Relationship with *B. tabaci* Adult Abundance

All morphological traits varied significantly ($p < 0.001$) among cassava genotypes, location, crop age and the two-way and three-way interactions (Appendix 6). The crop with the highest trait values at all growth points among all genotypes was recorded in Lira in both years. For example, in 2017, LAI at four MAP ranged from 3.7–4.4 in Lira, followed by 1.2–1.9 in Kamuli and 0.4–1.1 in Wakiso among all cassava genotypes (Appendix 7). Among all genotypes, growth was consistently high for Alado alado and low for NASE 14 in the first six months of growth in both years (Appendix 7). On average, Alado alado were the tallest plants in all locations in 2016 and 2017 (Figures 3.5 and 3.6); and plant height was 145–213 cm in Alado alado compared to 85–154 cm in NASE 14 during 4–6 MAP in Lira in 2016 (Figure 3.5). Also, Njule Red had consistently high lobe numbers at all growth points in both years across all locations; with 8.1 lobes in Lira, 7.1 lobes in Kamuli and 6.2 lobes in Wakiso at two MAP in 2017 (Appendix 7).

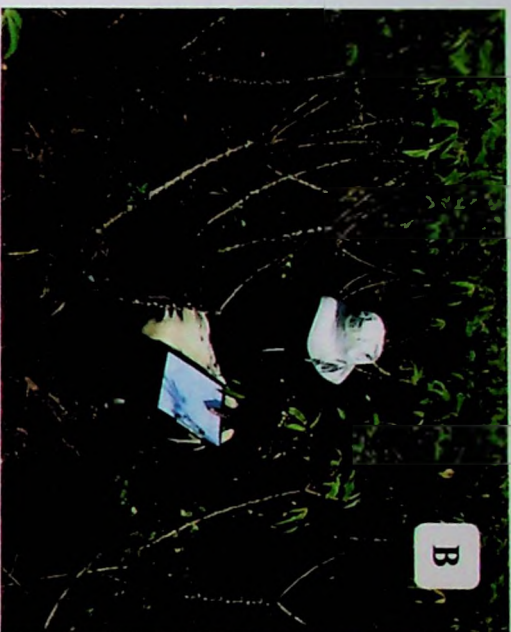


Plate 3.1: Measurement of various plant morphological traits; plant height (A), stem girth (B), leaf area (C) and LAI (D).

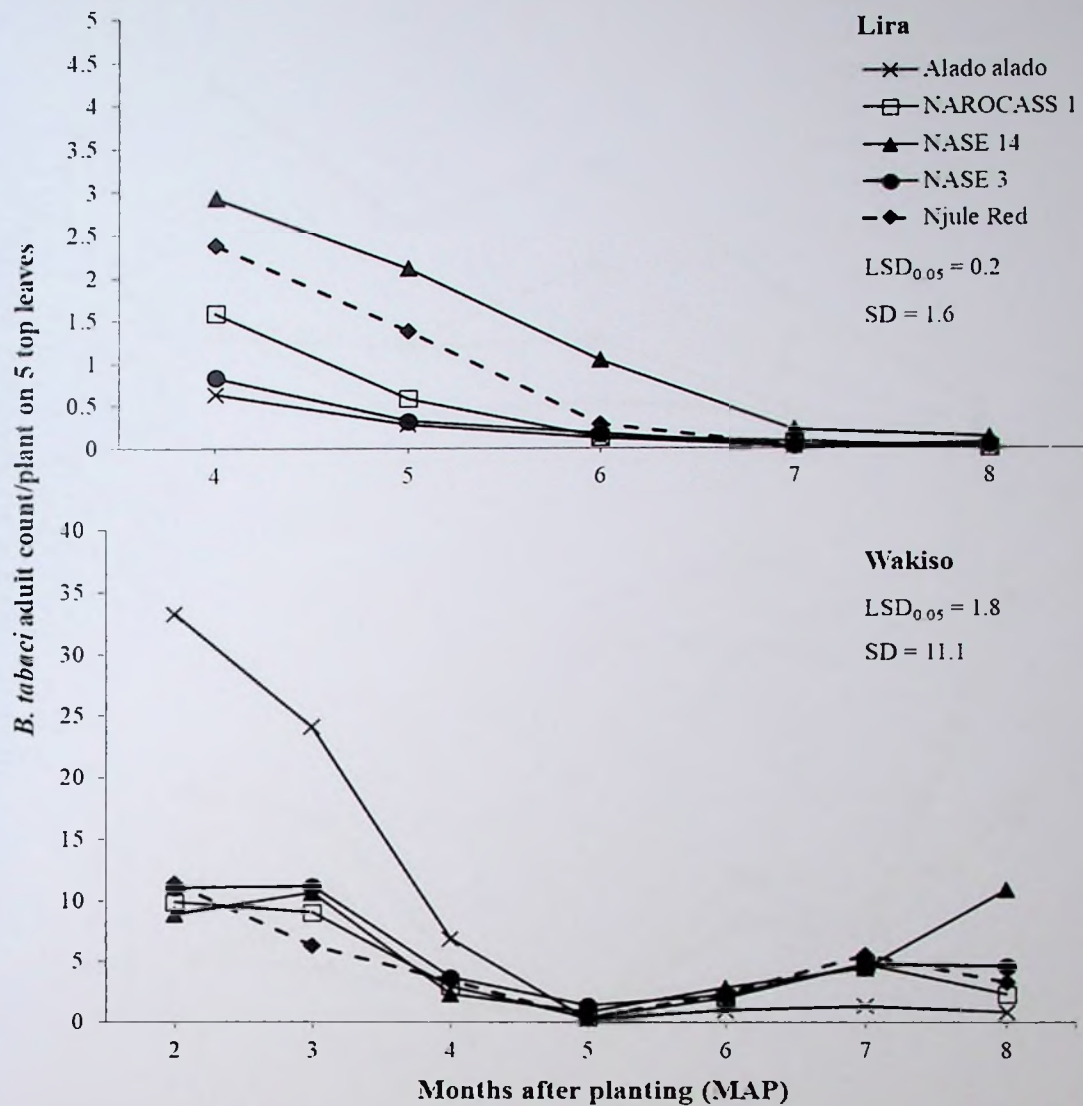


Figure 3.1: Mean monthly *B. tabaci* adult counts on five cassava genotypes at different growth stages in Lira and Wakiso in 2016.

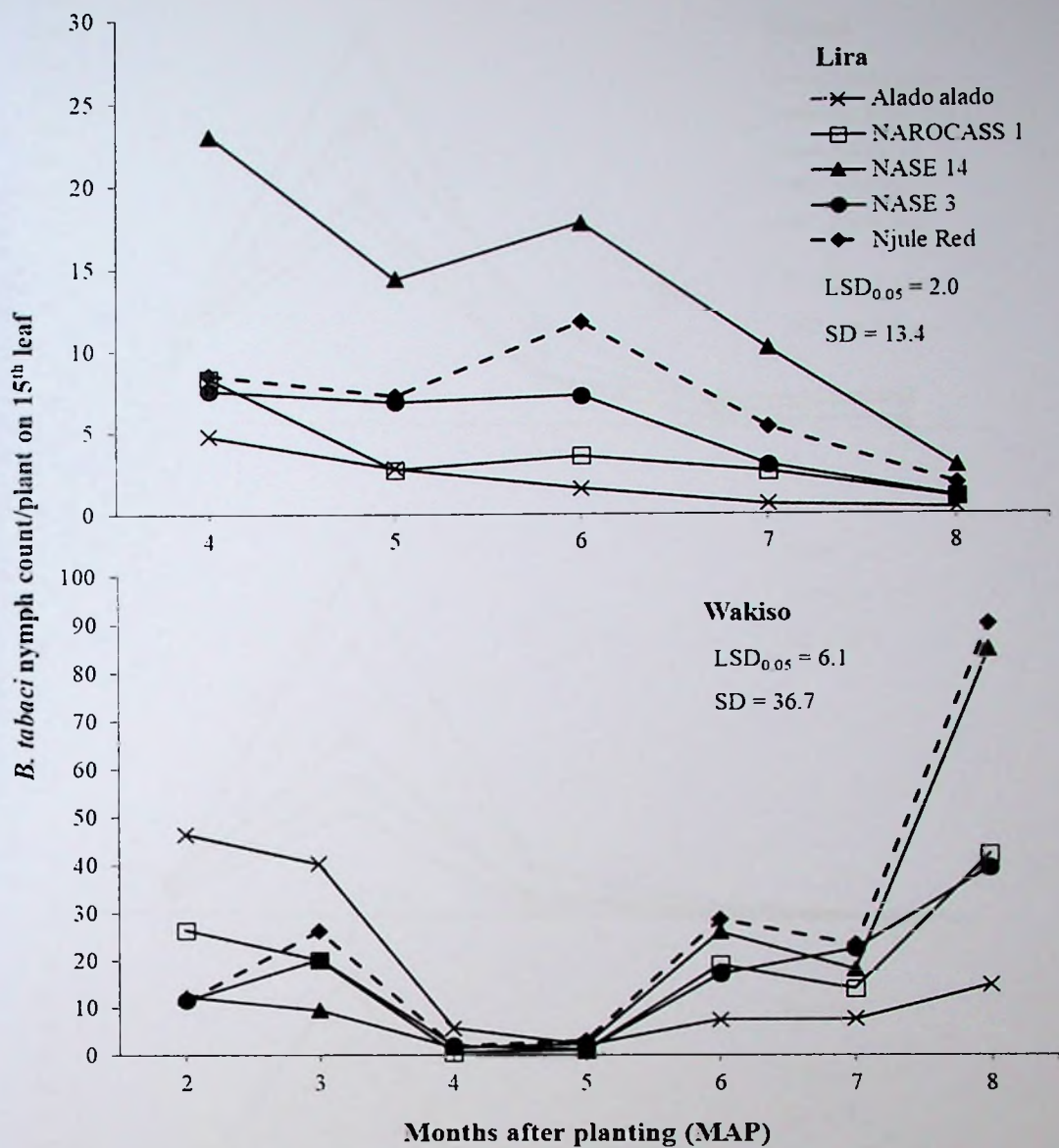


Figure 3.2: Mean monthly *B. tabaci* nymph (3rd and 4th instars) counts on five cassava genotypes at different growth stages in Lira and Wakiso in 2016.

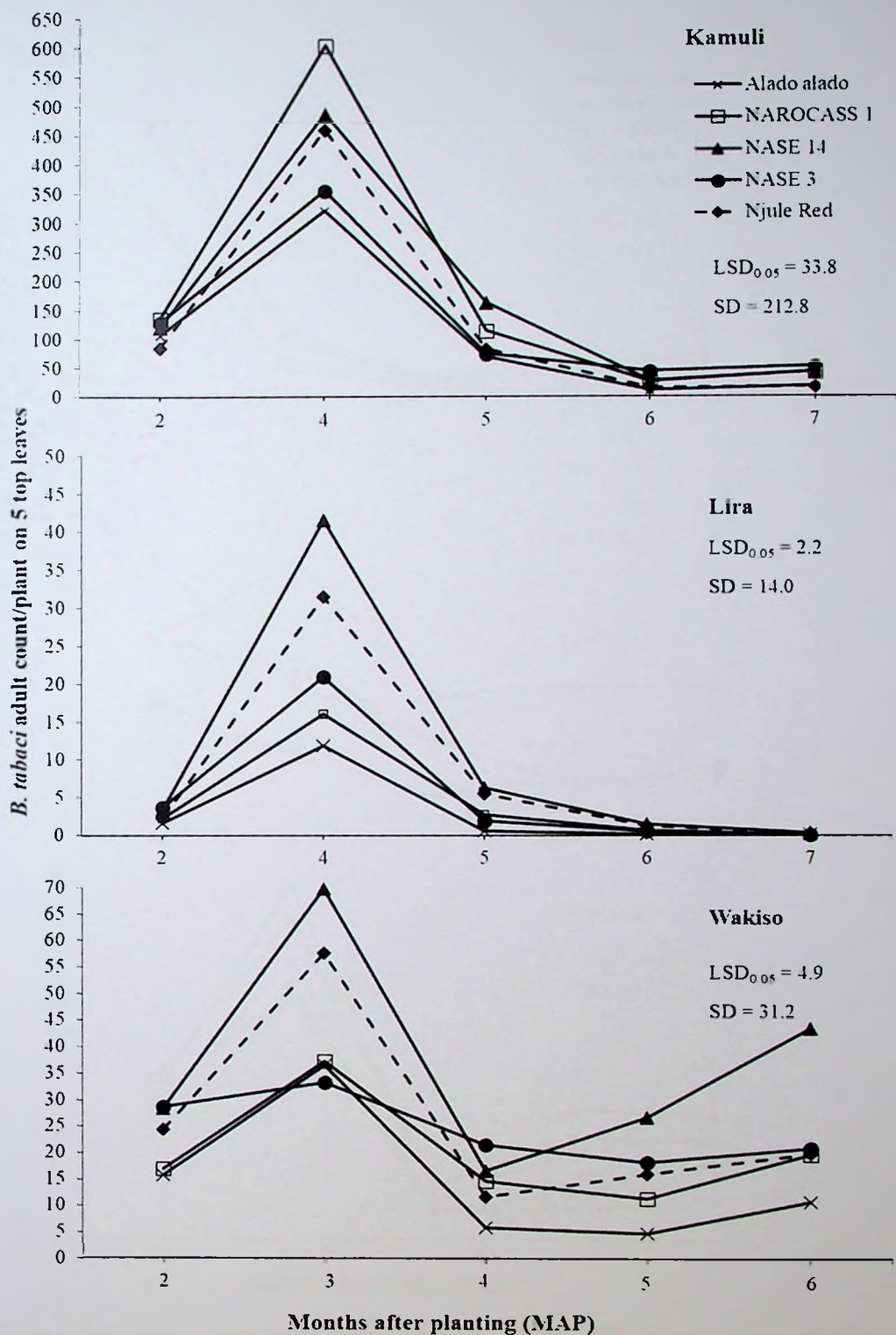


Figure 3.3: Mean monthly *B. tabaci* adult counts on five cassava genotypes at different growth stages in Kamuli, Lira and Wakiso in 2017.

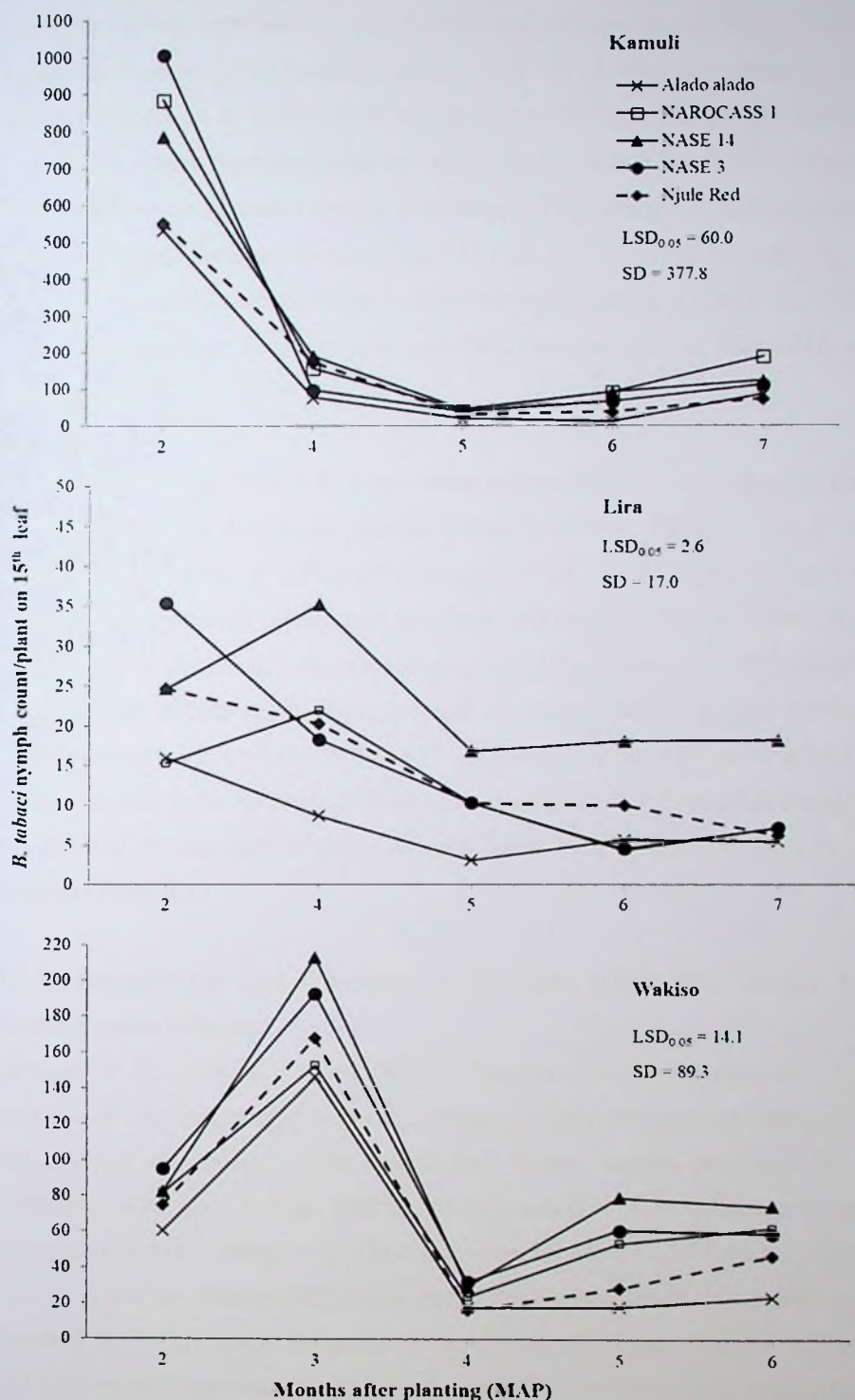


Figure 3.4: Mean monthly *B. tabaci* nymph (3rd and 4th instars) counts on five cassava genotypes at different growth stages in Kamuli, Lira and Wakiso in 2017.

From the subset regression, plant height was selected as an explanatory variable in the regression models for all locations in 2016 and 2017 (Table 3.1). Plant height had significant negative effects on *B. tabaci* adult counts across all locations in both years ($p < 0.001$; Table 3.1). In Lira where the tallest crop was observed (Figures 3.5 and 3.6), very low numbers of *B. tabaci* adults were recorded among all genotypes (Appendix 5). Additionally, Alado alado, the tallest genotype across all locations in 2016 and 2017 (Figures 3.5 and 3.6), generally had the lowest numbers of *B. tabaci* adults in all locations compared to NASE 14, the shortest genotype on which the highest *B. tabaci* adult numbers were recorded in both 2016 and 2017 (Figures 3.1 and 3.3).

In Kamuli where the highest *B. tabaci* adult populations were recorded, leaf area, lobe number and lobe width had significant positive effects ($p < 0.001$; Table 3.1) on *B. tabaci* adult count per plant. The highest *B. tabaci* adult counts of 184.8 and 167.8 were on NAROCASS 1 and NASE 14, respectively, which had high leaf area and lobe width values (Appendix 7). Njule Red had many small leaf lobes resulting in a high leaf area, and had relatively high *B. tabaci* adult numbers in both years. Multiple linear regression showed that the selected morphological characteristics accounted for 29% and 7% of the variations in *B. tabaci* adults count in Lira and Wakiso, respectively, in 2016. In 2017, the variation in *B. tabaci* adult counts accounted for by the selected morphological characteristics were 29% in Kamuli, 27% in Lira and 10% in Wakiso (Table 3.1).

3.3.3. Relationship and Dynamics of *B. tabaci* Adult and Nymph Occurrence with Environmental Factors

Because of the relatively small data set, correlation analysis focused on the strength and direction of the relationship between average monthly temperature, RH, total monthly rainfall and average monthly *B. tabaci* adult and nymph counts per location. In 2016, strong relationships between average monthly temperature ($r = -0.85$), average monthly RH ($r = 0.83$) and total monthly rainfall ($r = 0.63$) and average monthly *B. tabaci* adult counts were observed in Lira. A similar relationship was observed for average monthly *B. tabaci* nymph populations (Table 3.2). In Lira where temperatures were high with range 29–33.6 °C, low RH of 29–57% and high rainfall amounts (0–102 mm), negligible numbers of *B. tabaci* adults and nymphs were recorded. The highest average counts of 1.7 and 10.5 adults and nymphs per plant, respectively were at four MAP (Figure 3.7; Appendix 8). In Wakiso, total monthly rainfall had a strong positive effect on *B. tabaci* adult count ($r = 0.77$; Figure 3.8).

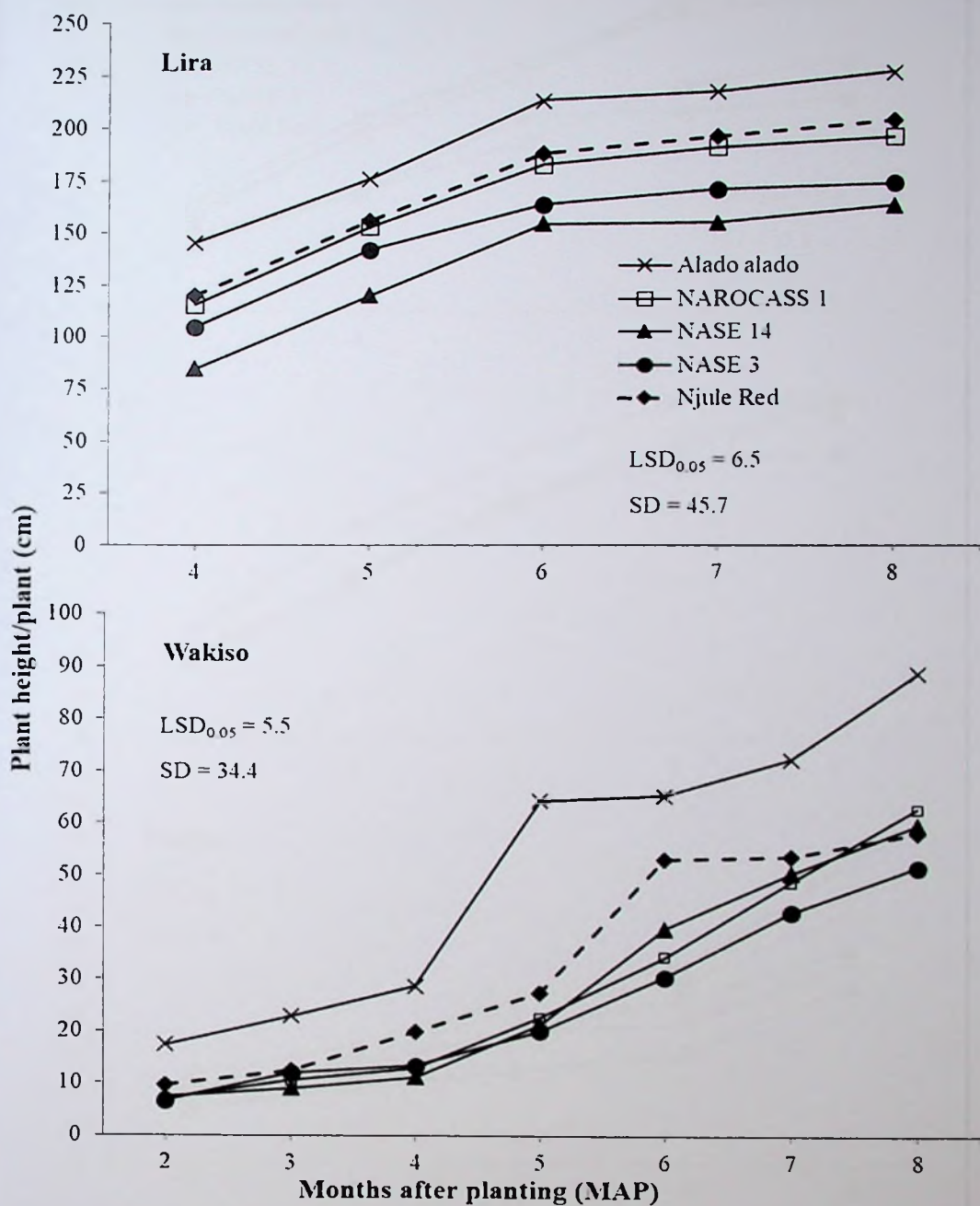


Figure 3.5: Mean monthly plant height on five cassava genotypes at different growth stages in Lira and Wakiso in 2016.

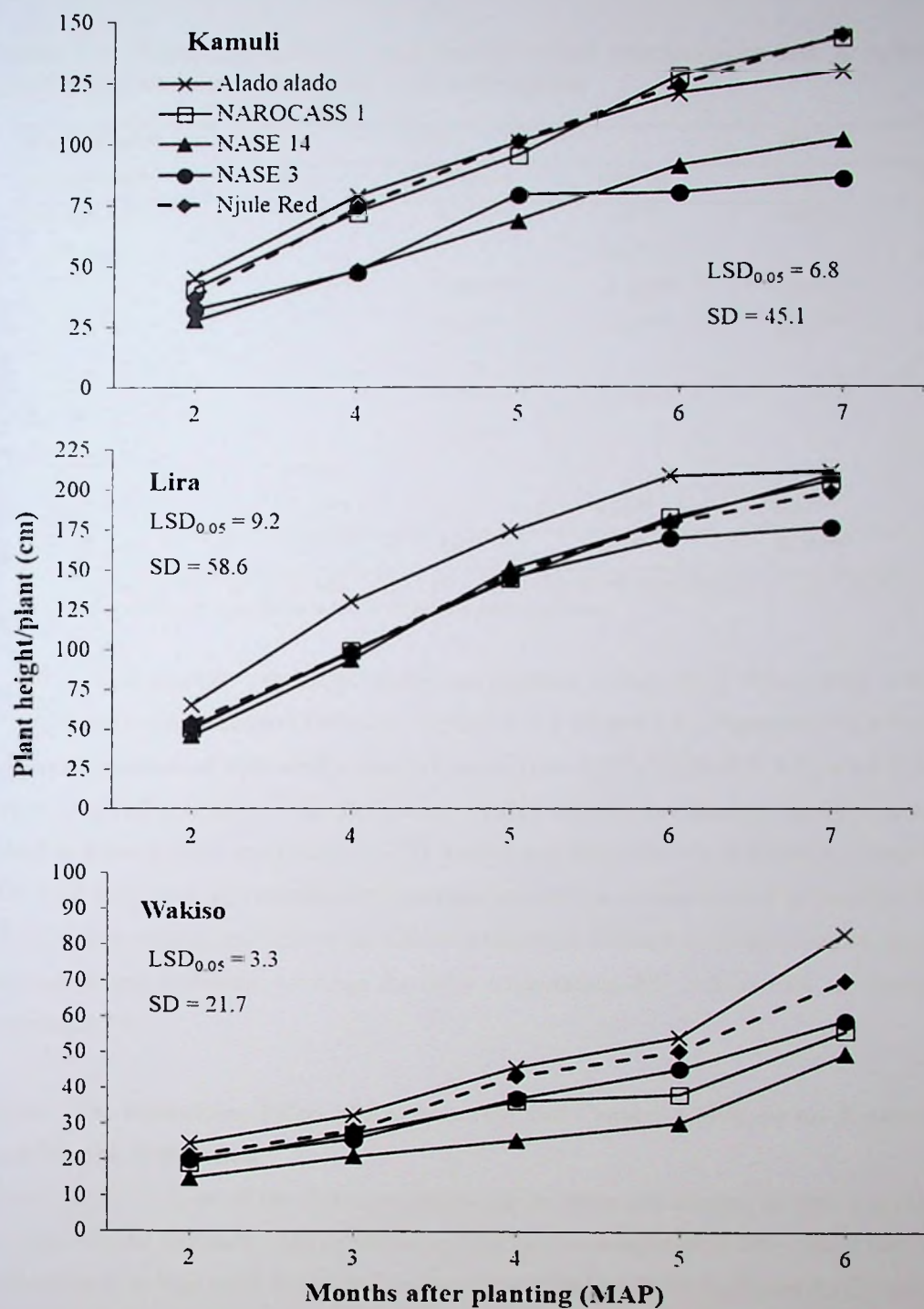


Figure 3.6: Mean monthly plant height on five cassava genotypes at different growth stages in Kamuli, Lira and Wakiso in 2017.

Table 3.1: Regression between plant morphological characteristics and *B. tabaci* adult population abundance in small-plot trials from Uganda.

Morphological characteristic	2016			2017	
	Lira	Wakiso	Kamuli	Lira	Wakiso
Intercept	3.81***	0.79***	3.42***	0.85**	0.80**
Leaf area	-	-	0.32***	-	0.23***
Plant height	-0.12***	-0.17***	-0.26***	-0.23***	-0.22***
Lobe number	-	0.16***	0.17***	0.26***	0.13***
Lobe length	-	-	-	-	0.19***
Lobe width	-	0.19**	0.43***	-	-
Stem girth	-	-0.02*	-	-	-
Petiole length	0.80***	-	-	-	-
LAI	1.15***	-	0.20**	0.63***	0.19***
R ²	0.29***	0.07***	0.29***	0.27***	0.10***

Significance: * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$; R^2 , coefficient of determination, (-) variable not selected in the regression model for a given location; LAI means leaf area index.

In 2017, total monthly rainfall generally had negative effects on *B. tabaci* adult and nymph populations in all locations (Table 3.2; Figures 3.9, 3.10 and 3.11; Appendix 9), with a strong association observed with adult count in Kamuli ($r = -0.67$). Highest *B. tabaci* adult numbers were observed in months when the lowest monthly rainfall was received; and this was at four MAP in Kamuli (36.9 mm) and Lira (111.9 mm), and three MAP in Wakiso (9.3 mm) (Figures 3.9, 3.10 and 3.11). The effects of temperature and RH on *B. tabaci* adult and nymph numbers in 2017 were inconsistent among the different locations (Table 3.2). A summary of the monthly maximum and minimum readings for daily temperature, RH and rainfall are presented in Appendix 10.

3.3.4. The Interacting Effect of Environment and Cassava Genotype on *B. tabaci* Adult and Nymph Population

From the PCA biplot of the different morphological traits and climate factors, a combination of high rainfall amounts, high temperatures and large morphological trait values had negative effects on *B. tabaci* adult and nymph counts in both 2016 and 2017 (Figure 3.12), with lowest *B. tabaci* adult and nymph counts observed in Lira. Relative humidity had moderately positive effect on *B. tabaci* adult and nymph counts in both 2016 and 2017. In general, three (3) distinct *B. tabaci* population size zones were revealed; the low population zone in Lira, the moderate population zone in Wakiso and the high population zone being Kamuli.

Table 3. 2: Correlation coefficients of *B. tabaci* adult and nymph (3rd and 4th instars) populations with RH, temperature and rainfall in small-plot trials from Uganda. Locations used in 2016 were Lira and Wakiso, and in 2017 were Kamuli, Lira and Wakiso

Weather parameter	2016						2017					
	Lira		Wakiso		Kamuli		Lira		Wakiso			
	Adult count	Nymph count	Adult count	Nymph count	Adult count	Nymph count	Adult count	Nymph count	Adult count	Nymph count	Adult count	Nymph count
Temperature	-0.85	-0.92	-0.04	0.20	-0.70	-0.60	-0.74	-0.42	0.55	0.47		
RH	0.83	0.97	0.25	-0.05	-0.02	0.78	0.69	0.32	-0.55	-0.40		
Rainfall	0.63	0.88	0.77	0.29	-0.67	0.00	-0.19	0.01	-0.23	-0.42		

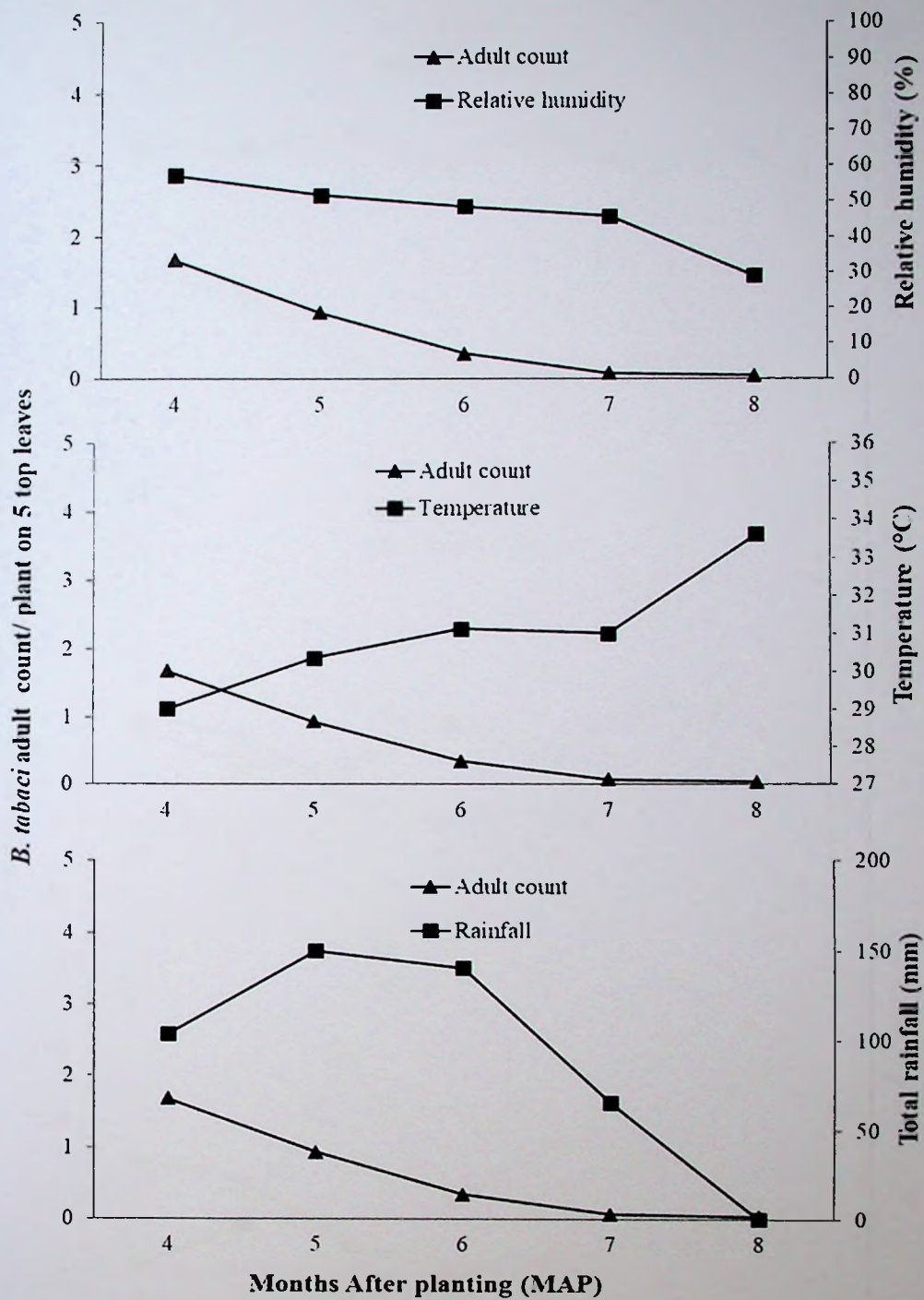


Figure 3.7: Variation in mean monthly *B. tabaci* adult counts with monthly average relative humidity, monthly average temperature and total monthly rainfall in 2016 in Lira.

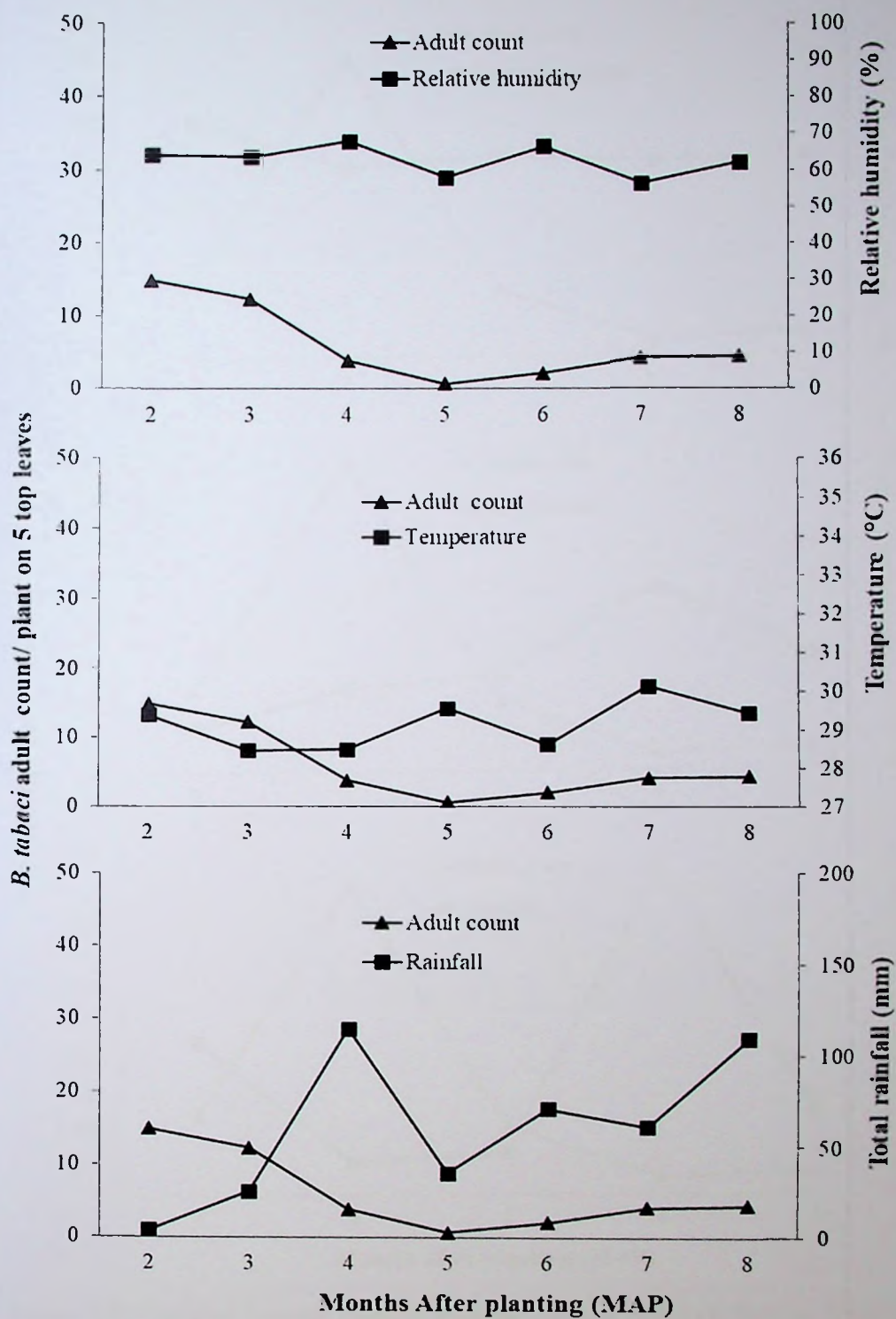


Figure 3.8: Variation in mean monthly *B. tabaci* adult counts with monthly average relative humidity, monthly average temperature and total monthly rainfall in 2016 in Wakiso.

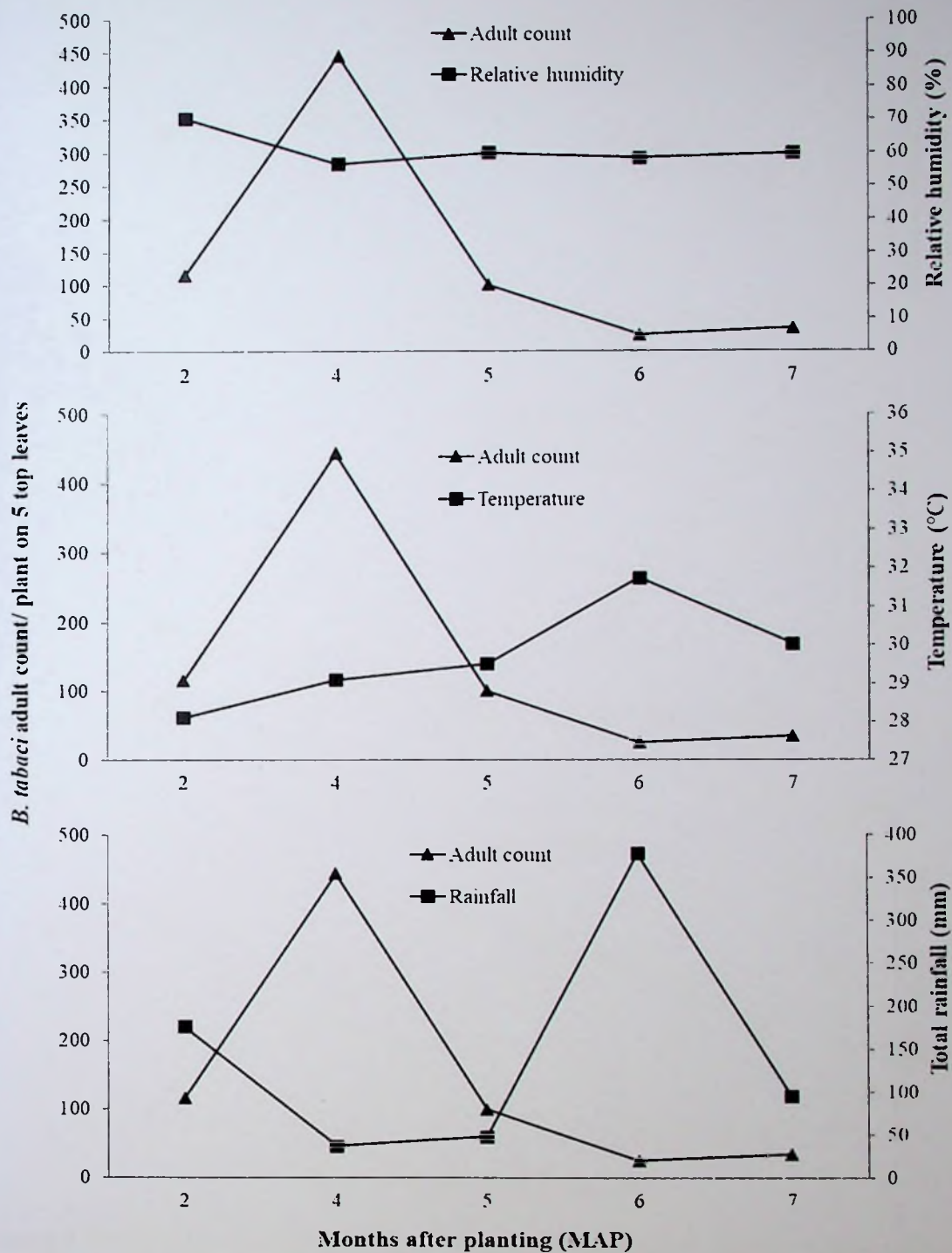


Figure 3.9: Variation in mean monthly *B. tabaci* adult counts with monthly average relative humidity, monthly average temperature and total monthly rainfall in 2017 in Kamuli.

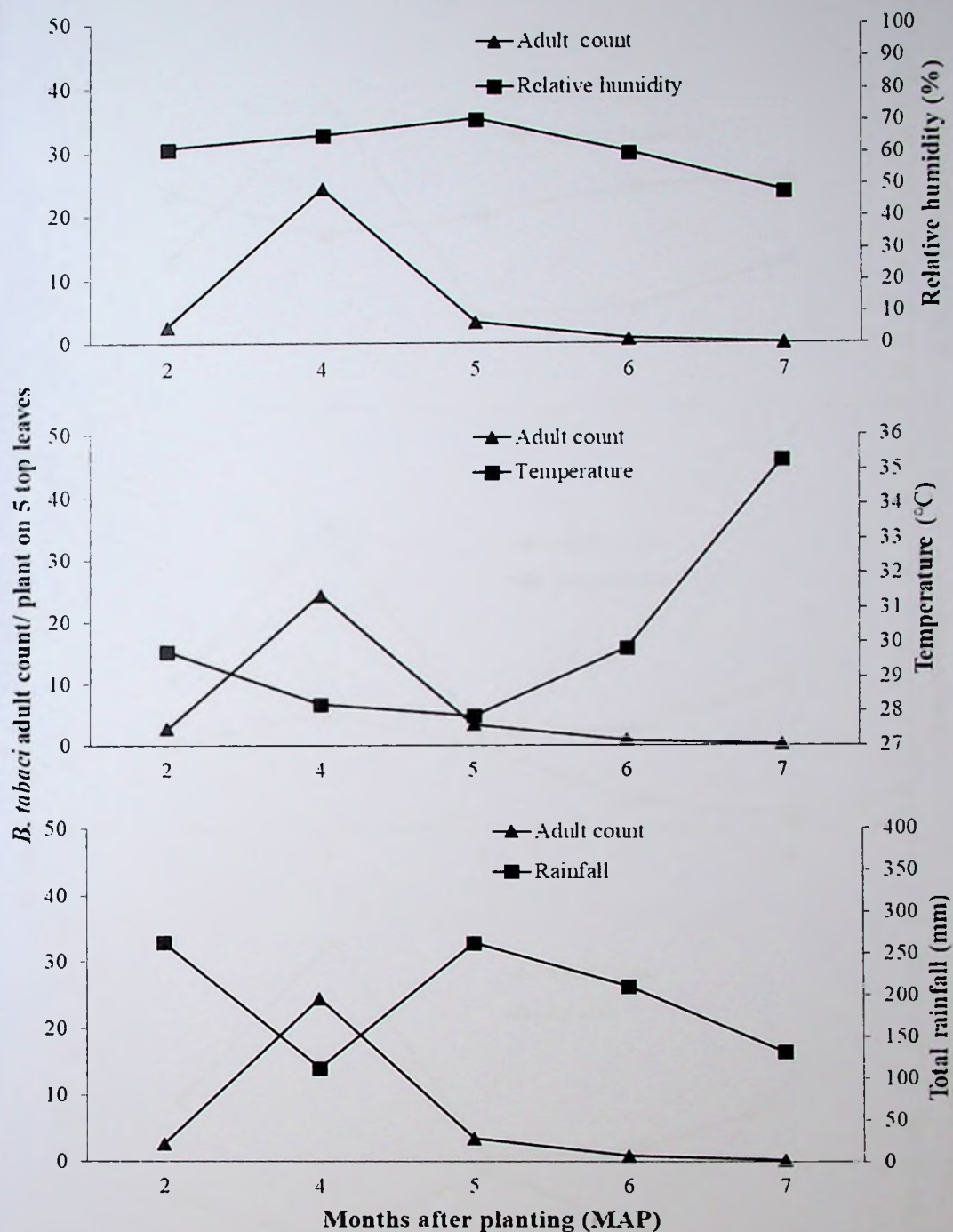


Figure 3.10: Variation in mean monthly *B. tabaci* adult counts with monthly average relative humidity, monthly average temperature and total monthly rainfall in 2017 in Lira.

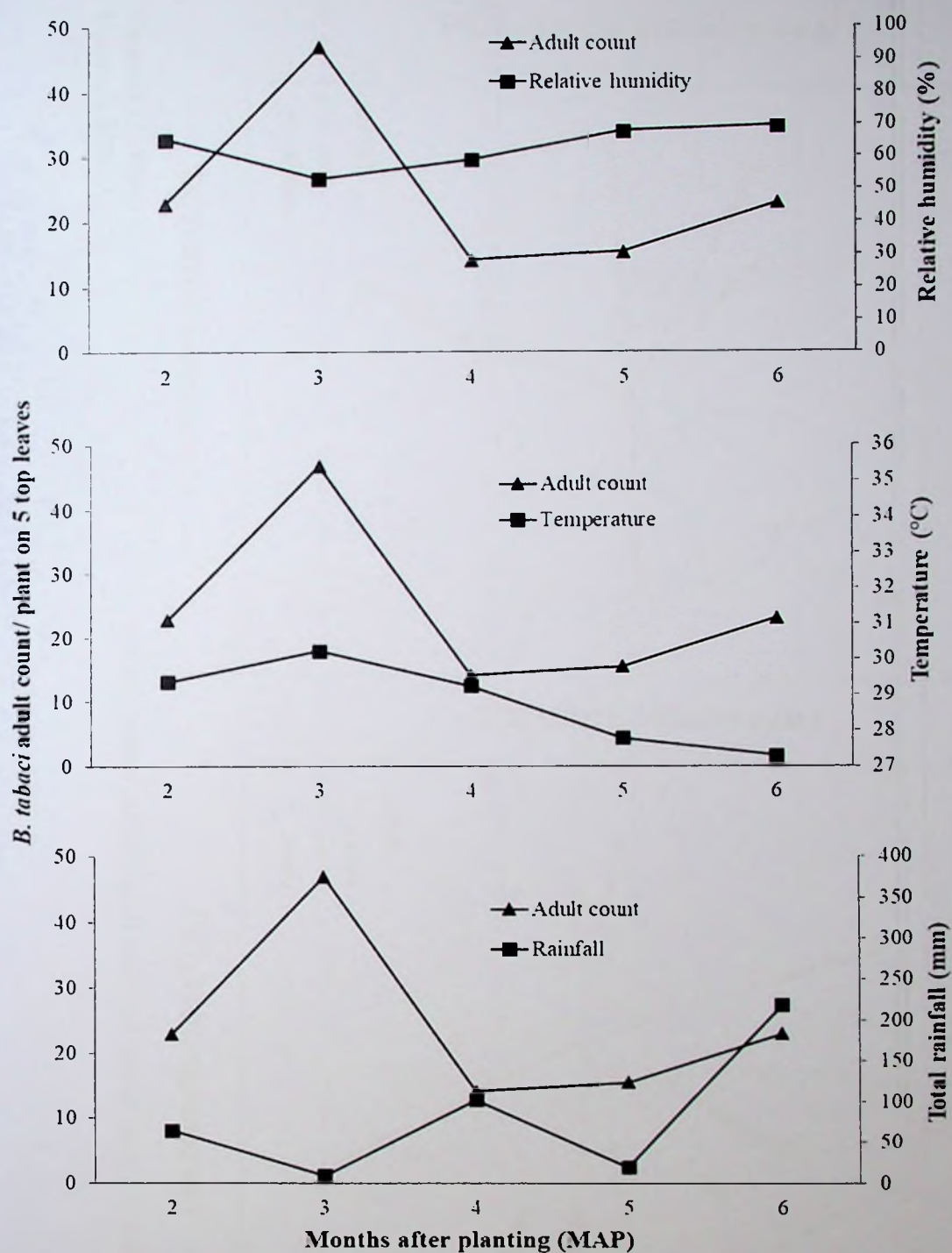


Figure 3.11: Variation in mean monthly *B. tabaci* adult counts with monthly average relative humidity, monthly average temperature and total monthly rainfall in 2017 in Wakiso.

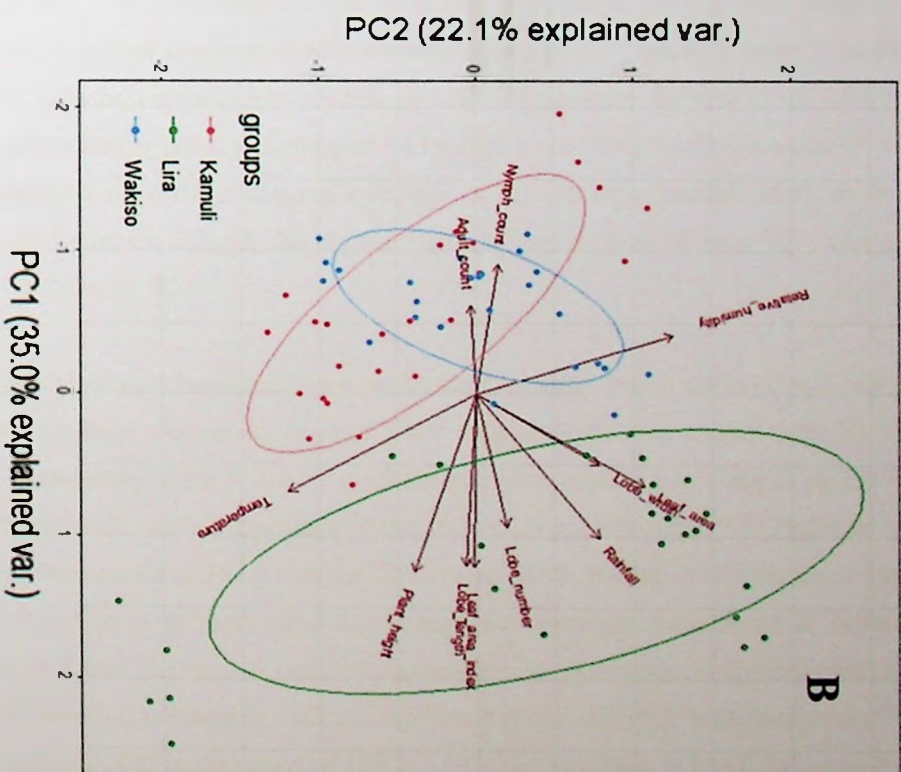
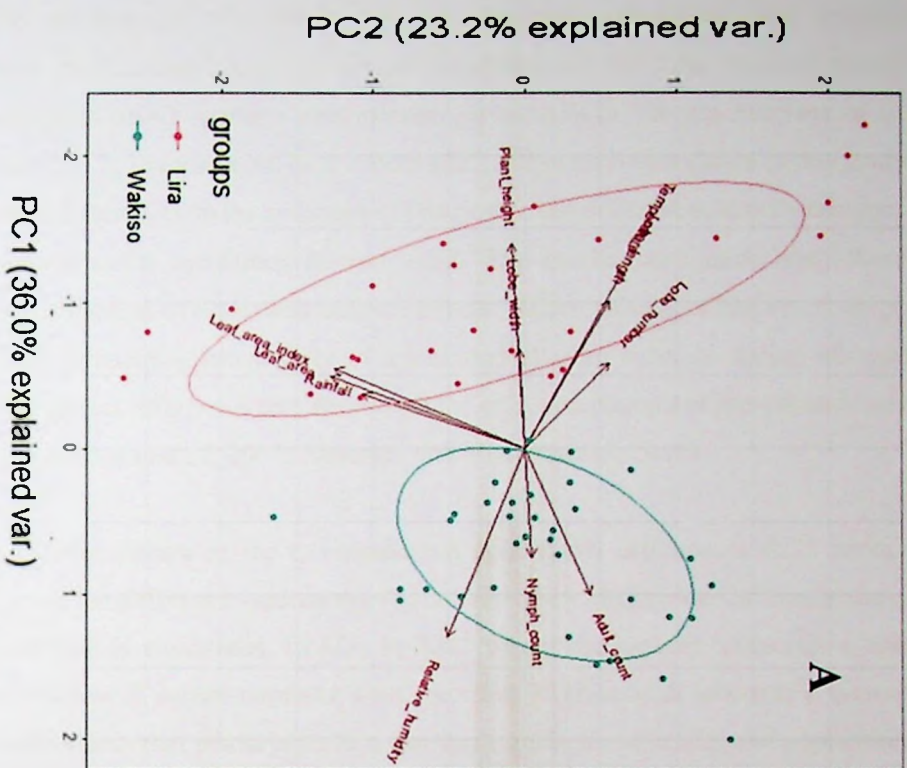


Figure 3.12: Biplot of the relationship between *B. tabaci* count and cassava morphological traits and climate factors in different locations of Uganda in 2016 (A) and 2017 (B).

3.4. DISCUSSION

This study aimed to evaluate the effects of environmental conditions and cassava morphological traits on *B. tabaci* adult and nymph populations in the field. *Bemisia tabaci* populations (identified as SSA1 species) were present on cassava in varying numbers in all locations in 2016 and 2017. The variation in *B. tabaci* adult and nymph abundance in this study demonstrated marked differences in the response of this pest to the different cassava genotypes as well as the environmental conditions in each AEZ. The mechanisms underlying these patterns may be a combination of direct and indirect effects. Direct influences can be observed through limiting and stimulating the activity of adults and altering survival during adverse weather conditions. Indirect influences can be through the effect on host plant growth and food quality (Karuppaiah and Sujayanad, 2012; Jaworski and Hilszczański, 2013).

With regard to the direct effects of the environmental conditions, differences in *B. tabaci* population dynamics in the different locations may have been due to differences in temperature, rainfall or relative humidity conditions. In Lira in 2017 where the highest temperature and rainfall were observed, low *B. tabaci* numbers were recorded. High rainfall amounts is known to wash away whiteflies and other insect pests thus causing significant mortality and population reduction (Leite *et al.*, 2005; Palumbo, 2010; Melesse and Singh, 2012). The negative relationship between *B. tabaci* abundance and temperature may have resulted from reduced adult longevity and reduced reproductive success at high temperature. Sohani *et al.* (2007) reported mean *B. tabaci* female adult longevity of 34.10 days at 20 °C and 16.88 days at 30 °C on cucumber. Curnutte *et al.* (2014) reported a decline in reproductive success of *B. tabaci* with increasing temperature on collard; the highest reproductive success of over 80% was at 28 °C compared to 46% at 33 °C.

Although the monthly average temperature was similar for Lira and Kamuli during 2 to 6 MAP (27.9–31.9 °C), in Lira there were many days of when temperatures were higher than 30 °C during 6–7 MAP. Conversely, high *B. tabaci* populations were recorded in Kamuli in 2017, which experienced moderate rainfall especially in the early crop growth stages of 176.5 mm of total monthly rainfall compared to 262.9 mm for Lira at two MAP. Based on the above, it was inferred that the combination of high rainfall and high temperatures suppressed *B. tabaci* population growth in Lira. The low *B. tabaci* populations in 2016 was also attributed to differences in environmental conditions. In Lira, the low RH (29–57.1%), high temperatures (29–33.6 °C), and high rainfall in the range of 102.7–139.9 mm during 4–6 MAP followed by

drastic decline to 0 mm at 8 MAP greatly suppressed *B. tabaci* populations. These environmental factors all contribute to low reproductive success (Norhisham *et al.*, 2013) and high mortality, therefore leading to low populations. There is however, urgent need for controlled studies on the effect of temperature and RH to validate these field results.

Variations in environmental conditions can also have indirect effects through differences in the expression of cassava morphological traits across locations as differences in plant morphology influenced *B. tabaci* population size in this study. High growth and vigor of cassava occurred in Lira where the highest rainfall amounts and temperatures were recorded, supporting results of Brown *et al.* (2016) who reported that cassava growth is enhanced by high temperatures if adequate rainfall is received. Because the cassava crop in Lira escaped the vulnerable vegetative growth stage for *B. tabaci* infestation, there was low *B. tabaci* populations in Lira, even on the whitefly susceptible genotype NASE 14. By contrast, Wakiso was largely dry in the first five MAP and cassava grew poorly due to moisture stress as observed by the reduced plant height, restricted leaf area. This was consistent with reports of Aina *et al.* (2007) and Podleśny and Podleśna (2011). Thus, a stressed crop that may have been nutritionally unfavorable for *B. tabaci* development resulted in the moderate *B. tabaci* populations observed in Wakiso. In Kamuli where moderate temperature, rainfall and RH conditions occurred in the first five months, however, there was moderate crop vigor that produced cassava plants with large tender leaves that may have been preferred by *B. tabaci* adults (Fishpool *et al.*, 1987; Katono *et al.*, 2015) as evidenced by highest *B. tabaci* adult and nymph abundances observed here.

Fluctuations in *B. tabaci* adult populations across all locations in 2017, were characterized by low initial numbers at two MAP followed by rapid increase and peaks at three and four MAP, and eventual decline at five MAP (Figure 3.3). Similar seasonal patterns were also observed in other studies (Omongo, 2003; Khalid *et al.*, 2006). This pattern may be associated with differences in host plant quality across time, with younger crops (≤ 2 MAP) with few leaves being less preferred by *B. tabaci* adults, while large tender leaves produced at later crop stages may have been preferred by *B. tabaci* adults. At later growth stages, leaves senesce and reduced food quality may have prompted *B. tabaci* adults to search for better host plants for both oviposition and feeding. Previous studies demonstrated that *B. tabaci* population dynamics are strongly influenced by crop age (Khalid *et al.*, 2006; Katono *et al.*, 2015; Kalyebi *et al.*, 2018).

This study revealed that *B. tabaci* adult populations varied significantly with cassava genotypes across all locations in both years (Figures 3.1 and 3.3). This was probably due to differences in plant morphological traits among the genotypes. Indeed, significant differences were observed in plant height which was the only trait with a consistent negative effect on *B. tabaci* adults across all locations. This was typified by the consistently low and high *B. tabaci* adult counts on Alado alado and NASE 14 across all locations in both years that were the tallest and shortest genotypes, respectively. This result supports the findings of Javed *et al.* (2011) and Khalil *et al.* (2015) who reported negative relationship between *Leucinodes orbonalis* Guenee and *B. tabaci* adult populations with plant height in aubergine and cotton, respectively.

In trials where environmental conditions were suitable for growth and development of *B. tabaci* populations, it was observed that leaf area, leaf lobe widths and leaf lobe numbers positively influenced *B. tabaci* numbers that could be supported on cassava. High numbers were observed on NASE 14 and NAROCASS 1 in Kamuli in 2017, and this was because large leaf area and lobe width provided *B. tabaci* adults large surface areas for feeding and oviposition as well as offering suitable protection from wind and rain. These findings are in agreement with those of Sippell *et al.* (1987) who reported reduction in *B. tabaci* adult numbers on cotton with lower leaf area. Large surface areas, leaf lobe widths and leaf lobe numbers ultimately result in dense canopy cover and high LAI values which provides protection from high temperatures and low RH (Andres *et al.*, 2016). However, since this result was from one study in Kamuli, further investigations in areas of high *B. tabaci* population abundance are recommended to validate these findings.

In this study, cassava genotypes with different levels of tolerance or resistance to major cassava diseases and *B. tabaci* infestation were used. Generally, Alado alado which is considered tolerant to *B. tabaci* performed as expected in terms of having consistently low *B. tabaci* adult and nymph abundance. However, Njule Red often supported similar numbers of *B. tabaci* to NAROCASS 1, NASE 3 and NASE 14 (the susceptible or moderately tolerant genotypes). Although Njule Red had very small leaf lobes as reflected in the low leaf lobe width values across all locations in both years, it had the highest leaf lobe numbers and leaf lobe lengths which resulted in large leaf areas and high *B. tabaci* numbers. These findings suggest that Njule Red should not be considered tolerant to *B. tabaci* in the field.

This study has also shown that the risk of *B. tabaci* outbreaks in cassava fields is heightened by the deployment of short, broad-leaved, cassava genotypes in areas that experience moderately hot and humid environment, with moderate amounts of rainfall. However, the study did not examine all factors that may be important for *B. tabaci* population dynamics in the field. Natural enemies, such as predators and parasitoids can cause significant mortality to *B. tabaci* populations, especially late in the season (Legg, 1995; Otim *et al.*, 2005). Additionally, the plot trials adopted in this study were small relative to the movement capabilities of *B. tabaci* adults. Although we assume that higher numbers of adults in one plot represent a biological preference for those plants over the others in the trial, there may also have been a high amount of stochastic movement as adults could easily move between plots in each trial. Furthermore, in real smallholder production landscapes, there is often a diversity of cassava and non-cassava host plants that can support *B. tabaci* populations (and their natural enemies) to some degree. The effects of this diversity of resources was not assessed in this field trials, but may have had some impacts. Studies reported in the next Chapter were therefore conducted to further expound on the effect of cassava genotype and temperature on *B. tabaci* biology.

These results have shown that high temperature, high rainfall, low RH and high plant height have negative effects on *B. tabaci* abundance on cassava. The tallest genotype, Alado alado was shown to consistently support low populations of *B. tabaci*; however, this genotype is susceptible to both CMD and CBSD. These results have also shown that cassava genotypes (e.g., NASE 14) with low plant height, large leaf area and large lobe width support high *B. tabaci* populations, yet these are farmer preferred disease tolerant genotypes. Further breeding efforts are therefore needed to resolve these contradictions.

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CHAPTER FOUR

EFFECT OF TEMPERATURE AND CASSAVA GENOTYPE ON THE DEVELOPMENT, FECUNDITY AND REPRODUCTION OF *Bemisia tabaci* (Hemiptera: Aleyrodidae) SSA1

4.1. INTRODUCTION

Temperature and host plant effects are primary factors affecting development, fecundity and mortality of *B. tabaci* (Nava-Camberos *et al.*, 2001; Naranjo *et al.*, 2010). With the expected rise in global surface temperatures of up to 11 °C by the year 2100 (Githcko *et al.*, 2000; United States Global Climate Research Program, 2009) and a projected 2 °C rise in mean annual temperature in Africa (Giesen *et al.*, 2020), momentous temporal and spatial distribution shifts are expected among insects (Parmesan, 2006). However, inconsistent responses due to global warming have been reported for different phloem feeders (e.g., whiteflies) (Bezemer and Jones, 1998) and host plants (Bezemer *et al.*, 1999).

Although temperature was reported to positively impact *B. tabaci* populations (Alicai *et al.*, 1999; Sharma *et al.*, 2017), other researchers reported otherwise (Bhatt *et al.*, 2018). It is therefore imperative that *B. tabaci* populations are investigated along its life cycle against temperature, cassava genotypes and their interactions (temperature versus cassava genotypes), and how these affect whitefly population dynamics with special attention to the currently known *B. tabaci* species and the significant fluctuations in night temperatures from those recorded at 15:00 hours in Uganda.

Results from Chapter Three revealed that a combination of moderate temperature, relative humidity and broad leaf cassava genotypes of short stature supports high *B. tabaci* populations. The objective of this study therefore was to evaluate the development, fecundity, survival and reproduction of *B. tabaci* sub-Saharan Africa 1 (SSA1) species on three cassava genotypes with contrasting traits under a range of temperatures.

4.2. MATERIALS AND METHODS

4.2.1. Plant Materials

The cassava genotypes that were shown to support high (NAROCASS 1 and NASE 14) and low (Alado alado) *B. tabaci* SSA1 populations in Chapter Three were used in this study. Ten centimeter (10 cm) long stem cuttings of cassava test genotypes were placed vertically in 10 cm-diameter plastic pots containing sterilised black soil in a screenhouse at the National Crops Resources Research Institute (NaCRRI) in Namulonge, Uganda (Plate 4.1). The experiments were conducted between September 2018 and May 2019.

4.2.2. *Bemisia tabaci* SSA1 Pure Colony

Pure colonies of *Bemisia tabaci* SSA1 species were raised from a single mated female on the cassava genotype NAROCASS 1 grown in 10 cm-diameter plastic cups in insect proof cages (50 cm x 50 cm x 50 cm) the screenhouse at NaCRRI (Plate 4.1). The colonies were maintained under natural fluctuating conditions; with temperature range of 16–32.5 °C and relative humidity rang of 38–100% and a photoperiod of 12:12 (L:D).

4.2.3. Experimental Conditions and Design

The study was conducted under controlled environmental conditions in separate temperature-humidity controlled rooms at NaCRRI. The three test cassava genotypes were placed under five study temperatures (16, 20, 24, 28 and 32 ± 2 °C), with relative humidity (RH) maintained at $70 \pm 5\%$ and a photoperiod of 12: 12 (L:D). These temperatures and RH ranges are typical of the prevailing environmental conditions of Uganda (Irish-Aid, 2017; Nkuringo-Safaris, 2020; World Climate Guide, 2021).

The experiment was set in a randomized complete block design (because of temperature and RH gradients in the controlled rooms) with replications depending on the parameters under study. For all studies, temperature was the main plot factor, while cassava genotype was the sub-plot factor. To guard against power failures, a fully fueled automatic generator was always on standby.

4.2.4. Development Duration and Survival of Immature *B. tabaci* SSA 1

This experiment was set in a randomised complete block design with six replications of three plants per genotype per temperature (Plate 4.2), and was repeated three times. Fifty pairs of 24 h old *B. tabaci* (50 males and 50 females), identified according to Kedar *et al.* (2014) were

clipped in cages of 5.5 cm diameter and 5 cm length with a nylon cloth at the base on the first and second fully expanded leaves of cassava plants. The insects were then left to oviposit for 24 hours at 24 °C (the study temperatures closest to room temperature of 25 °C) (Plate 4.2). The test plants were then transferred to temperature-controlled rooms set at the various study temperatures.

Immediately after, fifty eggs were selected for observation using a 10× hand lens and all the other eggs on the leaves were removed by gently brushing them off using the edge of soft tissue paper (Asiimwe *et al.*, 2007a). Daily observations were made and records made on survival and the transition from one stage to another (Eggs, 1st, 2nd, 3rd and 4th nymphal instars and the pupal stage) until adult emergence as described by Gangwar and Gangwar (2018). Survival during each immature stage was recorded as the number of individuals developing to the subsequent stage, and this was converted into percentage survivorship for each stage.

4.2.5. Longevity, Fecundity and Population Parameters of *B. tabaci* SSA1

Five newly emerged adult mating pairs in clip cages were confined on the underside of the 1st, 2nd, 3rd and 4th fully expanded cassava leaves of each genotype (each leaf was treated as a replicate) and allowed to oviposit for 24 h. The five mating pairs were transferred daily to a new leaf until death of all the females. The number of eggs laid was recorded daily and used to calculate fecundity, while the lifespan of the females was used to calculate longevity. The eggs were observed until adult emergence and the progeny were sexed according to Kedar *et al.* (2014) and their numbers were recorded to obtain the secondary sex ratio as the number of males per 100 females. The experiment was also set in four replications using a randomised complete block design and was repeated twice.



Plate 4.1: Test plants and *B. tabaci* pure colonies raised in separate screenhouses at NaCRRI.



Plate 4.2: Clip cages used for holding fifty pairs of 24 h old *B. tabaci* (Each tray had the three test cassava genotypes).

4.2.6. Data Analysis

All data were analyzed using R statistical software (R Core Team, 2017). Prior to analysis, all data were tested for normality and where skewness occurred, data were subjected to the Box Cox procedure (Venables and Ripley, 2002) in order to determine the most appropriate transformation based on the lambda value. The data were then subjected to fixed model ANOVA for temperature and genotype effects. Means were separated using the Least Significant Difference (LSD) test at 5% probability level. Development rate was calculated as a reciprocal of development duration in days (Nava-Camberos *et al.*, 2001). The effect of temperature on immature development rate was then subjected to linear regression. Population parameters; net reproductive rate (R_0), mean generation time (T) in days, finite rate of increase (λ) and the intrinsic rate of increase (r_m) were calculated according to (Birch, 1948; Islam and Ren, 2007).

4.3. RESULTS

4.3.1. *Bemisia tabaci* SSA1 Development Duration

Cassava genotype and genotype by temperature interactions had no significant effect on development duration ($p>0.05$) (Appendix 11). However, the effect of temperature variation was significant ($p<0.001$) on development duration of all stages and total development duration of *B. tabaci* SSA1. Developmental duration reduced by a factor of 3 to 5.6 with increase in temperature for the lowest and highest temperature values across all development stages (Table 4.1).

Generally, the effect of temperature on development duration was more pronounced on the eggs, and first, second and third nymphal instars. The shortest development time for eggs was observed at 32 °C; while the longest time occurred at 16 °C (Table 4.1), the egg stage lasted 20 days at 16 °C, while it only lasted 5.5 days at 32 °C (Table 4.1). Mean egg development time ranged from 5.52 days at 32 °C to 19.99 days at 16 °C; mean total developmental duration for all immature *B. tabaci* SSA1 growth stages ranged from 17.93 days at 32 °C to 65.33 days at 16 °C. However, there were no significant differences ($p>0.05$) in development duration for the first instar, second instar, fourth instar and the pupal stages at 28 °C and 32 °C (Table 4.1). The egg stage had the longest development period at all temperatures (Table 4.1).

4.3.2. *B. tabaci* SSA1 Development Rate

Developmental rates generally increased with increase in temperature for all growth stages and total life cycle (Figure 4.1), with the exception of the first nymph instar where the development rate observed at 20 °C was similar to the development rate observed at 28 °C and 32 °C (Figure 4.1). The lowest and highest development rates were observed at 16 °C and 32 °C, respectively (Figure 4.1). Simple linear regression analysis of developmental rates and temperature for each growth stage and the total life cycle further revealed a strong and significant positive relationship between development rate and temperature, with temperature accounting variation observed in development rate of between 47% for 1st instar to 82% for eggs (Table 4.2).

4.3.3. Survival of Immature Stages of *B. tabaci* SSA1

There were significant genotype by temperature ($p < 0.05$) effects on the survival of all immature *B. tabaci* growth stages (Appendix 11). For all *B. tabaci* SSA1 growth stages on all cassava genotypes, survival was lowest at 16 °C (Table 4.3). *Bemisia tabaci* SSA1 survival from egg to adult on all cassava genotypes at all temperatures was generally over 80%; and varied from 82.1% at 16 °C on Alado alado to 98.7% at 28 °C on NAROCASS 1. There were no significant differences in *B. tabaci* SSA1 survival at temperatures 28 °C and 32 °C, where highest survival for all *B. tabaci* stages on all cassava genotypes was observed. At all temperatures, over 85% of eggs reached the first instar on all cassava genotypes (Table 4.3). Although significant genotype effects were revealed by ANOVA, these were most pronounced for the 2nd instar stage at 16 °C where 63.7% of the nymphs molted into third instar nymphs on Alado alado compared with 81.5% on NASE 14 and 88.9% on NAROCASS 1 (Table 4.3). In general, inconsistent variations in *B. tabaci* SSA1 survival were noted among cassava genotypes at temperatures of 16 °C to 24 °C. While on Alado alado the lowest survival of 63.7% was observed for the second instar stage, the highest survival rate of 88.9% was for the fourth nymph stage (Table 4.3). At 32 °C, survival of the different *B. tabaci* SSA1 growth stages was similar on all cassava genotypes.

Table 4. 1: Development duration of *B. tabaci* SSA1 at five constant temperatures on cassava in the laboratory in 2019

Temperature (°C)	Development duration (days) of different <i>B. tabaci</i> SSA1 growth stages						All stages
	Egg	1 st instar	2 nd instar	3 rd instar	4 th instar	Pupa	
16 °C	19.99a	9.02a	12.68a	12.76a	5.63a	6.24a	65.33a
20 °C	9.63b	3.02c	4.00b	6.18b	1.69b	3.02b	27.54b
24 °C	7.30c	3.39b	3.48c	5.37c	1.24c	2.61c	23.39c
28 °C	7.15c	3.13bc	2.94d	3.94d	1.06cd	2.28d	20.50d
32 °C	5.52d	3.06c	2.80d	3.41e	1.00d	2.15d	17.93e
SD	5.11	2.49	3.86	3.57	1.88	1.66	17.7

Means within a stage followed by the different letters are significantly different at 5% significance level. Means pooled over-all cassava genotypes.

Table 4. 2: Linear regression parameters of temperature versus developmental rates of *B. tabaci* SSA1 on cassava

Stage	Intercept	slope	R ²
Egg	-3.818	0.069	0.815***
1 st instar	-2.618	0.053	0.47***
2 nd instar	-3.459	0.084	0.688***
3 rd instar	-3.554	0.077	0.802***
4 th instar	-2.775	0.096	0.64***
Pupa	-2.524	0.06	0.62***
Total life cycle	-5.039	0.072	0.781***

Significance: *** $p < 0.001$; R², coefficient of determination

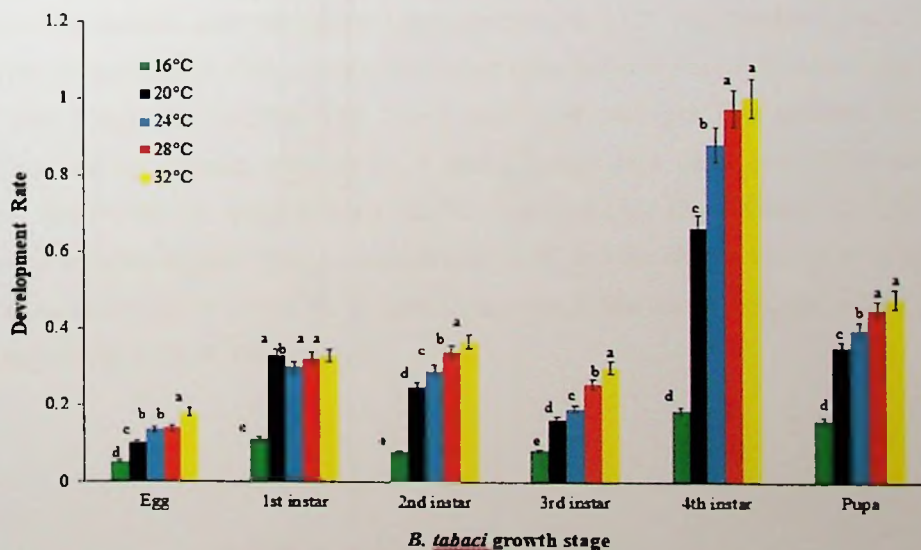


Figure 4.1: Developmental rates for different *B. tabaci* SSA1 growth stages at five constant temperatures, pooled over-all cassava genotypes in the Laboratory in 2019.

Table 4. 3: Survival of *B. tabaci* SSA1 immature stages at five constant temperatures on three cassava genotypes

Genotype	Temperature (°C)	Survival (%) of <i>B. tabaci</i> growth stage stages						All stages
		Egg	1 st instar	2 nd instar	3 rd instar	4 th instar	Pupa	
Alado alado	16	86.78c	87.16c	63.71c	80.26c	88.90c	85.51c	82.05d
	20	92.78b	90.88bc	88.84b	87.22b	89.93c	90.79bc	90.07c
	24	95.78ab	94.41ab	93.72ab	94.24a	95.20b	93.86ab	94.53b
	28	97.78ab	98.52a	96.44a	99.10a	99.24a	99.30a	98.40a
	32	100.00a	98.56a	97.48a	97.51a	96.64ab	98.93a	98.19a
NAROCASS 1	16	94.56b	94.12ab	88.94c	87.34c	79.51c	80.70b	87.53c
	20	93.00b	91.72b	92.00bc	92.68b	89.07b	93.05a	91.92b
	24	98.56a	96.88a	96.76ab	96.18ab	95.93a	97.56a	96.98a
	28	100.00a	96.67a	97.12a	100.00a	98.92a	99.29a	98.67a
	32	100.00a	97.56a	96.77ab	97.83ab	96.90a	99.41a	98.08a
NASE 14	16	88.33c	87.93c	81.47c	84.90c	80.76b	88.25b	85.27c
	20	92.44bc	93.78b	91.28b	91.80b	92.74a	94.01a	92.68b
	24	95.33ab	97.50ab	96.34ab	96.66a	96.41a	96.93a	96.53a
	28	98.44a	97.51ab	96.97a	95.68ab	95.45a	96.94a	96.83a
	32	100.00a	99.11a	96.63a	97.17a	96.23a	98.12a	97.88a

Means within the same stage followed by the same letter are not significantly different at 5% significance level.

4.3.4. Fecundity and Female Longevity of *B. tabaci* SSA1

Cassava genotype and their interaction with temperature did not significantly affect fecundity and female longevity ($p > 0.05$) (Appendix 11). However, fecundity increased significantly ($p < 0.001$) with temperature, with the highest value observed at 32 °C and the lowest at 16 °C for all genotypes (Figure 4.2A). The median number of eggs laid daily at 16 °C was 1 egg for Alado alado and 2 eggs for NAROCASS 1 and NASE 14 each per five females for all genotypes. This was in contrast with 35.5, 34 and 37 eggs laid daily for Alado alado, NAROCASS 1 and NASE 14, respectively at 32 °C (Figure 4.2A). The reverse was true for female longevity with the highest lifespan recorded at 16 °C and the shortest at 32 °C (Figure 2B). Female *B. tabaci* SSA1 lived for 28, 29 and 27 days on Alado alado, NAROCASS 1 and NASE 14, respectively at 16 °C (Figure 4.3).

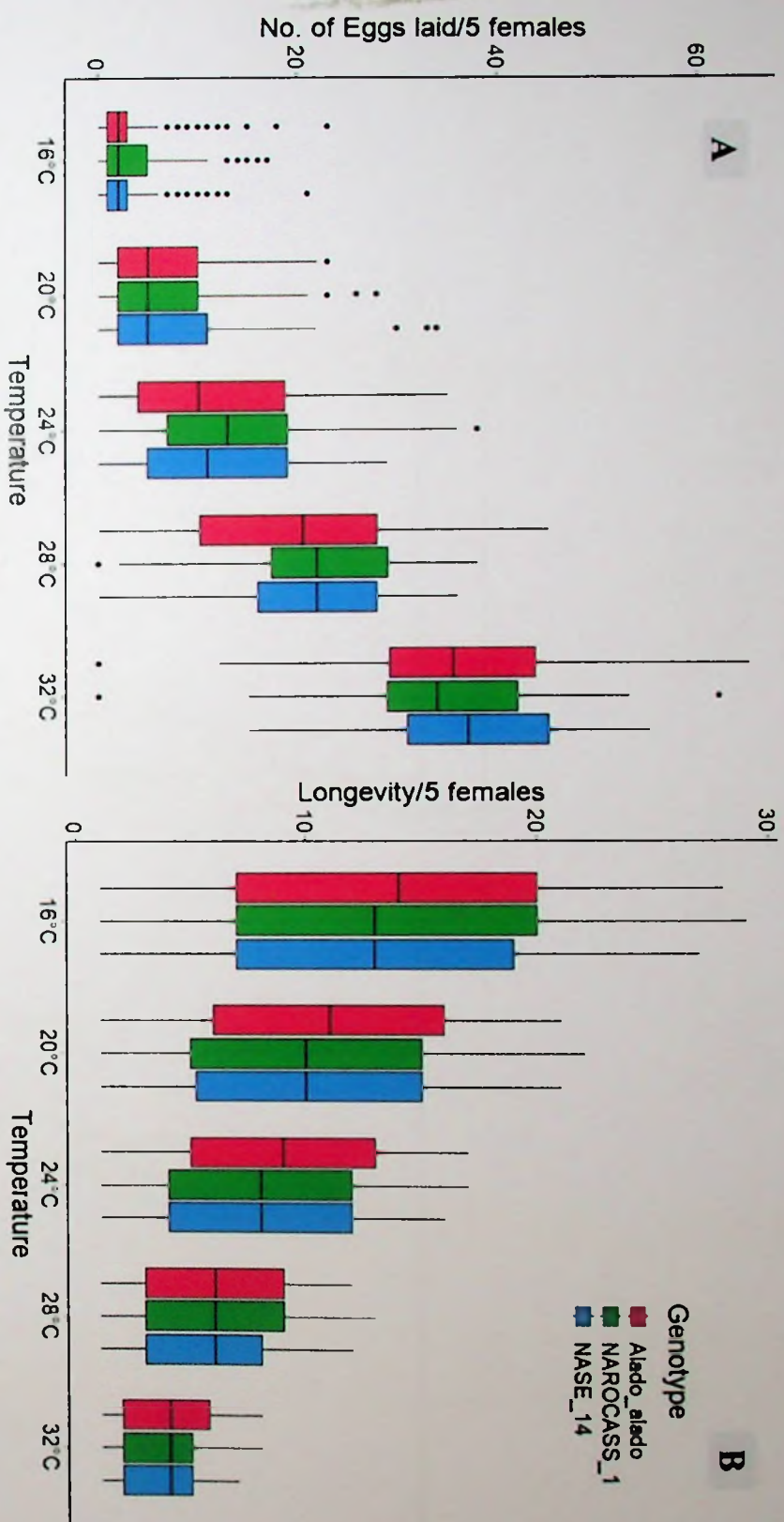


Figure 4.2: Box plots for the number of eggs laid daily by five females (A) and longevity of female (B) *Bemisia tabaci* SSA1 on three cassava genotypes at five constant temperatures.

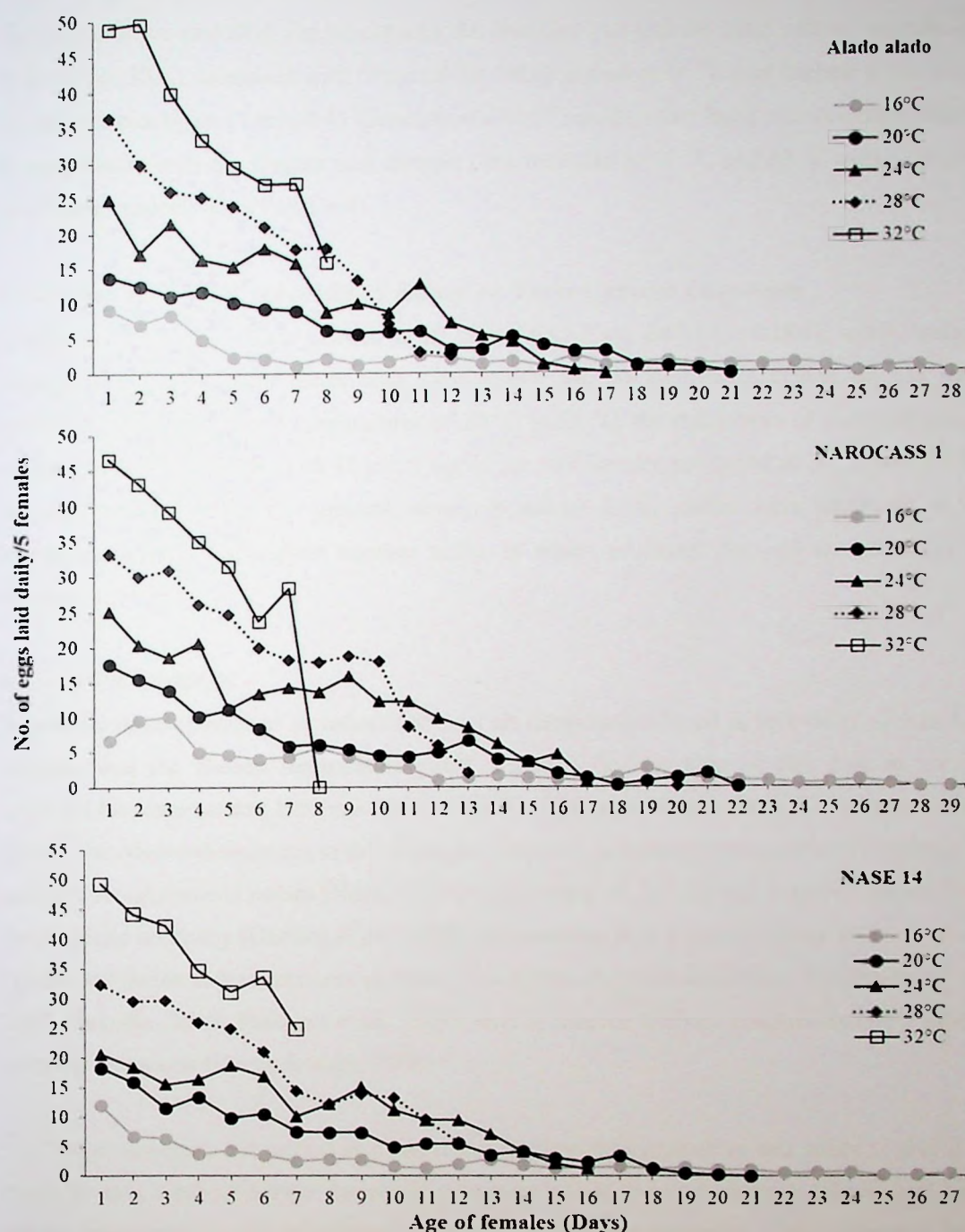


Figure 4.3: Number of eggs laid daily by five *B. tabaci* SSA1 females on three cassava genotypes at five constant temperatures.
 Note: At 32°C on NAROCASS, the zero fecundity at 8 days means that the females were present but did not lay any eggs.

4.3.5. Population Parameters of *B. tabaci* SSA1 Raised on Three Cassava Genotypes

Net reproductive rate (R_0), innate capacity for increase (r_m) and the finite rate of increase (λ) of *B. tabaci* SSA1 increased with temperature; being lowest at 16 °C and highest at 32 °C on all cassava genotypes (Table 4.4). Generation time (T) on the other hand was inversely related to temperature with the longest and shortest time recorded at 16 °C and 32 °C on all cassava genotypes, respectively (Table 4.4).

4.3.6. Sex Ratio of *B. tabaci* SSA1 Raised on Three Cassava Genotypes

Temperature had significant effects on *B. tabaci* SSA1 sex ratios ($p < 0.001$), while cassava genotypes and their interactions with temperature had no significant effects on sex ratio ($p > 0.05$) of progeny. From temperatures of 20 °C to 32 °C, the proportion of male offsprings reduced with temperature, with 38 and 9 males per 100 females produced at 20 °C and 32 °C, respectively (Table 4.5). In general, fewer *B. tabaci* SSA1 males were produced at all temperatures, with the highest number being 38 males produced per 100 *B. tabaci* SSA1 females at 20 °C.

4.4. DISCUSSION

Successful development of *B. tabaci* SSA1 at all temperatures used in this study (Table 4.1) suggests that the chosen temperature range supports development of this pest as earlier observed for temperatures between 15 °C to 35 °C (Muniz and Nombela, 2001; Yang and Chi, 2006). The observed decrease in development time with increase in temperature is because *B. tabaci* is ectothermic in nature (Neven, 2000; Sgolastra *et al.*, 2011), and is known to exhibit a thermophilic tendency (Gerling *et al.*, 1986). This implies that *B. tabaci* SSA1 will reproduce rapidly and thrive as temperatures increase, thus enhancing their abundance (Menendez *et al.*, 2007; Shrestha, 2019; Pathania *et al.*, 2020), due to reduced thermal constraints under global warming situations (Deutsch *et al.*, 2008).

The longer development period at observed at the low temperature in this study (Table 4.1) might be as a result of slower metabolic processes due to reduced enzyme activity and high energy consumption for physiological repair of injuries resulting from extended cold conditions (Ikemoto, 2005; Benkova and Volf, 2007; Lalouette *et al.*, 2011; Damos and Savopoulou-soultani, 2012). The findings in this study are consistent with earlier reports (Butler *et al.*, 1983; Bonato *et al.*, 2007; Couret *et al.*, 2014; Guz *et al.*, 2016; Cui *et al.*, 2018; Salimi *et al.*, 2018).

Table 4. 4: Life table parameters for *B. tabaci* SSA1 on three cassava genotypes at five constant temperatures

Genotype	Temperature (°C)	Parameters			
		Net reproductive rate (R_0)	Generation time in days (T)	Intrinsic rate of increase (r_m)	Finite rate of increase (λ)
Alado alado	16	1.8945	71.2027	0.0090	1.0090
	20	7.4934	33.8098	0.0596	1.0614
	24	17.6695	28.9972	0.0990	1.1041
	28	37.2391	25.2057	0.1435	1.1543
	32	48.6990	22.6390	0.1720	1.1870
NAROCASS 1	16	2.5949	68.9857	0.0138	1.0139
	20	7.1020	32.1628	0.0610	1.0628
	24	17.9569	29.2684	0.0987	1.1037
	28	40.9130	26.0386	0.1425	1.1532
	32	44.1370	21.9417	0.1726	1.1884
NASE 14	16	1.5416	69.2605	0.0062	1.0063
	20	6.7543	32.7889	0.0583	1.0600
	24	17.4408	30.3933	0.0941	1.0986
	28	37.4320	25.9945	0.1394	1.1495
	32	45.7560	21.4434	0.1783	1.1952

Table 4. 5: Sex ratio of *B. tabaci* SSA1 at different temperatures on cassava

Temperature (°C)	No. of females	No. of males	Sex ratio (%)
16	249	60	24.10
20	873	333	38.14
24	2164	681	31.47
28	4514	536	11.87
32	5187	450	8.68

Thus, warmer temperatures in the range of 28-32 °C will result in higher *B. tabaci* SSA1 populations. The lack of significant genotype and genotype by temperature interactions effects on development time indicates that the relative effect of temperature on development was similar across the three cassava genotypes used in this study. This result rules out the existence of antibiosis resistance to *B. tabaci* SSA1 in the three cassava genotypes used in this study, and is in agreement with the findings of Nava-Camberos *et al.* (2001).

The high R^2 values (>0.5) for the relationship between *B. tabaci* SSA1 development rate and temperature (Table 4.2) obtained in this study indicates a strong linear relationship between the two for the eggs, nymphs and the total life cycle. The highest *B. tabaci* SSA1 development rate at 32 °C means that the pest can quickly build-up its populations in our warm environments. The temperature of 32 °C that greatly favours *B. tabaci* SSA1 development is within the optimum temperature range reported by other authors (Drost *et al.*, 1998; Bonato *et al.*, 2007; Cumutte *et al.*, 2014).

Among the different *B. tabaci* SSA1 developmental stages, the egg, third and second instar stages had the longest development times, respectively. This finding is critical in the choice of management options (Sohani *et al.*, 2007), for example, deployment of nymph parasitoids *Encarsia sophia* and *Eretmocerus mundus* at 32 °C would be appropriate since they are known to prefer the 3rd (Binu *et al.*, 2003; Yang *et al.*, 2012) and 2nd (Urbaneja and Stansly, 2004) instar stages, respectively.

The high, but similar survival on all genotypes at 32 °C may indicate that *B. tabaci* SSA1 is adapted to high temperatures, a result in agreement with that of Bonato *et al.* (2007) who observed high survival rates at temperatures of 21 °C to 30 °C. Furthermore, although high temperatures are known to cause desiccation in insects, the high RH range used in this study (a norm for East Africa) offset the desiccation effects of the high temperatures (Kreppel *et al.*, 2016), and thus enhanced survival as temperature increased. High temperatures are also improve food quality of host plants, particularly increased availability of soluble nitrogen in plant sap hence enhancing the survival of immature insect stages (White, 1984). Pest outbreaks also occur in stressed plants as a result of a weakened plant biochemical defense systems (Rhoades, 1985).

Fecundity increased with temperature, and the reverse was true for female longevity (Figure 4.2A). The highest fecundity observed at 32 °C was probably because high temperatures shorten pre-oviposition period and increase the speed of oviposition (Subba Rao and Gowda, 1961; Huang *et al.*, 2021), in addition increasing soluble nitrogen in plant sap which enhanced fecundity (White, 1984).

The observed reduction in generation time with increase in temperature (the shortest generation time was observed at 32 °C: Table 4.5) was expected because insects complete their development more quickly under favorable temperatures (Muturi *et al.*, 2012) being within the optimum range of 30-33 °C reported for *B. tabaci* development (Drost *et al.*, 1998). Similarly, net reproductive rate (R_0), finite rate of increase (λ) and intrinsic rate of increase (r_m) increased with temperature from 16 °C to 32 °C, with more generations of *B. tabaci* SSA1 occurring because of its multivoltine nature (Asiimwe *et al.*, 2007a; Karuppaiah and Sujayanad, 2012). Yamamura and Kiritani (1998), reported that a 2 °C temperature increase may result in up to five additional life cycles of an insect in a season. While r_m was positive at all study temperatures in this study, it was over 0.05 at temperatures between 20 °C and 32 °C, suggesting that *B. tabaci* SSA1 is more productive in this temperature range.

The female-biased sex ratio as temperature increased from 20 °C to 32 °C was evidence that at higher temperatures, higher proportions of fertilised eggs resulted into more female progeny. Similar results were reported by other researchers on *B. tabaci* (Gerling *et al.*, 1985; Enkegaard, 1993). It has also been previously reported that increase in temperature increased host plant quality (White, 1984), resulting into female biased sex ratios (Horowitz and Gerling, 1992).

The study elucidated the effects of different temperatures on the biological performance of *B. tabaci* SSA1, and 32 °C was best for *B. tabaci* SSA1 expressing strong levels of reproductive capacity and fitness. Thus, projected Climate Change scenario (Marinho *et al.*, 2016; Skendžic *et al.*, 2021) of higher temperature will advance the overall biological fitness of *B. tabaci* SSA1. This will allow for its continued geographical range expansion and increased crop production losses and prevalence of *B. tabaci* SSA1 vectored diseases in parts of the world with average temperature of 32 °C and RH range of 65-75%. In Uganda, agro-ecologies such as the North-Eastern Savanna grassland (hot and dry environment) and Kabale-Rukungiri highlands (cold and wet environment) (Sserumaga *et al.*, 2013), that were previously unfavourable for *B. tabaci* existence are also likely to witness increased populations of this pest.

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CHAPTER FIVE

MORTALITY FACTORS ACTING ON FIELD POPULATIONS OF *Bemisia tabaci* (Hemiptera: Aleyrodidae) SSA1 ON CASSAVA IN UGANDA

5.1. INTRODUCTION

Several abiotic and biotic factors including predators, parasitoids, pathogens, and weather affect *Bemisia tabaci* populations within crop fields (Naranjo, 2001; Naranjo and Ellsworth, 2005). The timing and relative importance of these mortality factors are key determinants of the population dynamics (Naranjo and Ellsworth, 2005), especially for insects that cause economic damage to crops (Baskauf, 2003).

For the *B. tabaci* species complex, high populations have been reported throughout the cassava-growing regions of East and Central Africa over the past two decades (Colvin *et al.*, 2004; Legg *et al.*, 2014a; Ally *et al.*, 2019). The recent outbreaks of *B. tabaci* populations heightened its importance as a direct pest of cassava and also its role as a vector of the two damaging viral diseases of cassava: Cassava Mosaic Disease (CMD) and Cassava Brown Streak Disease (CBSD) (Legg *et al.*, 2014a; Maruthi *et al.*, 2017). As cassava is considered a staple crop in sub-Saharan Africa that is highly resilient to Climate Change (Nweke *et al.*, 2002; Jarvis *et al.*, 2012; Maruthi *et al.*, 2017), the threats posed by the pest undermine food security and livelihood benefits of cassava production.

Although many mortality factors are known to have impact on *B. tabaci* field populations Gerling *et al.*, 2001; Naranjo and Ellsworth, 2005, there is limited information on the rates of mortality associated with specific mortality factors, especially in light of the different *B. tabaci* species currently described. Age-specific life tables for insects under field conditions provide critical information for a given cohort of individuals and helps in identifying mortality factors responsible for population regulation (Choudhury *et al.*, 2013).

Life tables have previously been used to study population dynamics of *B. tabaci* on cassava in Uganda where Asiimwe *et al.* (2007a) determined that fourth instar parasitism and disappearance were the key nymphal and egg mortality factors for *B. tabaci*. CMD was the key production constraint for cassava in the country at that time in 2003, 18 years ago, when the study was done. With the recent CBSD epidemic, most of the CMD resistant cassava genotypes

have been replaced with CBSD tolerant genotypes (Alicai *et al.*, 2007; Kawuki *et al.*, 2016), that unfortunately support very high populations of *B. tabaci* (Otim *et al.*, 2006; Omongo *et al.*, 2012). Also, the *B. tabaci* species complex affecting cassava in Uganda was unknown at the time of the study reported in 2007.

Currently, cassava in Uganda is largely infested by *B. tabaci* Sub-Saharan Africa 1 (SSA1) species (Mugerwa *et al.*, 2012; Legg *et al.*, 2014a; Kalyebi *et al.*, 2018; Ally *et al.*, 2019). This study therefore sought to develop comprehensive life tables for *B. tabaci* SSA1 on cassava, and to estimate the impact of specific mortality factors affecting each life growth stage of *B. tabaci* SSA1 on cassava in the country.

5.2. MATERIALS AND METHODS

5.2.1. Study Site, Cassava Genotypes Used and Experimental Layout

This study was established at NaCRRI in Wakiso district (0.518991°N, 32.636165°E), Uganda in March 2016 and March 2017 using the cassava genotypes NAROCASS 1 and Alado alado. NAROCASS 1 is an improved genotype that is susceptible to *B. tabaci* infestation, whereas Alado Alado is a local genotype that is tolerant to *B. tabaci* infestation. The experiment was laid out in a randomized complete block design with three replicates. The plots measured 9 m by 9 m with plants spaced at 1 m by 1 m and two-meter alleys were left between blocks. Weeds were removed manually by hoeing monthly for the first five months.

5.2.2. Cohort Establishment

In this study, a semi-controlled field experiment was used to standardize the number of eggs and nymphs observed in each cohort to more accurately contrast the effect on *B. tabaci* mortality of two cassava genotypes. Monthly egg and nymph cohorts were established on 10 randomly selected plants per plot on separate days. The cohorts, selected from naturally occurring populations, were established on different plants between 08:00 and 11:00 h. Five cohorts were established in the period of 3–7 months after planting (MAP) in both 2016 (cohorts one to five) and 2017 (cohorts six to ten). Hence, mortality was observed on 10 cohorts in total on each cassava genotype.

5.2.2.1. Egg cohorts

Ten freshly laid eggs on the underside of the top-most expanded plant leaf were identified using a hand lens (x10 magnification) on each genotype per replicate plot (Plate 5.1). For each plot, 10 plants were selected, thus 100 eggs were marked per plot per cassava genotype, and 300 eggs for each cassava genotype per cohort. All other eggs on the leaf were removed by gently brushing them off the leaf using the edge of soft tissue paper. Individual egg positions on the leaf were marked by drawing a small circle around each egg using a non-toxic pen (Asiimwe *et al.*, 2007a). A red tag was then tied around the petiole of the leaf bearing the marked eggs so they could be easily found again.

5.2.2.2. Nymph cohorts

In each plot, 10 plants were selected and, on each plant, 30 first-instar nymphs were identified and marked on a single leaf (Plate 5.1). Thus, a total of 300 nymphs per plot per cassava genotype were marked, with each nymph cohort consisting of 900 nymphs per cassava genotype. The nymphs were marked using the same procedure described for eggs and green tag was used to mark the leaves having the marked nymphs (Plate 5.1). Marked nymphs were checked after one hour to ascertain that they had settled, and any nymph that had crawled out of the circle was replaced by marking another one.

5.2.3. Determination of Mortality Factors and Recording of Egg Eclosion and Nymph Development

Each marked egg was observed daily using a 10× hand lens for 15 days, which is more than the 11-day egg hatching period of *B. tabaci* eggs on cassava (Legg, 1995). Marked nymphs were observed for 30 days, a period sufficient for both *B. tabaci* and parasitoid adult emergence (Asiimwe *et al.*, 2007a). Each day, the stage and state of each egg and nymph were recorded and categorized as healthy or dead. Death was then characterized as disappearance, predation, parasitism, inviability, and unknown death (Table 5.1; Naranjo and Ellsworth, 2005, 2017; Asiimwe *et al.*, 2007a; Banjo, 2010). Mortality in the crawler stage was not considered in this study because separate cohorts of eggs and nymphs were established. Furthermore, Naranjo (2007) and Karut and Naranjo (2009) indicated that *B. tabaci* crawler mortality on cotton was negligible.

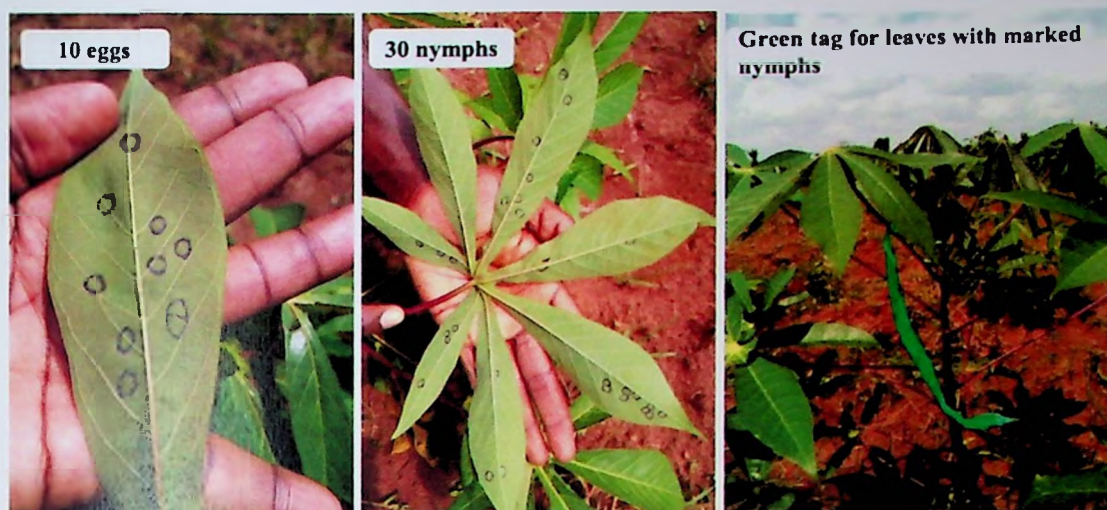


Plate 5.1: Marking of eggs and nymphs during monthly cohort establishment.

Table 5.1: Classification and description of mortality components* acting on *B. tabaci* SSA 1 egg and nymph populations on cassava in the field

Cause of death	Description
Disappearance	Egg or nymph goes missing due to total removal by a chewing predator, or dislodgement from the leaf due to wind or rain.
Predation	Sucking predators evacuate the contents of the prey and leave behind an empty egg chorion or nymph cuticle.
Parasitism**	The paired yellowish mycetomes are displaced by the developing parasitoid larva, and in the case of parasitism by <i>Encarsia sophia</i> , the nymph turns black.
Inviability	Eggs fail to hatch by the fourteenth day and are dark tan in colour.
Unknown death	A death that is attributed to any cause excluding those described above. There is evidence of the carcass on the leaf (i.e., the individual has not disappeared).

* Mortality components are herein also referred to as "cause of death". ** Although parasitoids attack all nymph stages of *B. tabaci* (Foltyn and Gerling, 1985; Liu and Stansly, 1996), *E. sophia* and *E. mundus* prefer to parasitise the third (Binu *et al.*, 2003; Yang *et al.*, 2012) and second (Urbaneja and Stansly, 2004) *B. tabaci* nymph stages. Visible signs of parasitism are detected in the third and fourth nymph stages (Karut and Naranjo, 2009).

5.2.4. Recording of environmental parameters

Air temperature and relative humidity (RH) were recorded using a data logger placed at the trial site. Sunshine hours, wind speed, and rainfall data were accessed from the weather station at NaCRRRI. The daily readings recorded at 15:00 h for rainfall, air temperature, RH, sunshine hours, and wind speed were used to calculate total monthly rainfall, and average monthly air temperature, RH, sunshine hours, and wind speed values. In handling the data, a month was from the date of cohort establishment to the date the last nymph died or emerged into an adult, and the date the last egg hatched into first-instar nymph or 15th day after cohort establishment.

5.2.5. Data Analysis

5.2.5.1. Multiple decrement life table

The raw data obtained were summarised to generate a table showing the total number of insects at the beginning of each stage (N_x) and the number of deaths from all causes (D_x) at a given stage of growth (Appendix 12.1). Deaths from the different causes was denoted as D_{ix} . This information was then used to estimate the probability of death from all causes (aq_x) (Appendix 12.2) at a given stage of growth (Carey, 1989). The aq_x values were then used to compute the survival (al_x) (Appendix 12.3) of the immature *B. tabaci* populations subjected to all causes of death in a given stage and to construct the multiple decrement life table following the methods of Carey (1989).

5.2.5.2. Determination of mortality rates

Age-specific marginal mortality rates (MMR) for each factor were estimated based on apparent (observed) mortality rates (AMR) (Buonaccorsi and Elkinton, 1990; Naranjo and Ellsworth, 2005). Marginal mortality rate estimates the level of death arising from a single factor assuming that it was the only one operating at the time (Naranjo and Ellsworth, 2005). However, a mortality factor may be masked by another factor since they operate concurrently with no clear order of events (Naranjo and Ellsworth, 2005; Asiimwe *et al.*, 2007a). Disappearance is the only factor for which the AMR is equal to the MMR because it cannot be concealed by any other factor (Naranjo and Ellsworth, 2005; Asiimwe *et al.*, 2007a).

The general equation for determining MMR was derived from Naranjo and Ellsworth (2005) as below:

$$M_{Ax} = \frac{d_{Ax}}{1 - d_{Bx}}$$

Where: M_{Ax} is the MMR due to factor A in stage x,

d_{Ax} is the AMR due to factor A in stage x, and

d_{Bx} is the sum of apparent mortalities from all other relevant contemporaneous factors.

MMR were calculated separately for each development stage and for each mortality factor. Due to the concurrent nature of mortality from other factors that act on the immature stages of *B. tabaci*, the AMRs needed to estimate MMR for each mortality factor with each growth stage is given in Table 5.2 (Naranjo and Ellsworth, 2005; Asiimwe *et al.*, 2007a).

Table 5.2: Matrix for determining marginal mortality rates for populations of *Bemisia tabaci* SSA1 from apparent rates of relevant competing contemporaneous factors

Marginal mortality rate of interest (M_A)	Apparent mortality rate (d_A)	Other apparent mortality rate (d_B)	Growth stage
Inviability	Inviability	Predation + Disappearance	Egg
Predation	Predation	Disappearance	Egg and all nymph stages
Disappearance	Disappearance	No competing factor	Egg and all nymph stages
Parasitism	Parasitism	Predation + Disappearance	Third and fourth instar nymphs
Unknown death	Unknown death	Predation + Disappearance	All nymph stages

5.2.5.3. *Estimation of irreplaceable mortality (I_C)*

Irreplaceable mortality (I_C) is that portion of total cohort mortality that would not occur if a given mortality factor was eliminated (Carey, 1989; Naranjo and Ellsworth, 2005). Irreplaceable mortality was calculated for each mortality factor within each *B. tabaci* growth stage using the equation below (Carey, 1989; Naranjo and Ellsworth, 2005):

$$I_C = (1 - \prod_{i=1}^j [1 - M_i]) - (1 - \prod_{i=1}^{j-1} [1 - M_i])$$

Where: M_i is the marginal mortality rate for factor i , and

j is the total number of all mortality factors acting in a given stage.

The first product includes all mortality factors, while the second product includes all mortality factors except the factor of interest.

5.2.5.4. *Analysis of variance*

All data on MMR, I_C , and k -values were tested for normality, and where skewness occurred, data were subjected to the Box-Cox procedure (Venables and Ripley, 2002) to determine the most appropriate transformation based on the lambda value. Data for eggs and nymphs were then subjected to a nested model ANOVA (Bates *et al.*, 2015) to check the strength of the variability due to cassava genotype, cause of death and stage of growth on marginal mortality rate, irreplaceable mortality and mean levels of death (k value). Cause of death and stage of growth were nested within genotype. Data on eggs, early nymphs (first and second instar stages), and late nymphs (third and fourth instar) were separated because different mortality factors acted in the different stages.

5.2.4.5. *Key-factor analysis*

The graphical method of Varley and Gradwell (1960) which compares patterns of total mortality ($K = \sum k$) for the cohort to that of individual k -values [$k = -\ln(1 - M)$] for each mortality factor was used to determine the relative contribution of individual causes of death to total mortality. The factor whose graph most closely resembles that of total mortality is the key factor (Naranjo and Ellsworth, 2017). To further quantify the key factors, individual k -values were regressed against total mortality (K), and the factor whose individual k -values had the largest slope was denoted as the key factor (Podoler and Rogers, 1975).

5.2.5.6. *Relationship between environmental parameters and the different mortality factors*

From the data obtained, correlation analysis was performed to determine the strength and the direction of the relationship between weather parameters with *B. tabaci* egg and nymph mortality rates (Revelle, 2017). Correlation analysis was performed for the relationship between average monthly air temperature, relative humidity (RH), sunshine hours and wind speed, and total monthly rainfall with monthly mean levels of mortality (k values) of the different mortality factors per cohort (cohorts 1 to 5; 2016 and 6 to 10; 2017).

5.3. RESULTS

5.3.1. Sources and Levels of Mortality

From the ANOVA result, the variation in MMR, I_c and k -value was due to cause of death nested within genotype (Table 5.3). There was considerable variation in MMRs for each cause of death when pooled over-all immature stages; with the highest median rates of death associated with disappearance on both cassava genotypes in all cohorts. The median MMR was 0.355 on Alado alado (Figure 5.1A). Parasitism caused the second highest MMR of 0.084 on NAROCASS 1 and 0.058 on Alado alado (Figure 5.1A). When pooled over-all mortality factors, sizeable variation in MMR was also observed in each development stage; with the highest median rate of mortality associated with the third instar stage for both genotypes being 0.092 on Alado alado and 0.073 on NAROCASS 1 (Figure 5.1B). Highest cohort mortality was observed in the 8th and 10th cohorts in the egg stage. Median MMR was 0.2 on NAROCASS 1 and 0.25 on Alado alado (Figure 5.1C).

For all development stages on both cassava genotypes, highest mortality was associated with disappearance followed by parasitism in the third and fourth nymph stages (Figure 5.2A). Similarly, when all growth stages were pooled, disappearance was associated with the highest levels of death across all the 10 cohorts on both cassava genotypes (Figure 5.2B). Across all 10 cohorts on both genotypes, the third instar stage had consistently high levels of death compared with the fourth instar stage where mortality was highest from cohort one (1) to six (6), and minimum from cohort seven (7) to 10 (Figure 5.2C). At all growth stages, disappearance had the highest irreplaceable mortality followed by parasitism in the 3rd instar stage on both cassava genotypes (Figure 5.3).

Table 5.3: Variance associated with genotype, cause of death, and stage of growth on mortality of immature stages of *B. tabaci* SSA1 on cassava in Uganda

Group	Early nymphal stages			Late nymphal stages			Egg stage		
	MMR	Ic	k-value	MMR	Ic	k-value	MMR	Ic	k-value
Genotype	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Cause of death: Genotype	0.0179	0.0168	0.0277	0.0453	0.0401	0.0994	0.0453	0.0401	0.0994
Growth stage: Genotype	0.0004	0.0001	0.0006	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Residual	0.0046	0.0037	0.0090	0.0135	0.0085	0.0484	0.0135	0.0085	0.0484

5.3.2. Relationship and Dynamics of *B. tabaci* SSA1 Adult and Nymph Occurrence with Environmental Factors

In both 2016 and 2017, effects of the different weather parameters on the various mortality factors were inconsistent. For example, the effect of rainfall on nymph disappearance in 2016 was positive ($r = 0.65$) while a negative relationship ($r = -0.56$) was observed in 2017 (Table 5.4). For nymph populations, strong positive and negative relationships between average monthly air temperature, RH, and total rainfall, and all nymph mortality factors in 2016 ($r = -0.87, 0.75, 0.51$) for disappearance, parasitism and predation, respectively (Table 5.4). Sunshine hours had strong effects on predation ($r = 0.54$) and unknown death ($r = 0.77$) (Table 5.4). In 2017, RH had strong effects on parasitism ($r = 0.69$) and unknown death ($r = -0.77$), while rainfall affected disappearance ($r = -0.56$) and predation ($r = 0.75$). For eggs, a strong negative effect of air temperature on disappearance ($r = -0.64$) and a positive effect of sunshine hours on predation ($r = 0.59$) were observed in 2016. In 2017, only sunshine hours and wind speed had strong positive effects on disappearance and predation (Table 5.4).

5.3.3. Key Factor Analysis

Comparison of individual k-values of the different mortality factors to total mortality showed that the curve for disappearance was most similar to that of total mortality, and disappearance resulted in the largest regression slope for both eggs and nymphs on both cassava genotypes in both years (Figures 5.4 and 5.5).

5.4. DISCUSSION

This study identified and quantified the impacts of different mortality factors acting on immature populations of *B. tabaci* SSA1 species on cassava in a semi-controlled field experiment. A three-pronged investigative approach (marginal mortality, irreplaceable and key factor analysis) was used to understand and assess the relative importance of each mortality factor. The cohort-based system, coupled with the daily observations of each individual in the cohort provided comprehensive data on the rates of mortality affecting this pest.

Based on marginal mortality rates and the life table results, disappearance followed by third and fourth instar parasitism were the largest components of overall *B. tabaci* SSA1 species mortality, followed by unknown factors (nymphs only), inviability (eggs only), and predation. The results show that disappearance was the most important factor driving both egg and nymph mortality. Disappearance can be attributed to abiotic factors like wind and rain, and also predators that remove the entire individual from the leaf, like ants and spiders. Parasitism in the third instar was the second factor driving nymph mortality. The high levels of parasitism were attributed to the high numbers of Aphelinidae parasitoids (*Eretmocerus mundus* Mercet and *Encarsia sophia* Girault and Dodd).

The high irreplaceable mortality from disappearance, coupled with its high regression coefficient from key factor analysis points to its importance in reducing both egg and nymph populations of *B. tabaci* SSA1. This is in agreement with the findings of Horowitz (1984), who reported disappearance as the key mortality factor in *B. tabaci* on cotton. However, these results are only in partial agreement with findings of Asimwe *et al.* (2007a) who reported that disappearance was the key factor driving *B. tabaci* egg mortality on cassava whereas parasitism in the fourth instar was the key factor driving nymph mortality. In contrast, key factor analysis revealed that disappearance followed by third instar parasitism were the key mortality factors in this study.

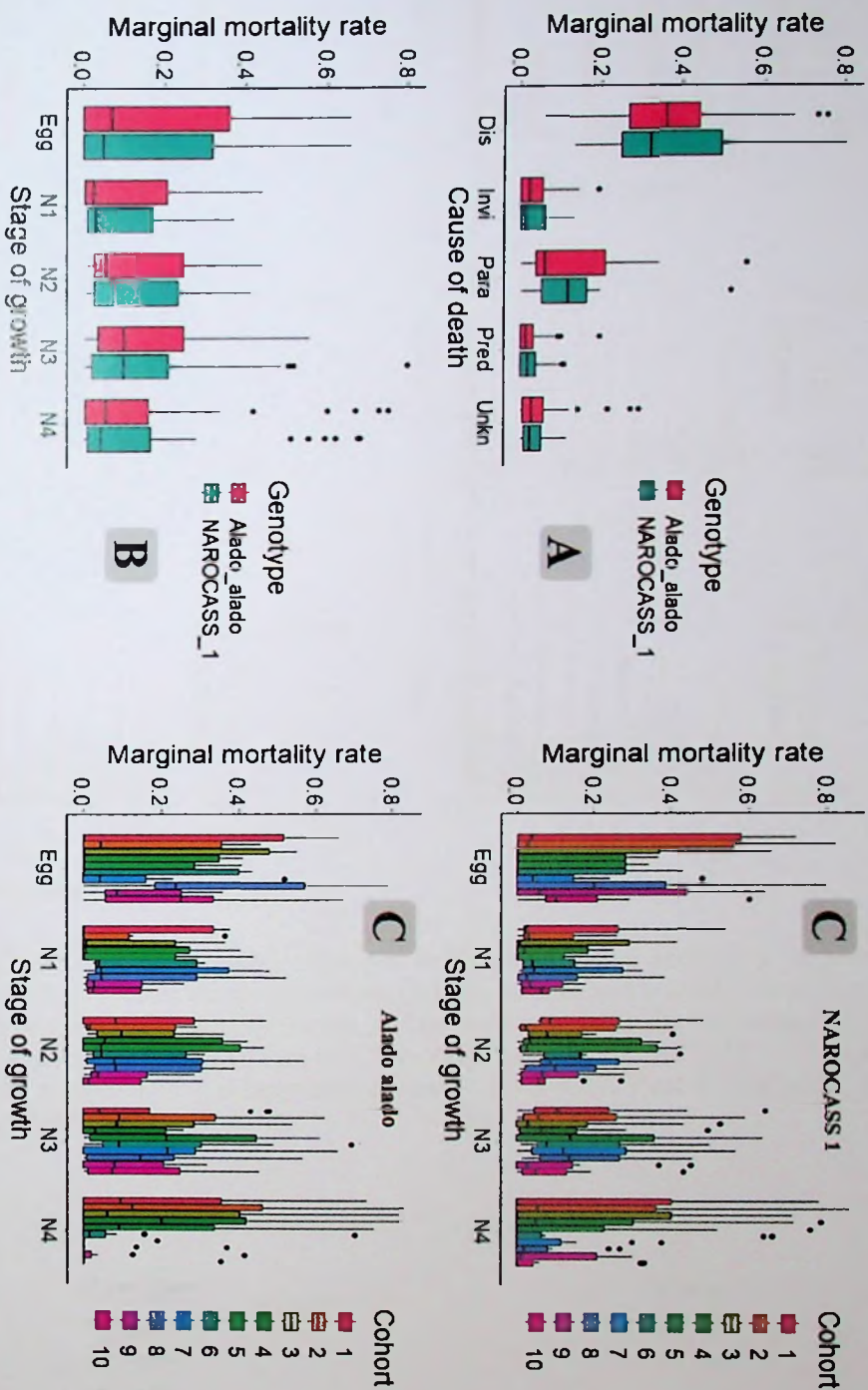


Figure 5.1: Box plots of marginal mortality rates (MMR) for *Bemisia tabaci* SSA1 on two cassava genotypes by cause of death pooled over-all immature growth stages (A) and during each growth stage pooled over-all causes of death (B) for 10 cohorts and during each growth stage pooled over-all causes of death (C) in 10 cohorts on two cassava genotypes. N1 – 1st, N2 – 2nd, N3 – 3rd, N4 – 4th instar nymph; Dis – disappearance, Invi – inviability, Pred – predation, Para – parasitism and Unkn – unknown death.

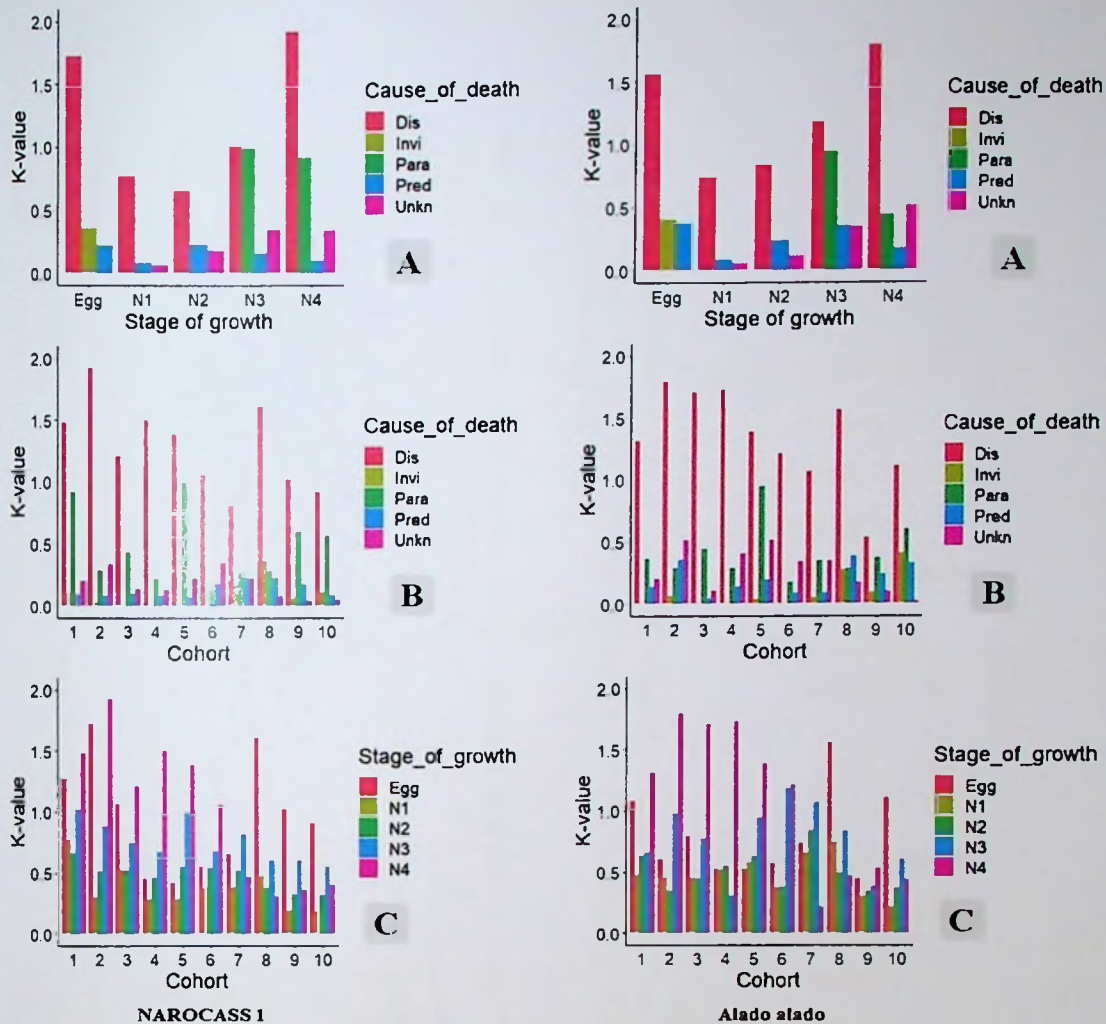


Figure 5.2: Mean levels of mortality expressed as K values within each stage of growth of *Bemisia tabaci* SSA1 species across all cohorts (A), for each cohort pooled over-all stages of growth (B) for the different mortality factors, and for each cohort for the five stages of growth pooled over-all mortality factors (C) on two cassava genotypes. N1 – 1st, N2 – 2nd, N3 – 3rd, N4 – 4th instar nymph; Dis – disappearance, Invi – inviability, Pred – predation, Para – parasitism and Unkn – unknown death.

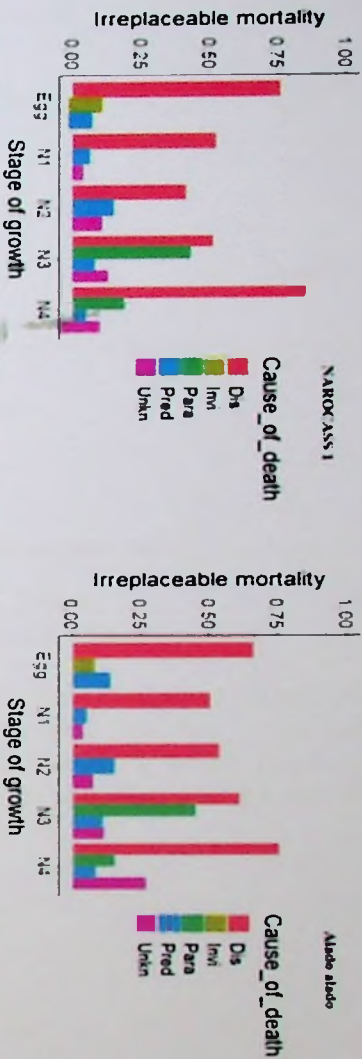


Figure 5.3: Irreplaceable mortality within each stage of growth of *Benisia tabaci* SSA1 for the different mortality factors on two cassava genotypes across all cohorts. N1 – 1st, N2 – 2nd, N3 – 3rd, N4 – 4th instar nymph; Dis – disappearance, Invi – inviability, Pred – predation, Para – parasitism and Unkn – unknown death.

Table 5.4: Correlation coefficients (r) of mean levels of immature *B. tabaci* SSA1 mortality for each mortality factor with different weather parameters in Wakiso across 10 cohorts on cassava in 2016 and 2017

Weather parameter	2016					2017				
	Air temperature	RH	Rainfall	Sunshine hours	Wind speed	Air temperature	RH	Rainfall	Sunshine hours	Wind speed
EGGS										
Disappearance	-0.64	0.48	0.37	0.45	-0.10	0.46	-0.23	-0.25	0.56	0.99
Inviability	-0.46	0.29	0.02	0.33	-0.06	0.01	0.46	-0.05	0.45	0.48
Predation	-0.16	0.00	-0.53	0.59	0.29	0.17	0.22	0.45	0.92	0.72
NYMPHS										
Disappearance	-0.87	0.92	0.65	-0.37	0.30	0.06	-0.40	-0.56	-0.14	-0.33
Parasitism	0.75	-0.83	-0.65	0.37	-0.39	-0.40	0.69	0.36	0.24	0.40
Predation	0.51	-0.62	-0.49	0.54	-0.11	0.33	-0.35	0.75	0.36	0.15
Unknown death	0.77	-0.74	-0.51	0.77	0.70	0.50	-0.77	-0.36	-0.21	-0.67

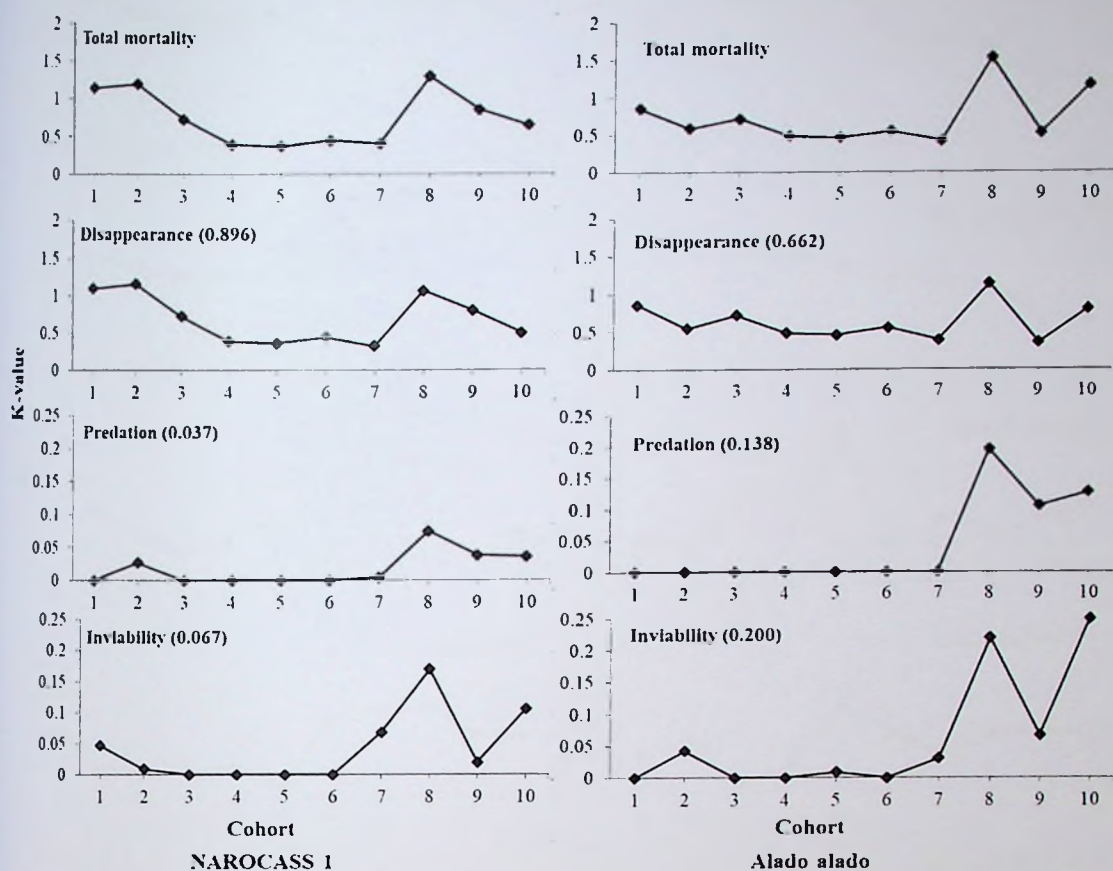


Figure 5.4: Key factor analysis for *Bemisia tabaci* SSA1 species egg populations on two cassava genotypes over 10 cohorts in the field. The pattern displayed by total mortality is compared to those of specific causes of death (summed over growth stages). The factor whose graph closely resembles that of total mortality and has the highest slope value (in parenthesis) is the key factor.

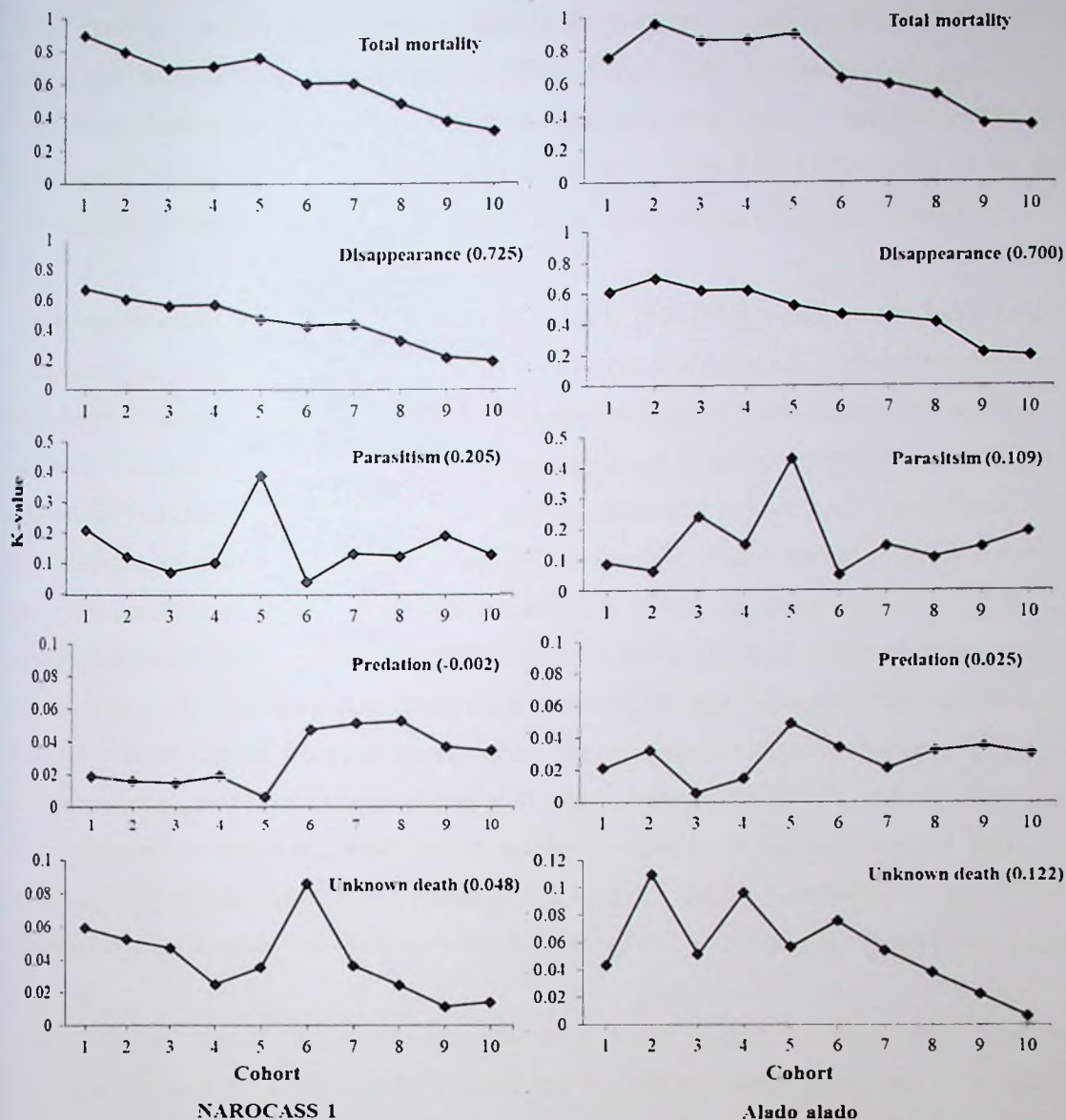


Figure 5.5: Key factor analysis for *Bemisia tabaci* SSA1 species nymph populations on two cassava genotypes over 10 cohorts in the field. The factor whose graph closely resembles that of total mortality and has the highest slope value (in parenthesis) is the key factor.

The subtle differences between the findings from this study and those of Asiimwe *et al.* (2007a) was probably due to differences in the cassava genotypes used in each study, as NASE 4 was used by Asiimwe *et al.* (2007a). Furthermore, the identity of whiteflies colonizing cassava during the 2003 study was not clear, yet it may have been responsible for the observed variations in the key

mortality factors reported. Until recently, species diversity among the members of *B. tabaci* was vague due to inconsistent global phylogenies (Boykin *et al.*, 2007; De Barro *et al.*, 2011). This led to the generic description of *B. tabaci* as a single species with no concern for the specific species that colonized cassava at that time. Currently, however, *B. tabaci* SSA1 is known as the species most commonly colonizing cassava in Uganda (Legg *et al.*, 2014a; Ally *et al.*, 2019)

The average monthly air temperature (26–31.5 °C), RH (50–75%), wind speed (3–5.5 km/h) and total monthly rainfall (3–140 mm) recorded in the two years of this study were within the optimum range for *B. tabaci* reproduction and growth. The narrow range of these parameters could not give conclusive evidence of the impact of weather parameters on *B. tabaci* mortality factors. However, it is possible that rainfall may have indirectly influenced disappearance through its effects on host-plant quality (Guz *et al.*, 2016). For example, where drought conditions are experienced, cassava may grow poorly into short plants with small leaves which increased exposure of *B. tabaci* individuals to death from wind and rainfall (Chapter Three). The high levels of disappearance in both years probably highlighted the importance of predators; ants and spiders that were frequently observed in the trial plots. Positive impacts of air temperature on mortality due to natural enemies is probably because of their enhanced ability to suppress pest populations under the temperature ranges observed (Huang *et al.*, 2008). Under warmer temperatures, higher parasitoid reproductive success (Zilahi-balogh *et al.*, 2009; Romo and Tylianakis, 2013; Kambrekar *et al.*, 2015) and greater survival of coccinellids (Simmons and Legaspi, 2004; Yao *et al.*, 2019) have been reported.

Although higher mortality rates were anticipated for Alado alado, a genotype that supports low field populations of *B. tabaci* adults as observed in Chapter Three, there were no significant differences in mortality of *B. tabaci* SSA1 between Alado alado and NAROCASS 1. In this study, a semi-controlled field experiment was used and therefore the numbers of eggs and nymphs entering the data set on each cassava genotype (which is impossible in uncontrolled field surveys and studies) were standard. These findings therefore suggest that genotype differences may only affect *B. tabaci* adult populations (as reported in Chapter Three and by; Omongo *et al.*, 2012), with little impact on mortality of immature *B. tabaci* SSA1 stages, at least for the two cassava genotypes used as reported on cotton by Karut and Naranjo (2009). These results suggest the presence of antixenosis resistance mechanism in Alado alado.

Previous studies also reported high levels of antixenosis resistance to *B. tabaci* in soybean and to *Amrasca devastans* (Distant) on cotton due to low trichome density (Murugesan and Kavitha, 2010; da Silva *et al.*, 2012), and *A. devastans* due to high plant height (Murugesan and Kavitha, 2010). Legg (1995) reported higher numbers of *B. tabaci* parasitoids in improved cassava genotypes as opposed to low numbers on local genotypes. However, parasitism rates between different cassava genotypes were similar in uncontrolled field surveys (Macfadyen *et al.*, 2020).

From this study, it was evident that greater use of cassava genotypes that are less attractive to adult *B. tabaci* SSA1 such as Alado alado (as shown in Chapter Three), will reduce the number of eggs oviposited by the pest in fields planted with such genotypes, and thus assist mortality agents in reducing *B. tabaci* SSA1 abundance at the field-level. For landscape-scale *B. tabaci* population reductions, however, cassava genotypes that increase mortality of immature *B. tabaci* stages (antibiosis resistance mechanisms) are urgently needed for East Africa. Such a cassava genotype could be in the mold of the South American genotype MEcu 72 on which *B. tabaci* nymphal mortality of 73% have been recorded (Bellotti and Arias, 2001).

This study has also shown that disappearance is the key mortality factor acting on all immature stages of *B. tabaci* SSA1 on cassava, followed by third instar parasitism, although for the two cassava genotypes used, there was no increase in mortality of immature stages on Alado alado (the reportedly more tolerant genotype). This means that Alado alado does not have antibiotic resistance mechanisms in addition to being susceptible to CBSD and CMD. Given the potential importance of parasitism in enhancing mortality of *B. tabaci*, it became necessary to undertake a study of the influence of *B. tabaci* density on parasitism by the parasitoids, *E. mundus* and *E. sophia* on cassava.

An extract from this Chapter has been published in:

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CHAPTER SIX

EFFECT OF *Bemisia tabaci* SSA1 HOST DENSITY AND CASSAVA GENOTYPE ON HOST FEEDING CAPACITY AND PARASITISM BY TWO HYMENOPTERA PARASITOID SPECIES

6.1. INTRODUCTION

Various control methods such as the use of biological control agents are being explored to control *B. tabaci* (Horowitz *et al.*, 2011; Sani *et al.*, 2020). Biological control is sustainable, eco-friendly, and cost-effective (Herren and Neuenschwander, 1991; Gerling, 1996; Neuenschwander, 2004; Al-zyoud *et al.*, 2007; Sohani *et al.*, 2008; Arnó *et al.*, 2010) and has high potential for use in subsistence farming in developing countries (Legg *et al.*, 2014b; Guastella *et al.*, 2015). Numerous species of natural enemies attack *B. tabaci* (Gerling *et al.*, 2001; Torres *et al.*, 2014), with parasitoids as key agents since they parasitise and feed on *B. tabaci* nymphs (Al-zyoud *et al.*, 2007) in different cropping systems (Asiimwe *et al.*, 2007a; Karut and Naranjo, 2009). Hymenoptera parasitoids in the genera *Encarsia* and *Eretmocerus* (Horowitz *et al.*, 2011) have been linked to successful biological control of the whitefly, *B. tabaci* (Arnó *et al.*, 2010; Guastella *et al.*, 2015).

Mortality of a pest population by the natural enemies is determined by their responses to host densities (Rosenheim and Rosen, 1992; Sohani *et al.*, 2008). *Eretmocerus mundus*, *Eretmocerus warrae*, *Encarsia sophia* and the predator, *Serangium percesetosum* have been reported to exhibit positive killing responses with increase in *B. tabaci* host densities (Arnó *et al.*, 2010; Hanan *et al.*, 2012; Al-zyoud, 2012). However, despite the significant occurrence of *E. sophia* and *E. mundus* in cassava fields in Uganda (Otim *et al.*, 2005; Asiimwe *et al.*, 2007a), their efficacies in the management of *B. tabaci* SSA1 populations are currently not known. There are also cassava genotypes that have been developed to control CBSD and CMD pandemics (Kawuki *et al.*, 2016) that are reported to support high *B. tabaci* (SSA1) populations (Omongo *et al.*, 2012). However, how the cassava genotypes influence parasitoid species efficiency has not been assessed.

The objective of this study therefore was to assess the killing capacity (parasitism and host feeding ability) of two *B. tabaci* SSA1 parasitoids *E. mundus* and *E. sophia* at varying *B. tabaci* SSA1

densities on different cassava genotypes in the screenhouse. This knowledge will help guide deployment of biological control agents in integrated pest management systems for *B. tabaci* SSA1 which in the long run will help to minimize pesticide use.

6.2. MATERIALS AND METHODS

6.2.1. Plant Materials

The cassava genotypes NAROCASS 1, NASE 14 and Alado alado were used in this study. As observed in Chapter Three, NAROCASS 1 and NASE 14 are improved genotypes that support high *B. tabaci* SSA1 populations, whereas Alado alado is a local genotype that supports low *B. tabaci* SSA1 populations. The three genotypes were grown in the screenhouse as described in Chapter Four.

6.2.2. *Bemisia tabaci* SSA1 Pure Colony

Pure colonies of *B. tabaci* SSA1 species were raised from a single adult mating pair that was clipped on the first fully expanded leaf on cassava genotype NAROCASS 1 at NaCRRI as described in Chapter Four. The clip cage was moved to a new leaf on the same plant every 48 h until the female died. Just before adult emergence of the first generation of pure colonies, fresh cassava plants were placed in the cages for their oviposition. On emergence, some of the new adult pairs were collected by aspiration using a pooter and released into other cages containing fresh cassava plants to multiply. The colonies were maintained under natural fluctuating conditions (temperature of 16-32.5°C; relative humidity of 38-100% and; a photoperiod of 12:12 (L:D).

6.2.3. Parasitoid Culture

The *E. mundus* and *E. sophia* parasitoids used in this study were raised from parasitized fourth instar *B. tabaci* SSA1 nymphs picked from a cassava field at NaCRRI as described by Otim *et al.* (2005; 2008). Leaf portions having parasitized nymphs were placed for 24 h in emergence bottles (Plate 6.1) that had two streaks of 20% honey solution on the walls.

6.2.4. Experimental Setup

To generate the required population of nymphs for the experiment, 30 pairs of 24 h old *B. tabaci* SSA1 adults were collected using a pooter and were separately confined on the underside of the 1st and 2nd fully expanded cassava leaves of each genotype for 24 h (on two separate days) to ensure host stage uniformity (Plate 6.2A).

For each genotype, 20 plants were infested and the leaves were treated as replicates; i.e., two leaves per plant. The adults were removed and the eggs were monitored daily until they developed to the desired parasitisation stage of the second instar nymphs for *E. mundus* and third instar nymphs for *E. sophia* (Binu *et al.*, 2003; Urbaneja and Stansly, 2004; Yang *et al.*, 2012). Five *B. tabaci* SSA1 nymph host densities; 10, 40, 60, 100 and 140 nymphs were left on each leaf in the area covered by the clip cage (Plate 6.2B). A 24 h old mating pair of *E. mundus* identified according to Urbaneja and Stansly (2004) or one female *E. sophia* were then introduced into each clip cage (5.5 cm in diameter and 3 cm in length with nylon cloth at the base) on the cassava leaves with varying *B. tabaci* SSA1 densities (Plate 6.2C). The parasitoids were then kept for 48 h and allowed to oviposit and feed, after which they were removed.

The number of *B. tabaci* SSA1 that were killed by parasitizing or host-feeding were checked eight days after parasitoid removal (Urbaneja and Stansly, 2004; Urbaneja *et al.*, 2007). Parasitized nymphs were recognized by existence of displaced mycetomes (Otiin *et al.*, 2008; Urbaneja and Stansly, 2004). Nymphs that were fed on were flat, desiccated and their colour was faded (Zang and Liu, 2008). The hosts that died due to natural death were identified using the procedure of Yang *et al.* (2012) and were excluded from the count. The experiment was set in four replicates using a randomized complete block design with split plot arrangement (with host densities nested into genotype for each parasitoid species) and was repeated three times.



Plate 6.1: Emergence bottles used for rearing out adult parasitoids

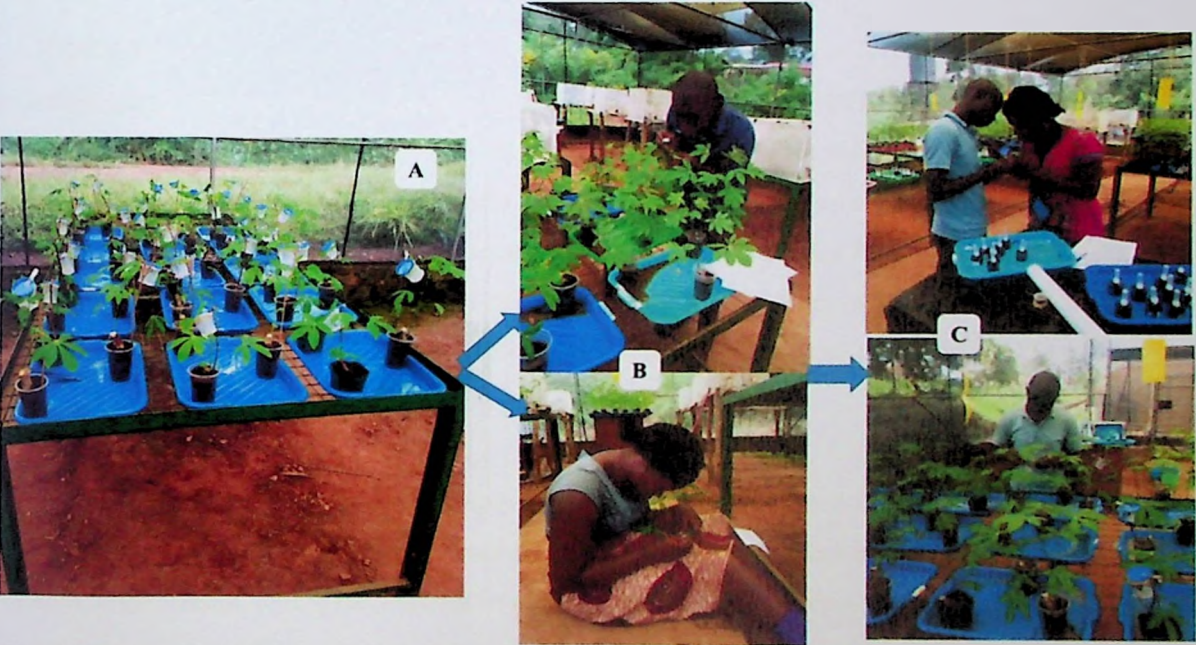


Plate 6.2: *B. tabaci* host plant infestation (A), nymph density selection (B) and parasitoid identification and confinement on *B. tabaci* nymphs (C).

6.2.3. Data Analysis

All data were analyzed using R statistical software (R Core Team, 2017). All data were tested for normality, and where skewness occurred were subjected to the Box Cox procedure (Venables and Ripley, 2002) in order to determine the most appropriate transformation based on the lambda value. Data were then subjected to fixed model ANOVA (Kuznetsova *et al.*, 2016) for host density, parasitoid species and genotype effects on parasitism, host feeding and total mortality (parasitism and host feeding). Means were separated using the Least Significant Difference (LSD) test at 5% probability level (Felipe de Mendiburu, 2017).

The strength of the effects of host density on host feeding and parasitism was determined using simple linear regression. Apparent parasitism and host feeding rates were expressed separately as the proportion of parasitized or fed on nymphs to the total nymphs (both parasitized and unparasitized *B. tabaci* nymphs combined) (Ruiz-narváez and Castro-webb, 2003).

6.3. RESULTS

Host feeding, parasitism and total mortality differed significantly ($p < 0.001$) between parasitoid species and *B. tabaci* nymph density, and their interactions were significant (Appendix 13). Whereas cassava genotype did not significantly influence the three parameters assessed, there was significant interaction between parasitoid species and cassava genotypes for host-feeding ($p < 0.05$), parasitism ($p < 0.001$) and total mortality ($p < 0.01$) (Appendix 13). The three-way interaction effects for parasitism, host feeding and total mortality were not significant ($p > 0.05$) (Appendix 13).

6.3.1. Host Feeding

As host density increased, both parasitoid species killed more nymphs through feeding (Figure 6.1). The lowest and highest numbers of nymphs fed-on were observed at host densities of 10 and 140 nymphs, respectively, and mean number of nymphs fed-on by *E. sophia* was 3 and 16 nymphs at host densities of 10 and 140 nymphs, respectively (Figure 6.1A). At all host densities across all genotypes, *E. sophia* fed on more *B. tabaci* SSA1 nymphs than *E. mundus*, and this difference was significant for host densities of 60 to 140 nymphs (Figure 6.1). At host density of 60 nymphs, *E. sophia* fed on 8 nymphs compared to 6 nymphs for *E. mundus* (Figure 6.1A).

All genotypes interacted with parasitoid species, and resulted in higher host feeding levels by *E. sophia*, with mean number of nymphs fed on by *E. sophia* being 8 compared to 7 nymphs fed on by *E. mundus* on Alado alado (Figure 6.1B). Although the interaction of *E. mundus* with cassava genotype resulted in similar host feeding levels, the *E. sophia* by genotype interaction resulted in varying levels of host feeding, with feeding on NAROCASS 1 being the highest (9 nymphs) and lowest on Alado alado (7.8 nymphs) (Figure 6.1B).

6.3.2. Parasitism

For both parasitoid species, the number of nymphs parasitised increased with host density (Figure 6.2A). The lowest and highest numbers of parasitised nymphs were observed at host densities of 10 and 140 nymphs respectively and mean number of nymphs parasitised by *E. mundus* was 1.5 and 40 nymphs at host densities of 10 and 140 nymphs, respectively. At all host densities across all genotypes, *E. mundus* parasitised more *B. tabaci* SSA1 nymphs than *E. sophia* (Figure 6.2). At the host density of 100 nymphs, *E. mundus* parasitised 31 nymphs compared to 11 nymphs parasitised by *E. sophia* (Figure 6.2A). All cassava genotypes influenced the activities of the parasitoid species, with higher parasitism levels by *E. mundus*; on Alado alado where it parasitised 20.5 nymphs compared to 9 nymphs parasitised by *E. sophia* (Figure 6.2B). Although *E. mundus* had similar parasitism levels on all the cassava genotype, *E. sophia* had varying levels of parasitism, with Alado alado and NASE 14 having the highest (9 nymphs) and lowest (6.5 nymphs) numbers of parasitised nymphs, respectively (Figure 6.2B).

6.3.3. Total Mortality

For both parasitoid species, the total number of nymphs killed by both host feeding and parasitism increased with host density (Figure 6.3). The lowest and highest numbers of nymphs killed were observed at host densities of 10 and 140 nymphs, respectively; mean number of nymphs killed by *E. sophia* through both host feeding and parasitism were 3.5 and 35 nymphs at host densities of 10 and 140 nymphs, respectively (Figure 6.3A). At all host densities across all genotypes, *E. mundus* killed more *B. tabaci* SSA1 nymphs than *E. sophia*. At host density of 100 nymphs, *E. mundus* killed a total of 39 nymphs, compared to 22 nymphs killed by *E. sophia* (Figure 6.3A).

All cassava genotypes influenced parasitoid species activities to result in higher total mortality by *E. mundus*. On NASE 14, total nymph mortality caused by *E. mundus* was 27.5 compared to 15.4 caused by *E. sophia* (Figure 6.3B). Parasitoid species activities were differentially influenced by cassava genotypes, with NAROCASS 1 having the lowest total nymphal mortality caused by *E. mundus* (25 nymphs), whereas NASE 14 had the lowest total nymphal mortality caused by *E. sophia* (15 nymphs) (Figure 6.3B).

6.3.4. Relationship between Host Feeding and Parasitism with Host Density

Simple linear regression revealed that *B. tabaci* SSA1 nymph density had strong positive effects ($p<0.001$) on host feeding and parasitism by both *E. sophia* and *E. mundus*. For *E. mundus*, host density accounted for 61.3% and 86.5% of variations in the numbers of nymphs fed on and parasitised, respectively. For *E. sophia*, host density accounted for 82.3% and 69.8% of the variations in the numbers of nymphs fed on and parasitised, respectively.

6.3.5. Parasitism and Host Feeding Ratios at Different Host Density

Host feeding ratio was only affected by main effects of host density and parasitoid species ($p<0.001$). Parasitism ratio was significantly affected by host density, parasitoid species, host density by parasitoid species ($p<0.001$), and by parasitoid species by genotype interactions ($p<0.01$). Both parasitoid species had higher parasitism ratios with increase in host density, with the highest and lowest ratios for both parasitoids observed at nymph densities of 140 and 10 nymphs, respectively. Parasitism ratio was 0.14 at host density of 140 nymphs compared to 0.08 at 10 nymphs for *E. sophia* (Table 6.1). For *E. mundus* however, parasitism ratio increased with increase in host density up to a density of 60 nymphs, after which no significant difference was observed (Table 6.1). Parasitoid species by genotype interaction significantly influenced parasitism ratios and for *E. mundus* on Alado alado, the parasitism ratio was 0.26 compared to 0.1 for *E. sophia* (Table 6.1). Host feeding ratio was higher for *E. sophia* (0.15) than for *E. mundus* (0.11), but was only significantly different at host density of 10 nymphs, where the highest ratio of 0.23 was recorded (Table 6.1).

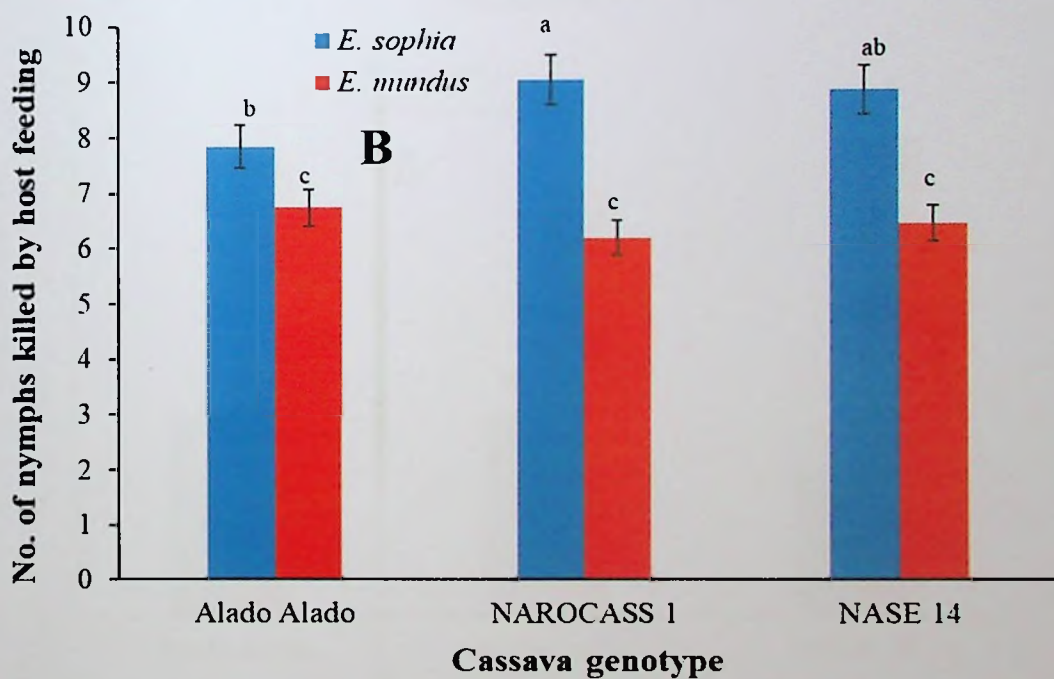
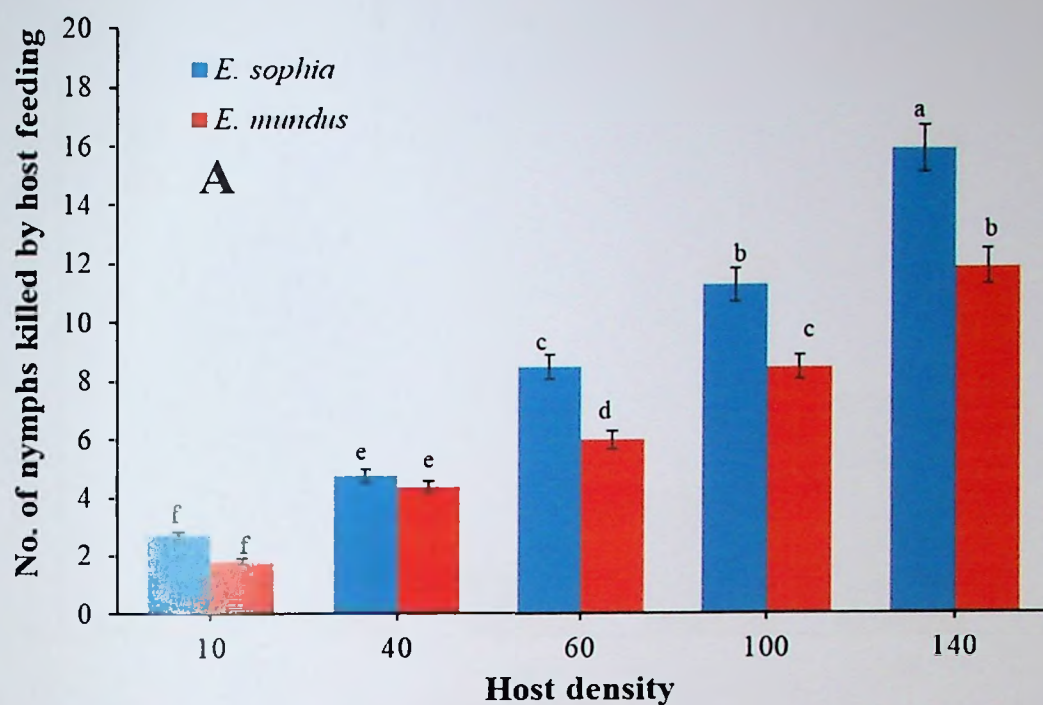


Figure 6. 1: Number of *B. tabaci* SSA1 nymphs fed-on by *E. sophia* and *E. mundus* at different host densities pooled over-all cassava genotypes (A); on three cassava genotypes pooled over-all host densities (B).

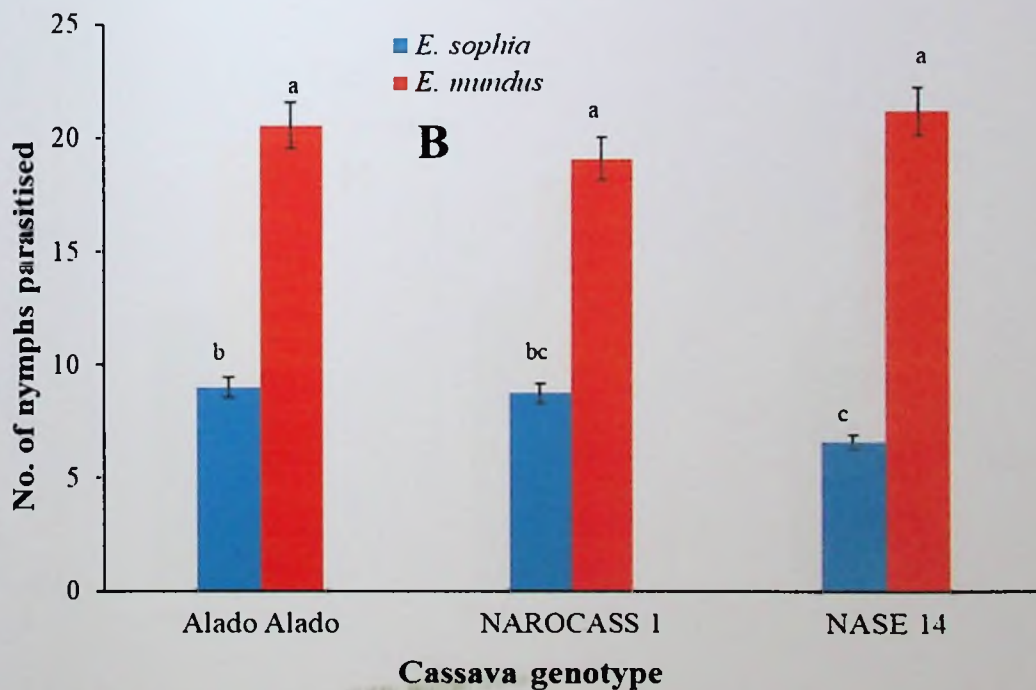
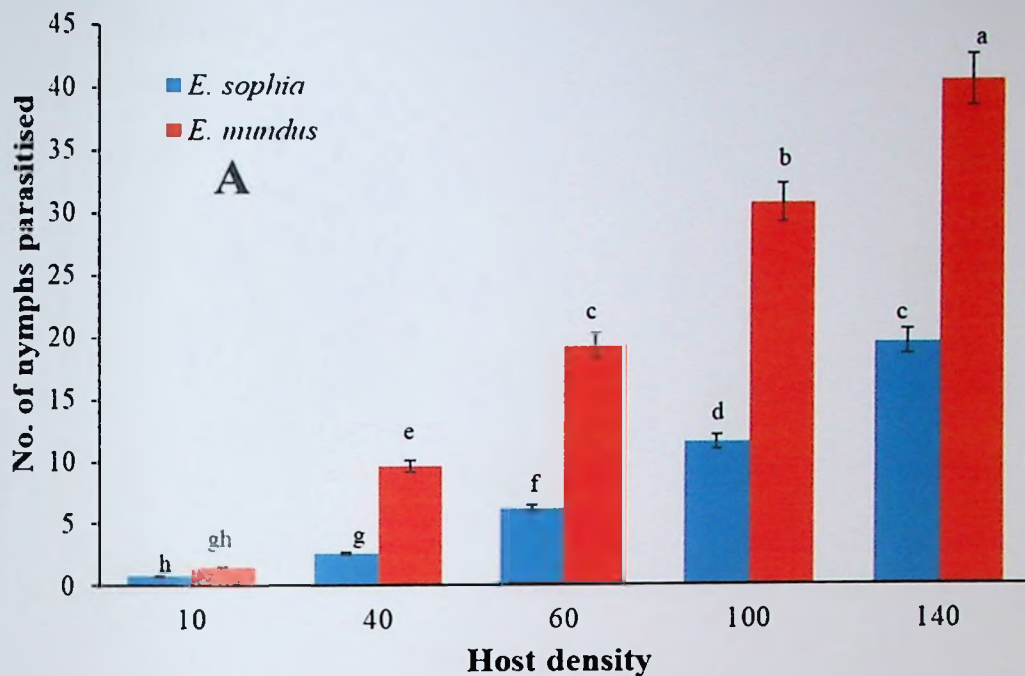


Figure 6. 2: Number of *B. tabaci* SSA1 nymphs parasitised by *E. sophia* and *E. mundus* at different host densities pooled over-all cassava genotypes (A); on three cassava genotypes pooled over-all host densities (B).

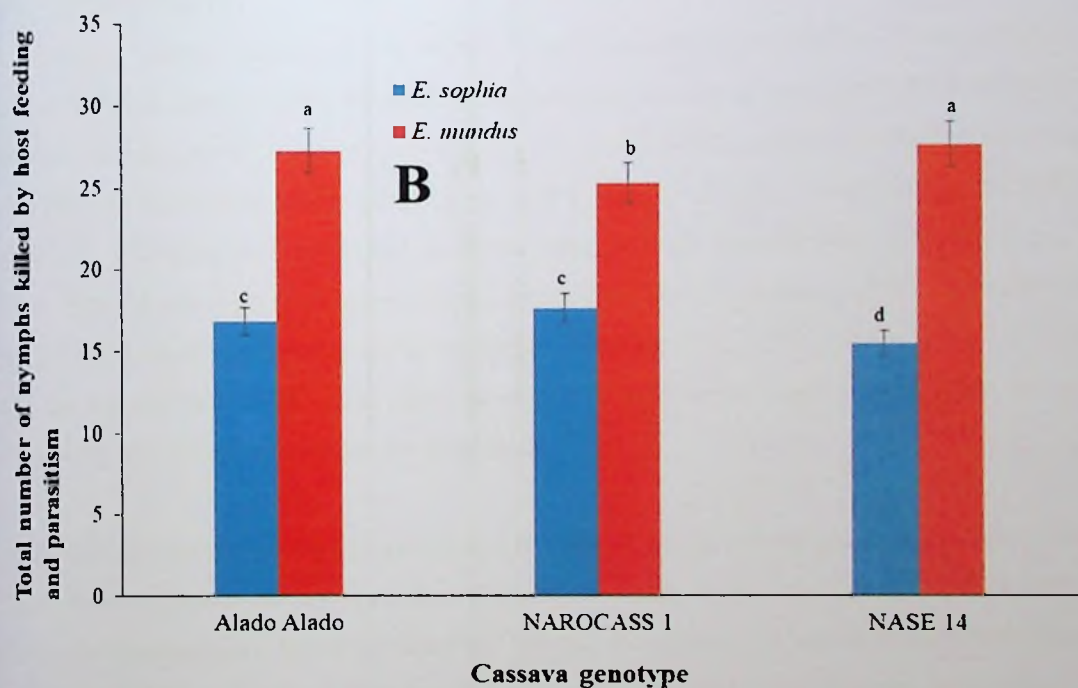
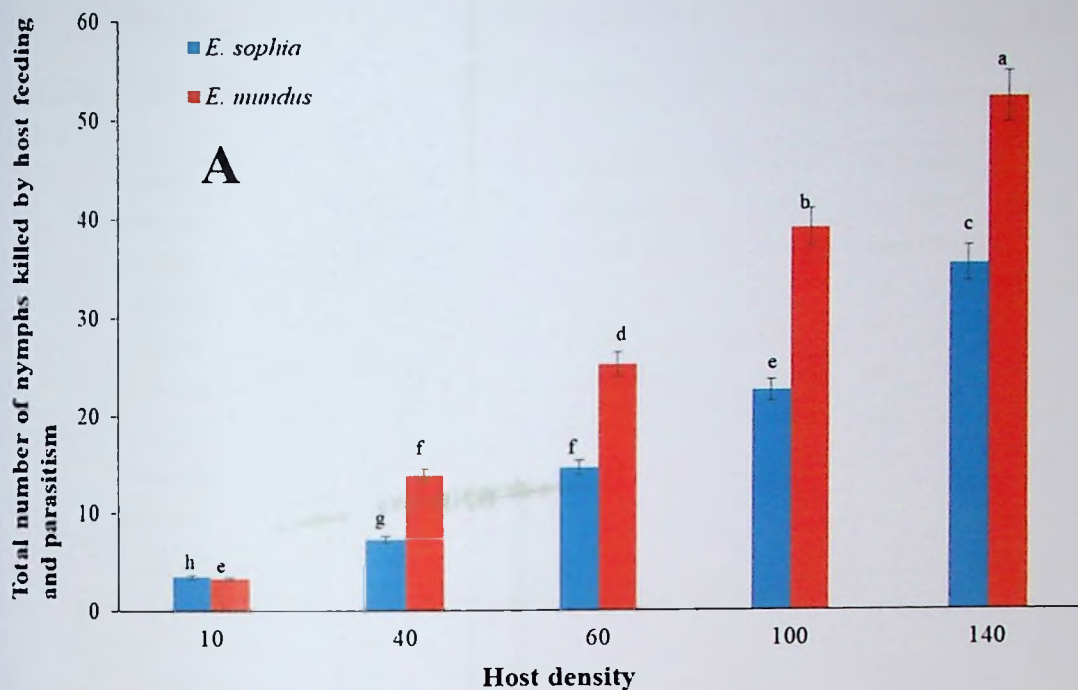


Figure 6. 3: Total number of *B. tabaci* SSA1 nymphs killed through host feeding and parasitism by *E. mundus* and *E. sophia* at different host densities pooled over-all cassava genotypes (A); on three cassava genotypes pooled over-all host densities (B).

Table 6.1: Parasitism and host feeding ratio of *Eretmocerus mundus* and *Encarsia sophia* at different densities *Bemisia tabaci* SSA1 nymphs on cassava

Parasitism ratio					Host feeding ratio	
Host density by Parasitoid species	Ratio	Parasitoid Genotype	species by	Ratio	Parasitoid species	
10	<i>E. sophia</i>	<i>E. mundus</i>	Alado alado	0.26a	<i>E. mundus</i>	0.11b
	<i>E. mundus</i>		NAROCASS I	0.24a	<i>E. sophia</i>	0.15a
40	<i>E. sophia</i>	<i>E. mundus</i>	NASE 14	0.28a	Host density	
	<i>E. mundus</i>				10	0.26a
60	<i>E. sophia</i>	<i>E. sophia</i>	Alado alado	0.10b	40	0.11b
	<i>E. mundus</i>		NAROCASS I	0.12b	60	0.12b
100	<i>E. sophia</i>	<i>E. sophia</i>	NASE 14	0.08b	100	0.10b
	<i>E. mundus</i>				140	0.10b
140	<i>E. sophia</i>	<i>E. mundus</i>				
	<i>E. mundus</i>					

Column means with dissimilar letter(s) at each host density differ significantly at $p < 0.05$

6.4. DISCUSSION

In this study, both *E. mundus* and *E. sophia* females fed and oviposited on *B. tabaci* SSA1 hosts even at low host densities and the parasitoids exhibited increased tendencies for both oviposition and host-feeding with increase in host density. This result is consistent with other reports (Sandlan, 1979; Bai and Mackauer, 1990; Sohani *et al.*, 2008; Zang *et al.*, 2011; Yang *et al.*, 2012; Hanan *et al.*, 2012), indicating increased host encounter rates at high host densities (Burger *et al.*, 2004). These results agree with the theory that the parasitoids protein-seeking ‘drive’ is independent of their ‘drive’ to seek out hosts suitable for oviposition (Sandlan, 1979). Thus, at high host density, they do not interfere with each other resulting in satiation of the ovipositional drive while maximising the need for proteins for oogenesis.

At the low host density of 10 nymphs, more *B. tabaci* were fed-on by parasitoids than parasitised. This is because parasitoid host feeding is known to precede oviposition (Bai and Mackauer, 1990), and in the circumstance fewer nymphs are left for oviposition at low host densities (Jervis and Kidd, 1986). Also at low host density, the host encounter rate is low (Burger *et al.*, 2004), which possibly forces the parasitoid to reduce on oviposition and focus on feeding for maintenance of oogenesis (Sandlan, 1979; Jervis and Kidd, 1986), as also observed by Yang *et al.* (2012).

The present study showed that *E. mundus* parasitised more *B. tabaci* SSA1 nymphs than *E. sophia*, but the latter parasitoid fed more on the nymphs in a 48 h period. The results are in agreement with findings of Zang and Liu (2008) and Zang *et al.* (2011). The low levels of host feeding vis-a-vis oviposition, especially in *E. mundus*, may be explained by the fact that parasitoids are known to mainly feed on host instars that are less preferred for oviposition (Nell *et al.*, 1976; Sandlan, 1979; Jervis and Kidd, 1986; Kidd and Jervis, 1991; Heimpel and Collier, 1996; Yang *et al.*, 2012). In this study, only the second instar nymphs preferred for oviposition (Urbaneja and Stansly, 2004) were provided hence the higher parasitisation rates. For *E. sophia*, although the preferred third instar nymphs (Binu *et al.*, 2003; Yang *et al.*, 2012) were provided, host feeding was generally higher than parasitism. This is explained by the fact that 24 h old *E. sophia* have low initial egg load upon emergence (Otim, 2007; Yang *et al.*, 2012), and so require more host feeding to obtain nutrients for egg maturation (Jervis and Kidd, 1986; Heimpel and Collier, 1996; Burger *et al.*, 2004). Also *Encarsia spp.* are known to exhibit low oviposition levels of less than 50% even when the preferred host stage is provided (Hoddle *et al.*, 1998), and to have a strong host-feeding drive (Zang and Liu, 2008).

Although cassava genotypes are known to significantly affect *B. tabaci* SSA1 counts (Omongo *et al.*, 2012), in this study there was no significant direct effect of genotype *per se* on parasitoid efficiency, which is in agreement with findings of Harbaugh and Mattson (1976) and Otim *et al.* (2008). This is possibly due to the fact that, with the exception of NASE 14 which has very few trichomes, the cassava genotypes used in this study are glabrous and such genotypes do not interfere with parasitoid walking speed which enabled higher parasitoid foraging success (Hulspas-Jordan and van Lenteren, 1978; Sutterlin and van Lenteren, 1996). Indeed, crop genotypes with low trichome densities have been reported to support higher levels of host-feeding and parasitism by *E. formosa* on *B. tabaci* in cotton (Sippell *et al.*, 1987) and poinsettia (Heinz and Parrella, 1994), and by *Trialeurodes vaporariorum* on cucumber (van Lenteren *et al.*, 1995). On the other hand, significantly higher host feeding, parasitism and total mortality of *B. tabaci* SSA1 species due to *E. mundus* compared to *E. sophia* further confirmed that *E. mundus* is a better biological control agent of *B. tabaci* SSA1 than *E. sophia* irrespective of the cassava genotype planted, as long it is a glabrous genotype.

Overall, results obtained from this study have shown that both *E. mundus* and *E. sophia* have a density dependent relationship with *B. tabaci* SSA1, although *E. mundus* generally killed more *B. tabaci* SSA1 nymphs than *E. sophia* and thus, is a more effective natural enemy for management of this pest in a cassava system. Also, the fact that *E. sophia* killed more nymphs through host feeding than *E. mundus*, makes it a valuable biological control agent for *B. tabaci* SSA1.

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CHAPTER SEVEN

GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

7.1. GENERAL DISCUSSION

Bemisia tabaci management is one of the major challenges to crop production on small-holder African farms, especially for low value crops such as cassava as limited whitefly management options are available. Besides, pesticides are not only expensive but are hazardous to farmers and the environment. In Uganda, although numerous factors including predators, parasitoids, host plant resistance and weather are known to act on *B. tabaci* pest populations, in-depth understanding of how they regulate *B. tabaci* population changes were still elusive. The research reported in this Thesis therefore focused on: (1) determining the effects of cassava genotype morphological traits and environmental conditions on *B. tabaci* population dynamics in contrasting ecological regions of Uganda; (2) determining the development rate, reproductive capacity and longevity of the predominant *B. tabaci* species at different temperatures on cassava in a controlled environment; (3) determining the impact of specific mortality factors acting on *B. tabaci* populations on cassava under field conditions, and (4) evaluating the influence of cassava genotype and *B. tabaci* host density on the effectiveness of selected parasitoids.

From field studies, all cassava test genotypes planted in the trial locations were variously infested by *B. tabaci* SSA1 species. Even genotypes such as Njule Red and NASE 14 that were considered to be tolerant and moderately tolerant to *B. tabaci* infestation were shown to harbor moderate to high *B. tabaci* infestations, suggesting that the resistance in these genotypes may have been overcome. The study also showed that tall cassava genotypes supported low *B. tabaci* populations as observed on cassava genotype Alado alado, the tallest among the tested genotypes across all ecological locations. This suggests that Alado alado may offer good *B. tabaci* resistance traits for a cassava breeding programme. It is also clear from this study that although some cassava genotypes of short statures with large leaf area and large leaf lobe width (e.g., NASE 14) have been widely adopted and are grown because of their tolerance to CMD and CBSD, they support high *B. tabaci* populations and require improvement with *B. tabaci* resistance traits like increased plant height.

This study also demonstrated that high temperatures, high rainfall, low RH negatively impacted *B. tabaci* abundance as was observed in Lira where such unfavourable environmental conditions prevailed. The differential impact of environmental conditions on populations of *B. tabaci* suggest that ecological conditions may dictate choice of management strategy for *B. tabaci* for different areas. For example, where environmental conditions are unsuitable for the build-up of high populations of *B. tabaci* (such as Lira), a wider range of cassava genotypes can be planted provided that disease free cassava planting materials are used to establish crops. On the other hand, in areas where conditions favour *B. tabaci*, genotypes such as Alado alado, which support low populations of *B. tabaci*, are beneficial; although, Alado alado is susceptible to CBSD and CMD. It is important to note that Kamuli, that was considered to be a moderate *B. tabaci* infestation zone actually had high *B. tabaci* populations while Wakiso is had moderate populations.

Temperature is one of the most important drivers of changes in behavior, abundance and distribution of insect pests (Ezeakacha and Yee, 2019; Sharma and Dhillon, 2020). Results from this study affirmed the fact that increased temperature significantly reduced *B. tabaci* SSA1 development time while greatly enhancing its development rate, survival, fecundity and general fitness on all cassava genotypes. Temperature of 32 °C was the most suitable for development of *B. tabaci* while the temperature of 16 °C significantly reduced *B. tabaci* population parameters on all cassava genotypes. At temperatures of 28 °C and above, *B. tabaci* SSA1 expressed strong levels of reproductive capacity and fitness. Therefore, with enhanced biological performance at higher temperatures, *B. tabaci* outbreaks can be expected with the projected global Climate Change (Marinho *et al.*, 2016; Skendžic *et al.*, 2021). This would result in increased crop production losses due to the direct feeding effects of *B. tabaci* as pests and their roles as vectors of plant virus diseases. The lack of genotype differences in development duration, fecundity and population parameters observed in this study, coupled with inconsistent effects on pest survival suggest absence of antibiosis resistance to *B. tabaci* SSA1 in the cassava genotypes that were used in the study.

Investigation of the mortality factors that act on *B. tabaci* SSA1 field populations showed that disappearance was the key mortality factor acting on all the immature stages of *B. tabaci* SSA1 on cassava, followed by third instar parasitism. These two factors were associated with the highest

levels of marginal mortality rates and irreplaceable mortality, and their importance was confirmed by key factor analysis. Disappearance is attributed to the effects of abiotic factors such as wind and rain, and also to predators (Naranjo and Ellsworth, 2005; Asiimwe *et al.*, 2007a).

This study also showed that for the two cassava genotypes used, the levels of mortality of immature stages were similar even on Alado alado (the reportedly more tolerant genotype). This further confirms the absence of antibiosis resistance to *B. tabaci* SSA1 in Alado alado as was demonstrated in Chapter Four. This means that integrated management approach that supports *B. tabaci* natural enemy population build up is desirable. Breeders may also focus on developing *B. tabaci* resistant/tolerant cassava genotypes with traits that may increase *B. tabaci* adult non-preference (such as taller plants) (Murugesan and Kavitha, 2010; Khalil *et al.*, 2015) that enhance the likelihood of disappearance of eggs and nymphs due to increased exposure (Sippell *et al.*, 1987).

The results obtained from this study have also shown that the parasitic capacities of *E. mundus* and *E. sophia* were enhanced with increased *B. tabaci* SSA1 nymph density on cassava, a quality with far reaching significance for biological control given the key role played by parasitism in the mortality of *B. tabaci* immature stages as observed in Chapter Five. Furthermore, the fact that these two parasitoids use non-concurrent feeding mechanisms (Jervis and Kidd, 1986), enhance their efficacy in the management of *B. tabaci* SSA1 and when combined can be efficient biological control agents of *B. tabaci* SSA1. Additionally, the two parasitoids prefer different host instars for oviposition and host-feeding leaving no host instar free of parasitoid pressure thus complementing each other which further assures their efficiency against *B. tabaci* SSA1. In absence of *B. tabaci* SSA1 resistant cassava genotypes so far in Uganda, the combined augmentative releases of these two parasitoids could offer better control of this pest, especially under the current high population reported in the country.

7.2. GENERAL CONCLUSIONS

This study revealed that:

- High temperature, high rainfall, low RH and deployment of tall cassava genotypes with small leaf area had a negative effect on *B. tabaci* population growth.
- Temperature ranges of 28-32 °C at RH of 70% greatly enhance the biological fitness of *B. tabaci* SSA1 whereas host plant resistance wanes.
- Disappearance is the major cause of death for all immature stages of *B. tabaci* SSA1 on cassava in the field.
- *Eretmocerus mundus* and *Encarsia sophia* efficacy is density dependent and both can cause appreciable reductions of *B. tabaci* infestation in cassava systems. However, *E. mundus* is a more effective natural enemy for *B. tabaci* management in a cassava system.

7.3. GENERAL RECOMMENDATIONS

Several recommendations have emerged from the results of the various studies conducted, their discussions and conclusions.

The difference in *B. tabaci* abundance in the different AEZs calls for location-specific *B. tabaci* control measures. At sites where environmental conditions are unsuitable for the growth and development of *B. tabaci* (e.g., Lira), any cassava genotype could be deployed provided that CBSD/CMD-free planting material is used. In sites with ideal conditions, the use of genotypes that support low populations of *B. tabaci* is suitable. Also, breeders may consider high plant height as one of the traits for genotype improvement to *B. tabaci* resistance.

Adoption of practices which enhance disappearance and parasitism is recommended as this would offer the most effective way of increasing overall mortality of *B. tabaci* SSA1. Practices such as early planting of cassava at the beginning of the rainy season would intensify the effect of disappearance. While augmentative release of *E. mundus* and *E. sophia* parasitoids to supplement the naturally occurring parasitoid populations, may help to enhance parasitism.

Further studies to understand the combined effect of temperature and RH variations on *B. tabaci* SSA1 population dynamics are needed. Furthermore, there is also a need to study the effect of temperatures beyond 32 °C on *B. tabaci* SSA1 development, reproduction and fitness in order to establish the species optimum temperature.

The contribution of factors associated with disappearance needs to be well understood, hence the need for further investigations.

Lastly, the efficiency of *E. mundus* in the management of *B. tabaci* needs to be validated under natural field infestation.

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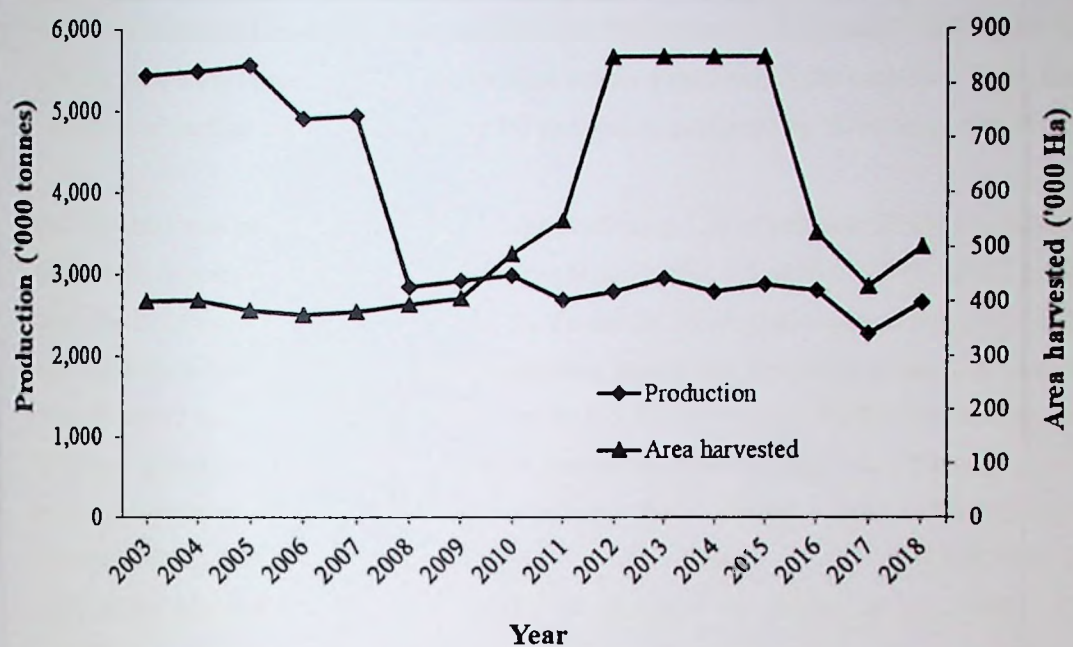
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APPENDICES



Appendix 1: Cassava Production in Uganda, 2003 – 2018 (Source: Authors' compilation using FAOSTAT 2020 data (FAO 2020)).

Appendix 2: Ancestry of improved cassava genotypes NAROCASS 1, NASE 14 and NASE 3

Genotype	Source	Parents	Characteristics	Year of release
NAROCASS 1 (OPV)	IITA-Ibadan, Nigeria	IITA-TMS-IBA92248 (♀)	CMD resistant, CBSD tolerant, High yielding	2015
NASE 14 (OPV)	TARI, Tanzania	Kibaha (♀)	CMD resistant, CBSD tolerant	2011
NASE 3	IITA-Ibadan, Nigeria	Unknown	CMD resistant, CBSD tolerant	1993

Source: CASSAVABASE (cassavabase.org/breeders/trials, Accessed on 16. May, 2022). (OPV means Open Pollinated Variety).

Appendix 3: *Bemisia tabaci* species identification

Bemisia tabaci adults were collected using an aspirator from the experimental fields in the three study sites (Kamuli, Lira and Wakiso) and stored in 90% ethanol in a separate 1.5 ml Eppendorf tube for each site. Three *B. tabaci* adults were selected randomly from each site. DNA from individual whiteflies was extracted using the protocol as explained by (Otim *et al.*, 2018b).

Each reaction was performed in 25 µl volume containing 1 µl of template DNA, 1 µl each of 10 pmol/µL of primer, 2.5 µl of 10X DreamTaq Green buffer, 0.5 µl of dNTP (10 mM/L), 0.25 µl of *Taq* DNA polymerase 5 U/µl, 2.5 µl 5% Tween 20, 16.25 µl of nuclease free water. PCR was run with the reaction mix under the following conditions; Denaturation for 2 minutes at 95°C followed by annealing step at 95°C for 30 seconds (35 cycles), 52°C (30 seconds), and then final extension at 1 min at 72°C for 10 minutes after which, reactions were held at 4°C. PCR amplification was achieved using the primer pair; C1-J-2195(5'-TTGATTTTTTGGTCATCCAGAAGT-3') and L2-N-3014(5'-TCCAATGCACTAATCTGCCATATTA-3') as described by (Simon *et al.*, 1994). The amplification success for all samples was checked on 1.3% agarose gel.

The PCR products were stored at -20 °C until transportation for sequencing. A consensus sequence was sent back for farther analysis. Molecular data have been deposited in GenBank with accession numbers MW080632 - MW080640 for samples from Kamuli, Wakiso and Lira, respectively. A phylogenetic tree based on the mitochondrial cytochrome oxidase I partial gene for *Bemisia tabaci* was generated (Figure A1) and all samples were determined to be Sub-Saharan Africa 1 (SSA1) species.

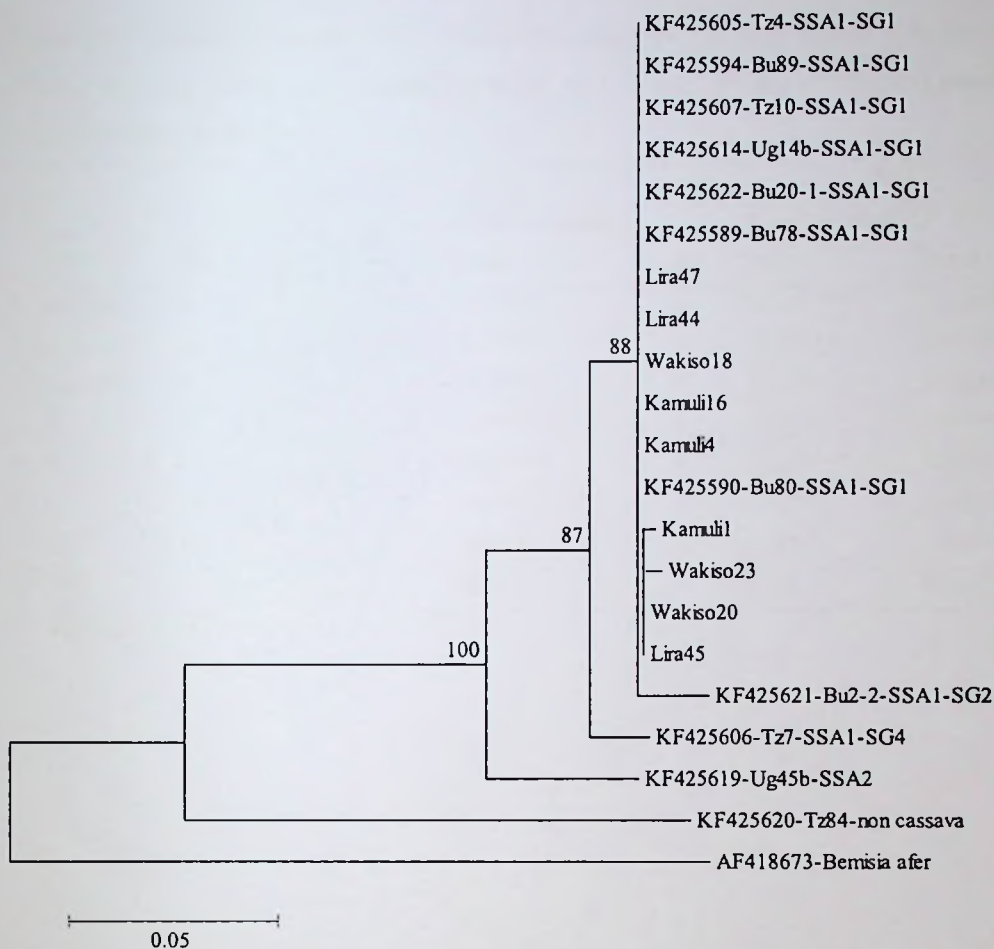


Figure A1: Phylogenetic tree based on the mitochondrial cytochrome oxidase I partial gene sequence for *Bemisia tabaci* collected on cassava at three experimental sites in Uganda generated using maximum likelihood available in MEGA6 software program. *Bemisia afer* was included as an out-group.

Appendix 4: F-statistics for the effects of location, genotype and crop age on *B. tabaci* adults per plant on 5 top leaves and nymphs per plant on 15th leaf (3rd and 4th instars) population change over time in 2016 and 2017

SOV	DF	2016		DF	2017	
		<i>B. tabaci</i> adult count	<i>B. tabaci</i> nymph count		<i>B. tabaci</i> adult count	<i>B. tabaci</i> nymph count
Location (A)	1	190.66***	66.67***	2	483.06***	109.85***
Genotype (B)	4	33.20***	70.55***	4	76.07***	133.34***
Crop age (C)	4	65.07***	101.74***	4	816.37***	591.68***
A × B	4	6.14***	7.32***	8	17.33***	14.30***
A × C	4	101.02***	290.23***	8	112.30***	101.53***
B × C	16	5.07***	7.40***	16	6.76***	11.25***
A × B × C	16	13.97***	4.92***	32	5.81***	5.48***
CV (%)		1576.31	132.93		82.60	54.98

*** = significant at $p < 0.001$

Appendix 5: *Bemisia tabaci* adult and nymph (3rd and 4th instars) population abundance on five cassava genotypes in small-plot trials from Uganda.

Locations used in 2016 were Lira and Wakiso, and in 2017 were Kamuli, Lira and Wakiso

Year	Location	<i>B. tabaci</i> adult count/plant								<i>B. tabaci</i> nymph count/plant							
		Months After Planting (MAP)								Months After Planting (MAP)							
		4	5	6	7	8	4	5	6	7	8	4	5	6	7	8	
2016	Lira	1.67b	0.93a	0.35b	0.07b	0.04b	10.46a	6.82a	8.37b	4.36b	1.47b						
	Wakiso	3.85a	0.65a	2.08a	4.19a	4.38a	2.36b	1.98b	19.65a	17.04a	54.17a						
2017		2	4	5	6	7	2	4	5	6	7						
	Kamuli	115.96a	443.69a	100.48a	24.84a	34.32a	752.50a	139.75a	35.11b	60.00a	116.73a						
	Lira	2.66c	24.40b	3.41c	0.84b	0.19b	23.22c	20.89b	10.17c	8.51c	8.82b						
	Wakiso	22.81b	14.15b	15.50b	22.98a		78.66b	23.76b	47.94a	52.96b							
	LSD _{0.05}	9.96	27.46	9.93	3.95		52.32	12.98	6.29	6.71	14.38						

Column means with dissimilar letter(s) per year differ significantly at $p < 0.05$; MAP means Months after planting

Appendix 6: F-statistics for the effects of location, genotype and crop age on cassava morphological traits over time in 2016 and 2017

2016										
SOV	DF	Plant height	Leaf area	LAI	Petiole length	Leaf width	Lobe width	Lobe length	Stem girth	Lobe number
Location (A)	1	732.63***	71.86***	86.17***	116.00***	59.62***	64.85***	78.16***	534.43***	2.20ns
Genotype (B)	4	230.32***	337.82***	291.04***	251.30***	316.09***	323.08***	316.62***	13.71***	127.35***
Crop age (C)	4	624.00***	127.40***	141.18***	161.19***	136.64***	66.77***	86.73***	154.16***	21.17***
A × B	4	22.03***	9.44***	9.91***	14.94***	14.56***	61.58***	7.22***	14.96***	5.14***
A × C	4	15.29***	442.10***	512.54***	471.12***	343.44***	217.07***	416.84***	16.64***	133.12***
B × C	16	2.17**	5.46***	3.38***	3.11***	7.24***	3.44***	3.43***	4.73***	2.67***
A × B × C	16	1.65*	7.75***	5.77***	5.32***	6.39***	5.69***	6.00***	5.51***	3.99***
CV		37.49	14.35	10.76	23.29	19.49	42.98	15.68	89.89	23.09

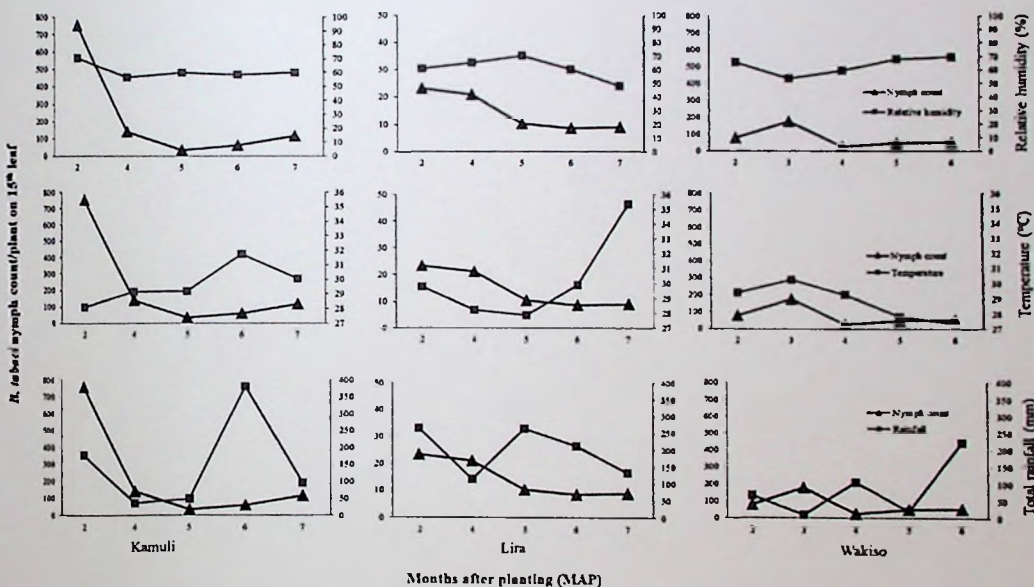
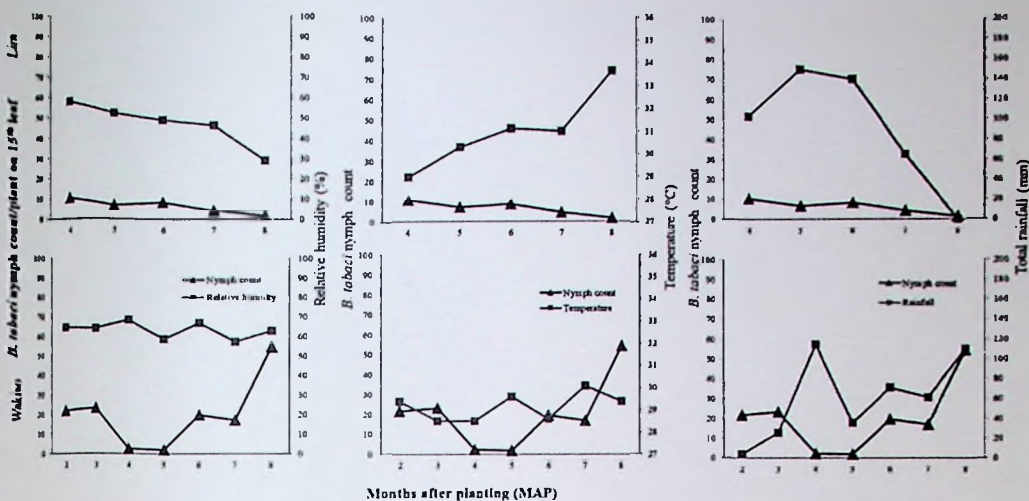
2017										
SOV		Plant height	Leaf area	LAI	Petiole length	Leaf width	Lobe width	Lobe length	Stem girth	Lobe number
Location (A)	2	751.23***	101.92***	192.87***	140.33***	70.67***	70.67***	128.45***	214.61***	39.82***
Genotype (B)	4	245.72***	91.98***	28.05***	430.75***	290.88***	290.88***	383.69***	14.26***	284.89***
MAP (C)	4	2895.29***	218.17***	140.83***	187.70***	109.64***	109.64***	76.69***	1048.46***	211.90***
A × B	8	52.55***	67.28***	28.81***	47.15***	60.77***	60.77***	54.83***	29.76***	41.55***
A × C	8	166.71***	232.12***	69.62***	159.93***	144.20***	144.20***	139.11***	24.15***	80.10***
B × C	16	5.10***	26.10***	7.01***	14.01***	27.54***	27.54***	26.64***	3.35***	9.58***
A × B × C	32	4.78***	16.06***	5.68***	8.47***	11.81***	11.81***	13.89***	2.94***	6.95***
CV		36.67	18.15	248.16	21.73	20.08	37.05	15.6	149.93	23.27

Significance: * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$

Appendix 7: Cassava morphological traits on five cassava genotypes in small-plot trials in Kamuli, Lira and Wakiso in Uganda in 2017.

Genotype	Leaf area (cm ²)										LAI	Months After Planting (MAP)										Lobe no	Lobe width (cm)						
	2	4	5	6	2	4	5	6	7	2		4	5	6	7	2	4	5	6	7									
Kamuli	2	4	5	6	2	4	5	6	7	2	4	5	6	7	2	4	5	6	7										
Njile Red	182.23a	133.14a	66.11c	27.46d	1.27a	1.88a	7.99a	1.45c	2.71b	7.07a	7.53a	7.10a	6.62a	6.77a	2.06c	1.88c	1.75c	1.54d	2.01d										
Alado alado	145.68b	82.37c	60.69c	29.24d	1.10b	1.54b	1.67a	1.09d	1.56c	6.37bc	6.33b	5.60b	5.65b	5.18b	3.96a	3.82a	2.91d	2.13c	2.49c										
NAROCASS 1	167.39ab	112.20b	136.38a	101.96a	1.30a	1.65ab	2.31a	3.41a	4.24a	6.15c	6.01b	5.05c	5.02c	4.77bc	4.08a	3.94a	4.39a	4.03a	4.12a										
NASE 14	115.04c	71.58cd	99.23b	80.61b	0.88c	1.20c	1.69a	1.87b	1.71c	6.67b	6.25b	5.12c	4.67c	4.72c	3.53b	3.13b	3.83b	3.79a	3.38b										
NASE 3	115.73c	66.54d	72.30c	44.44c	0.87c	1.19c	1.65a	1.86b	2.51b	6.60b	5.65c	4.17d	4.02d	4.72c	3.53b	3.06b	3.57c	2.98b	3.05b										
LSD	23.51	15.23	13.53	11.23	0.16	0.26	7.54	0.3	0.56	0.32	0.37	0.42	0.44	0.45	0.3	0.7	0.27	0.27	0.35										
Lira	2	4	5	6	2	4	5	6	7	2	4	5	6	7	2	4	5	6	7										
Njile Red	251.79cd	223.29a	205.83ab	122.07ab	2.32ab	3.91bc	4.12c	4.42a	4.48c	8.13a	8.50a	7.20b	6.82a	6.47a	2.55d	2.68d	2.99d	2.53c	2.39d										
Alado alado	305.51a	207.61a	186.40bc	130.48a	2.52ab	4.37a	4.96ab	3.89b	3.72d	7.23b	7.38b	6.97b	5.70c	4.78d	5.81a	5.05a	4.80ab	4.60a	3.79b										
NAROCASS 1	241.79d	218.36a	176.48c	119.13ab	2.31ab	4.04abc	5.05a	4.82a	5.75a	6.17c	6.43c	6.37c	5.47c	5.38c	5.43b	5.04a	4.69b	4.36b	4.34a										
NASE 14	272.41bc	210.03a	214.34a	113.49b	2.55a	3.73c	4.73abc	4.50a	5.20b	7.94a	8.28a	8.05a	6.35b	5.95b	5.21c	4.77b	4.99a	4.03c	3.77b										
NASE 3	284.84ab	142.37b	110.61d	44.97c	1.98b	4.23ab	4.37bc	4.45a	4.31c	7.35b	7.07b	6.07c	4.87d	4.55d	5.48b	4.00c	3.93c	2.79d	2.74c										
LSD	24.91	21.28	25.5	14.51	0.56	0.41	0.65	0.5	0.54	0.36	0.33	0.38	0.41	0.41	0.2	0.3	0.25	0.21	0.35										
Wakiso	2	3	4	5	2	2	4	5	6	2	3	4	5	6	2	3	4	5	6										
Njile Red	55.43a	79.09ab	69.38a	76.74a	0.70b	0.75ab	0.58a	1.49a	1.17a	6.18a	6.65a	6.12a	6.42a	6.89a	1.57d	1.46c	1.97c	1.91b	2.25d										
Alado alado	59.16a	89.82a	61.12a	63.73b	0.68b	0.68ab	1.12a	0.60a	0.86b	5.58b	6.13bc	5.83ab	6.22ab	6.37b	3.24a	3.07a	2.86a	3.04a	3.47c										
NAROCASS 1	46.23b	68.17bc	56.94ab	71.28ab	0.70b	0.66bc	0.49a	0.43a	1.03ab	5.10c	5.80c	4.97c	4.95c	5.20c	2.90b	2.64b	2.87a	3.12a	4.21b										
NASE 14	42.51b	56.96c	45.98b	70.01ab	0.71c	0.57c	0.39a	0.61a	1.24a	6.40a	6.22b	5.92ab	6.50a	7.12a	2.45c	2.55b	2.55b	3.19a	4.64a										
NASE 3	60.78a	58.70c	60.21a	69.45ab	0.77a	0.77a	0.62a	0.70a	1.24a	6.25a	6.18b	5.70b	6.03b	5.37c	3.14a	2.47b	2.76ab	3.18a	4.06b										
LSD	9	14.48	13.43	11.24	0.07	0.1	0.89	1.1	0.26	0.33	0.37	0.38	0.32	0.33	0.2	0.2	0.27	0.25	0.36										

Column means with dissimilar letter(s) per location differ significantly at $p < 0.05$; MAP means Months after planting



Appendix 10: Variation in minimum and maximum monthly temperature, relative humidity, rainfall in 2017 and 2017. Locations used in 2016 were Lira and Wakiso, and in 2017 were Kamuli, Lira and Wakiso.

Year	Location	Months after Planting	Temperature		Relative humidity		Rainfall (mm)	
			Min	Max	Min	Max	Min	Max
2016	Lira	4	26.5	31.6	43	87	0	19.5
		5	27	32	41	87	0	31.8
		6	27.6	33.2	28	74	0	29.8
		7	27.8	33.2	27	86	0	17.6
		8	31.8	35.2	17	42	0	0
	Wakiso	2	24.2	32.3	50	82	0	1.5
		3	23.6	30.5	41	94	0	8.6
		4	25.5	30.2	48	91	0	33.6
		5	25.5	33	45	86	0	26
		6	21.8	31.8	50	95	0	23.6
		7	26.8	34.8	43	92	0	25.5
		8	26	31.5	37	94	0	32.2
	Kamuli	2	17.9	31.8	53.3	100	0	46.1
		3	22.4	32	41.5	87.3	0	33.2
		4	18.7	35.5	33.1	99.8	0	9.7
		5	21.5	35.4	39	93.4	0	18.2
		6	20.8	39	35.5	98.7	0	131
		7	22.4	35.2	43.9	88.2	0	28.7
2017	Lira	2	20.1	34	43.4	100	0	60.1
		3	18.5	32.9	43.3	100	0	61.5
		4	20.9	32.2	48.9	96.7	0	32
		5	19.2	30.7	53.5	100	0	62.3
		6	23.3	33.2	50.6	82.7	0	41
		7	22.6	45.5	29.3	95.4	0	29
	Wakiso	2	22.1	34.1	48.7	99.8	0	25.2
		3	20.2	35.7	32.7	99.1	0	7.1
		4	18.6	36.3	33.8	98.8	0	34.1
		5	23.1	30	51	89.6	0	7.4
		6	24	29.5	57	84	0	80

Appendix 11: F-statistics for the effects of temperature and cassava genotype on *B. tabaci* SSA1 development duration, immature survival, female fecundity and longevity

SOV	DF	Development duration	Survival	Fecundity	Female longevity	Total duration
Temperature (A)	4	284.31***	156.69***	687.99***	703.71***	3583.54***
Cassava genotype (B)	2	0.16ns	8.44***	2.68ns	2.98ns	2.10ns
A x B	8	0.18ns	3.00**	0.79ns	0.37ns	2.12*
CV (%)		53.50	10.11	59.27	22.9	13.97

Significance: ns, not significant; * $p<0.05$; ** $p<0.01$; and *** $p<0.001$

Appendix 12: Life table of *B. tabaci* SSA1 immatures on two cassava genotypes

The summary of deaths from all the different causes is presented in Appendix 12.1. The highest death rates in both genotypes for all stages of growth were as a result of disappearance followed by third instar parasitism. Death rate due to disappearance ranged from 30% in the second instar to 44% in the egg stage and was 14% for third instar parasitism on Alado alado (Appendix 12.2). The highest stage-specific mortality for both genotypes was observed in the third instar stage; 55% for Alado alado and 49% for NAROCASS 1. Only about 12% of the nymphs survived to adult emergence in both genotypes (Appendix 12.3). For both the egg and nymph stages, disappearance was associated with the highest mortality of 73% and 69% of nymph deaths in Alado alado and NAROCASS 1, respectively (Appendix 12.3).

Appendix 12.1: Deaths from five causes of mortality of *B. tabaci* SSA1 immature field populations on cassava in Uganda in 2016 and 2017 in Wakiso

Genotype	Stage of growth	No. beginning	No. healthy	Total death	Number of death due to					
					Inviability	Predation	Parasitism	Disappearance	Unknown death	
	x	N _x		D _x	D _{ix}	D _{px}	D _{sx}	D _{ax}	D _{ux}	
Alado alado	Egg	2855	1476	1379	62	52	-	1265	-	
	1 st instar	7341	4953	2388	-	98	-	2228	62	
	2 nd instar	4953	3225	1728	-	146	-	1476	106	
	3 rd instar	3225	1440	1785	-	54	438	1183	110	
	4 th instar	1440	870	570	-	6	30	496	38	
	Adult	870	870	-	-	-	-	-	-	
NAROCASS I	Egg	2915	1518	1397	55	20	-	1322	-	
	1 st instar	7415	5454	1961	-	158	-	1726	77	
	2 nd instar	5454	3540	1914	-	245	-	1525	144	
	3 rd instar	3540	1787	1753	-	49	418	1181	105	
	4 th instar	1787	960	827	-	13	80	714	20	
	Adult	960	960	-	-	-	-	-	-	

Appendix 12.2: Cause-specific probability of death from specified mortality factors in the presence of all factors acting on immature stages of *B. tabaci* SSA1 species

Genotype	Stage of growth	Probability of death	Cause of death				
			Inviability	Predation	Parasitism	Disappearance	Unknown death
x		aq _x	aq _{1x}	aq _{2x}	aq _{3x}	aq _{4x}	aq _{5x}
Alado alado	Egg	0.4830	0.0217	0.0182	-	0.4431	-
	1 st instar	0.3253	-	0.0133	-	0.3035	0.0084
	2 nd instar	0.3489	-	0.0295	-	0.2980	0.0214
	3 rd instar	0.5535	-	0.0167	0.1358	0.3668	0.0341
NAROCASS 1	4 th instar	0.3958	-	0.0042	0.0208	0.3444	0.0264
	Egg	0.4792	0.0189	0.0069	-	0.4535	-
	1 st instar	0.2645	-	0.0213	-	0.2328	0.0104
	2 nd instar	0.3509	-	0.0449	-	0.2796	0.0264
	3 rd instar	0.4952	-	0.0138	0.1181	0.3336	0.0297
	4 th instar	0.4628	-	0.0073	0.0448	0.3996	0.0112

Appendix 12.3 Life table of mortality from specified causes at a given stage of *B. tabaci* SSA1 development.

Genotype	Stage of growth	Probability of death	Fraction living at beginning of stage	Fraction of death due to						Unknown death
				Fraction of all deaths	Inviability	Predation	Parasitism	Disappearance		
Alado alado	x	aq _x	al _x	ad _x	ad _{1x}	ad _{2x}	ad _{3x}	ad _{4x}	ad _{5x}	
	Egg mortality	0.483	1	0.483	0.0217	0.0182	-	0.4431	-	
	Nymph mortality									
	1 st instar	0.3253	1	0.3253	-	0.0133	-	0.3035	0.0084	
	2 nd instar	0.3489	0.6747	0.2354	-	0.0199	-	0.2011	0.0144	
	3 rd instar	0.5535	0.4393	0.2432	-	0.0074	0.0597	0.1611	0.015	
	4 th instar	0.3958	0.1962	0.0776	-	0.0008	0.0041	0.0676	0.0052	
	Adult	-	0.1185	-	-	-	-	-	-	
	Total nymph death			0.8815	-	0.0414	0.0638	0.7333	0.043	
	Egg mortality	0.4792	1	0.4792	0.0189	0.0069	-	0.4535	-	
	Nymph mortality									
	NAROCASS 1	1 st instar	0.2645	1	0.2645	-	0.0213	-	0.2328	0.0104
2 nd instar		0.3509	0.7355	0.2581	-	0.033	-	0.2057	0.0194	
3 rd instar		0.4952	0.4774	0.2364	-	0.0066	0.0564	0.1593	0.0142	
4 th instar		0.4628	0.241	0.1115	-	0.0018	0.0108	0.0963	0.0027	
Adult		-	0.1295	-	-	-	-	-	-	
Total nymph death				0.8705	-	0.0627	0.0672	0.694	0.0467	

Appendix 13: F-statistics for the effects of *B. tabaci* SSA1 nymph density, parasitoid species and cassava genotype on host feeding and parasitism of *B. tabaci* SSA1 by *E. mundus* and *E. sophia*

SOV	DF	Parasitism	Host feeding	Total mortality
Host density (A)	4	358.24***	228.02***	669.15***
Parasitoid species (B)	1	392.27***	61.30***	240.84***
Genotype (C)	2	1.98ns	0.58ns	0.27ns
A x B	4	20.05***	2.61*	18.39***
A x C	8	1.06ns	1.11ns	0.98ns
B x C	2	8.30***	4.20*	6.47**
A x B x C	8	0.76ns	1.04ns	0.93ns
CV		56.65	33.63	42.49

Significance: * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$, ns: not significant.