Doctoral thesis

UNDERSTANDING THE POTENTIAL IMPACT OF CLIMATE CHANGE ON CASSAVA- COLONISING WHITEFLY, *BEMISIA TABACI* (GENNADIUS) (HEMIPTERA: ALEYRODIDAE)

A thesis submitted, in partial fulfilment of the requirements for the degree of Doctor of Philosophy,
to:

- the international Phd program in "Agriculture, Food and Environment", held at the Department of Agriculture, Food and Environment of the University of Catania (Italy)

- the Department of Plant and Environmental Sciences of the University of Copenhagen (Denmark)

also in the frame of the Erasmus Mundus Joint Doctorate program "AgTraIn" (Agricultural Transformation by Innovation)

Principal supervisor: Professor Carmelo Rapisarda (University of Catania, Italy)
Co-supervisor: Associate Professor Ole Søgaard Lund (University of Copenhagen, Denmark)
Co-supervisor: Associate Professor Lene Sigsgaard (University of Copenhagen, Denmark)
Field supervisor: Dr. James P. Legg (International Institute of Tropical Agriculture, Tanzania)
2018

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AREGBESOLA OLUWATOSIN ZACHEUS

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2018

Declaration

I hereby declare that this thesis is my own, that it has never been submitted nor concurrently being submitted for any degree to any other University and that all sources have been duly acknowledged.

SIGNED: AREGBESOLA OLUWATOSIN ZACHEUS

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Summary

Cassava has been described as a "super-crop" for its role as food crop, cash crop and industrial raw material. Its production is vital to the well-being of more than 700 million people globally. Cassava viruses and their vector (*B. tabaci*) are one of the greatest constraints to cassava production. Among the insect pests of cassava, *B. tabaci* stands out as an economically important pest, causing direct damage to a wide range of crops by producing sooty moulds and transmitting plant viruses. *B. tabaci* is a species complex consisting of more than 34 morphologically indistinguishable species. *B. tabaci* is known to vector over 100 plant viruses, including at least 11 viruses of cassava, driving disease epidemics across cassava production systems globally. Cassava farmers across Africa incur annual losses of over 1 billion USD due to viruses transmitted by *B. tabaci.*

Even though cassava is expected to be resilient to climate change, at the moment, there is a dearth of information on temperature-dependence, and the potential impact of climate change on an African population of cassava-colonising *B. tabaci.* To fill this knowledge gap, this study was initiated to: evaluate the effects of temperature on the developmental characteristics of cassava-colonising *B. tabaci*, evaluate the effects of temperature on the reproductive performance of cassava-colonising *B. tabaci*, review the potential impact of climate change on whiteflies, model the distribution and abundance of cassava-colonising *B. tabaci* under climate change scenarios, and investigate strategies for adapting to cassava whitefly and virus disease under climate change scenarios.

To provide a solid foundation for the study, potential impact of climate change on whiteflies and the viruses they vector was reviewed. These included the possible impacts on: life history traits (immature development time and survival, adult longevity and fecundity of adult female), movement and distribution, population dynamics, efficacy of management

strategies, and implications for vectored plant viruses. The identity and purity of the *B. tabaci* colonies used for the experiments was confirmed by sequencing a fragment of the mitochondria cytochrome oxidase 1. The *B. tabaci* used was confirmed to be sub-Saharan Africa 1 Sub Group 3 (SSA1-SG3). Data on life history traits were collected from both laboratory and field experiments to facilitate model development and validation. To achieve this, a comprehensive study of the biology of the whiteflies was initiated. Data on longevity of newly emerged adults (males and females), and fecundity of adult females were collected under both field and laboratory conditions. For a better understanding of temperature-dependence, and the potential impact of climate change on the distribution and abundance of *B. tabaci* SSA1-SG3, data from the constant temperature experiments were used for phenology model building, while data from the field experiments were used for model validation. Cassava whiteflies are a threat to cassava production, and their populations may increase with climate change in some cassava-growing areas. Against this backdrop, a survey of smallholder farmers was carried out to understand their production characteristics, challenges and adaptive capacity to the potential impact of climate change on cassava whiteflies and associated viruses. Expert judgement of 20 whitefly and/cassava virus experts was then used to identify possible adaptation strategies and ways to enhance the adaptive capacity of the farmers.

The review of climate change impacts on whiteflies suggests that temperature increase will likely reduce whitefly fecundity, longevity and development time, while elevated CO_2 will lengthen development time but not likely affect fecundity and adult longevity of whiteflies. For most whitefly species living below their thermal optimum, temperature increase in both temperate and tropical zones will favour population increase. However, extreme temperatures will likely reduce whitefly populations. While climate change may alter levels of damages from whiteflies and plant viruses they transmit, the direction of change will be location specific and also depend on host-vector-virus interactions.

The immature development time from egg to adult significantly differed at the six constant temperatures tested under laboratory conditions. Immature development time decreased with temperature up to 28 °C, it was slowest at 16 °C where it lasted 59.3 days and fastest at 28 °C lasting only 16.3 days. Additionally, immature development time at 32 °C was slower than at 28 °C, but faster than at other temperatures. Eggs did not successfully developed to adults at 36 °C.

In climatic chambers, whiteflies oviposition peaked at temperatures from 20 °C to 28 °C and the number of eggs laid dropped outside these range of temperatures. The maximum number of eggs laid by an individual whitefly was 387 eggs, observed at 20 °C. Peak oviposition of 117.5 eggs per female was also recorded at 20 °C. Longevity was highest (19.7 days) at 24 °C for females and at 20 °C for males (11.0 days). The maximum longevity of an individual whitefly was 47 days (observed in both 20 °C and 24 °C treatments). Adult longevity at extreme temperatures was relatively lower. At 16 °C, longevity was 12.4 and 7.0 days for females and males respectively. At a high temperature extreme of 36 °C, it was 8.5 days (females) and 6.0 days (males).

The maximum longevity of a single individual during the field experiment was 28 and 31 days for males and females respectively. However, mean longevity for males was 9.2 days

and 13.1 days for females. The maximum number of eggs laid by an individual *B. tabaci* outdoor was 287 eggs, although the mean fecundity per female was 94.5 eggs.

Results from field experiments also show that immature development time decreased with increasing average temperature across *B. tabaci* generations. Development duration varied from 18 days in April (average temperature of 28.3 °C, and average relative humidity of 86.1%) to 25 days in July (average temperature of 25.6 °C and average relative humidity of 77.4%). It took an average of 21.3 days from egg to adult emergence under field conditions in Dar es Salaam, Tanzania where the average temperature and relative humidity were 28 °C and 78% respectively.

For the climatic chamber experiment, peak survival (62.5%) was recorded at 24 °C, while least survival (14.9%) was observed at 16 °C. Host plant effects in form of leaf drying and dropping accounted for additional mortality of *B. tabaci* on cassava at 16 °C because cassava being a tropical crop could not tolerate the constant 16 °C treatment.

Survival of immature stages under field conditions were also greatly affected by natural enemies and survival varied from 0.69% to 18.0%.

Under laboratory conditions, third instars had lower development threshold (T_o) temperature of 2.2 °C, which was lower than for other instars, while pupa stage had the highest (T_o = 11.6 °C). Lower development threshold temperature for egg to adult emergence was 4.3 °C under laboratory conditions. Degree-days requirement varied from 504.4 at 28 °C to 695.8 at 16 °C under laboratory conditions.

Similarly, results from field experiments suggest that pupa stage had the highest lower development threshold temperature (12.8 °C), and lower threshold temperature required for egg to adult emergence is 3.1 °C. The average degree-day requirement (egg – adult emergence) for field populations of *B. tabaci* in Dar es Salaam, Tanzania was 523.

Several models describing temperature-dependence of insects were fitted to life history data, and an overall phenology model was developed for this pest using ILCYM® software. Immature development time was best described by the log-logistic model. A combination of Sharpe & DeMichele 12 and Logan's Tb model provided an excellent description of temperature-dependent development rate of immature stages. Temperature-dependent mortality of immature stages was well described by Wang 2, Wang 3 and quadratic models. The longevity of adult females and oviposition time was best described by the Weibull distribution. The established phenology model predicted maximum population growth between 22 and 24 °C, and an optimum temperature for total fecundity per female to be 21.4 °C.

The estimated establishment risk index based on the established phenology model suggests a decrease in distribution of *B. tabaci* SSA1-SG3 with climate change in North and West Africa, and a southward range expansion in southern Africa. The distribution of *B. tabaci* SSA1-SG3 is predicted not to significantly change in East Africa.

In West Africa, the number of generations is predicted to increase with climate change based on generation index. However, activity index (a more reliable estimate of population growth) indicates a decrease in population growth with climate change. Climate change is

predicted to cause a decrease in population growth potential in North Africa, parts of Central Africa Republic, southern region of Sudan, eastern regions of Ethiopia, Kenya and Somalia. Both the estimated generation and activity index agree with an increase in the number of generations and population growth potential in most parts of East and Southern Africa. Cassava-colonising *B. tabaci* SSA1-SG3 will continue to pose significant threat in cassava-growing countries across Africa.

An interview study with 320 cassava farmers in Tanzania showed that most farmers produce cassava primarily for food. Some of the challenges of cassava production were diseases, insect pests, drought, finance, market access, planting materials among others. Farmers rely mainly on their friends and their own farms for cassava planting materials. Adaptive capacity was found to be moderate for most farmers, and some farmers apply simple methods to control cassava viruses and whiteflies. The 20 whitefly and/cassava virus expert interviewed recommended an integrated pest management approach, phytosanitation, novel vector management techniques and biocontrol of whiteflies as good adaptatation strategies; and that enhancing adaptive capacity of the farmers could be achieved with capacity building through level specific training of stakeholders.

This is the first comprehensive study on temperature-dependence of life history traits of a cassava-colonising and endemic African population of *B. tabaci* (combining field and laboratory experiments). This is also the first study that described the potential impact of climate change on a cassava-colonising and endemic African population of *B. tabaci.*
The findings will be useful for climate change adaptation planning and phytosanitary risk assessments.

Keywords: *B. tabaci,* climate change, temperature-dependence, smallholder farmers, phenology modelling, distribution, pest risk mapping, population dynamics

RESEARCH ACTIVITIES

Submitted manuscripts

- Aregbesola OZ, Legg JP, Sigsgaard L, Lund OS, Rapisarda C, 2018. How will climate change affect whiteflies and the viruses that they vector? *Journal of Pest Science* (submitted manuscript).

- Aregbesola OZ, Legg JP, Uzokwe VNE, Adeloye KA, Lund OS, Sigsgaard L, Rapisarda C, 2018. Adaptation of smallholder farmers to climate change impacts on cassava whiteflies and associated viruses in Tanzania. *International Journal of Pest Management* (submitted manuscript).

Manuscripts in preparation

- Aregbesola OZ, Legg JP, Lund OS, Sigsgaard L, Sporleder M, Carhuapoma P, Rapisarda C, 2018. Life history and temperature-dependent phenology model of cassava-colonising population of *Bemisia tabaci* (Gennadius) (manuscript in preparation).

- Aregbesola OZ, Legg JP, Lund OS, Sigsgaard L, Sporleder M, Carhuapoma P, Rapisarda C, 2018. Potential impact of climate change on the distribution and abundance of cassava-colonising *Bemisia tabaci* (Gennadius) in Africa (manuscript in preparation).

Selected conference presentations

- Aregbesola OZ, Legg JP, Lund OS, Sigsgaard L, Sporleder M, Carhuapoma P, Rapisarda C, 2018 July. Temperature-dependent phenology and climate change model of cassava-colonising populations of *Bemisia tabaci.* Accepted for oral presentation at XI the European Congress of Entomology, Naples, Italy.

- Aregbesola OZ, Legg JP, Uzokwe VNE, Adeloye KA, Lund OS, Sigsgaard L, Rapisarda C, 2017 September. Adaptation by smallholder farmers to climate change impacts on cassava whiteflies and associated viruses in Tanzania. Presented at the Agricultural Biosystems International Conference, Manitoba, Canada.

- Aregbesola OZ, Legg JP, Sigsgaard L, Lund OS, Rapisarda C, 2017 March. Influence of biotic and abiotic interactions on the development and survival of cassava whitefly, *Bemisia tabaci* (Gennadius). Presented at the 13th Triennial Symposium of the International Society of Root and Tuber Crop – Africa branch, Dares Salaam, Tanzania.

- Aregbesola OZ, Sigsgaard L, Lund OS, Legg JP, Rapisarda C, 2016 February. Potential impact of climate change on whiteflies (Hemiptera: Aleyrodidae) and implications for vectored plant viruses. Presented at the 2nd International Whitefly Symposium, Arusha, Tanzania.

Collaborations with institutions other than host universities

- International Institute of Tropical Agriculture (IITA), Dar es Salaam, Tanzania.
- International Potato Centre (CIP), Lima, Peru.

Selected courses and seminars attended

- Applied Insect Ecology with emphasis on insects-plant, insect-insect, and climate insect-interactions. Organised by the University of Copenhagen, Denmark
- Writing in the Sciences. Organised by Stanford University, USA
- Modelling climate effects on cropping systems. Organised by Aarhus University, Denmark

Dedication

This research work is dedicated to the Almighty God, the giver of life, and the kind support of my family and friends.

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Preface

Members of the *B. tabaci* species complex are the most economically important whiteflies globally due to direct damage on host plants, transmission of hundreds of plant viruses and significant losses caused to farmers. Climate change affects the life history and biological characteristics of insects. There is a dearth of information on temperature-dependence, and the potential impact of climate change on an African population of cassava-colonising *B. tabaci*. This study was initiated to fill this knowledge gap. The endemic African population of *B. tabaci* used for the study is *B. tabaci* SSA1-SG3 found in coastal Tanzania. The study used phenology modelling approach with the Insect Life Cycle Modelling (ILCYM®) software to investigate temperature-dependence, and the potential impact of climate change on an African population of cassava-colonising *B. tabaci*. Data from constant temperature experiments in the laboratory were used for phenology model building, while field data were used for model validation. The first part of the report (Chapter 1) provides a background on cassava, *B. tabaci*, climate change, impact of climate change on African agriculture, climate change impact on whiteflies, statement of problems and the objectives of the thesis. Chapter 2 is a thorough review of literatures on how climate change will affect whitefly species and the viruses they vector. The aspects considered include: impact of climate change on life history traits of whitefly species, distribution and movement, population dynamics, efficacy of management strategies and implication for vectored plant viruses. Chapter 3 presents life history and temperature-dependent phenology model of cassava-colonising *B. tabaci,* using laboratory (six constant temperatures) and field data (10 generations). Potential impact of climate change on the distribution and abundance of cassava whitefly is presented in chapter 4. A life-table study showing the influence of natural enemies on the mortality of cassava whitefly is presented in chapter 5. These included the identification of key mortality factor and key mortality stage of *B. tabaci* under field conditions in Dar es Salaam, Tanzania. Interviews with 320 smallholder cassava farmers and 20 international cassava whitefly/virus experts were used to identify adaptation strategies and measures which can be deployed to enhance the adaptive capacity of the farmers to the potential impact of climate change on cassava whiteflies and viruses. This study on smallholder farmers is presented in chapter 6. Chapter 7 is a detailed discussion on the whole study, while chapter 8 higlights the conclusions and recommendations.

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List abbreviations

ABIC Agricultural Biosystems International Conference

ACMBV *African cassava mosaic Burkina Faso virus*

ACMV *African cassava mosaic virus*

AFT Accelerated Failure Time

AgTraIn Agricultural Transformation by Innovation

AI Activity Index

AIC Akaike's Information Criterion

CBSD Cassava Brown Streak Disease

CBSV *Cassava brown streak virus*

CBSVs Cassava Brown Streak Viruses

CGIAR Consultative Group on International Agricultural Research

CIP International Potato Centre

CMBs Cassava Mosaic Begomoviruses

CMD Cassava Mosaic Disease

CMGs Cassava Mosaic Geminiviruses

CMMV *Cassava mosaic Madagascar virus*

DD Degree-Days

DNA Deoxyribonucleic Acid

DRC Democratic Republic of Congo

EACMCV *East African cassava mosaic Cameroon virus*

EACMKV *East African cassava mosaic Kenyan virus*

EACMMV *East African cassava mosaic Malawi virus*

EACMV *East African cassava mosaic virus*

EACMVUV *East African cassava mosaic virus-Ugandan- variant*

EACMZV *East African cassava mosaic Zanzibar virus*

EFSA European Food and Safety Authority

EPPO European Plant Protection Organisation

ERI Establishment Risk Index

EU European Union

FACE Fully Open Air CO_2 Elevation

FAO Food and Agricultural Organisation of the United Nations

FAOSTAT Food and Agricultural Organisation of the United Nations Statistics

GCM General Circulation Model

GI Generation Index

ICMV *Indian cassava mosaic virus*

IITA International Institute of Tropical Agriculture

ILCYM Insect Life Cycle Modelling

IPCC Intergovernmental Panel on Climate Change

MEAM1 Middle East–Asia Minor 1

MED Mediterranean

mtCOI mitochondrial cytochrome oxidase 1

NASA National Aeronautics and Space Administration

NR- Not Recommended

PCR Polymerase Chain Reaction

PPMC Pearson Product Moment Correlation

R Recommended

RH Relative Humidity

RNA Ribonucleic Acid

ROC Republic of Congo

SACMV *South African cassava mosaic virus*

SCMV *Sri Lankan cassava mosaic virus*

SR Seriously Recommended

SRES Special Report on Emission Scenarios

SSA sub-Saharan Africa

SSA1-SG3 sub-Saharan Africa 1-Sub Group 3

Tsh Tanzanian Shillings

TYLCV *Tomato yellow leaf curl virus*

UCBSV *Ugandan cassava brown streak*

URT United Republic of Tanzania

USA United States of America

USD United States Dollars

VVEG Virus Vector Ecology Group (of IITA, Tanzania)

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1. Introduction

1.1 Background on cassava

1.1.1 Origin and distribution of cassava

Cassava *(Manihot esculenta* Crantz*)* is a crop grown in tropical countries of Africa, Asia, South America, and other locations like Australia and United States of America. The origin of cassava has been a subject of debate. Although it appears that its primary route of introduction was around the western coast of Africa, other introductions were also reported from the axis of Reunion and Madagascar from where the crop spread to other parts of Africa (Hillocks *et al.*, 2002; Nweke, 2005). Several locations including Brazil, Peru, Mexico, Guatemala, Honduras, Venezuela, Amazonia and North America have been proposed as the centres of cassava origin (Allem, 2002). Most of these locations are found in South America,

hence scientists generally agree that cultivated cassava originated from South America (Allem, 2002; Olsen and Schaal, 2001; Ceballos *et al*., 2010). Using molecular tools, Olsen and Schaal (1999, 2001) provided further answers about the origin of cassava. They concluded that cassava emerged primarily from its conspecific wild relative. Furthermore they suggest that the southern border of the Amazon basin is possibly site of domestication of cassava.

1.1.2 Economic importance of cassava

Cassava production supports the livelihood of about 700 million people globally including smallholder farmers and industrial users (FAO, 2013). Several agronomic traits of cassava makes it a staple food and an excellent food security crop that can be counted on to supply calories when other crops fail. In Africa, cassava ranks third among major staple food, with rice and maize being first and second respectively (Adenele *et al*., 2012). It is resistant to drought, can tolerate poor soils and high temperature, and also positively responds to elevated CO_2 levels. All these make it a promising crop for now and the future (Jarvis *et al.*, 2012). Nweke (2005) opined that cassava production can be used as a strategy for increasing farmers' income, reducing poverty and improving food security. Besides the good food values of cassava, it can also be used to make livestock feed.

Figure 1: Cassava plant

1.1.3 Production of cassava

Global cassava production increased from 71 million metric tonnes in 1961 to about 289 million metric tonnes in 2015 (FAOSTAT, 2015). Africa accounts for 55% of global cassava production, other continents where cassava is massively produced are Asia (29%) and Latin America (14%). Moreover, nine out of top ten cassava producers are located in Africa and Asia.

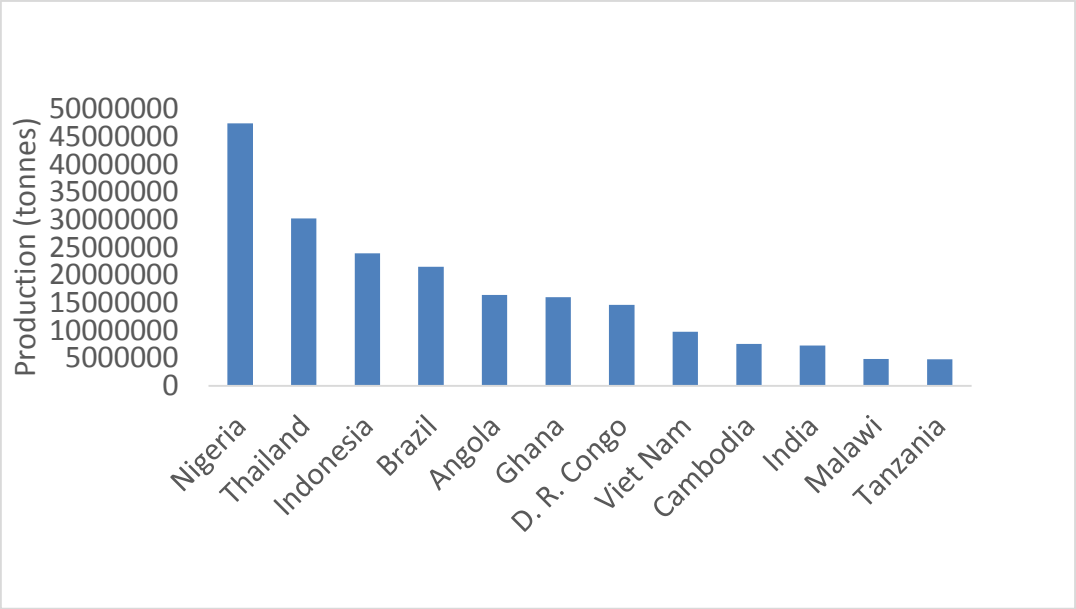

Figure 2: Top global cassava producing countries

Source: FAO STAT, 2013.

This explains why 73% of global cassava production is concentrated in these continents (SADC, 2007). Nigeria is the largest producer in Africa and globally, growing an estimated 48 million metric tonnes in 2015. Other leading producers are Brazil, Indonesia, Thailand, Angola, Ghana, Democratic Republic of the Congo, Viet Nam and Cambodia (CGIAR, 2017). There has been an average of 2.2% increase per annum in world cassava production since the 1970s.

Table 1: Production, yield and harvested area of cassava showing top African producers

Area	Production (tonnes)	Harvested area (Ha)	Yield (hg/ha)
World	268277743	23867002	112405
South America	30641834	2148121	142645
Asia	89833397	4100218	219094
Africa	145770528	17307152	84226
Nigeria	47406770	7102300	77203
Angola	16411674	755874	101060
Ghana	15989940	889000	185872
Democratic R. Congo	14611911	1812743	81000
Malawi	4813699	222750	225040
Tanzania	4755160	800454	62374
Cameroon	4596383	326183	150760
Mozambique	4303000	870300	60947
Benin	3910036	296641	137092
Sierra Leone	3810418	393839	104994
Madagascar	3114578	375575	78007
Uganda	2979000	852000	33005
Rwanda	2948121	198207	159407

Source: FAO STAT, 2013.

This growth is a product of an expansion of cultivated area rather than on increasing productivity (Prakash, 2008). According to FAOSTAT (2014), even though Africa produces more cassava than Asia and South America put together, the average yield in Africa (84226 hg/ha) is much lower than in both Asia (219094 hg/ha) and South America (142645 hg/ha). Between 1961 and 2014, there was a 40 percent expansion in the global harvested area of

cassava, from 9.6 million to 23.9 million hectares, the biggest percentage expansion in cultivated area among the world's five major food crops (FAOSTAT, 2014).

1.1.4 Constraints to cassava production

Cassava production is constrained by abiotic and biotic factors. Among the abiotic factors limiting cassava production are: access to land, finance, inadequate structural facilities, inadequate storages and processing services. While, biotic constraints include weeds, invertebrate pest and disease. Pest and diseases cause massive damages to cassava crops and farmers incur huge losses annually.

1.1 Cassava Mosaic Disease

While pests and diseases are the major problems facing cassava farmers, Cassava Mosaic Disease is most devastating (Legg, 2009). Damage caused by CMD could be more than 50% depending on the virulence of the infecting virus strain(s), micro-climate and the susceptibility of the cultivar (Legg *et al*., 2011). In economic terms, yield losses due to CMD in Africa are estimated to be around 440 million USD annually (Thresh *et al*., 1997). A newer estimate from Kenya put losses at 1, 300 USD/hectare (Masinde *et al*., 2016; Bart and Taylor, 2017). For nearly three decades, cassava production in East Africa has been hampered by the spread of a very severe CMD pandemic which started from Uganda and spread to neighbouring countries. Currently, about nine countries in East and Central Africa have been struck by the pandemics (Legg *et al*., 2015). The countries include: Uganda, Sudan, Democratic Republic of Congo (DRC), Republic of Congo (ROC), Rwanda, Tanzania, Kenya,

Burundi and Gabon (Legg, 2009). Recent analysis by Tajebe *et al*. (2015a) suggests that the pandemics is spreading towards the south-east of Tanzania at a rate of 26 km/year.

CMD is caused by eleven viruses which are circular ssDNA viruses in the family *Geminividae* and genus *Begomovirus*. The disease is vectored by cassava whitefly (*B. tabaci*) and disseminated through stem cuttings used for its propagation. The viruses causing this disease are collectively referred to as the cassava mosaic geminiviruses (CMGs). Most of the CMGs are endemic in Africa, and over 27 strains have been identified (Ndunguru *et al*., 2016). Their distribution and economic importance varies globally. The eleven CMGs are: *African cassava mosaic virus(*ACMV), *African cassava mosaic Burkina Faso virus* (ACMBV), *Cassava mosaic Madagascar virus* (CMMV), *East African cassava mosaic virus* (EACMV), *East African cassava mosaic Malawi virus* (EACMMV), *East African cassava mosaic virus-Ugandan-variant* (EACMVUV), *East African cassava mosaic Zanzibar virus* (EACMZV), *East African cassava mosaic Cameroon virus* (EACMCV), *South African cassava mosaic virus* (SACMV), *East African cassava mosaic Kenyan virus* (EACMKV)*, Indian cassava mosaic virus* (ICMV) and *Sri Lankan cassava mosaic virus* (SCMV). Infected plants are characterised by varying levels of leaf distortion, mosaic, chlorotic patterns, and poor root yield due to reduced photosynthetic capacity of the plant (Bart and Taylor, 2017).

Figure 3: Cassava plant showing symptoms of CMD

1.2 Cassava Brown Streak Disease

The emerging pandemic of Cassava Brown Streak Disease is one of the most important problems threatening cassava production and food security in East and Central Africa (Taylor *et al*., 2012; Legg *et al*., 2015). Yield losses in susceptible varieties could be up to 70% annually (Hilllocks *et al.*, 2002; Maruthi *et al.,* 2005). CBSD was first reported by Storey (1936) at the Amani research station of Tanganyika (now Tanzania). The disease has been spreading through East, Central and Southern Africa, and is now considered a threat to West Africa where the virus has not been reported (Kaweesi *et al*., 2014). Countries affected are: Tanzania, Uganda, Kenya, Malawi, Mozambique, Burundi, Rwanda and Democratic Republic of Congo (Kaweesi *et al.,* 2014).

CBSD is caused by two members of the virus family *Potyviridae* in the genus *Ipomovirus*, namely: *Cassava brown streak virus* (CBSV) and *Ugandan cassava brown streak virus*

(UCBSV), both species are collectively referred to as CBSVs. Like CMGs, CBSVs are also transmitted by cassava whitefly (*B. tabaci*) and disseminated through infected cuttings (Maruthi *et al*., 2005). Cassava plants infected with CBSD are characterised by a range of symptoms on the leaves, stem and roots. All parts of the plant show some forms of symptoms, but the extent of the symptoms depend on growth stage of the crop vis-a-vis the time of infection, prevailing environmental conditions, and varietal sensitivity (Hillock *et al.,* 2002). The name `brown streak' describes the brown lesions seen on young stems of infected plants. However, this is not the most conspicuous symptom of the disease and is sometimes absent (Hillock *et al.,* 2002). Common foliar symptoms are chlorosis or feathery necrosis which can appear shortly after planting infected cuttings or when the viruses are transmitted by its vector. However, root necrosis cause more economic losses (Kaweesi *et al*., 2014). Necrotic roots are usually inedible and have poor market value (Ogwok *et al.,* 2012).

Figure 4: Cassava plant showing symptoms of CBSD

1.4 *Bemisia tabaci* species complex

1.4.1 Economic importance

B. tabaci (Gennadius) (Hemiptera: Aleyrodidae) is a notorious, highly adaptive phloem feeding insect pest with a wide host range (Oliviera *et al*., 2001; CABI, 2017). Although *B. tabaci* has been known as a crop pest for over a century (Gennadius, 1889), it only recently became an economically important pest (Duffus and Flock, 1982; Gonzalez *et al.*, 1992; Legg *et al.,* 2014a). It is now considered among the most economically important and globally distributed insect pest causing severe crop losses (Global Invasive Species Database, http://www.issg.org/database). Although *B. tabaci* likely originated from Africa (Dinsdale *et al.,* 2010), increased climatic suitability and human activities has facilitated its global distribution, development of insecticide resistance and new genetic groups (Roditakis *et al.,* 2005). Feeding of *B. tabaci* adult and immatures stages also induces chlorotic spots on leaves and at higher infestation levels, the leaf may turn yellow and eventually fall off (CABI, 2017). Honeydew produced by immature *B. tabaci* on leaves attracts moulds, reduces photosynthetic area and crop quality. More importantly, *B. tabaci* vectors over 100 plant viruses (Czoneck, 2002; Jones, 2003; Hogenout *et al*., 2008; Polston *et al*., 2014) driving the disease epidemics of economically important plant viruses globally. For instance in Africa, *B. tabaci* vectors the nine cassava virus diseases causing annual losses worth 1 billion USD (Legg *et al.,* 2006; Legg *et al.,* 2014a).

Figure 5: *B. tabaci* on cassava leaf

1.4.2 Taxonomy of *Bemisia tabaci*

Gennadius (1889) described a previously unidentified sap sucking insect found on tobacco in Greece as *Aleyrodes tabaci* which was later moved to the genus *Bemisia* (Gennadius, 1889; Tay *et al*., 2017). Since then, there has been major taxonomic revisions (Tay *et al*., 2017) and up to 20 other synonyms exist for *B. tabaci* (Olivera *et al*., 2001; CABI, 2017). Molecular markers (allozyme and DNA markers) later used to resolve the conundrum showed substantial sub-clustering, giving rise to the application of the biotype concept in *B. tabaci* taxonomy (Tay *et al.,* 2017). Phenotypic plasticity on different hosts; differences in geographical distribution, reproductive characteristics, resistance to insecticides, natural enemies, endosymbionts and esterase banding patterns led to an explosion of *B. tabaci* biotype designations across the world and at least 36 biotypes of *B. tabaci* have been reported (McKenzie *et al.*, 2004; De Barro *et al.,* 2011; Liu *et al*., 2012). However, much progress has been achieved on *B. tabaci* taxonomy and systematics. Current evidences from

phylogenetic analyses indicate that *B. tabaci* is a species complex with 11 genetic groups and over 24 morphologically indistinguishable species (Boykin *et al*., 2007; Dinsdale *et al.*, 2010; De Barro *et al.,* 2011; Boykin *et al*., 2012; Lee *et al*., 2013). To elucidate more on *B. tabaci* taxonomy, using more robust techniques, Boykin *et al*. (2007) introduced the concept of "genetic groups" to *B. tabaci* taxonomy building on the work of De Barro *et al*. (2005). De Barro *et al.* (2011) reported the 24 identified genetic groups (putative species of the *B. tabaci* complex) and the biotypes that were previously used to describe them (in parenthesis) if applicable. These are : Asia 1 (PCG-2, H, M, NA), Asia II 1 (K, P, PK1, PCG-1, SY, ZHJ2), Asia II 2, Asia II 3 (ZHJ1), Asia II 4, Asia II 5 (G), Asia II 6, Asia II 7 (Cv), Asia II 8, China 1 (ZHJ3), China 2, Middle East–Asia Minor 1 (B, B2), Middle East–Asia Minor 2, sub-Saharan Africa 1, sub-Saharan Africa 2 (S), sub-Saharan Africa 3, sub-Saharan Africa 4, Uganda, India Ocean (MS), Australia (AN), Australia/Indonesia, Italy (T), Mediterranean (Q, J, L, Sub-Saharan Africa, Silverleaf biotypes) and New World (Jatropha, Sida, A, C, D, F, N, R). However, more recent studies indicates that there are possibly more than 35 morphologically indistinguishable species (Hu *et al*., 2011; Alemandri *et al*., 2012; Chowda-Reddy *et al*., 2012; Firdaus *et al*., 2013; Lee *et al.*, 2013; Legg *et al.,* 2014a).

1.4.3 Host range and distribution

B. tabaci has been reported on over 600 host plants including: vegetables, legumes, ornamental, root and tuber crops across the world (Oliviera *et al*., 2001; Abd-Rabou and Simmons, 2010; CABI, 2017). Although mostly polyphagous, monophagus species has also been reported on various crops (Abd-Rabou and Simmons, 2010). The Mediterranean (MED)

and Middle East Asia Minor 1 (MEAM1) genetic groups are reported widely across the world and are probably the most invasive groups (Boykin *et al*., 2007; De Barro *et al*., 2011; Firdaus *et al*., 2013). Human activities and climatic suitability may be responsible for the recent detection of Mediterranean species of *B. tabaci* in Brazil (Barbosa *et al.,* 2015), Malaysia (Shadmany *et al*., 2013), Argentina and Uruguay (Grille *et al*., 2011). *B. tabaci* is a regulated pest in Europe and currently found mainly in southern European countries (Spain, France, Italy, and Greece), although there are reports of detection of the pest in other parts of Europe (Gilioli *et al*., 2014; CABI, 2017). *B. tabaci* also widely occurring in China, India, Japan, Pakistan and other Asian countries where it is causing massive damages (CABI, 2017).

Following the introduction of cassava from Latin America to Africa over four centuries ago, cassava-colonising *B. tabaci* species has long been recognised to occur in most cassava-growing parts of Africa and are now endemic populations that have adapted to the crop (Legg *et al.,* 2014a). Available literatures and *mtCOI* sequences data suggest that SSA1-5 genetic groups of *B. tabaci* have been recognised from cassava in Africa (Legg *et al.,* 2002; Berry *et al.*, 2004; Sseruwagi *et al.,* 2006; Esterhuizen *et al*., 2013; Legg *et al.,* 2014a; Tajebe *et al.,* 2015a; Manani *et al.,* 2017). For instance, SSA1 group is distributed across sub-Saharan Africa; SSA2 has been identified in East and West Africa; SSA3 is present in Cameroon and Togo; whereas SSA4 appears to be restricted to Cameroon; and SSA5 is probably limited to South Africa (Berry *et al.,* 2004; Gnakiné *et al*., 2012; Esterhuizen *et al.*, 2013; Legg *et al.,* 2014a). Furthermore, Tajebe *et al*. (2015a) identified Sub-Saharan Africa 1 (SSA1), East Africa 1, Indian Ocean and Mediterranean on cassava across Tanzania. While

Manani *et al.* (2017) reported the presence of sub-Saharan Africa 1 and 2 on cassava in Kenya.

1.4.4 Morphology

Freshly laid eggs are ovoid, whitish – yellow and gradually turn brown before hatching. Eggs are small (about 0.26 mm in length with a 0.1 mm diameter) and often found either scattered or in clutches on abaxial surface of the leaf. Egg hatches after 5 – 9 days depending on host and environmental conditions like temperature and relative humidity (EPPO, 2003). *B. tabaci* is hemimetabolous, has four instars and a "pupa" stage varying in length from 0.3 mm (first instar) to 0.7 mm (pupa stage). The fourth instar and pupa stage are continuous and moulting does not occur, hence it is not a true pupa stage, however, the "pupa" designation has been retained in whitefly literature for convenience and clarity (Gelman *et al.*, 2002; Walker *et al.,* 2009). First to fourth instars have a yellowish structure called bacteriome (formerly mycetomes) that harbour endosymbionts. Some endosymbionts play important roles in transmission of plant viruses by adult whiteflies (Tajebe *et al*., 2015b). Like most whiteflies, *B. tabaci* nymphs are usually dorso-ventrally flat and oval in shape. Length, width and appearance serve to differentiate one instar stage from another since it is uniform for the same host, and this was the method used throughout this study. Immature stages of *B*. *tabaci* moult before growing to next instar stage and provides further evidence that there is growth from one instar to another. First instars or crawlers have well developed legs and crawl around on the leaf surface until it can find a suitable site. Once they find a suitable feeding site within few hours they settle and become sessile.

The fourth instar and pupa are also ovoid in shape. The pupa stage is characterised by remarkable changes, the nymphs gradually metamorphose into an adult whitefly as the body turns yellowish, and red eyes become obvious. On eclosion, *B. tabaci* makes a "T" slit on the pupa case. Pupa case characteristics are also important in distinguishing whitefly species (Martins, 1987). According to Bryne and Bellows (1991), the male is smaller (body length: 0.85 ±0.05; wing expanse: 1.81±0.06) than the female (body length: 0.91±0.06; wing expanse 2.13±0.06). Shortly after adult emergence, the body and wings are covered with a whitish- yellow powdery excretion (EPPO, 2003).

Figure 6: *B. tabaci* on cassava leaf

1.4.5 Bionomics of *B. tabaci*

1.4.5.1 Development of immature nymphs

Development is an important aspect of an insect's life history. It undergoes slow changes in body form (egg to fourth instar/pupa) and a drastic change during the late fourth instar

stage/pupa before eclosion into an adult *B. tabaci* (Gelman *et al.,* 2002, Walker *et al.,* 2009). Development of *B. tabaci* varies with environmental conditions, being faster during summer or warmer conditions and very slow during winter or cooler conditions (Gerling *et al*., 1986). Temperature and relative humidity appear to be the key environmental factors influencing the development of whiteflies (Gerling *et al*., 1986; Bale *et al.,* 2002; Bonato *et al.,* 2007). Due to its high plasticity, *B. tabaci* is also able to aestivate if environmental conditions are unfavourable (Butler *et al.,* 1983). In this study, the ability of *B. tabaci* to aestivate was observed on cassava at 32 °C. Additionally, development of *B. tabaci* also differs with the hosts on which it is growing. This led to the notion of *B. tabaci* having different biological types or biotypes (Brown *et al.,* 1995).

Development of *B. tabaci* has been studied on several genetic groups (Biotype) of *B. tabaci* under a near optimum temperature conditions in the laboratory (25 °C – 28 °C, RH 60 – 80%). Generally, total immature development time of MEAM1 (B- biotype) ranges from 17.31 on eggplant to 44.4 on cassava (Tsai and Wang, 1996; Musa and Ren, 2005; Zang *et al*., 2006; Iida *et al.,* 2008; Mansaray and Sundufu, 2009; Carabali *et al.,* 2010). For MED (Q-biotype), it ranges from 24.6 on cucumber to 35.2 on bell pepper (Iida *et al.,* 2008). Zang *et al*. (2006) reported total immature development for *B. tabaci* (ZH-J1) to be 21.5 days on cotton and 22.9 days on squash. Similarly, Chaubey *et al.* (2015) studied life history of *B. tabaci* on cotton and reported immature developmental time of 25.75 days for *B. tabaci* (Asia 1), 24.05 days for *B. tabaci* (Asia II-1) and 23.80 days for *B. tabaci* (Asia II-7).

For studies on development and survival of *B. tabaci* at wider temperature ranges, see chapter 2.

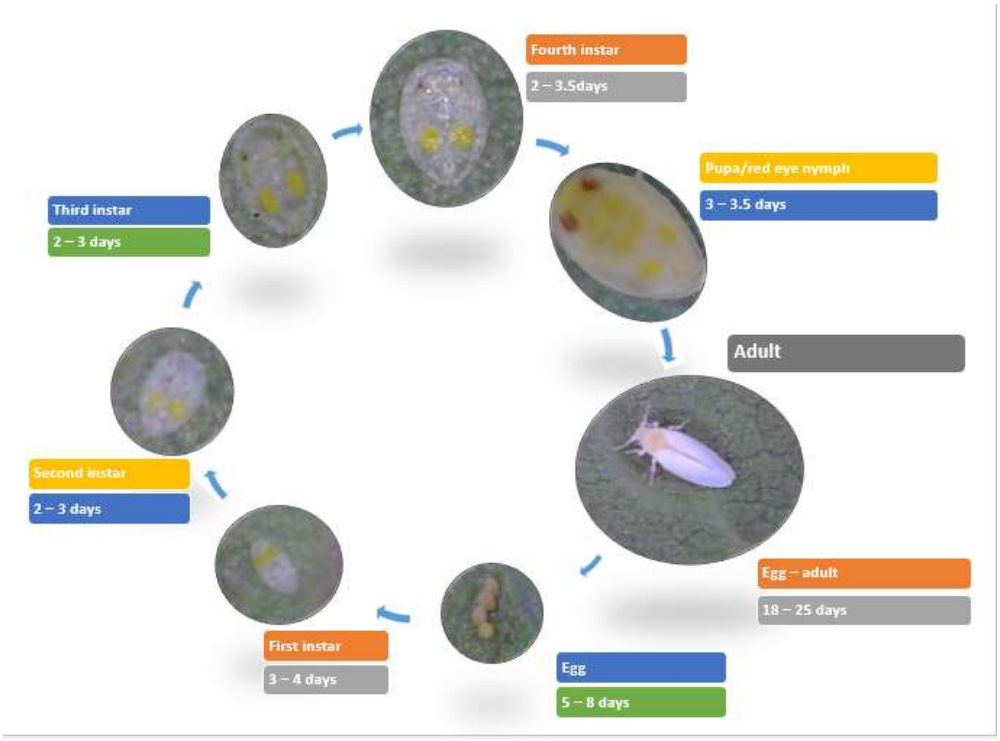

Figure 7: Life cycle of *B. tabaci* on cassava under field conditions in Dar es Salaam, Tanzania

1.4.5.2 Survival of immature *B. tabaci* nymphs

Survival of insect herbivores including *B. tabaci* is influenced by several factors primarily, the host plant, the environment and natural enemies. Considering that *B. tabaci* is a species complex, survivorship of these species also varies with the host plants. Natural enemies caused substantial mortality in populations of *B. tabaci* from most life-table studies reported (Asiimwe *et al*., 2007; Naranjo and Ellsworth, 2005; Karut and Naranjo, 2009). Predation was reported to be the main source of *B. tabaci* mortality on alfalfa, ornamental

lantana, cotton and cantaloupes (Naranjo and Ellsworth, 2005; Naranjo *et al.,* 2009). Similarly, parasitism by aphelinid parasitoids was the main cause of mortality on cassava (Asiimwe *et al.* 2007) and cotton (Karut and Naranjo, 2009). This was also observed on cassava in this study. Wind, dust and rain also cause dislodgement of most life stages thus affecting survival of *B. tabaci* (Naranjo *et al.,* 2009). In the absence of natural enemies and under favourable environmental condition, influences of host plants on survival of *B. tabaci* become more pronounced. Although the species of *B. tabaci* complex are able to adapt to different host, their fitness is sometime affected leading to poor survival on some host. Egg – adult survivorship of some *B. tabaci* species could be very high, for instance up to 94.3% for MEAM1 on tomato, 93.2% for MEAM1 on eggplant and 96.3% for MED on eggplant (Iida et al 2006). At 25 °C and RH 60±5, Bonato *et al.* (2007) observed egg – adult survival for MED to be 85% on tomato. However, note that MEAM1 and MED species are invasive species, and their high fecundity and survival rates contribute to the invasive success. In the absence of natural enemies and under favourable conditions (25 °C – 26 °C, relative humidity 60-80%) instances of lower survivorship are also widely reported. For example, survivorship of 6.1 % for MEAM1 on bell pepper (Iida *et al.,* 2006), 26.5% for MEAM1 on garden beans (Mansaray and Sundufu, 2009), 27.5% for MEAM1 on cassava (Carabali *et al.,* 2010), 46.4% and 45.8% respectively for MEAM1 on cucumber and garden beans (Tsai and Wang, 1996). Survivorship of 26.0% was also observed for ZH-J1 on squash (Zang *et al.,* 2006). Notice the differences in survival of the *B. tabaci* species on different host at similar temperature.

1.4.5.3 Reproduction and fecundity of adult female *B. tabaci*

Most insects undergo sexual reproduction, meaning mature males and females must be present in time and space for reproduction to take place (Gullan and Cranston, 2005). However, *B. tabaci* utilises haplo-diploid reproduction, and it is able to reproduce in the absence of fertilisation. This process is called Arrhenotoky (Gerling *et al.,* 1986; Bryne and Bellow, 1991). Virgin females can only produce male offspring, while mated females are able to produce both males and females (Bryne and Bellow, 1991). One of the implications of arrhenotoky in *B. tabaci* is that virgin females may initiate field populations, provided their longevity extends till the emergence of their male progeny (Gerling *et al.,* 1986).

Fecundity in *B. tabaci* is influenced by host plant, *B. tabaci* species and environmental conditions. Oviposition generally decreases with temperature (Bonato *et al.,* 2007). In their studies on cotton, Chaubey *et al*., 2015 observed fecundity of 54.04 eggs per female (Asia 1), 62.3 eggs per female (Asia II-1) and 64.3 eggs per female (Asia II-7). On several host, MEAM1 has been associated with very high fecundity (Musa and Ren, 2005; Tsai and Wang, 1996; Mansaray and Sundufu, 2009). Fecundity up to 223.67 eggs per female was reported by Tsai and Wang (1996) on eggplant. Fecundity of an indigenous Chinese population of *B. tabaci* (ZH-J1) was 58.5 eggs per female on cotton, 2.9 eggs per female on tobacco, 0.5 eggs per female on cabbage, 5.0 eggs per female on squash and 3.4 eggs per female on kidney beans (Zang *et al.,* 2006). While At 25 ^{o}C and RH 60±5, Bonato *et al.* (2007) observed fecundity up to 105.3 eggs per female for MED on tomato.

1.4.5.4 Adult longevity of *B. tabaci*

Reports of adult longevity under laboratory and field condition vary widely with host plants and the prevailing environmental conditions. Besides temperature and host plant effects, humidity also influences adult longevity. A detailed summary of the influence of temperature and other environmental factors on adult longevity are presented in chapter 2. *B. tabaci* longevity up to 48 days was observed on cassava, 33 days on sweet potatoes and more than 13 days on cotton under field conditions (Legg, 1995) and longevity up to 61.5 days has been reported on cotton (Gerling *et al*., 1986). Carabali *et al.* (2010) observed adult longevity of 3.1 days for MEAM1 on cassava at 25 °C. While at 26 °C, Mansaray and Sundufu, (2009) observed longevity of MEAM1 to be 15.3 days on Soybean and 10.7 days on Garden beans. Musa and Ren (2005) studied longevity of MEAM1 raised on soybean, cowpea and garden peas and reported longevity of 12.30, 11.70 and 9.80 days respectively. At 28 °C, RH 70%, longevity of ZH-JI ranges from 11.2 days on cotton to 1.2 days on cabbage (Zang *et al*., 2006). While at 25 °C and RH 60±5, Bonato *et al*. (2007) observed adult longevity up to 21.9 for MED on tomato and up to 39 days at 17 °C.

1.5 Climate change

1.5.1 Basics of climate change

The unique environmental condition on earth makes it the only planet in our solar systems known to support life (Singh *et al*., 2013). The earth's atmosphere has three key life supporting element: oxygen, water and a suitable temperature. Climate change is described as a change, either natural or anthropogenic, in the earth's climate that persists for decades or longer (Australian Academy of Science, 2017). Anthropogenic emission of green house

gases (carbon dioxide, nitrous oxide, ozone, methane and water vapour) is the main cause of global climate change. The most important factors responsible for this significant increase of greenhouse gases in the atmosphere are: massive deforestation caused by global increase in agricultural production, the need to meet up developmental and technological necessities (leading to unprecedented increase in burning of fossil fuel) (Singh *et al*., 2013).

1.5.2 Evidence of climate change

Since the industrial revolution in the 1750s, the global average amount of the greenhouse gases in the atmosphere has increased by 41% (CO_2), 16% (methane) and 20% (nitrous oxide) (Jones, 2016). Estimates for 2017 put the current atmospheric CO_2 levels at 404.42 ppm and it is predicted to reach 650 ppm by 2100 (NASA, 2016). Similarly, Earth's surface in the last three decades has been successively warmer than any decade since 1850. Available data from independent sources show that the last thirty years (1983 to 2012) was very likely the warmest period of the last Millennium (IPCC- Intergovernmental Panel on Climate Change, 2014). With a very high level of confidence, the fifth assessment report of the IPCC posit that warming of the climate system is unequivocal. Statistics from the IPCC's highest emission scenario predict an increase of 2.6 – 4.8 °C in average global temperature by 2100 if emissions continue at current rate (IPCC, 2014). Change already observed include: warming of the atmosphere and ocean, diminished amounts of snow and ice, a rise in seas level globally, and rampant extreme climate events.

1.5.3 Climate change and Africa

Experts suggest that the impacts of climate change on the world's eco-socio-economic systems will not be equally shared across the world (Kotir, 2011). Distribution of climate change impact will vary with the ability and resources across nations of the world (Kotir, 2011). Sub-Sahara Africa is considered very vulnerable to climate change due to its possession of limited technical and financial resources to cope with climate change (Adhikari *et al.,* 2015). Chapter 22 of the fifth assessment report of IPCC (Niang *et al.,* 2014) discussed the observed and projected impact of climate change on Africa. There is increased confidence that warming over Africa is due to anthropogenic climate change (Niang *et al.,* 2014). Projections of the A1B and A2 Special Report on Emission Scenarios indicates that mean annual temperature rise over Africa is likely to exceed 2 °C in comparison to data from end of the 20th century, with a projected rate of warming of about 0.2 °C per decade (Niang *et al.,* 2014). Simulations from most General Circulation Models indicate relatively moderate changes in rainfall compared to the current variabilities. Rainfall is expected to increase over most parts of the continent except in Southern parts of Africa and North-East Africa where about 10% reduction in rainfall are predicted by 2050. (Niang *et al.,* 2014). The impact of climate change is already felt on ecosystems across Africa, and future impact will be significant if the global climate change trend continues (Niang *et al.,* 2014).

1.5.4 Impact of climate change on African agriculture

Agricultural systems in Africa are among the world's most vulnerable to the impact of climate change (Kotir, 2011; Niang *et al.,* 2014; Adhikari *et al.,* 2015). African agriculture's vulnerability to climate change is mainly because: agricultural systems are primarily rain-fed, characterised by high intra- and inter-seasonal climate variability, frequent droughts and floods, and majority of the farmers are smallholders with limited financial resources, infrastructure and access to information needed to adapt (Pereira, 2017). Interaction of climate change and other non-climate stressors will aggravate the vulnerability of African agriculture, especially in semi-arid areas of the continent (Niang *et al.,* 2014).

Schlenker and Lobel (2010) reported yield reductions up to -22, -17, -17, -18, and -8% for maize, sorghum, millet, groundnut, and cassava respectively in regions across Africa. In their study on climate change impact on millet and sorghum production in West-Africa, Sultan *et al*. (2013) reported a negative impact on yield, especially for higher temperatures and reduced rainfall combinations. The Sudanian region bordering Benin, Mali, Burkina Faso, southern Senegal and northern Togo showed greater probability of yield reduction due to the high sensitivity of the locations to temperature changes. Addition, crop yields were more sensitive to rainfall changes in the Sahel region (northern Senegal, Burkina Faso, Niger and Mali) (Sultan *et al.,* 2013). In East Africa, wheat will be the most vulnerable crop and up to 72% reduction compared current production level has been predicted (Adhikari *et al.,* 2015). For maize sorghum and rice, anticipated yield reductions could be as high as 45% (Adhikari *et al.,* 2015). However, cereals like millet and sorghum and root crops like cassava and potato show some resilience and will likely be less affected compared to other crops (Jarvis *et al.*, 2012; Schlenker and Lobel, 2010; Sultan *et al.,* 2013; Adhikari *et al.,* 2015). Distribution, abundance and damage done by weeds, insects, pathogens and other pests is

expected to change in response to climate change and other human induced factors (Niang *et al*., 2014; Pereira, 2017). The distribution of major cassava diseases and pest in Africa are predicted to change with some range expansion in some locations, while pressure from the pest and disease will reduce in others (Campo *et al.,* 2011; Jarvis *et al.,* 2012). Although most climate change impact studies on African agriculture suggest significant negative impacts, there are likely to be some positive aspects like reduced pest pressures, extended crop area and season. Increased temperature and rainfall changes are projected to extend growing seasons in Ethiopia and Southern Africa (Pereira, 2017).

1.5.5 Climate change and cassava

There are limited studies on the impact of climate change on cassava. Schlenker and Lobel (2010) reported a minor negative impact of climate change on cassava in comparison to maize, sorghum, millet and groundnut. However, newer studies show that cassava will more likely be positively impacted by climate change. Jarvis *et al.* (2012) used a combination of General Circulation Models and other bioclimatic models to investigate the potential impact of climate change productivity, climatic suitability and pests of cassava in Africa. Their results suggest that cassava shows changes in climatic suitability between -3.7% to +17.5% across Africa and most countries are positively impacted. Jarvis *et al.* (2012) then concluded that cassava is highly promising and resilient to impact of climate change. Hence it can provide adaptation options for millions of Africans depending on cassava for their livelihood. Rosenthal *et al.* (2012) further corroborated the position of Jarvis *et al*. (2012) that cassava will benefit from the impact of climate change. In their study, Rosenthal *et al*. (2012)

combined a fully open air CO_2 elevation (FACE) and open top chamber experiments to assess the impact of elevated CO_2 on productivity of cassava. They concluded that cassava greatly benefited from elevated CO_2. Their opinion was that increased rate of photosynthesis, consistently larger canopy of cassava grown at elevated CO_2, and exposure to a significantly longer period of high photosynthetic capacity increased productivity of the crop.

1.5.6 Climate change and whiteflies

Life history of whiteflies can vary greatly with differences in temperature, CO_2, Ozone, relative humidity, and host plant (Bonato *et al.,* 2007; Wang *et al*., 2014; Cui *et al.,* 2012; Curnutte *et al.,* 2014). Available records on *B. tabaci* MEAM1 and MED indicates a reduction in fecundity with temperature increase (Wang and Tsai, 1996; Qui *et al*., 2003; Guo *et al*., 2013; Bonato *et al*., 2007). Few studies are available relating to the effects of ozone and CO_2 on whiteflies, Curnutte *et al.* (2014) suggests that elevated CO_2 will not affect *B. tabaci* fecundity. While elevated ozone has a negative effect on *B. tabaci* fecundity (Cui *et al.,* 2012). As the case for most insects, all available studies show that immature developmental time of *B. tabaci* decreases with increasing temperature (Muniz and Nombela, 2001; Bonato *et al.*, 2007; Han *et al*., 2013; Nava-Camberos *et al*., 2001; Yang and Chi, 2006; Bayhan *et al.*, 2006). The same trend of decreasing developmental time with temperature increase was also observed in this study for SSA1-SG3 population of *B. tabaci* in Tanzania. Similarly, adult longevity decreases with temperature increase (Qui *et al.*, 2003, Wang and Tsai, 1996; Guo *et al*., 2013; Bonato *et al*., 2007) and elevated CO_2 may not have significant effects on adult

longevity of *B. tabaci* (Wang *et al.*, 2014). Furthermore, elevated atmospheric CO_2 and ozone levels may alter trophic interactions between the plant, whiteflies and their natural enemies (Wang *et al.,* 2014). Climate change has also been predicted to affect the distribution (Gilioli *et al*., 2014) and population dynamics (Zidon *et al*., 2016) of *B. tabaci*.

1.6 Problem statement and objectives of the study

Continual anthropogenic emission of greenhouse gases has been identified as the primary driver of the global climate change, creating long-lasting changes in climate system, and increasing the possibilities of severe and irreversible impacts on ecosystems (IPCC, 2014). Projections from all assessed emission scenarios indicate that global surface temperature will rise over the 21st century (IPCC, 2014). Global climate change has been predicted to affect both natural and agricultural ecosystems triggering major changes in life history, geographical distribution, abundance and ecological interactions of insect pests across the globe (Harrington *et al.,* 2001; Bale *et al.,* 2002; Gilioli *et al.,* 2014; Sharma, 2014).

Cassava is both a food and economic security crop, supporting the livelihood of about 700 million people globally (FAO, 2013). Cassava is potentially highly resilient to impact of climate change and could give farmers options for adaptation when other major food crop face challenges (Jarvis *et al.,* 2012). However, *B. tabaci* and the viruses they transmit, cause severe yield losses over 1 billion USD on cassava farms across Africa (Legg *et al.,* 2006). Recently, a super-abundant population of *B. tabaci* was implicated in pandemics of CMD and CBSD in East and Central Africa (Legg *et al.,* 2014a). *B. tabaci* is a species complex and

five distinct putative species namely sub-Saharan Africa 1 – 5 (SSA 1- 5) have been identified to colonise cassava in Africa (Legg *et al.,* 20014a).

Temperature is considered most important climatic factor affecting the life history and biological characteristics of insects. Temperature-dependence and the impact of climate change on *B. tabaci* MEAM1 (Wang and Tsai, 1996; Qui *et al*., 2003; Yang and Chi, 2006; Bayhan *et al*., 2006; Campos *et al.,* 2011; Xie *et al*., 2011; Bellotti *et al.,* 2012; Jarvis *et al.,* 2012; Guo *et al*., 2013; Gamarra *et al.,* 2016a) and *B. tabaci* MED (Bonato *et al.,* 2007; Tsueda *et al*., 2011; Han *et al.,* 2013; Gilioli *et al.,* 2014) have been reported; however, these species are not associated with cassava in Africa. Furthermore, there is much to be investigated as available literature suggests differences in life history traits of members of the *B. tabaci species* complex with regards to the host plants, climate and geographical locations. With respect to Africa, first, temperature-dependence of an endemic African population of *B. tabaci* has not been described. Second, the potential impact of climate change on cassava-colonising *B. tabaci* has also not been described. To fill the knowledge gap, the study initiated both laboratory and field studies using a cassava-colonising African population of *B. tabaci* SSA1 - SG3 (a haplotype of *B. tabaci* SSA1). A phenology model was established for the pest using ILCYM software, and the established phenology was used to investigate temperature-dependence, and the impact of climate change on the distribution and abundance of *B. tabaci* SSA1-SG3.

Objectives

Based on the background above, the objectives of the study are as detailed below:

1. Review the potential impact of climate change on whiteflies.
2. Evaluate the effects of temperature on the developmental characteristics of cassava-colonising *B. tabaci.*
3. Evaluate the effects of temperature on the reproductive performance of cassava-colonising *B. tabaci.*
4. Assess the effects of biotic factors on mortality of *B. tabaci* on cassava
5. Model the distribution and abundance of *B. tabaci* under climate change scenario.
6. Investigate adaptation strategies for cassava *B. tabaci* and viruses under climate change.

2. How will climate change affect whiteflies and the viruses that they vector?[1]

2.1 Abstract

Whiteflies (Hemiptera: Aleyrodidae) are important insect pests causing serious damage to plants and transmitting hundreds of plant viruses. Climate change is expected to influence life history and trophic interactions between plants, whiteflies, and their natural enemies. Here we review the potential impacts of climate change on whiteflies and the likely consequences for agricultural systems. This review concludes that temperature increase will reduce whitefly fecundity, longevity and developmental time, while elevated CO_2 will lengthen developmental time but not likely affect fecundity and adult longevity of whiteflies. For most whitefly species, temperature increase in both temperate and tropical zone will favour population increase, although extreme temperatures will likely reduce whitefly populations. A poleward range expansion of whiteflies is predicted. Climate change will influence the invasion success of whiteflies as climatic suitability will play a key role in the establishment of introduced species. Although climate change may alter levels of damage from whiteflies and the plant viruses they transmit, the direction of change will depend on the optimum physiology of the whiteflies, habitat temperature of the location and prevailing species interactions. Greater efforts are required to improve understanding

of the complex effects of climate change on the multi-trophic agro-ecological systems inhabited by whiteflies, and to use this new knowledge to develop robust and climate-smart management strategies.

[1]Aregbesola OZ, Legg JP, Sigsgaard L, Lund OS, Rapisarda C, 2018. How will climate change affect whiteflies and the viruses that they vector? (Submitted to the Journal of Pest Science)

Keywords: whiteflies, population dynamics, plant viruses, pest management, species interaction

2.2 Introduction

Whiteflies are important global agricultural pests. They have a wide host range and are very adaptive to different environmental conditions. The *Bemisia tabaci* (Gennadius) species group is the most economically important whitefly. It causes damage to crops directly through phloem feeding as well as the excretion of honeydew leading to the growth of sooty moulds that reduce photosynthesis. Whiteflies also cause indirect damage through the transmission of economically important viral plant pathogens (Tzanetakis *et al.,* 2013; Polston *et al.,* 2014). Crop damage due to plant viruses transmitted by whiteflies globally results in losses worth more than 1 billion USD (Gonzalez *et al.,* 1992; Legg *et al.,* 2006).

IPCC's fifth assessment report predicted a 1.5 °C increase in global surface temperature, and an increasing contrast in precipitation between wet and dry regions (IPCC, 2013). Independent observations by the National Oceanic and Atmospheric Administration (NOAA) and the National Aeronautics and Space Administration (NASA) showed that globally, temperatures in 2016 were 0.99 °C warmer compared to records from the 20th century, and

the third year in a row to set a new record high temperature (NASA, 2017). Global CO_2 concentration is the primary driver of the recent anthropogenic climate change. While the global concentration of CO_2 in the atmosphere reached 400 parts per million (ppm) for the first time in recorded history in 2013, the trend has continued, with the 2016 estimate at 404.42 ppm (NASA 2013, 2016).

Climatic change is affecting agricultural and natural ecosystems, and directly affects the development, reproduction, survival, population dynamics, potential distribution and abundance of whitefly species (Muniz and Nombela, 2001; Bonato *et al.,* 2007; Bellotti *et al.,* 2012; Gilioli *et al.,* 2014). Some studies have reported direct effects of temperature (Xie *et al.,* 2011; Guo *et al.,* 2013; Han *et al.,* 2013), CO_2 (Koivisto *et al.,* 2011; Curnutte *et al.,* 2014), and O_3 (Cui *et al.,* 2012, 2014) on life history traits. Others have discussed effects of rainfall (Castle *et al.,* 1996; Naranjo and Ellsworth, 2005; Naranjo *et al.,* 2009; Sharma and Yogesh, 2014) on whiteflies.

At the present time, information on the potential influence of climate change on whiteflies is limited and effects of climate change on several biological parameters of whiteflies are poorly understood. New research initiatives aim to deepen insights into the influence of climate change on whiteflies, and on the tri-trophic interactions within the agricultural systems in which they cause so much damage. This review explores the influence of climate change on life history traits of whiteflies considering different host and climatic factors; we also analyse possible influences of climate change on the distribution, population dynamics,

efficacy of management strategies and impacts on vectored plant viruses. Through this analysis, we have been able to identify important trends for some whitefly species and important biological parameters, and based on these, we highlight needs for further research.

2.3 How will whiteflies respond to climate change?

2.3.1 Life history traits

There are differences in response of whiteflies to climate change resulting from differences in whitefly species, host plants, climatic zones and climate factors. The response of different whiteflies and host plants to changes in climatic factors are summarised in Table 2. Temperature and host-plant effects have been identified as important factors affecting development, mortality, and fecundity rates in whitefly populations. Whiteflies respond to increasing temperatures with an increase in development rate, overwintering survival, and number of generations within a season as long as temperatures are within upper and lower thermal thresholds. Temperature increase within the thermal optimum leads to a decrease in developmental time (Madueke and Coaker, 1984; Sengonca and Liu, 1999; Muniz and Nombela, 2001; Nava-Camberos *et al.,* 2001; Bayhan *et al.,* 2006; Bonato *et al.,* 2007; Xie *et al.,* 2011; Han *et al.,* 2013). Other effects of temperature increase on life history traits include decreasing fecundity (Bonato *et al.,* 2007; Xie *et al.,* 2011; Guo *et al.,* 2013) and decreasing longevity (Sengonca and Liu, 1999; Bonato *et al.,* 2007; Guo *et al.,* 2013). Elevated CO_2 and O_3 increased developmental time of whiteflies (Cui *et al.,* 2012; Wang *et al.,* 2014), but elevated CO_2 did not affect adult longevity (Koivisto *et al.,* 2011; Curnutte *et al.,* 2014) and fecundity of whiteflies (Curnutte *et al.,* 2014; Wang *et al.,* 2014).

Table 2: Effects of climatic factors on life history traits that include fecundity, immature development time and adult longevity of whiteflies

Whitefly spp.	Host plant	Climatic variable	Effects on life history	Key references
		Fecundity		
B. tabaci MEAM1	Eggplant, Tomatoes,	Temperature increase	-	*Wang and Tsai, 1996; Qui *et al.,* 2003; Guo *et al.,* 2013
B. tabaci MED	Tomatoes	Temperature increase	-	Bonato *et al.,* 2007
Trialeurodes vaporariorum (Westwood)	Kidney bean, *Brassica* spp.	Temperature increase	-	Manzano and Lenteren, 2009; Xie *et al.,* 2011
B. tabaci MEAM1	*Brassica* spp.	Temperature increase	+	Xie *et al.,* 2011
T. vaporariorum	Tomatoes	Elevated CO_2	-	Koivisto *et al.,* 2011
B. tabaci MEAM1	Collard, Cotton	Elevated CO_2	0	Curnutte *et al.,* 2014; Wang *et al.,* 2014
B. tabaci MEAM1	Tomatoes	Elevated ozone	-	Cui *et al.,* 2012
		Immature developmental time		
B. tabaci MEAM1 and MED	Sweet pepper	Temperature increase	-	Muniz and Nombela, 2001
B. tabaci MED	Tomatoes, Sweet pepper,	Temperature increase	-	Bonato *et al.,* 2007; Han *et al.,* 2013

	Eggplant and Oriental melon			
T. vaporariorum	Greenhouse crops	Temperature increase	-	Madueke and Coaker, 1984
B. tabaci MEAM1	Fruits and vegetables	Temperature increase	-	*Nava-Camberos *et al.,* 2001; *Yang and Chi, 2006; Bayhan *et al.,* 2006
Aleurotuberculatus takahashi (David et Subramaniam)	Citrus	Temperature increase	-	Sengonca and Liu, 1999
B. tabaci MEAM1 and *T. vaporariorum*	*Brassica* spp.	Temperature increase	-	Xie *et al.,* 2011
Bemisia afer (Priesner and Hosny)	Sweet potato	Temperature increase	-	Gamarra *et al.,* 2016a
B. tabaci MEAM1	Cotton	Elevated CO_2	+	Wang *et al.,* 2014
B. tabaci MEAM1	Tomatoes	Elevated ozone	+	Cui *et al.,* 2012
		Adult longevity		
B. tabaci MEAM1	Eggplant, Tomatoes	Temperature increase	-	Qui *et al.,* 2003; *Wang and Tsai, 1996; Guo *et al.,* 2013
A. takahashi	Citrus	Temperature increase	-	Sengonca and Liu, 1999
B. tabaci MED	Tomatoes	Temperature increase	-	Bonato *et al.,* 2007
T. vaporariorum	Kidney bean	Temperature increase	-	Manzano and Lenteren, 2009
B. afer	Sweet potato	Temperature increase	-	Gamarra *et al.,* 2016a
T. vaporariorum	Tomatoes	Elevated CO_2	0	Koivisto *et al.,* 2011
B. tabaci MEAM1	Cotton	Elevated CO_2	0	Wang *et al.,* 2014

+ represents an increase, - represents a decrease, 0 represents no change
MEAM1 (Middle East-Asia Minor 1) = B biotype
MED (Mediterranean) = Q biotype
**B. argentifolii* = MEAM1

There is a lack of studies regarding the effects of elevated O_3 on whitefly longevity and fecundity (Table 2). Extreme cold or hot temperatures tend to reduce survival of both immature and adult stages (Wang and Tsai 1996; Nava-Camberos *et al.,* 2001; Qui *et al.,* 2003).

With increasing temperatures whiteflies can complete more generations per year, while reduced fecundity at higher temperatures may to some extent counter this effect. Climate change will thus affect the population dynamics and also the establishment risk of whiteflies. The impact of these climate change factors on the life history of whiteflies can be better appreciated when the effects of climatic change are considered on demographic characteristics of the whiteflies and patterns of distribution.

Using temperature as an example, *B. tabaci* Mediterranean (MED) and Middle East-Asia Minor 1 (MEAM1) are highly adaptive species characterised by high tolerance for extreme temperatures (optimum development temperature and high intrinsic rate of population increase between 32.5 °C and 35 °C, and adult longevity 6 to 10 days at 35 °C (Yang and Chi 2006; Bonato *et al.,* 2007). A 2 °C increase in temperature in California, Sicily or Beijing will likely favour population increase and range expansion of the species in these locations (Table 3; Bellotti *et al.,* 2012; EFSA, 2013; Gilioli *et al.,* 2014; Gamarra *et al.,* 2016a). A

detailed discussion on how climate change will affect the population dynamics of whiteflies is presented later in this article.

2.3.2 Movement and distribution

Spread of whiteflies is facilitated partly by human transportation of infested plant materials, and there is increasing concern that climate change allows establishment in hitherto unsuitable regions (Bebber *et al.,* 2013). Climate change will also have additional implications for the invasion success of whitefly species as climatic suitability and overall community interaction will play a key role in the establishment and geographical expansion of the introduced whitefly species.

In Europe, expansion of *B. tabaci* northwards is thought to be limited by low temperatures, reducing the risk of *B. tabaci* establishment because of climatic limitations (Gilioli *et al.,* 2014). *B. tabaci* could possibly expand its range in some of the Mediterranean countries (Spain, France, Italy, and Greece) and in countries along the Adriatic coast line (Gilioli *et al.,* 2014) as a consequence of climate change. A temperature increase of 2 °C, could lead to the northwards movement of established populations of *B. tabaci* an estimated 300 – 500 km (EFSA, 2013; Gilioli *et al.,* 2014).

Increased climatic suitability for *B. tabaci* has been predicted to occur in northern Argentina, south-central Bolivia, north-eastern Brazil, south-west Peru, northern Australia, southern

China, as well as parts of the USA (Bellotti *et al.,* 2012). A similar trend is predicted for Central African Republic, Ethiopia and Cameroon (Jarvis *et al.,* 2012) and southern India (Campos *et al.,* 2011). There will also be more *B. tabaci* further south, in regions where there is a cool and dry winter (Bellotti *et al.,* 2012). However, the overall suitability for *B. tabaci* is predicted to decrease in Africa (Jarvis *et al.,* 2012). According to Gamarra *et al.* (2016b,c), in 2050, temperature will potentially reduce *B. afer and T. vaporariorum* establishment in current high-risk areas of the tropics globally. By contrast, the risk of establishment of *B. afer* will increase in the sub-tropical sweet potato growing areas of South Africa, southern Brazil, Peru, Uruguay, Chile, and Argentina. The temperate regions of Europe, North America and Asia will become increasingly suitable for *T. vaporariorum*, although the risk of establishment will still be very low outside greenhouses (Gamarra *et al.* 2016c).

2.3.3 Population dynamics

The major factors that regulate population dynamics are climate, natural enemies, initial population size, host-plant suitability, farming systems and management practices (Price *et al.*, 2011). Generally, rainfall has been noted to negatively affect populations of *B. tabaci* (Naranjo and Ellsworth, 2005; Sharma and Yogesh, 2014). Using sprinkler irrigation to simulate rainfall, Castle *et al.* (1996) found consistent reduction in densities of immature whiteflies. Some of the most abundant populations of *B. tabaci* in history were from irrigated desert cropping systems where consistently high temperatures shorten generation times and rainfall is infrequent (Naranjo *et al.,* 2009). Generally, increasing temperature within developmental thresholds leads to an increase in insect population by reducing

developmental time and hastening metabolic and physiological activities. By combining general circulation models (GCMs) with a stochastic weather generator and population dynamics models, Zidon *et al.* (2016) studied population dynamics of *B. tabaci* in three locations in the Mediterranean region under two future scenarios. Their study suggests that temperature increase will increase population size and average number of generations completed by *B. tabaci* yearly, and a lengthening of growing season in the three locations.

Table 3: Potential impact of a 2 °C temperature increase on whitefly populations at three annual temperatures

Whiteflies species	T_O	K	Potential change in number of generations			Sources of T_O and K
			15 °C	25 °C	28 °C	
B. tabaci MEAM1	12.36	263.81	+1.32	+0.37	+0.09	Qui *et al.,* 2003
B. tabaci MEAM1	11.53	307.00	+1.06	+0.25	+0.01	Bosco and Casiagli, 1998
B. tabaci MEAM1	8.68	388.37	+0.66	+0.02	-0.18	Muniz and Nombela, 2001
B. tabaci MEAM1	8.07	403.23	+0.60	-0.02	-0.21	Muniz and Nombela, 2001
B. tabaci MEAM1	11.10	312.50	+1.01	+0.21	-0.02	Nava-Camberos *et al.,* 2001
B. tabaci MEAM1	13.20	250.00	+1.47	+0.48	+0.18	Nava-Camberos *et al.,* 2001
B. tabaci MEAM1	11.94	299.10	+1.13	+0.29	+0.04	Awadalla *et al.,* 2014
B. tabaci MEAM1	12.33	313.30	+1.11	+0.31	+0.07	Awadalla *et al.,* 2014
B. tabaci MED	8.72	363.25	+0.71	+0.02	-0.18	Muniz and Nombela, 2001

B. tabaci MED	8.14	376.65	+0.64	-0.02	-0.22	Muniz and Nombela, 2001
Aleurocanthus camelliae (Kanmiya and Kasai)	11.94	569.93	+0.59	+0.15	+0.02	Kasai *et al.,* 2012

15 °C, 25°C and 25 °C are mean annual temperatures of hypothetical locations;
- values indicate a potential population reduction and + values a potential population increase

Using the framework proposed by Yamamura and Kiritani (1998) and Kiritani (2006), potential increase in insect populations can be estimated with an equation in the form of:

$$\Delta N = \Delta T[206.7 + 12.46(m - To)]/K, \quad \text{equation 1}$$

Where,

Δ*N* is the potential increase in number of generations due to global warming. *m* °C is annual mean temperature (m °C), Δ*T* is the increase in the annual average temperature due to global warming. *K* is the thermal constant and T_O is the lower developmental threshold temperature.

Bemisia afer can go through 8 – 10 and 4 – 8 generations per year in tropical and sub-tropical regions respectively, under current temperature conditions, while *T. vaporariorum* can have up to 11 generations per year (Gamarra *et al.* 2016b, c). Considering the effects of climatic change up to 2050, *B. afer* is predicted to increase by only 1 generation per year in temperate regions of Europe, North America, and parts of Asia. An increase of 1 – 2

generations per year is predicted for sub-tropical regions in Asia (Malaysia, Philippines, Indonesia); Europe (Portugal); South America (southern Brazil, central Colombia, Peruvian coast); Central, East, and Southern Africa; the Caribbean; central and southern China; and Oceania (Papua New Guinea) (Gamarra *et al.* 2016b). Furthermore, an increase of 1 – 2 generations per year is predicted for *T. vaporariorum* in most tropical regions. *T. vaporariorum* will likely have a small increase in temperate regions (mainly Europe and North America), while increasing temperatures around the Equator will possibly reduce *T. vaporariorum* activity (Gamarra *et al.* 2016c).

2.3.4 Efficacy of management strategies

Evidence from Wang *et al.* (2014) indicates that the biological control of *B. tabaci* by *Encarsia formosa* (Gahan) would not be influenced by transgenic Bt cotton and/or elevated CO_2, while Cui *et al.* (2014) suggest that elevated O_3 enhanced the attraction of *En. formosa* to whiteflies with resulting augmented biological control. Furthermore, it has been experimentally confirmed that parasitism and predation rates of whitefly natural enemies could increase with temperature within the optimum ranges of the natural enemies as in the case of *E. formosa* (Burnett, 1949; Enkegaard, 1994; Qui *et al.,* 2004; Zilahi-Balogh *et al.,* 2006), *Eretmocerus eremicus* Rose & Zolnerowich (Qui *et al.,* 2004), *Er. mundus* Mercet (Qui *et al.,* 2004), *Eretmocerus* spp. (McCutcheon and Simmons, 2001), *Delphastus catalinae* (Horn) (Simmons and Legaspi, 2004), and *Nesidiocoris tenuis* Reuter (Madbouni *et al.,* 2017). Similarly, walking speed, walking activity and flight activity of whitefly natural enemies has been shown to be positively correlated with temperature (Roermund and Lanteren, 1995; Bonsignore, 2016), while handling time decreases with temperature increase (Enkeggard,

1994; Madbouni *et al.,* 2017). For most natural enemies, however, immature survival, fecundity, adult longevity and intrinsic rate of natural increase are maximised below 30 °C, and above this range the chances of population expansion drops significantly (Tables 4 & 5). Of course, the effects of diurnal temperature regimes could increase adaptability of these insects (Kingsolver *et al.,* 2015). Hence, how a natural enemy responds to temperature increase will be a function of the geographical location, current climatic conditions, its life history traits in relation to the amount of increase, which could either favour population build up or decline (Table 5; Deutsch *et al.,* 2008; Youngsteadt *et al.,* 2016). In line with this, biocontrol companies recommend temperatures between 21 and 29 °C for optimal performance of commercially available natural enemies.

Table 4: Optimum temperature conditions for selected life history traits of whitefly natural enemies

Natural enemies	Development time	Immature survival	Adult longevity	Fecundity	Intrinsic rate of increase	References
Parasitoids						
En. formosa	28 °C	22 °C	16 °C	28 °C	28 °C	Enkegaard, 1993
En. formosa	32 °C	NA	15 °C	NA	NA	Qui *et al.,* 2004
En. inaron (Walker)	30 °C	25 °C	20 °C	25 °C	25 °C	Malekmohammadi *et al.,* 2012
En. bimaculatus (Heraty and Polaszek)	32 °C	26 °C	20 °C	29 °C	29 °C	Qui *et al.,* 2006
En. acaudaleyrodis	32°C	25 °C	20 °C	25 °C	25 °C	Zandi-Sohani and Shishehbor,

(Hayat)						2011
Er. eremicus (Rose & Zolnerowich)	32 °C	NA	15 °C	NA	NA	Qui *et al.,* 2004
Er. sp. Nr. furuhasii (Rose & Zolnerowich)	29 °C	26 °C	20 °C	26 °C	29°C	Qui *et al.,* 2007
Er. mundus (Mercet)	30 °C	25 °C	20 °C	25 °C	30 °C	Zandi-Sohani *et al.,* 2009
Er. mundus (Mercet)	32 °C	NA	15°C	NA	NA	Qui *et al.,* 2004
Predators						
Serangium japonicum (Chapin)	32 °C	26 °C	20 °C	26 °C	29 °C	Yao *et al.,* 2011
Axinoscymnus cardilobus (Ren and Pang)	29 – 32 °C	23 °C	17 °C	23 °C	23 °C	Huang *et al.,* 2008
A. apioides (Kuznetsov and Ren)	29 °C	26 °C	20 °C	23 °C	26 °C	Zhou *et al.,* 2017
Clitostethus brachylobus (Peng et al.)	29 °C	26 °C	17 °C	26 °C	26 °C	Deng *et al.,* 2016
C. arcuatus (Rossi)	30 °C	25 °C	15 °C	20 °C	30 °C	Mota *et al.,* 2008
Nephaspis oculatus (Blatchley)	33 °C	26 °C	20 °C	26 °C	26 °C	Ren *et al.,* 2002

To ensure efficacy of their products, commercial producers of whitefly biocontrol products now combine more than one natural enemy. For instance, *En. formosa* is combined with *Er. eremicus* to harness the rapid population growth potential of *En. formosa* and high

temperature tolerance of *Er. eremicus* (Biobest, 2017). The same framework proposed by Yamamura and Kiritani (1998) and Kiritani (2006), described in the section on population dynamics of whiteflies in this article, was used to estimate potential population increase of whitefly natural enemies. Our estimates show that potential increase in the number of generations that can be completed by natural enemies will likely vary with habitat temperature of each location.

Host-natural enemy interactions are not basically linear or directly predictable due to complex species and environment interactions. Greenberg *et al.* (2000) compared the life history of *Er. eremicus* and two host whiteflies (*T. vaporariorum* and *B. tabaci* MEAM1, while Burnett (1949) compared the life history of *T. vaporariorum* and *En. formosa* under the same experimental conditions respectively. Their results show that the parasitoids perform better than the whiteflies at higher temperatures (24 – 32 °C) for most of the traits tested. Similarly, Youngsteadt *et al.* (2016) compared the changes in abundance of whiteflies, predators and parasitoids, and reported that parasitoids had higher abundance per °C warming compared to whiteflies, while predators show lower response to warming compared to parasitoids and whiteflies respectively.

Table 5: Three scenarios for the potential impact of a 2 °C temperature increase on population of whitefly natural enemies

			Potential change in number of generations		
Natural enemy	T_O	*K*	15 °C	25 °C	28 °C

Parasitoids					
En. formosa [abcde]	10.50	280.17	+1.15	+0.22	-0.05
En. bimaculatus [f]	11.60	181.40	+1.81	+0.44	+0.03
En. acaudaleyrodis [g]	11.50	189.80	+1.72	+0.41	-0.25
Er. eremicus [hij]	8.32	303.68	+0.90	+0.004	-0.23
Er. sp. nr. *furuhasii* [j]	11.10	263.40	+1.20	+0.25	-0.03
Er. mundus [kl]	8.86	283.88	+0.98	+0.06	-0.20
Predators					
S. japonicum [m]	9.41	285.71	+0.96	+0.09	-0.17
A. cardilobus [n]	9.07	315.30	+0.84	+0.05	-0.19
A. apioides [o]	12.46	344.83	+0.90	+0.04	-0.21
C. brachylobus [p]					
	9.58	276.50	+1.01	+0.11	-0.17
C. arcuatus [q]	7.90	293.60	0.81	-0.04	-0.30

15°C, 25°C and 25°C are mean annual temperatures of hypothetical locations;

-values indicate a potential population reduction and + values a potential population increase

[a] Enkegaard, 1993; [b] Zhang *et al.,* 2004; [c] Shishehbor and Brenan, 1996; [d] Soto *et al.,* 2001; [ek] Qui *et al.,* 2004; [f] Qui *et al.,* 2006; [g] Zandi-Sohani and Shishehbor, 2011; [h] Greenberg *et al.,* 2000; [i] Tullett *et al.,* 2004; [j] Qui *et al.,* 2007; [l] Zandi-Sohani *et al.,* 2009; [m] Yao *et al.,* 2011; [n] Huang *et al.,* 2008; [o] Zhou *et al.,* 2017; [p] Deng *et al.,* 2016; [q] Mota *et al.,* 2008

Insecticides have long been applied successfully in diverse environments from hot, irrigated desert regions to cool temperate regions. Although the toxicity of insecticides may be influenced by temperature (Sparks *et al.,* 1983; Boina *et al.,* 2009; Glunt *et al.,* 2014), diurnal

variations in temperature will still permit insecticide applications to be made within temperature ranges relevant to the functionality of the compounds. Moreover, compensatory feeding at elevated CO_2 levels would increase the consumption of insecticide (Coviella and Trumble, 2000) and could therefore increase the efficacy of insecticides. However, climate change and faster population growth of whiteflies may also increase insecticide application rates and associated costs of management with insecticides (Chen and McCarl, 2001; Koleva and Schneider, 2009). Climate change may also indirectly affect the efficacy of insecticides since periods suitable for spraying will likely increase with drier locations and decrease where it is wetter (Harrington *et al.,* 2001).

Cultural practices are commonly used as part of an overall strategy for whitefly management. Where efficient weather forecasting systems are available to farmers, changing planting date will remain an easy and effective tool to reduce pest pressure. However, climatic uncertainties may render this practice less useful (especially for smallholder farmers because of their limited use of weather information). The greenhouse strategy (physical barrier) is to a large extent already in place in the new areas that might be invaded by whiteflies, and will continue to be useful especially in intensive production systems if well managed and combined with other control methods. Phytosanitary measures, such as quarantine and the removal of weeds and crop residues, are widely used today and will continue to be useful since there are no indications that climate change will affect their effectiveness. Although constitutive and induced plant defences can be affected by climatic change due to changes in C:N ratio, which could in turn affect both synthesis and functioning of defence compounds (Zavala *et al.,* 2013), there is insufficient evidence as to how this will influence resistance to whiteflies. Even under current production conditions,

insect pests and pathogens often develop mechanisms for breaking down host resistance. How climate change will affect whitefly resistance is unknown, although it will most probably be host-whitefly specific. This topic presents an important opportunity for additional research.

2.4 Impact of climate change on whitefly-transmitted viruses

More than 100 plant viruses are known or assumed to be transmitted by whiteflies (Jones, 2003). However, only five species from three genera transmit viruses (*B. tabaci*, *B. afer*, *T. vaporariorum*, *T. abutilonea* (Haldeman) and *P. myricae*) (Lapidot *et al.,* 2014). Whiteflies that belong to the genera *Bemisia* and *Trialeurodes* are efficient virus vectors (Navas-Castillo *et al.,* 2014). The vast majority of these viruses (>90%) are in the genus *Begomovirus*. This genus consists of single-stranded (ss) DNA viruses infecting dicotyledonous plants and all are transmitted exclusively by the polyphagous virus vector, *B. tabaci*. The mode of transmission is circulative (persistent) and involves circulation of the virus particles in the insect haemolymph, stabilised in a complex with GroEL proteins produced by endosymbiotic bacteria of *B. tabaci* (Morin *et al.,* 1999). A number of plant RNA viruses (>20) including those from the genera: *Crinivirus, Ipomovirus, Torradovirus* and some members of *Carlavirus* are also transmitted by *B. tabaci* and/or one of a few other species of whiteflies, such as *B. afer*, *T. vaporariorum* or *T. abutilonea* (Jones, 2003; Navas-Castillo *et al.,* 2014). Whitefly-mediated transmission of these RNA viruses is semi-persistent (non-circulative) and involves specific attachment of the virus particles to the foregut or the stylet of the vector for a period of hours to days before transmission occurs (Jones, 2003; Tzanetakis *et al.,* 2013; Maruthi *et al.,* 2017).

Since virus transmission by whiteflies is mainly mediated by *B. tabaci* and *T. vaporariorum*, any change in the distribution of these vectors may affect the overall geography of viral diseases. Populations of *B. tabaci* are distributed in tropical and sub-tropical zones all around the globe and viruses transmitted by *B. tabaci* are found – as a group – roughly within the same areas (Navas-Castillo *et al.,* 2011) although local patterns of seasonal temperature, precipitation and altitude appear to play an important role (Morales and Jones, 2004). Sporadic records of viruses from greenhouse plants in cooler climates most likely reflect the importation of infected plant material and not *per se* the natural spread of viruses (Botermanns *et al.,* 2009). However, any future increase in temperature will allow populations of *B. tabaci* to expand towards the poles and the epidemic areas of the viruses vectored will most likely follow. A scenario of climate change has been outlined for *B. tabaci* and begomoviruses using *Tomato yellow leaf curl virus* (TYLCV) in Europe as an example. Manifest and frequent infection of field-grown tomato by TYLCV in Europe is restricted to the most southern, coastal/lowland regions, particularly the islands of Cyprus, Crete, Sicily, Sardinia and the southern parts of Spain and Portugal (Khan *et al.,* 2013). The same regions are characterised by year-round outdoor cultivation of tomato (main virus host) and the presence of populations of *B. tabaci* (EFSA, 2013; Gilioli *et al.,* 2014). In case of a temperature increase of 2 °C, both of these studies predict a movement of established populations of *B. tabaci* approximately 300 – 500 km northwards, taking into account significant local variations due to local topography. The spread of TYLCV in open fields is expected to follow the same pattern (EFSA, 2013). In the tropical coastal zone of Ivory Coast, West Africa, periods of high temperature were associated with maximum whitefly

populations and the most rapid spread of cassava mosaic begomoviruses (CMBs) in plantings of initially virus-free cassava (Fargette *et al.,* 1994). Regarding the impact of climate change on whitefly-transmitted RNA-viruses, a similar picture can be expected. Several of these viruses are vectored by members of the genus *Trialeurodes* (more temperate in its distribution than *B. tabaci*) and several of these viruses have a large number of alternative host plants (Tzanetakis *et al.,* 2013) making them less dependent on a specific species of crop plant being cultivated throughout the year. As overall suitability for whiteflies is predicted to decrease in Africa, so the pressure from the two major virus diseases (cassava mosaic disease and cassava brown streak disease) they vector is also predicted to decrease (Jarvis *et al.,* 2012). However, spatial variations in suitability changes can be expected, since variations in climate and local topography will play significant roles. There will be increasing suitability in high altitude areas where warming creates more favourable conditions for *B. tabaci* populations and viral disease epidemics. In addition, *B. tabaci* whiteflies are likely to become increasingly important in parts of sub-tropical southern Africa, where current temperatures are too low during the cool dry season. For instance, evidence has been presented for current minimum temperate limitations to *B. tabaci* activity and the spread of cassava brown streak disease (CBSD) in Tanzania, and climate change has been highlighted as a likely cause of increasing geographical coverage and consequent damage of this important disease (Jeremiah *et al.,* 2015).

In addition to the expected overall expansion (south-north) of the epidemic areas of diseases caused by whitefly-transmitted viruses, climate change is also likely to affect the severity of diseases within these areas. An increase of atmospheric CO_2 was reported to

cause an increase of the C:N ratio in leaves of tomato and correspondingly, a reduction of total soluble protein and virus protein was found in infected leaves (Huang *et al*., 2012). Consequently, a reduction of disease severity (symptoms and impact on yield) of TYLCV was found in the same study and the effect was linked to the phytohormones, salicyclic acid and jasmonic acid. Elevated CO_2 had a similar effect on a TYLCV susceptible tomato variety (Guo *et al.,* 2016). Studies on the severity of aphid-borne viral diseases (experimentally transmitted by mechanical inoculation) have shown similar results in tobacco plants (Fu *et al.*, 2010; Ye *et al.,* 2010, review by Sun *et al.,* 2011). Although studies of some plant viruses in the tropics suggest increasing temperature reduces symptom severity (Chellappan *et al.,* 2005; Firaol, 2013), one would expect a reverse of this for viral diseases in the Northern hemisphere where a rise in mean annual temperature for instance from 15 to 20 °C will most likely enhance disease incidence and symptoms.

Thus, the overall effect of climate change on diseases caused by whitefly-transmitted viruses is expected to be an expansion of epidemic-affected areas mostly into temperate zones (resulting from increased temperature) and a reduction of disease severity (due to increased levels of CO_2). However, within epidemic areas, major and to a large extent unpredictable changes in the distribution of specific viral diseases can be expected due to the on-going intra-species competition between different putative species of the *B. tabaci* species complex, for which the ability to transmit specific viruses appears to differ markedly (Duffus and Liu, 1994; Polston *et al.,* 2014). It is still an open question as to the extent to which the association with plant viruses is playing a role in the competitiveness of *B. tabaci* putative species and the degree to which climate change will influence this.

3 Life history and temperature-dependent phenology model of cassava-colonising population of *Bemisia tabaci* (Gennadius)

3.1 Abstract

The whitefly, *Bemisia tabaci* transmit viruses that are the greatest constraint to the production of Africa's most important food security crop – cassava. We aimed to model the impact of climate change on cassava-colonising *B. tabaci* and assess the changing risks posed by this global pest. We studied the life history of an endemic African population of *B. tabaci* SSA1-SG3 at six constant temperatures (16, 20, 24, 28, 32, 36 °C) in controlled environment chambers, and for 10 generations in the field. Our results show that the whiteflies preferred temperatures from 20 °C to 28 °C for oviposition, and that total fecundity was highest (117.5 eggs per female) at 20 °C. Similarly, *B. tabaci* adult females lived longest (19.7 days) at 24 °C compared to other temperatures, and the longevity was least at 36 °C (8.5 days). Immature developmental time decreased with temperature up to

28 °C, being slowest at 16 °C (59.3 days), and fastest at 28 °C (16.3 days). Eggs did not develop successfully to adults at 36 °C and this temperature was therefore considered lethal. In the field, development duration varied from 18.0 days during one of the hottest months, to 25.0 days during the coolest month. Mean immature survival peaked at 24 °C (62.5%), while least survival (14.9%) was observed at 16 °C. Survival of immature stages under field conditions varied from 0.69% to 18.0%, and natural enemies had a significant influence on immature survival rates. Several models describing temperature-dependence of insects were fitted to these life history data, and an overall phenology model was developed for this pest using Insect Life Cycle Modelling (ILCYM®) software. Immature developmental time was best described by the log-logistic model. A combination of Sharpe & DeMichele 12 and Logan's Tb model provided an excellent description of temperature-dependent development rate of immature stages. Temperature-dependent mortality of immature stages was well described by Wang 2, Wang 3 and quadratic models. The longevity of adult females and oviposition time was best described by the Weibull distribution. The established phenology model predicted maximum population growth between 22 and 24 °C, and an optimum temperature for total fecundity per female to be 21.4 °C. A comparison of *B. tabaci* SSA1-SG3 to *B. tabaci* MEAM1 and MED suggests that both *B. tabaci* MEAM1 and MED are probably more fit compared to *B. tabaci* SSA1-SG3. The results will be useful for spatio-temporal analysis of climate change impacts on the distribution and abundance of this pest.

Key words: *B. tabaci*, life history, phenology modelling, climate change, cassava, Africa

3.2 Introduction

B. tabaci is a cosmopolitan insect pest that causes crop losses through its effects on host plants including: phloem feeding, inducing growth of sooty moulds that reduce photosynthesis and plant growth (Oliviera *et al.,* 2001). However, the most important economic damages caused by *B. tabaci* are its transmission of viruses of several host plants and driving plant disease epidemics globally. Annual losses due to viruses transmitted by *B. tabaci* on cassava in Africa is more than $US 1 billion (Legg *et al*., 2006).

B. tabaci is a species complex with at least 34 morphologically indistinguishable species on several host crops (Dinsdale *et al.*, 2010; De Barro *et al.,* 2011; Firdaus *et al*., 2013; Lee *et al.*, 2013; Legg *et al.,* 2014a). Two distinct categories of *B. tabaci* occur widely in sub-Saharan Africa, the cassava-colonising and the non-cassava-colonising species (Wosula *et. al.,* 2017). The cassava-colonising *B. tabaci* represents five distinct genetic groups namely sub- Saharan Africa 1 – 5 (SSA 1- 5) (Wosula *et al.,* 2017). Of the cassava-colonising *B. tabaci*, SSA1 is wide spread in most cassava agro-ecologies across Africa (Mugerwa *et al.*, 2012; Legg *et al.,* 2014a, Tajebe *et al.*, 2015a; Manani *et al.*, 2017; Tocko-Marabena *et al.,* 2017; Wosula *et al.,* 2017). The remaining four genetic groups of the cassava-colonising *B. tabaci* tend to be more frequently occurring in some locations. For instance, SSA2 has been reported from several locations in East and West Africa; SSA3 and SSA4 appear to be widely distributed in Cameroon and Togo, whereas SSA5 occurs in South Africa (Berry *et al.,* 2004; Gnakiné *et al*., 2012; Esterhuizen *et al.*, 2013; Legg *et al.,* 2014a; Wosula *et al.,* 2017).

Continual emission of greenhouse gases is the primary driver of the global climate change, creating long-lasting changes in climate system, and increasing the possibilities of severe

and irreversible impacts on ecosystems (IPCC, 2014). Projections from all assessed emission scenarios indicate that global surface temperature will rise over the 21st century (IPCC, 2014). Influence of climate change on biological characteristics of insect is widely reported (Bale *et al*., 2002; Gilioli *et al.,* 2014). Climatic factors influence insect population dynamics through the regulation of development rates, survival, fecundity and dispersal (Price *et al*., 2011). Temperature is one of the most important abiotic factors that determines insect development as well as population dynamics (Gullan and Cranston, 2005). Temperature-dependent impacts on life history of members of the *B. tabaci* species complex has been reported, especially for *B. tabaci* MEAM1 (Wang and Tsai, 1996; Qui *et al*., 2003; Yang and Chi, 2006; Bayhan *et al*., 2006; Xie *et al*., 2011; Guo *et al*., 2013) and MED (Bonato *et al.,* 2007; Tsueda *et al*., 2011; Han *et al.,* 2013). Available literatures suggest difference in life history traits of *B. tabaci* of the species, host plants and geographical locations (Tsai and Wang 1996; Nava-Camberos *et al.,* 2001; De Barro *et al.,* 2011; Tsueda *et al.,* 2011).

Precise knowledge of the life history and temperature-dependent phenology of *B. tabaci* is necessary for understanding the population dynamics under current and future climate change scenarios. Furthermore, development of robust pest management programmes and climate change adaptation planning for *B. tabaci* must be based on a detailed understanding of the biology of the species. Despite the amount of available information on impact of temperature on some *B. tabaci* species, there is a dearth of essential information on effects of different temperatures on the African populations of *B. tabaci*. The objectives of this study were to determine the non-linear relationships between temperature and development, survival, and fecundity of cassava-colonising *B. tabaci* sub-Saharan Africa 1-

sub group 3 (SSA1-SG3), through natural and controlled temperature experiments, and to establish an overall temperature-driven phenology model for the pest. Results of the study were compared to data published on *B. tabaci* temperature-dependent development, and the differences among different *B. tabaci* genotypes feeding on different host plants are discussed. The results will provide useful information for predicting potential population increase of field populations with their seasonal variation in different ecologies within Africa.

3.3 Materials and Methods

3.3.1 Whitefly culture

The *B. tabaci* used for these experiments were collected from cassava at the Agricultural Research Station of the Tanzanian Ministry of Agriculture at Chambezi, Bagamoyo, Tanzania. Several species of *B. tabaci* have been reported to colonise cassava in Tanzania (Mugewa *et al.,* 2012; Legg *et al.,* 2014a; Tajebe *et al*., 2015a). *B. tabaci* colonies were maintained on cassava for 8 – 12 generations in screen-cages in the screen-house facility at IITA-Dar es Salaam, Tanzania. The identity of the *B. tabaci* used was confirmed by sequencing a fragment of the mitochondria cytochrome oxidase I (*mtCOI*) of adult females *B. tabaci* collected from the colonies. *B. tabaci* adult females were lysed in micro-centrifuge tubes to release total DNA. Polymerase chain reaction was carried out to amplify a fragment (~850 bp) of the *mtCOI* gene using primers AV_2F_1 (5´ATTTTCCCGAAACCGTTCA – 3´) and UVCPR (5´GTTACGGAGCAACATGCAT-3´) as described in Frohlich *et al.* (1999) with modifications.

PCR products were sent to commercial Macrogen laboratory, USA for sequencing. The identity of the *B. tabaci* was confirmed to be SSA1-SG3, and the same method was used to routinely check colony purity.

3.3.2 Host plants

Clean cassava materials used for the experiments were collected from clean cassava seed programme of IITA-Tanzania. The materials were tested for *Uganda cassava brown streak virus* (UCBSV)*, Cassava brown streak virus* (CBSV), and *East African cassava mosaic virus* (EACMV) and confirmed virus-free. Nucleic acid extraction protocol of Lodi *et al.* (1994) was optimised for cassava. While PCR for testing EACMV was as described by Firaol (2013) and Real-time PCR for testing cassava plants for UCBSV and CBSV was as described by Shirima *et al*. (2017). Cassava (variety Albert) used for experiments were raised in plastic pots for four to five weeks in the screen-house.

3.3.3 Climatic parameters of laboratory and field experiments

Climatic conditions used for the experiments are constant temperatures (16 °C, 20 °C, 24 °C, 28 °C, 32 °C and 36 °C); relative humidity of 65±5%, and a 12L: 12D diurnal light regime. For field experiments, weather data was obtained from Ubungo Weather Station (Ministry of Water and Irrigation, Tanzania), located approximately 3 km from the study site.

3.3.4 Development and survival of *B. tabaci* under field conditions

About 30 – 50 pairs of adult *B. tabaci* were confined on one of the top four cassava leaves with clip-cages for oviposition to take place. *B. tabaci* were removed after 24 h oviposition

period for uniformity in the cohort. About 20 – 30 eggs were marked per plant with a fine tip non-toxic Sharpie® marker, and 10 – 14 plants were used in each generation. A fine brush was used to remove all unmarked eggs. Since the marked eggs were not confined in clip-cages subsequently, cassava leaves were checked for eggs laid after original cohort establishment and new eggs on marked plants were removed. All marked individuals were monitored daily with a ×60 hand lens. Plants with marked eggs were tagged for ease of subsequent data collection. The experiments included 10 generations of *B. tabaci* from May, 2016 during the raining season to April, 2017 during the raining season. A single cohort of individuals was followed through all life stages (egg to adult emergence) and data on development and survival were recorded for each individual daily.

3.3.5 Development and survival of *B. tabaci* at constant temperatures in the laboratory

For this experiment, two clip-cages were used per plant, and 6 – 10 pairs of adult *B. tabaci* were confined on six potted cassava plants for oviposition to take place at ambient conditions. After 24 hours of oviposition, the pairs of *B. tabaci* were carefully removed from the leaves and transferred to climatic chambers (Percival® PGC - 6L) set at six constant temperatures. On each leaf, six eggs were marked with a fine tip non-toxic Sharpie® marker and all unmarked eggs were removed. Initially, one clip-cage per plant was used and 20 individuals were marked per plant. However, due to problem of leaf drop at 16 °C, two cages were subsequently used to confine the *B. tabaci* on each cassava plant, and 12 eggs were marked on two leaves, this reduced the chances of losing all immature nymphs due to leaf drop at low temperature.

3.3.6 Identification of immature stages

Identification of immature stages was done using illustrative guides provided by J. P. Legg, and as described by Gill (1990) and Gelman *et al.* (2002). Eggs are identified as creamy and ovoid which gradually turn dark-brown over time. First to fourth instars were identified based on their relative shapes and sizes, while the "pupa" or later fourth instar was identified by the characteristic red-eye. Changes from one instar to another was characterised by a molt, a sudden change in size and shape compared to the previous assessment, except for changes from fourth instar to "pupa". Adult emergence was confirmed by empty pupa case with a "T"shaped slit on location of a previously marked nymph.

3.3.7 Fecundity and longevity under laboratory and experimental plot conditions

Sub-colonies of *B. tabaci* were raised on cassava plants in screen-cages for a steady supply of newly emerged whiteflies. The peak period of *B. tabaci* emergence is in the morning (Powell and Bellow, 1992). Newly emerged *B. tabaci* (10 minutes to 2 hours) were collected in the morning between 0800 and 1000 hours. They were identified by the creamy outlook before the deposition of the whitish wax on their wings. During early stage of emergence, the wings are not fully expanded and thus, the newly emerged whiteflies were easily identified and collected from older cassava leaves toward base of the plant where these newly emerged whiteflies are more abundant. The sexes of the whiteflies were identified under a microscope in the laboratory. While females are slightly bigger compared to the

males and have blunt rounded abdomen, males have pointed abdomen (Bryne and Bellows, 1991).

A pair (one male and one female) of newly emerged *B. tabaci* were confined on cassava plants using glass clip-cages at ambient conditions before transferring the cassava plants with the clip-cages either to the climatic chambers, which were set at six constant temperatures, or to the experimental plot. To reduce the influence of leaf ageing on egg production and accumulation of sooty moulds, whiteflies were moved with the clip-cages every two days to a new leaf until their death. Both experiments on experimental plot and in the climatic chambers had 30 – 45 replicates.

3.3.8 Phenology Modelling with Insect Life Cycle Modelling

3.3.8.1 ILCYM Software

The development of an overall *B. tabaci* phenology model, and the estimation of its life-table parameters was executed in Insect Life Cycle Modelling (ILCYM) software package version 4.0 (Sporleder *et al.,* 2013; Sporleder *et al.,* 2016). ILCYM is an open-source software developed by the International Potato Centre (CIP), Lima, Peru. It is available for download at https://research.cip.cgiar.org. Life-table data collected at constant temperatures including data on developmental time of all immature stages, adult longevity of both males and females, and fecundity of adult were used for phenology model building using the

modelling module of ILCYM version 4.0. Phenology simulation with ILCYM uses a rate summation and cohort updating process. Variables used by the modelling module include development time, development rate, mortality, senescence, oviposition rate, oviposition time and total oviposition.

3.3.8.2 Development time, adult longevity and oviposition time

Life history data consisting of data on immature developmental time, adult longevity of both males and females, and fecundity were subjected to survival analyses. The surveg procedure (a part of the survival package in R – statistics, R-core development team) was used to fit the data to parametric accelerated failure time (AFT) models. Distribution link functions including lognormal, log-logistic and Weibull were used to describe immature development time, adult longevity and oviposition time. The best distribution link function for each life stage was selected based on maximum likelihood. The final model was then fitted considering: temperature–which is the default model, insect cohort per temperature – replications in time, and insect cohorts with an individual scale parameter fitted to the data of each cohort. These models were evaluated using a likelihood ratio test, and best fit models were chosen by considering Akaike's information criterion (AIC) (Akaike, 1973) – a popular indicator of goodness of fit, log likelihood ratios, and biological aspects of the species (Sporleder *et al.,* 2013; Mujica *et al.,* 2017).

3.3.8.3 Development, immature mortality, adult senescence and oviposition rates

The relationship between temperature and development, mortality, senescence and oviposition rates, and total fecundity per female were analysed by non-linear regression

analysis in R- statistics (R-core development team) using the values of median immature development time, adult longevity and fecundity observed for each insect batch at different temperatures. Several in-built non-linear models that describe the influence of temperature on each life history variables were tested. For a list of temperature-dependent models used by ILCYM, see the user manual at https://research.cip.cgiar.org/confluence/display/ilcym/ILCYM+manual. Immature survivorship was computed from the relative proportion of surviving test insects for each batch per temperature treatment. The best models describing temperature-dependence in each life stage were selected by comparing AICs, statistical criteria (coefficient of determination R^2 and adjusted R^2) – indicators of the extent to which the regression line approximates the observed data points, and other biological considerations.

3.3.8.4 Estimation of life-table parameters

The methods of Maia *et al.* (2000) that employ an approximate estimate for mean generation time (T) was used to simulate life-table parameters from the established phenology model considering a range of constant temperatures. An initial number of 100 individuals were used, and the "simulation" module of ILCYM was used to simulate life-table parameters. Life-table parameters evaluated include: mean generation time (T), doubling time (D_t), net reproduction rate (Ro), intrinsic rate of natural increase (r_m) and finite rate of increase (k). The simulations used a cohort updating algorithm in 1-day time step in which within-day temperature variability was taken into consideration using a 15-min discrete

time increment. A cosine-wave function describing the minimum and maximum temperature input data was used to predict temperature at each interval (Sporleder *et al.* 2013). A combination of temperature-dependent development rate functions selected for each life-stage and the distribution shape parameter of the AFT model was used to calculate proportion of insect in each cohort that develops to the next life stage (Table 9). The log-logistic function describing the relationship between the accumulated development frequency and the cohort's physiological age is given in the form of:

$$\text{Accumulated development frequency} = 1 - \left(\frac{1}{[1+ \sum_{k-0}^{n} r(T)^{\alpha}]} \right) \qquad \text{equation 2}$$

where $\sum_{k-0}^{n} r(T)^{\alpha}$ is the accumulated development rate from the onset of the life stage ($k = 0$) to the nth day subject to temperature T, and $\alpha = 1/\delta$ is the shape parameter of the curve for a particular stage, while δ is the scale parameter of the distribution link function for a specific stage. The proportion of individual insects developing each day to form a new cohort of the next life stage is estimated by subtracting the accumulated development frequency of day x_i from the accumulated development frequency of day x_{i-1}.

Daily survival rates for each life stage were estimated using the equation in the form of:

$$\text{Survival} = (1 - m_i)^{r(T)}, \qquad \text{equation 3}$$

where m_i is mortality due to the influence temperature in stage i calculated from well-known mortality functions (Table 12), and $r(T)$ is temperature-dependent development rate for a specific stage calculated as previously described (Table 9). The daily survival rate

formula assumes temperature dependence for stage-specific daily survival rate, l_x and that the temperature-dependence effect is not the unique for each life stage.

Daily fecundity per female was estimated using the equation in the form of:

Daily fecundity per female = $(P_i - P_{i-1}) \times F(T)$, equation 4

where P_i is the age-dependent accumulated proportion of eggs per female. For the Weibull link function, P_i is computed using the equation:

$P_i = 1 - exp(-\exp(ln(\sum_{k-0}^{n} r(T) \times \exp(1)) \times \alpha) \times \exp(-\alpha))$ equation 5

where $\sum_{k-0}^{n} r(T)$ is the accumulated median oviposition time from adult eclosion to the nth day subject to temperature$T$, and $\alpha = 1/\delta$ is the shape parameter of the curve for a particular stage, while δ is the scale parameter of the Weibull distribution link function for a specific stage (Table 14); and $F(T)$ is the total temperature-dependent fecundity per female computed from well-known models (Table 14).

3.3.8.5 Model validation

For model validation, life history data were collected from cassava plots maintained at the International Institute of Tropical Agriculture, Dar es Salaam, Tanzania (section 3.3.4). The data include the development, survival, fecundity and longevity of *B. tabaci* SSA1-SG3 from the same colony as the one used for the experiments at constant temperatures. Weather

data was obtained from Ubungo Weather Station (Ministry of Water and Irrigation, Tanzania) was used for model validation.

3.3.9 Complementary analysis – Estimation of thermal thresholds

Development rates (reciprocal of development time) were calculated for each immature stage while total development rate was calculated for the egg-adult at the six constant temperatures. Estimation of thermal thresholds, relationships among temperature and development rates were done by linear regression analysis using PROC REG (SAS 9.4 Institute, NC, Cary, USA). Development rate data was used as the dependent variable and temperature (constant temperatures of 16 – 36 °C or average temperature from a near weather station) as independent variable (Sigsgaard, 2000; Navas- Camberos *et al.,* 2000). To calculate the low development threshold (T_o) temperatures for each immature stages and total egg – adult stage, the intercept was divided by the slope after regression analysis (Han *et al.,* 2013). Development time on a degree-days (^oD) time scale was calculated using the equation:

$^oD = DT\,(T - T_o)$ for $T > T_o$,

otherwise $^oD = 0.$, equation 6

where T is temperature in °C, and DT is the observed development period in days (Sigsgaard, 2000). Maximum temperature threshold (T max) for immature stages was estimated using the Logan 1 model (Logan *et al.,* 1976) in ILCYM, while the optimum temperature (T opt) was estimated using the Janich 1 model (Janisch, 1932) in ILCYM.

Figure 8: Climatic chambers used for the experiments

Figure 9: Longevity and fecundity experiment at constant temperatures

Table 6: Mean monthly weather parameters during the field experiments

Month	Precipitation (mm)	Temperature (°C)	Relative humidity (%)	Wind speed (Km/h)
June	8	26.5	71.6	3.7
July	4	25.6	77.4	3.4
August	443	25.9	78.3	3.3
September	38	25.9	77.3	2.9
October	1	27.3	77.4	3.0

November	64	28.6	78.5	3.0
December	118	29.6	78.2	2.9
January	5	30.3	73.3	3.5
March	244	30.0	80.0	2.4
April	354	28.3	86.8	2.9

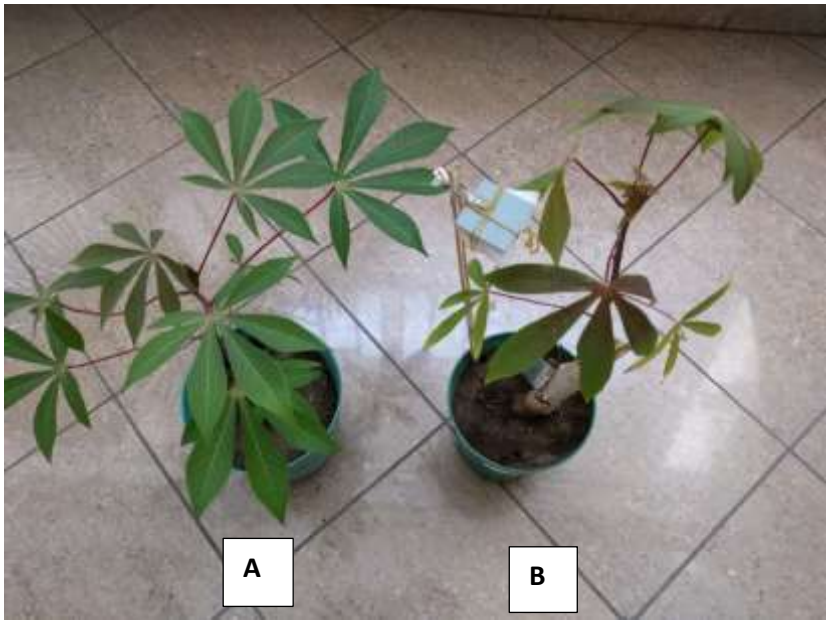

Figure 10: Cassava plant grown at ambient conditions (A), and cassava plant showing effects of cold temperature (16 °C) on leaf during experiments on reproduction and longevity (B)

3.4 Results

3.4.1 Development time

B. tabaci SSA1-SG3 successfully developed from egg to adult stage between 16 °C and 32 °C. Development period from egg to adult stage was longest at 16 °C, with an average of 59.3 days, and fastest at 28 °C taking an average of 16.3 days (Table 7). Development duration was longest in the egg stage, ranging from an average of 17.7 days at 16 °C to 5.5 days at

32 °C, and fastest at the second instar stage taking an average of 7.5 days at 16 °C to 2.4 days at 28 °C. Immature developmental time decreased linearly with temperature between the ranges of 16 °C – 28 °C. An increase in developmental time was observed between 28 °C and 32 °C treatments. For all immature stages, variation in development times were best described by the log-logistic distribution function according to AIC.

Table 7: Mean immature developmental time (days) of *B. tabaci* SSA1-SG3 at six constant temperatures

Life stage	16 °C	20 °C	24 °C	28 °C	32 °C	36 °C
Egg	17.6±0.4	11.8±0.1	8.93±0.1	6.4±0.1	5.5±0.1	5.8±0.3
First instar	9.8±0.3	6.0±0.1	4.6±0.1	3.3±0.1	3.3±0.9	-

Second instar	7.5±0.3	4.8±0.1	3.0±0.0	2.4±0.1	2.8±0.1	-
Third instar	8.2±0.3	5.3±0.2	3.4±0.1	2.4±0.1	3.9±0.2	-
Fourth instar	9.7±0.4	5.8±0.2	3.8±0.1	2.5±0.1	6.0±0.3	-
Pupa	8.4±1.0	5.1±0.1	4.6±0.1	3.5±0.1	3.5±0.1	-
Egg - Adult	59.3±1.3	38.9±0.5	28.2±0.2	16.3±0.6	25.1±0.3	-
N	45	150	218	173	79	18

N = the number of individuals that completed their development to adult stage except at 36 °C, where N is the number of eggs hatched. Values presented are mean immature development time with their standard errors.

Table 8 a: Median development times resulting from accelerated failure time modelling and observed survival rates (eggs)

			Egg		
Temperatures (°C)	N	Batch no.	Median dev.time(days)	CL (95%)	Survival (%)
16	160	1	20.6 ± 0.6	19.5 - 21.7	50 ± 4
16	57	2	18.5 ± 1.0	16.6 - 20.5	50 ± 6.4
16	54	3	18.1 ± 0.8	16.5 - 19.7	70 ± 6.1
16	58	4	17.5 ± 0.8	15.9 - 19.1	60 ± 5.7
16	65	5	20.9 ± 1.1	18.6 - 23.1	50 ± 6.5
20	120	7	12.6 ± 0.5	11.6 - 13.6	70 ± 5.2
20	72	8	11.5 ± 0.4	10.7 - 12.2	80 ± 3.5

20	72	9	14.1 ± 0.5	12.9 - 15.1	90 ± 2.7
20	50	10	10.7 ± 0.5	9.7 - 11.6	60 ± 5.9
20	77	6	12.6 ± 0.5	11.5 - 13.6	80 ± 5.2
24	71	11	9.4 ± 0.3	8.8 – 10.0	80 ± 3
24	71	12	8.4 ± 0.3	7.8 - 9.1	90 ± 4
24	72	13	8.4 ± 0.3	7.8 - 9.1	100 ± 2.4
28	107	14	6.3 ± 0.2	5.9 - 6.7	80 ± 2.6
28	72	15	6.8 ± 0.3	6.3 - 7.4	80 ± 4.8
28	72	16	6.7 ± 0.3	6.2 - 7.2	90 ± 4.1
32	128	17	5.1 ± 0.2	4.8 - 5.5	90 ± 2.7
32	72	18	5.6 ± 0.2	5.1 - 6.1	80 ± 4.5
32	72	19	6.1 ± 0.3	5.6 - 6.6	90 ± 3.9
32	82	20	5.4 ± 0.2	5.0 - 5.8	90 ± 3.9
32	68	21	5.5 ± 0.2	5.1 – 6.0	100 ± 2
36	160	22	5.8 ± 0.4	5.0 - 6.5	10 ± 2.2
36	72	23	5.2 ± 0.6	4.0 - 6.4	10 ± 3.5
Ln (δ)			-2.8850		
δ.			0.05585±0.003		

		Likelihood ratio test		
	- ln (L)	Deviance	Df	P
Model				
Intercept only	-4221.4	4864.5	17	< 0.0001
λ: for each temp.	-2187.8	489.5	5	< 0.0001
λ: for each batch	-2033.6	4375.5	22	< 0.0001

Table 8 b: Median development times resulting from accelerated failure time modelling and observed survival rates (first instars)

			First		
Temperatures (°C)	N	Batch no.	Median dev.time (days)	CL (95%)	Survival (%)
16	160	1	9.9 ± 0.6	8.7 - 11.2	40 ± 5.5
16	57	2	9.6 ± 0.9	7.8 - 11.3	70 ± 8.4
16	54	3	13.3 ± 1.3	10.8 - 15.8	40 ± 8
16	58	4	11.0 ± 1.0	9.0 – 13.0	50 ± 7.4
16	65	5	9.1 ± 1.1	7.0 - 11.2	30 ± 8.8
20	120	7	5.0 ± 0.4	4.2 - 5.7	90 ± 4
20	72	8	6.3 ± 0.5	5.4 - 7.3	60 ± 5
20	72	9	7.4 ± 0.7	6.3 - 8.6	90 ± 4.1
20	50	10	5.5 ± 0.5	4.4 - 6.6	50 ± 7.9

20	77	6	5.6 ± 0.5	4.7 - 6.6	70 ± 6.4
24	71	11	4.5 ± 0.3	3.9 - 5.3	90 ± 2.6
24	71	12	4.5 ± 0.4	3.8 - 5.2	90 ± 4
24	72	13	4.6 ± 0.4	3.9 - 5.3	80 ± 5.2
28	107	14	3.0 ± 0.2	2.5 - 3.4	70 ± 3.5
28	72	15	3.8 ± 0.3	3.2 - 4.4	70 ± 6
28	72	16	3.5 ± 0.3	2.9 - 4.0	60 ± 6.2
32	128	17	2.2 ± 0.3	1.9 - 2.6	80 ± 3.8
32	72	18	4.3 ± 0.4	3.6 - 5.0	80 ± 5.5
32	72	19	3.6 ± 0.3	3.2 - 4.2	90 ± 4
32	82	20	3.4 ± 0.3	2.9 – 4.1	80 ± 5.1
32	68	21	3.3 ± 0.3	2.8 - 3.8	90 ± 2.9
36	160	22	6.0 ± 1.6	2.8 - 9.2	10 ± 7.4
Ln (δ)			-2.1902		
δ			0.11189±0.00499		
			Likelihood ratio test		
		- ln (L)	Deviance	Df	P
Model					
Intercept only		-2223.4	1828.4	16	< 0.0001
λ: for each temp.		-792.9	242.7	5	< 0.0001
λ: for each batch		-1430.5	1585.7	21	< 0.0001

Table 8 c: Median development times resulting from accelerated failure time modelling and observed survival rates (second instars)

			Second		
Temperatures (°C)	N	Batch no.	Median dev. time (days)	CL (95%)	Survival (%)
16	160	1	6.6 ± 0.8	5.1 - 8.2	40 ± 9.7
16	57	2	7.9 ± 1.2	5.6 - 10.3	100 ± 0
16	54	3	7.1 ± 1.2	4.7 - 9.6	80 ± 9.8
16	58	4	8.3 ± 1.3	5.8 - 10.9	80 ± 7.9
16	65	5	9.0 ± 1.8	5.5 - 12.6	90 ± 9.5
20	120	7	4.3 ± 0.6	3.2 - 5.5	80 ± 5.3
20	72	8	3.9± 0.6	2.8 - 5.0	60 ± 6.6
20	72	9	5.7 ± 0.8	4.2 - 7.2	90 ± 3.3
20	50	10	4.9 ± 0.8	3.4 - 6.4	90 ± 7.6

20	77	6	5.4 ± 0.7	4.0 - 6.9	100 ± 2.8
24	71	11	2.8 ± 0.4	2.1 - 3.5	100 ± 1
24	71	12	3.1 ± 0.4	2.3 - 3.9	100 ± 1.8
24	72	13	3.3 ± 0.4	2.4 - 4.1	90 ± 3.2
28	107	14	2.1 ± 0.3	1.6 - 2.7	100 ± 1.7
28	72	15	2.9 ± 0.4	2.1 - 3.7	100 ± 2.4
28	72	16	2.5 ± 0.3	1.8 - 3.1	90 ± 3.7
32	128	17	2.1 ± 0.3	1.5 - 2.6	70 ± 4.9
32	72	18	4.0 ± 0.5	2.9 - 5.1	90 ± 3.7
32	72	19	3.3 ± 0.4	2.4 - 4.1	90 ± 3.8
32	82	20	2.9 ± 0.4	2.1 - 3.7	90 ± 3.6
32	68	21	2.4 ± 0.3	1.7 - 3.0	90 ± 3.5
Ln (δ)			-2.0137		
δ			0.1335±0.00716		

		Likelihood ratio test		
	- ln (L)	Deviance	Df	P
Model				
Intercept only	-1731.3	1373.6	15	< 0.0001
λ: for each temp.	-546.5	280.5	5	< 0.0001
λ: for each batch	-1184.8	1093.1	20	< 0.0001

Table 8 d: **Median development times resulting from accelerated failure time modelling and observed survival rates (third instars)**

			Third		
Temperatures (°C)	N	Batch no.	Median dev.time (days)	CL (95%)	Survival (%)
16	160	1	8.4 ± 1.7	5.1 - 11.7	70 ± 13.4
16	57	2	8.1 ± 1.8	4.5 - 11.7	100 ± 4.7
16	54	3	9.0 ± 2.3	4.6 - 13.5	90 ± 7.4
16	58	4	8.3 ± 2.0	4.4 - 12.3	80 ± 8.4
16	65	5	8.6 ± 2.4	3.8 - 13.3	100 ± 0
20	120	7	5.2 ± 1.1	2.9 - 7.4	90 ± 4.1
20	72	8	4.4 ± 1.0	2.4 - 6.3	70 ± 8.2
20	72	9	7.1 ± 1.5	4.1 - 10.0	90 ± 4.2
20	50	10	4.8 ± 1.1	2.5 - 7.0	100 ± 0
20	77	6	5.5 ± 1.2	3.1 - 7.8	100 ± 0
24	71	11	3.3 ± 0.7	2.0 - 4.6	100 ± 0.8

24	71	12	3.2 ± 0.7	1.8 - 4.5	90 ± 3.6
24	72	13	2.9 ± 0.6	1.7 - 4.2	80 ± 5.3
28	107	14	2.1 ± 0.4	1.3 - 3.0	100 ± 0.9
28	72	15	2.7 ± 0.6	1.6 - 3.9	80 ± 5.6
28	72	16	2.6 ± 0.6	1.5 - 3.7	100 ± 2.8
32	128	17	3.1 ± 0.7	1.8 - 4.4	80 ± 4.7
32	72	18	4.1 ± 0.9	2.4 - 5.9	90 ± 5.4
32	72	19	4.6 ± 1.0	2.6 - 6.6	80 ± 5.3
32	82	20	6.2 ± 1.3	3.5 - 8.8	90 ± 4.3
32	68	21	5.9 ± 1.3	3.4 - 8.4	90 ± 3.4
Ln (δ)			-1.7777		
δ			0.16902±0.00948		

		Likelihood ratio test		
	- ln (L)	Deviance	Df	P
Model				
Intercept only	-1832.9	1247.1	15	< 0.0001
λ: for each temp.	-426.7	393.7	5	< 0.0001
λ: for each batch	-1406.2	853.4	20	< 0.0001

Table 8 e: Median development times resulting from accelerated failure time modelling and observed survival rates (fourth instars)

			Fourth		
Temperatures (°C)	N	Batch no.	Median dev. time (days)	CL (95%)	Survival (%)
16	160	1	7.5 ± 1.5	4.6 - 10.5	90 ± 11.7
16	57	2	9.0 ± 2.0	5 – 13.0	100 ± 0
16	54	3	10.0 ± 2.5	5.1 – 14.9	80 ± 10.8
16	58	4	10.1 ± 2.7	4.7 - 15.6	60 ± 12.1
16	65	5	11.4 ± 3.3	4.8 - 18.0	60 ± 16.6
20	120	7	6.6 ± 1.4	3.8 - 9.4	100 ± 2.6
20	72	8	5.8 ± 1.3	3.2 - 8.5	90 ± 7.3
20	72	9	7.1 ± 1.5	4.1 - 10.1	100 ± 0
20	50	10	4.8 ± 1.1	2.6 – 7.0	90 ± 7.4
20	77	6	5.1 ± 1.1	2.9 - 7.2	100 ± 0
24	71	11	3.5 ± 0.7	2.1 - 4.91	100 ± 1.7
24	71	12	3.4 ± 0.7	2.0 - 4.7	100 ± 2.8
24	72	13	3.7 ± 0.8	2.1 - 5.3	100 ± 2.4

28	107	14	2.0 ± 0.4	1.2 - 2.8	100 ± 1.2
28	72	15	2.7 ± 0.6	1.5 - 3.8	100 ± 2.9
28	72	16	2.8 ± 0.6	1.6 - 4.0	100 ± 2.9
32	128	17	8.5 ± 2.0	4.6 - 12.3	40 ± 6.9
32	72	18	4.5 ± 1.0	2.5 - 6.5	70 ± 7.9
32	72	19	5.9 ± 1.5	3.0 - 8.8	40 ± 7.6
32	82	20	4.3 ± 1.1	2.2 - 6.4	30 ± 6.9
32	68	21	5.7 ± 1.4	3 - 8.5	30 ± 6.3
Ln (δ)			-1.6599		
δ			0.19016±0.01018		
			Likelihood ratio test		
		- ln (L)	Deviance	Df	P
Model					
Intercept only		-1567.7	1012.7	15	< 0.0001
λ: for each temp.		-341.6	329.5	5	< 0.0001
λ: for each batch		-1226.1	683.2	20	< 0.0001

Table 8 f: Median development times resulting from accelerated failure time modelling and observed survival rates (pupa)

			Pupa		
Temperatures (°C)	N	Batch no.	Median dev.time (days)	CL (95%)	Survival (%)
16	160	1	5.9 ± 1.1	3.7 - 8.1	90 ± 13.2
16	57	2	7.3 ± 1.5	4.3 - 10.3	100 ± 0
16	54	3	7.6 ± 1.7	4.3 - 10.9	80 ± 12.6
16	58	4	8.5 ± 1.9	4.7 - 12.22	80 ± 12.6
16	65	5	8.3 ± 2.0	4.3 - 12.2	100 ± 0
20	120	7	5.2 ± 1.0	3.2 - 7.3	100 ± 2.7
20	72	8	5.5 ± 1.1	3.2 - 7.7	90 ± 5.1
20	72	9	5.2 ± 1.0	3.3 - 7.2	100 ± 2
20	50	10	4.6 ± 1.0	2.7 - 6.5	90 ± 6
20	77	6	4.5 ± 0.9	2.7 - 6.2	100 ± 2.9
24	71	11	4.1 ± 0.8	2.5 - 5.6	100 ± 1.4
24	71	12	5.2 ± 1.0	3.2 - 7.3	90 ± 3.5
24	72	13	4.6 ± 0.9	2.7 - 6.4	100 ± 0
28	107	14	3.5 ± 0.7	2.2 - 4.9	100 ± 1.8
28	72	15	3.4 ± 0.6	2.0 - 4.7	100 ± 0

28	72	16	3.1 ± 0.6	1.9 - 4.3	100 ± 0
32	128	17	3.8 ± 0.8	2.2 - 5.4	60 ± 10.3
32	72	18	3.1 ± 0.6	1.9 - 4.4	100 ± 4.1
32	72	19	3.3 ± 0.7	1.9 - 4.6	90 ± 7.8
32	82	20	3.6 ± 0.8	2.1 - 5.1	100 ± 0
32	68	21	3.5 ± 0.7	2.1 - 4.9	100 ± 0
Ln (δ)			-1.9419		
δ			0.14343±0.00688		

		Likelihood ratio test		
	- ln (L)	Deviance	Df	P
Model				
Intercept only	-1212.6	561.2	15	< 0.0001
λ: for each temp.	-191.2	178.7	5	< 0.0001
λ: for each batch	-1021.4	382.5	20	< 0.0001

3.4.2 Development rate

Development rate was lowest at 16 °C for all immature stages, peaked between 30 °C and 32 °C for first instar to pupa stage, while this happened between 32 °C and 36 °C at the egg stage (although hatchability was extremely low at 36 °C) (Figures 11a–f). Variability in development rate increased with temperature. A combination of Sharpe & DeMichele 12 (Sharpe and DeMichele, 1977) and Logan's Tb Model (Logan *et al.,* 1976) provided an excellent description of temperature-dependent development rate of immature life stages (Table 9). The Sharpe & DeMichele 12 described the egg (adj R^2 =0.959, AIC = -137.7), first instar stage (adj R^2 = 0.764, AIC = -67.7) and second instar stage (adj R^2 = 0.771, AIC = -54.7). The third (adj R^2 = 0.847, AIC = -69.3), fourth (adj R^2 = 0.869, AIC = -72.0), and pupa stage (adj R^2= 0.8550, AIC =-88.0) were described by the Logan's Tb Model (Table 9). Maximum,

optimum and minimum temperatures predicted by models used for complementary analysis decreased as temperature increased except in the pupa stage (Table 10). The Logan 1 model predicted maximum development temperature to be between 41.6 °C (egg stage) to 32.3 °C (pupa instar) in a sequential order across the immature life stages. Optimum development temperature predicted by the Janisch 1 model (Janisch, 1932) for all immature stages ranged from 34.3 °C (egg stage) to 26.5 °C (fourth instars). Simple linear models predicted the lower development threshold to be between 2.19 (third instars) and 11.47 (pupa).

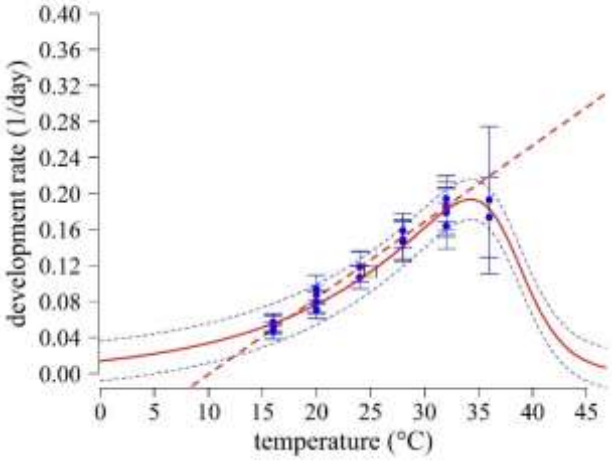

Figure 11a: Development rate of *B. tabaci* SSA1-SG3 eggs under constant temperature treatments

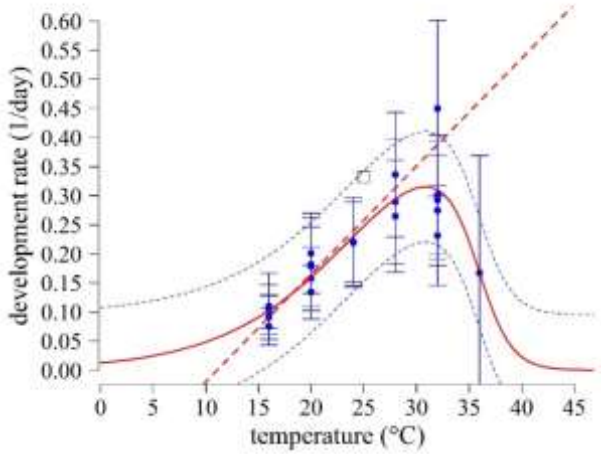

Figure 11b: Development rate of *B. tabaci* SSA1-SG3 first instars under constant temperature treatments.

Red bell shaped curve is the development rate predicted by the model(s), the blue dashes are 95% confidence intervals, the blue dots are experimental data points, the whiskers on the blue dots are error bars and the red dashes is the linear regression line.

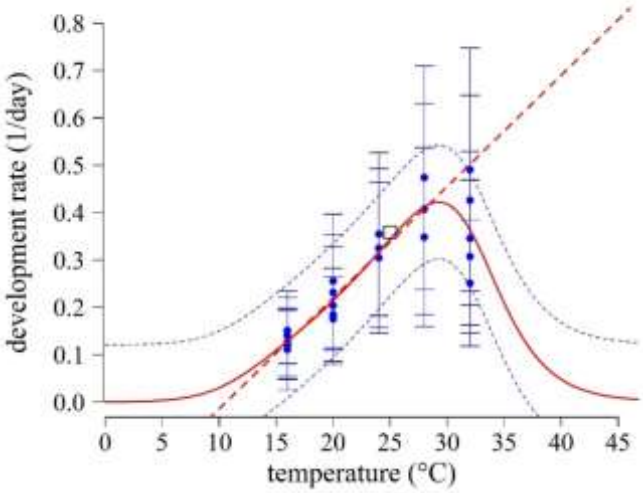

Figure 11c: Development rate of *B. tabaci* SSA1-SG3 second instars under constant temperature treatments.

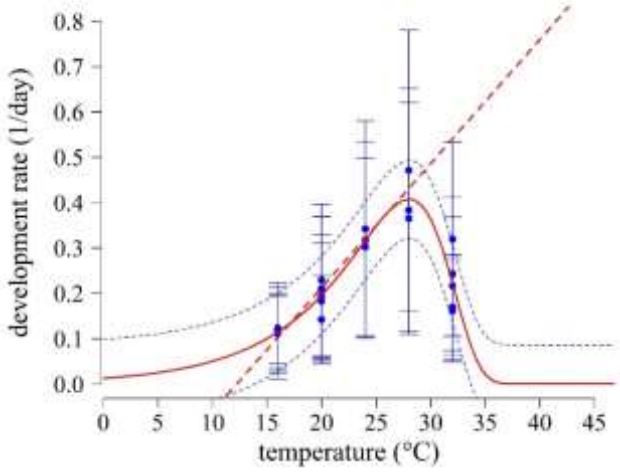

Figure 11d: Development rate of *B. tabaci* SSA1-SG3 third instars under constant temperature treatments.

Red bell shaped curve is the development rate predicted by the model(s), the blue dashes are 95% confidence intervals, the blue dots are experimental data points, the whiskers on the blue dots are error bars and the red dashes is the linear regression line.

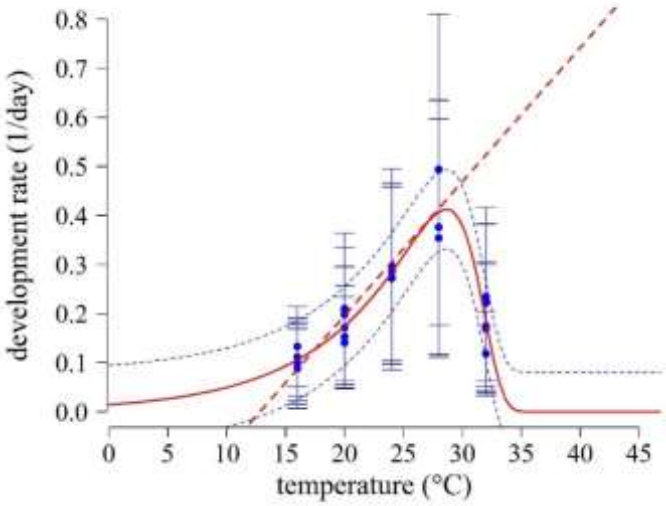

Figure 11e: Development rate of *B. tabaci* SSA1-SG3 fourth instars under constant temperature treatments

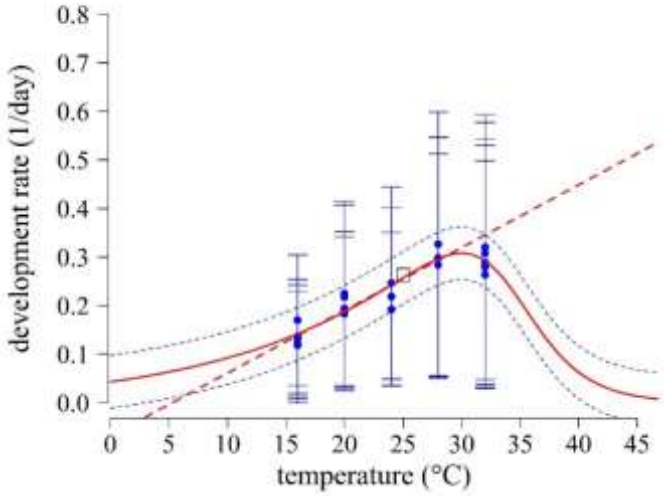

Figure 11f: Development rate of *B. tabaci* SSA1-SG3 pupa under constant temperature treatments. Red bell shaped curve is the development rate predicted by the model(s), the blue dashes are 95% confidence intervals, the blue dots are experimental data points, the whiskers on the blue dots are error bars and the red dashes is the linear regression line.

Table 9: Models and parameters fitted to describe effects of temperature on median development rates of *B. tabaci* SSA1-SG3

Life stages	Models		Parameters*	F value	Df 1, 2	P value	Adj R^2
Egg	Sharpe & DeMichele 12	P	0.1135	131	4, 18	> 0.001	0.959
		Ha	12905.02				
		T1	374.08				
		H1	1494553.8				
		Hh	96255.75				
		Th	311.00				
First instar	Sharpe & DeMichele 12	P	0.3322	18.02	4, 17	> 0.001	0.764

		Ha	20682.88				
		T1	307.59				
		H1	148311.79				
		Hh	34647.76				
		Th	303.77				
Second instar	Sharpe & DeMichele 12	P	0.3587	17.82	4, 16	> 0.001	0.771
		Ha	15827.87				
		T1	284.57				
		H1	-62497.44				
		Hh	82092.86				
		Th	305.49				
Third instar	Tb Model (Logan)	Sy	0.886	37.84	3, 17	> 0.001	0.847
		B	0.1388				
		Tb	30.6628				
		DTb	0.4109				
Fourth instar	Tb Model (Logan)	Sy	0.7259	45.27	3, 17	> 0.001	0.869
		B	0.1257				
		Tb	31.3149				
		DTb	0.2272				
Pupa	Sharpe & DeMichele 12	P	0.2634	30.49	4, 16	> 0.001	0.855
		Ha	11144.38				
		T1	325.24				
		H1	294903.97				
		Hh	75090.91				
		Th	307.31				

*Parameters of all models were significantly different from zero ($p < 0.0001$).

Model: Sharpe & DeMichele 12 used to describe development rates of egg, first, second and pupa instars is given by the equation:

$$r(T) = (p \times (T/298.16) \times \exp((Ha/1.987) \times ((1/298.16) - (1/T))))/(1 + \exp((Hl/1.987) \times ((1/Tl) - (1/T))) + \exp((Hh/1.987) \times ((1/Th) - (1/T)))) \quad \text{equation 7}$$

where P, Ha,T1, H1, Hh are parameters.

Model: Tb Model (Logan) used to describe development rates of third and fourth instars is given by the equation:

$$r(T) = sy \times \exp(b \times (T-Tb)-\exp(b \times (T-Tb)/DTb)), \quad \text{equation 8}$$

where sy, b, Tb, DTb are parameters.

Table 10: Complementary analysis on development thresholds

Life stages	T_{max} (°C)	R^2 adj	T_{opt} (°C)	R^2 adj	T_{min} (°C)	R^2 adj
Egg	41.6	0.9750	34.3	0.9770	9.0	0.9742
First	37.6	0.7750	29.6	0.7580	8.2	0.7585
Second	35.0	0.7850	28.7	0.7980	7.6	0.7715
Third	33.2	0.8460	26.6	0.8100	2.2	0.4587[a]
Fourth	32.7	0.8690	26.5	0.7730	3.0	0.1909[b]
Pupa	32.3	0.8680	30.8	0.8650	11.6	0.8559

Egg to adult	4.3	0.8028

p value for a = 0.0004, b = 0.0273, all other *p* values are < 0.0001

3.4.3 Mortality of immature stages

Mortality of the egg and first instar nymphs under constant temperature treatments were higher than later immature stages and the least mortality was observed for the pupa (Table 11, Figures 12a–f). Egg to adult mean survival peaked at 24 °C (62.5%), and was very low at 16 °C (14.9%) and 32 °C (20.3%). Mean survival for the egg stage was 7.5%, and none of the insects survived to adult stage at 36 °C. Overall mortality of immature stages was relatively low between 20 °C and 28 °C (Table 11, Figures 12a–f). Temperature-dependent mortality of egg, first, fourth and pupa instars was described by the Wang 3 model (Wang *et al.,* 1982). The Wang 2 model (Wang *et al.,* 1982) and quadratic model best described mortality in the second and third instars respectively (Table 12).

Table 11: Mean survival (%) of *B. tabaci* SSA1-SG3 at six constant temperatures

Life stages	16 °C	20 °C	24 °C	28 °C	32 °C	36 °C
Egg	65.8±7.8	77.6±6.2	87.5±4.2	87.0±2.6	90.0±3.1	7.5
First instar	49.1±5.1	74.0±9.0	84.2±4.5	67.2±3.8	79.0±4.2	-
Second instar	84.5±4.0	84.6±7.1	96.8±1.3	96.5±1.0	88.0±4.7	-

Third instar	83.8±2.1	89.5±6.3	91.8±4.5	92.8±4.1	80.8±3.9	-
Fourth instar	74.8±9.2	94.3±2.4	97.6±0.2	98.1±0.9	44.6±7.5	-
Pupa	78.7±12.35	97.1±1.3	96.9±1.8	99.1±0.9	89.5±6.8	-
Egg – Adult	14.9±5.3	43.3±11.1	62.5±3.5	48.4±2.6	20.3±3.5	-
N	46	150	218	173	79	18

N = number of individuals that completed their development to adult stage except at 36 °C, where N is number of eggs that hatched.

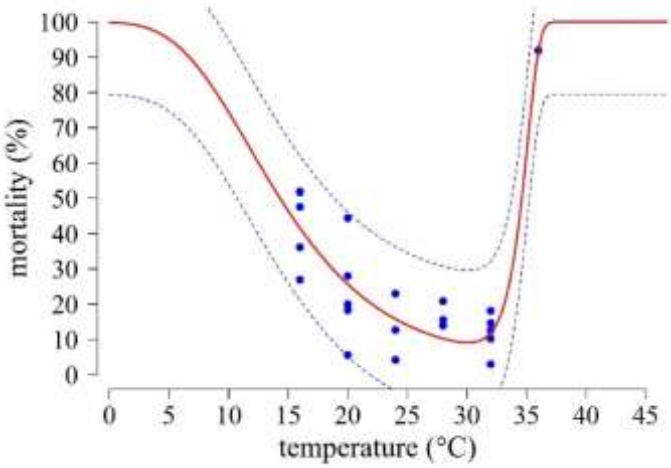

Figure 12a: Mortality of *B. tabaci* SSA1-SG3 eggs under constant temperature treatments

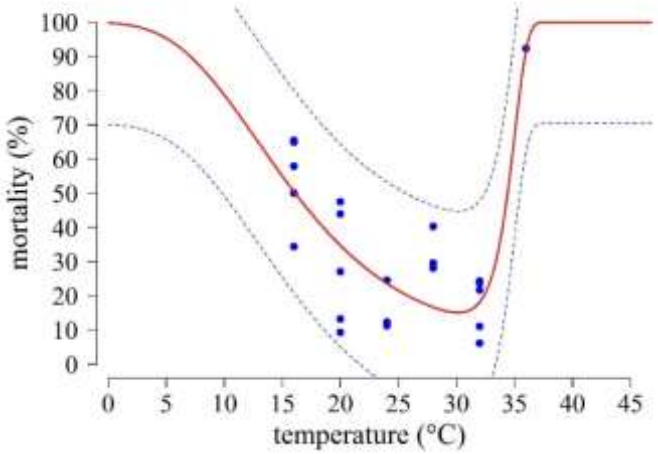

Figure 12b: Mortality of *B. tabaci* SSA1-SG3 first instars under constant temperature treatments

Red bell shaped curve is the mortality percentage predicted by the model(s), the blue dashes are 95 % confidence intervals, the blue dots are experimental data points.

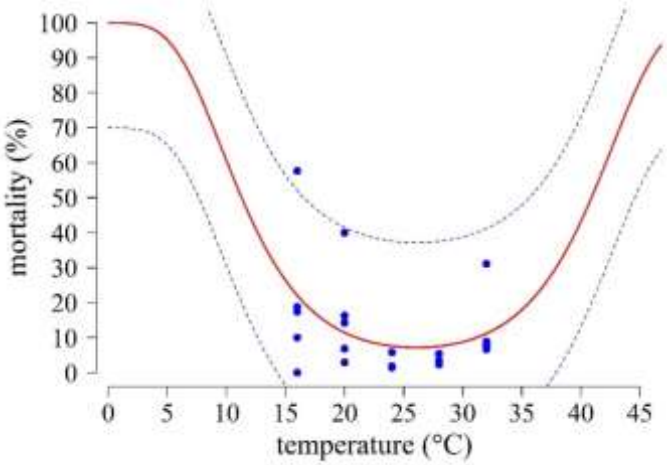

Figure 12c: Mortality of *B. tabaci* SSA1-SG3 second instars under constant temperature treatments

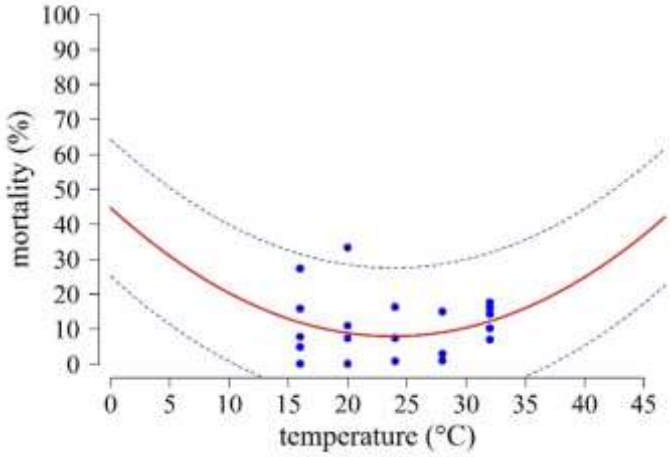

Figure 12d: Mortality of *B. tabaci* SSA1-SG3 third instars under constant temperature treatments

Red bell shaped curve is the mortality percentage predicted by the model(s), the blue dashes are 95% confidence intervals, the blue dots are experimental data points.

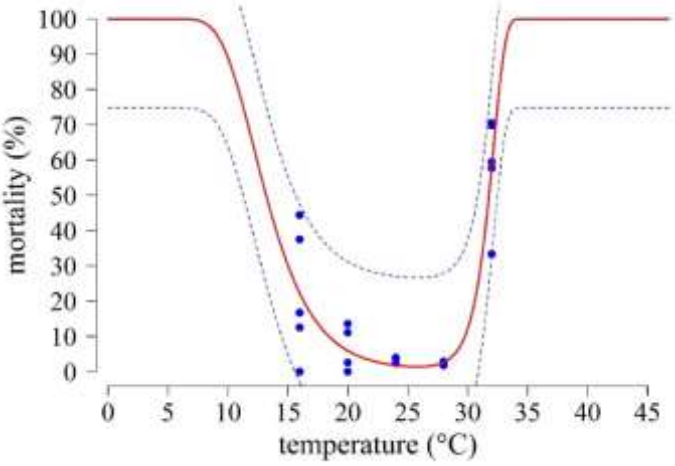

Figure 12e: Mortality of *B. tabaci* SSA1-SG3 fourth instars under constant temperature treatments

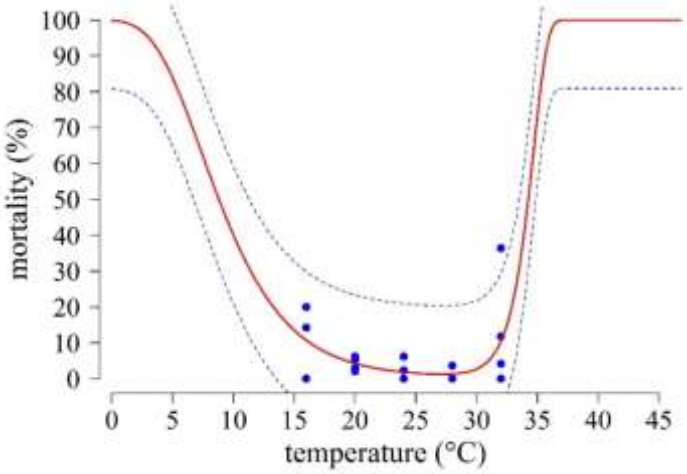

Figure 12f: Mortality of *B. tabaci* SSA1-SG3 pupa instars under constant temperature treatments

Red bell shaped curve is the mortality percentage predicted by the model(s), the blue dashes are 95% confidence intervals, the blue dots are experimental data points.

Table 12: Models and parameters fitted to describe effects of temperature on mortality rate of *B. tabaci* SSA1-SG3

Life stages	Model		Parameters	F value	Df 1, 2	P value	Adj R^2
Egg	Wang 3	T opt	32.283***	40.23	3, 19	> 0.001	0.8425
		B1	6.1539***				
		Bh	0.9793***				
		H	0.0355***				

First instar	Wang 3	T opt	32.635***	11.38	3, 18	> 0.001	0.5972
		B1	7.1208***				
		Bh	1.0585***				
		H	0.0619***				
Second instar	Wang 2			1.11	3, 17	0.3707	0.0169
		T1	26.0889				
		Th	26.086				
		B	4.1555				
		H	0.0186				
Third instar	Quadratic			0.36	2, 18	0.6983	-0.067
		A	0.00065				
		B	-0.03089				
		C	0.44702				
Fourth instar	Wang 3			23.47	3, 17	> 0.001	0.7712
		T opt	27.046***				
		B1	2.7377***				
		Bh	0.9635***				
		H	0.0044***				
Pupa	Wang 3			1.34	3, 17	0.2943	0.0486
		T opt	28.8437				
		B1	3.9175				
		Bh	1.103				
		H	0.0041				

Model: Wang 3 model used to describe mortality rates of egg, first instars, fourth and pupa stage is given by the equation:

$$m(T) = 1 - 1/(\exp((1+\exp(-(x-T\ opt)/B1)).(1+\exp(-(T\ opt-x)/Bh)).H)) \quad \text{equation 9}$$

where T, T opt, B1, Bh, H are parameters.

Wang 2 model used to describe mortality rates of second instar is given by the equation:

$$m(T) = 1 - 1/(\exp((1+\exp(-(x-T1)/B)).(1+\exp(-(Th-x)/B)).H)) \quad \text{equation 10}$$

where T1, T, Th, B, H are parameters.

Quadratic equation used to describe mortality rates of third instar is given by the equation

$m(T) = aT^2+bT+c$, where a, b, c are parameters. equation 11

Asterisks represents parameters values significantly from zero ($p < 0.001$ = ***, $p < 0.01$ = **, $p < 0.05$)

3.4.4 Adult lifespan and fecundity

In all temperature treatments the females lived longer than the males. The maximum longevity of a single whitefly observed in the study was 47 days and was recorded for both the 20 °C and 24 °C treatments. The longevity of adult females varied markedly with temperature, it was low at extreme of 16 °C (12.4 days), 32 °C (9.0 days) and 36 °C (8.5 days). The insects lived longer at 24 °C (19.7 days) and 20 °C (19.2 days). The longevity of adult females significantly decreased with temperature (p =4.5e-09), and was best described by

the Weibull distribution. Life span of adult males was in the range of 6 – 11 days across the temperature treatments.

Table 13: Longevity and total fecundity of adult *B. tabaci* SSA1-SG3

Temp. (°C)	Median adult survival time (days)				Median fecundity per female
	Male		Female		
	N		N		
16	38	7.0±1.1	44	12.42±0.6	16.4
20	48	11.0±1.4	45	19.2±1.3	117.5
24	34	9.0±2.4	31	19.73±1.4	98.9
28	28	8.5±1.0	30	12.75±1.0	109.6
32	36	8.0±1.3	35	9.02±0.6	64.6
36	27	6.0±1.0	27	8.47±0.6	52.3

Total fecundity per female observed was highest at 20 °C (117.5 eggs) and least at 16 °C (16.4 eggs). Total fecundity per female was relatively high at temperature extremes of 32 °C (64.6 eggs) and 36 °C (52.3 eggs) (Table 13). The Weibull link function best described survival time and median oviposition times of adult females (Table 14). The established Wang 5 model (Table 14) estimated the optimum temperature for total fecundity per female to be 21.4 °C. The maximum number of eggs laid by a single individual in its entire life was 387 eggs at 20 °C, and only a few individuals laid eggs at 16 °C.

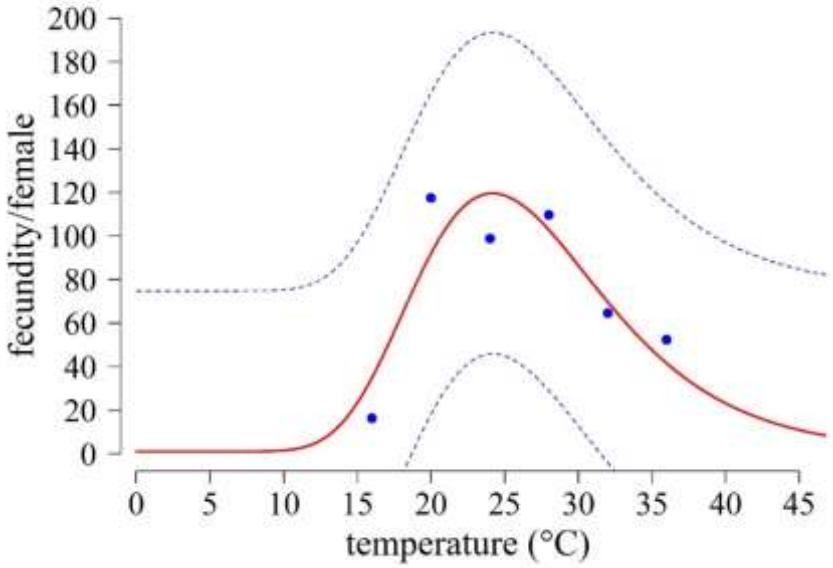

Figure 13: Total fecundity per female *B. tabaci* SSA1-SG3 pupa instars under constant temperature treatments

Red bell shaped curve is the Total fecundity per female predicted by Wang 5 model, the blue dashes are 95% confidence intervals, the blue dots are experimental data points.

Table 14: Models and parameters fitted to describe adult senescence rate, total fecundity per female, and median oviposition rate

Life history trait	Model	Parameters	F value	df 1, 2	P value	Adj R^2
Adult senescence rate	Exponential simple		6.63	1, 4	0.0616	0.530
		b1 0.0284				

		b2	0.0392				
Total fecundity per female	Wang 5	T opt	21.3605	5.59	2, 3	0.0974	0.647
		B	5.8732				
		H	-1566.092				
Median oviposition time^{-1}	Weibull distribution						

Models: Exponential simple model describing adult senescence rate is given by:

$$r(T) = 1/(b1 + b2\ T) \quad \text{equation 12,}$$

where b1 and b2 are parameters.

Wang 5 model describes total fecundity per female given by:

$$f(T) = 1 - H/(\exp(1+\exp(-(x-Topt)/B)).(1+\exp(-(Topt-x)/B))) \quad \text{equation 13}$$

where Topt, B, and H are parameters.

3.4.5 Life-table parameters at constant temperatures

An estimation of life-table parameters showed that at constant temperatures, *B. tabaci* SSA1-SG3 populations would be maximised between 22 °C and 24 °C, except the generation time that was least between 28 °C and 30 °C. For instance, intrinsic rate of natural increase peaked around 22 °C (0.0113) and 24 °C (0.0116), and was negative at 16 °C (-0.0188) and 34 °C (-0.062). Net reproductive rate was also maximal between 22 °C (1.564) and 24 °C

(1.482). Similarly, finite rate of increase also peaked between 22 °C (1.011) and 24 (1.012). Gross reproductive rate was least at 34 °C (0.702) and maximal at 32 °C (6.447). Generation time ranged from 26.19 days (30 °C) to 76.64 days (34 °C), and was least between 28 °C (26.3 days) and 30 °C (26.2 days). The least doubling time was 59.7 days at 24 °C. Life-table parameters could not be estimated for the 36 °C treatment because immatures did not complete their development to adult stage at this temperature (Figure 14).

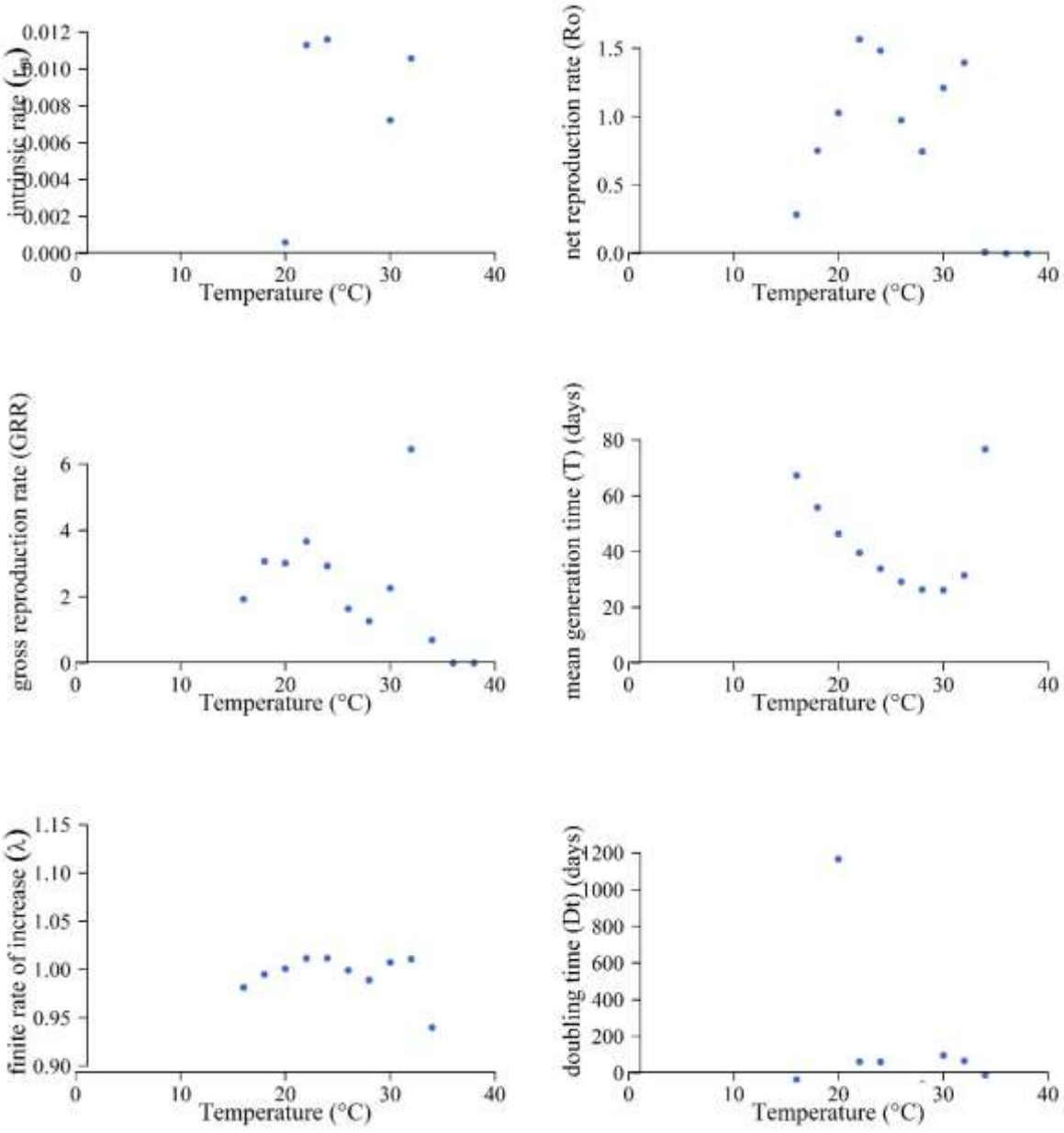

Figure 14: Life-table parameters of *B. tabaci* SSA1-SG3 estimated for the constant temperature treatments

3.4.6 Degree-days requirement of *B. tabaci* SSA1-SG3 under both field and laboratory condition

Generally, degree-days required for field population of *B. tabaci* SSA1-SG3 to complete their development reduced as temperature increased (Table 17). Degree-days requirement also generally decreased from the egg to second instar stage and then increased at the third instar stage before decreasing again. Degree-days required were highest at the egg (168.6) and lowest at the pupa stage (43.4). The average degree-days required for egg to adult development were 523.02. For development from egg to adult stage, the lowest degree-day requirement (483.95) were estimated for the month of March (30 °C, RH = 80%) and highest for the month of January (30.3 °C, RH-73.3%).

B. tabaci subjected to constant temperature treatments showed a decrease in degree-days from egg to second instar stage, followed by an increase in degree-days from third instar to pupa stage (Table 16). Degree-days required for development were lower between 24 °C and 28 °C compared to other temperatures. At both temperature extremes 16 °C (695.8) and 32 °C (692.1), higher degree-days were required for completion of insect development and the least degree-days of 504.4 were estimated at 28 °C.

Table 15: lower development threshold of *B. tabaci* SSA1-SG3 under both field and laboratory conditions

Stage	Conditions	linear model	lower threshold (°C)	Adj R^2	P- value
Egg	Climatic	Y 0.00786x – 0.07037	9.0	0.9742	< 0.0001
First	Climatic	Y 0.01397x – 0.11417	8.2	0.7585	< 0.0001
Second	Climatic	Y 0.01744x – 0.13227	7.6	0.7715	< 0.0001
Third	Climatic	Y 0.01097x – 0.02397	2.2	0.4587	0.0004
Fourth	Climatic	Y 0.00740x + 0.02241	3.0	0.1909	0.0273
Pupa	Climatic	y 0.00974x – 0.01127	11.6	0.8559	< 0.0001
Egg-Adult	Climatic	y 0.00162x – 0.00697	4.3	0.8028	<0.0001
Egg	Field	y 0.00598x –0.01641	2.7	0.2581	0.0766
First	Field	y 0.00046929x + 0.00979	0.05	0.1545	0.1425
Second	Field	y 0.01660x –0.03532	2.1	0.1959	0.1118
Third	Field	y 0.01569x –0.04687	3.9	0.0291	0.2925
Fourth	Field	y 0.01623x –0.08430	5.19	0.0151	0.3172
Pupa	Field	y 0.02319x –0.29631	12.8	0.5611	0.0077
Egg-Adult	Field	y 0.00192x–0.00598	3.1	0.4847	0.0152

Table 16: Degree-days requirement for field populations of *B. tabaci* SSA1-SG3 in Dar es Salaam, Tanzania

	Egg	First	Second	Third	Fourth	Pupa	Egg-Adult
June	145.4	116.0	62.15	58.5	58.3	38.9	493.9
July	186.5	106.4	62.52	67.8	71.4	44.8	561.6
Aug.	187.0	97.7	67.80	76.4	61.5	45.1	557.2
Sept.	168.9	100.2	59.43	61.1	63.0	39.9	510.9
Oct.	153.3	98.2	56.58	57.3	48.9	49.2	485.1
Nov.	142.2	114.2	52.95	89.7	70.2	39.6	522.6
Dec.	177.2	88.8	69.57	61.1	61.8	45.6	521.2
Jan.	172.3	114.2	69.84	80.9	89.2	46.7	589.6
Mar.	174.4	107.8	55.73	54.0	44.7	37.9	484.0
Apr.	179.0	84.8	52.37	50.7	69.4	46.6	504.1
Mean	168.6±5.1	102.8±3.	60.9±2.1	65.7±4.0	63.8±3.9	43.4±1.3	523.0±11.3

Table 17: Degree-days requirement of *B. tabaci* SSA1-SG3 at six constant temperatures

Temp. (°C)	Egg	First	Second	Third	Fourth	Pupa	Egg-Adult
16	122.1±6	75.8±6	61.2±2.5	111.8±6.3	130±9.0	33.2±1.6	695.8±8.2
20	133.9±7	71.1±3.4	62.6±5.3	98.6±7.1	103.0±7.7	43.3±1.6	626.7±28.
24	130.9±6	72.5±0.6	50.8±1.9	73.1±0.9	79.5±2.6	60.0±4.4	556.5±2.2
28	124±3	68.6±4.7	52.3±5.3	65.5±4.9	69.1±7.7	56.5±2.1	504.4±22
32	127.5±3	77.1±7.5	64.3±7.6	118.3±10	177.5±28	71.4±2.7	692.1±9.6
36	148.4±0						

3.4.7 Life history of field population of *B. tabaci* SSA1-SG3 in Dar es Salaam, Tanzania

3.4.7.1 Survival of immature *B. tabaci* SSA1-SG3 on experimental plots outdoor

Survival of immatures was higher in the second, third and fourth instar stages compared to other stages (Table 18). The least survival was in the fourth (49.4%) and pupa (50.4%) stages where the activities of predators and parasitoids were highest (Table 18).

Table 18: Survival (%) of *B. tabaci* SSA1-SG3 of cassava under field conditions

Generation	N	Egg	First instar	Second instar	Third instar	Fourth instar	Pupa	Egg-Adult
June	258	96.5	72.3	76.7	76.1	58.1	78.7	18.6
July	260	44.2	80.0	85.9	72.1	57.9	18.2	2.3
August	258	69.7	76.5	80.0	82.0	79.1	38.9	10.9
September	260	37.5	71.4	86.7	84.9	83.9	50.0	9.2
October	290	83.0	84.8	85.8	82.2	75.4	28.7	10.0
November	289	59.0	80.1	80.3	71.8	45.6	5.6	0.69
December	234	70.9	91.0	81.5	62.6	33.8	65.4	7.3
January	263	52.6	84.9	83.9	76.8	39.5	93.3	10.3
March	226	62.4	44.0	80.7	51.0	8.0	100.0	2.2
April	269	85.2	73.4	64.9	56.9	12.7	25.0	0.7
Average		66.1	75.8	80.6	71.7	49.4	50.4	7.2

N = the number of whiteflies at the start of the experiment

Overall, egg to adult survival was very low since natural enemies and other mortality factors absent in the constant temperature experiments caused severe mortality.

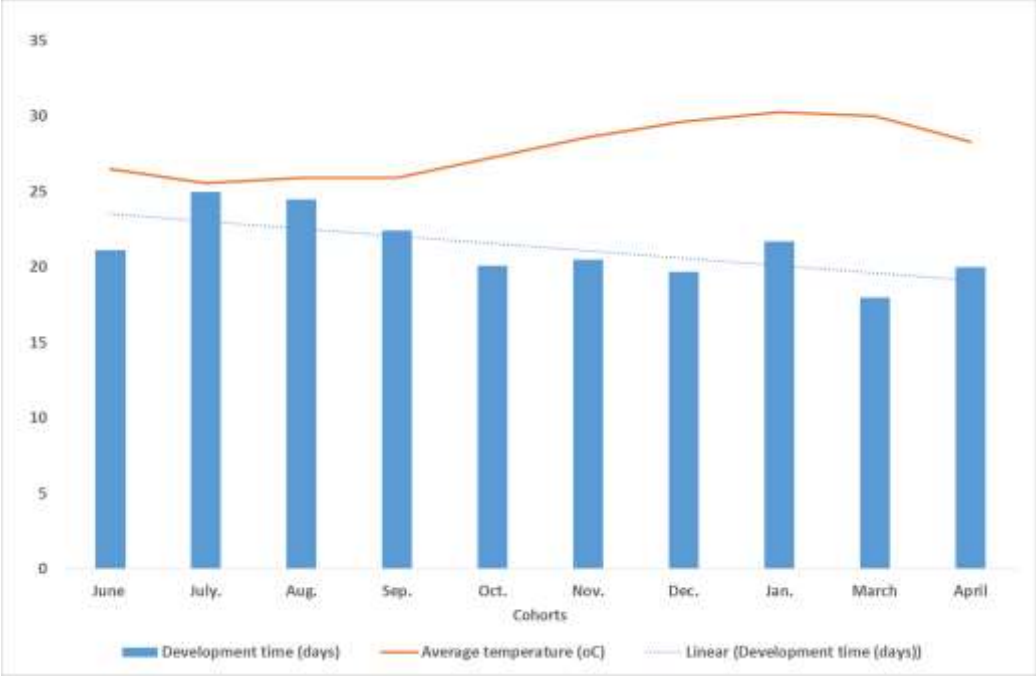

Figure 15: Relationship between average temperature and development of whiteflies under field conditions

3.4.7.2 Longevity of *B. tabaci* adult males and females on experimental plots outdoor

Under experimental plot conditions, adult males in clip-cages lived up to 28 days, although the mean longevity was 9.2 days. Under the same conditions, adult females lived up to 31 days although the mean longevity was 13.1 days. Similar to the pattern observed for the experiments with constant temperature treatments, females also lived longer than the males. The highest number of eggs laid by an individual *B. tabaci* was 287 eggs and mean fecundity per female was 94.5 eggs (Table 19).

Table 19: Longevity and fecundity of *B. tabaci* SSA1-SG3 under field conditions

Statistics	Longevity (days)		Fecundity (eggs/female)
Sex	Male	Female	Female
Minimum	1	1	2
Maximum	28	31	287
Mean	9.2±1.1	13.1±1.6	94.5±14.6
N	39	41	40

3.4.7.3 Estimation of life-table parameters at fluctuating temperature

The simulated intrinsic rate of natural increase, finite rate of natural increase and doubling time were not significantly different ($p= 0.05$) from observed values. The simulated gross reproductive rates, net reproductive rate and generation time were significantly different, but were within reasonable and biologically meaningful range (Table 20). Except for fourth instars, the observed developmental time was significantly faster than the simulated values but again within a reasonable range. The simulated mortality was significantly different ($p= 0.05$) from the observed in most cases. This was expected because the data used for the simulations were collected from field experiments where natural enemies greatly influenced mortality.

Table 20: Simulated and observed life history parameters of *B. tabaci* SSA1-SG3 at fluctuating temperatures

Parameters	Simulated	Observed	*p*-value
Life-table parameters			
R	0.086 ± 0.004	0.087	0.4054
Ro	25.516 ± 2.609	18.677	0.0079
GRR	117.514± 10.19	100.389	0.0163
T	37.67± 0.778	33.535	0.0020
λ.	1.09 ± 0.005	1.091	0.4056
Dt	8.061± 0.412	7.941	0.4001
Development time (days)			
Egg	9.929 ± 0.212	6.382	0.0002
First instar	4.415± 0.17	4.422	0.8759
Second instar	3.16 ±0.102	2.418	0.0010
Third instar	3.213± 0.11	2.438	0.0011
Fourth instar	3.463± 0.146	2.762	0.0023
Pupa	5.111 ±0.2	2.833	0.0004
Mortality rates			
Egg	0.202±0.087	0.035	0.0167
First instar	0.244± 0.069	0.277	0.1266
Second instar	0.086±0.085	0.217	0.0232
Third instar	0.053± 0.027	0.255	0.0010
Fourth instar	0.014±0.011	0.400	0.0000
Pupa	0.064±0.044	0.238	0.0035

3.5 Discussion

3.5.1 Phenology model

The study investigated temperature-dependent effects on the life history traits of *B. tabaci* SSA1-SG3 over a range of temperatures in climatic chambers and under field conditions, and then developed an overall phenology model for the pest. Several models describing the effects of temperature on insect life history have been developed and used for many insects (Logan *et al.,* 1976, Sharpe and DeMichele, 1977, Wang *et al.,* 1982) including whiteflies (Bonato *et al.,* 2007, Han *et al.,* 2013). These models are very useful for predicting changes in pest populations, and when built into a phenology model (like in this study), can be used for predicting the changes in distribution and abundance of insects both now and under future climate change. A similar approach of phenology modelling with ILCYM have been used to study the impact of climate change on insects across wide agro-ecologies (Fand *et al.,* 2014, Khadioli *et al.,* 2014a; Tonnang *et al.,* 2015 Mwalusepo *et al.,* 2015; Ngowi *et al.,* 2017). The estimated life-table parameters from our overall phenology model predicted maximum population growth between 22 and 24 °C, and optimum temperature for fecundity to be 21.4 °C. This is very much in line with our experimental observations, as fecundity and longevity of adult were highest within this temperature range. We observed variation in development time among individuals under the same conditions. Although it can be expected that homogenous individuals under the same conditions behave the same way, it does not always happen that way in nature. The overall model established in ILCYM includes modelling variation in development among individuals. Increasing model complexity for each immature stages significantly improved the model

3.5.2 Development time and rate

The predicted optimum temperature for development of immature life stages was between 26.4 °C and 34.28 °C. However, based on experimental observations, peak development was observed around 28 °C and the data suggest that optimum development can be obtained between 28 °C and 30 °C. This is much in agreement with the optimum temperature of 28 °C (Qui *et al.,* 2003) and 31.4°C (Muniz and Nombela, 2001) reported for *B. tabaci* MEAM1, but higher than 32.5 °C for *B. tabaci* MED on tomato (Bonato *et al.,* 2007), because at 32 °C, development time was prolonged, and fewer individuals reached the adult stage. Immature development time of 25.1 days for *B. tabaci* SSA1-SG3 on cassava at 32 °C is comparable to values for *B. tabaci* MEAM1 on broad beans (23.0 days) (Bosco and Caciagli, 1998), and cotton (23.1 days) (Nava-Camberos *et al.,* 2001), but differs substantially from that of *B. tabaci* MEAM1 on Cantaloupe (19.5 days) at 32 °C. In this study, no individual completed development from egg to adult stage at 36 °C. This is likely because the 36 °C degree treatment exceeds the optimum temperature for development of *B. tabaci* SSA1-SG3 or even close to the predicted maximum temperature for some of the immature stages (Table 10). Similar observations were made by Nava-Camberos *et al.* (2001) and Butler *et al.* (1983). However, several studies on the developmental time for *B. tabaci* MED and MEAM1 showed that both species are able to complete development at 35 °C or even higher (Wang and Tsai, 1996; Muniz and Nombela, 2001; Qui *et al.,* 2003; Bonato *et al.,* 2007; Delatte *et al.,* 2009; Guo *et al.,* 2013; Han *et al.,* 2013). Development rate followed similar patterns that has been reported for other whiteflies (Wang and Tsai, 1996; Qui *et al.,* 2003) and insects (Khadioli *et al.,* 2014a; Sporleder *et al.,* 2016; Mujica *et al.,* 2017). The difference between our results and those of others can be primarily attributed to differences in the thermal

tolerance of *B. tabaci* SSA1-SG3 compared to *B. tabaci* MEAM1 or MED. Additionally, members of the *B. tabaci* complex are known to sometimes have differential performance on different hosts even under the same conditions (Tsai and Wang, 1996; Nava-Camberos *et al.,* 2001). Differences in development time from one life stage to another can be explained by differences in their thermal sensitivity and other traits related to their response to climate (Kingsolver *et al.,* 2011).

3.5.3 Mortality and survival of immature stages

Mortality at the egg and first instar stages are relatively higher than all other stages at all temperatures tested. This pattern is in agreement with what has been previously reported for other members of the *B. tabaci* species complex (Wang and Tsai, 1996; Muniz and Nombela, 2001; Qui *et al.,* 2003; Bonato *et al.,* 2007; Delatte *et al.,* 2009; Guo *et al.,* 2013; Han *et al.,* 2013). This high mortality of *B. tabaci* eggs can be attributed to the hatchability of the eggs at different temperatures. First instars are known to be mobile for the first few hours after egg hatch, which can contribute to their mortality. Additionally, thermal sensitivity of each life stage also differs, which may lead to differences in mortality (Kingsolver *et al.,* 2011). Percentage survival from egg to adult emergence of *B. tabaci* MEAM1 on eggplant reported by Qui *et al.* (2003) (27 – 67%) is also similar to our result (14 – 62%). However, results of Bonato *et al.* (2007) (48 – 85%) for *B. tabaci* MED, Nava-Camberos *et al.* (2001) (76.5 – 100%) for *B. tabaci* MEAM1 on cantaloupe, Butler *et al.* (1983) (37 – 89%) for *B. tabaci* MEAM1 on eggplant, Wang and Tsai (1996) (36.8 – 88.7%) on eggplant are far higher than what was recorded on cassava in this study. *B. tabaci* SSA1-SG3 individuals were more tolerant to moderate temperatures (20 °C – 28 °C), than higher (32 °C

– 36°C) or lower temperature extreme (16 °C) because mortality rates were lower within this range. In contrast, Qui *et al.* (2003), Bonato *et al.* (2007) and Guo *et al.* (2013) suggest that both *B. tabaci* MEAM1 and MED appear to be better adapted to higher temperatures because they are still able to survive relatively well at these extremes.

Results from outdoor experiments showed that natural enemies caused substantial mortality compared to results from constant temperature treatments where natural enemies were absent. This will have further implication on the population dynamics of *B. tabaci* under future climate change and would make an interesting topic for further investigation.

3.5.4 Adult longevity and fecundity

Total fecundity per female decreased as temperature increased with a maximum at 20°C (117.47 eggs/ female). Unlike the trend in whitefly development and survival in which case development and survival is greatly affected above 30 °C, our results show that they are still able to lay a relatively impressive number of eggs (64.6 eggs per female at 32 °C and 52.3 eggs per female at 36 °C). This may have biological significance in the light of climate change since the whitefly may fall back on a similar strategy for survival and maintenance of its population. In contrast to this study where fecundity were higher within the range of 20 – 28 °C, Tsueda *et al*. (2011) reported much higher fecundity – up to 135 eggs per female and 81 eggs per female for *B. tabaci* MEAM1 and MED species respectively at 30 °C. Again, total fecundity per female in this study is also resembling those reported for *B. tabaci* MED species by Bonato *et al.* (2007). Although fecundity observed in this study was much lower

at 16 °C, and relative higher at 36 °C compared to similar temperatures in their study. Qui *et al.* (2003) reported much higher fecundity for *B. tabaci* MEAM1 than what was observed for *B. tabaci* SSA1-SG3 at comparable temperatures. Wang and Tsai (1996) showed that *B. tabaci* MEAM1 could lay up to 324 eggs per female at 20 °C, which far exceeds 117.5 eggs per female observed for *B. tabaci* SSA1-SG3 tested at the same temperature in this study. Similar pattern was also reported within the range of 20 – 27 °C by the same study, however total fecundity at 30 °C and 35 °C were less than what was observed in this study. Total fecundity per female at 16 °C was very low (16.4 eggs) and a few whiteflies laid eggs at this temperature, this observation is much in agreement with the development and survival of immature stages at this temperature.

Longevity of adult stages differed with temperature. High longevity at 20 °C and 24 °C, and low longevity at temperature extremes (16 °C, 32 °C, 36 °C) mirrored patterns observed for other life history traits in this study and many other on insects (Qui *et al.,* 2003; Bonato *et al.,* 2007, Khadioli *et al.,* 2014a). However, unlike most study where longevity was highest at the lowest temperature (Wang and Tsai, 1996; Qui *et al.,* 2003; Bonato *et al.,* 2007), adult longevity was not highest at the lowest temperature. Temperature-inflicted damage to cassava leaves during studies of immature development on cassava at 16 °C provided evidence for strong host plant effects on the whiteflies at this temperature, and also explains the low longevity of adult. In all cases, females lived longer than males, a trend that has been reported for whiteflies and many other insects.

4. Potential impact of climate change on the distribution and abundance of cassava-colonising *Bemisia tabaci* (Gennadius) in Africa

4.1 Abstract

Cassava production supports the livelihood of about 700 million people globally including smallholder farmers and industrial users. *Bemisia tabaci* is one of the greatest biotic constraints to cassava production due to its role in the transmission of viruses causing huge yield losses on cassava farms across Africa. Current temperature and downscaled future temperature data (2050) from the WorldClim database were used to assess the potential impact of climate change on the distribution and abundance of *B. tabaci* SSA1-SG3 based on three risk indices. The risk indices (establishment risk index, generation index and activity index) were visualised using the simulation module in Insect Life Cycle Modelling (ILCYM) software. Established temperature-dependent phenology model of *B. tabaci* SSA1-SG3, implemented in ILCYM was used for estimation and mapping of the risk indices. The estimated establishment risk index suggests a decrease in distribution of *B. tabaci* SSA1-SG3 with climate change in North and West Africa, and a southward range expansion in Southern Africa. The distribution of *B. tabaci* SSA1-SG3 is predicted not to significantly change in East Africa. In West Africa, although the number of generations is predicted to increase based on generation index, activity index (a more reliable estimate of population growth) indicates a decrease in population growth with climate change. Similarly, climate change is predicted to cause a decrease in population growth potential in North Africa, parts of Central Africa Republic, southern regions of Sudan; eastern regions of Ethiopia, Kenya and

Somalia. Both the estimated generation and activity indices agree with an increase in the number of generations and population growth potential in most parts of East and Southern Africa. Taken together, cassava-colonising *B. tabaci* SSA1-SG3 will continue to pose significant threat in cassava-growing countries across Africa. The findings have implications for vectored cassava viruses, and will be useful for climate change adaptation planning in countries where damage from the pest has been predicted to increase.

Keywords: Pest risk mapping, climate change, *B. tabaci* SSA1-SG3, Africa, cassava

4.2 Introduction

Cassava production supports the livelihood of about 700 million people globally including smallholder farmers and industrial users (FAO, 2013). Global cassava production increased from 71 million metric tonnes in 1961 to about 289 million metric tons in 2015 (FAOSTAT, 2015). Several agronomic traits of cassava make it a staple food and an excellent food security crop that can be counted on to supply calories when other crops fail (Nweke, 2005). In Africa, cassava ranks third among major staple food, with rice and maize been first and second respectively (Adenele *et al.,* 2012). Among the constraints to cassava production, pests and diseases constitute a major challenge. *B. tabaci* and the viruses they vector (cassava mosaic geminiviruses and cassava brown streak viruses) are considered the most important biotic constraints to cassava production (Legg *et al.,* 2006).

B. tabaci has been reported on over 600 host plants including: vegetables, legumes, ornamentals, root and tuber crops across the world (Oliviera *et al*., 2001; Abd-Rabou and Simmons, 2010; CABI, 2017). Although mostly polyphagous, monophagus species have also been reported on various crops (Abd-Rabou and Simmons, 2010). Feeding of *B. tabaci* adults and immatures stages also induce chlorotic spots on leaves, and at higher infestation levels, leaves may turn yellow and eventually fall off (CABI, 2017). The honeydew produced by immature *B. tabaci* on leaves attracts moulds and reduces photosynthetic area and crop quality. More importantly, *B. tabaci* vectors over 100 plant viruses (Czoneck, 2002; Jones, 2003; Hogenout *et al*., 2008; Polston *et al*., 2014) driving the disease epidemics of economic important plant viruses globally.

B. tabaci is a species complex consisting of more than 34 morphologically indistinguishable species (Dinsdale *et al.*, 2010; De Barro *et al.,* 2011; Chowda-Reddy *et al*., 2012; Firdaus *et al*., 2013; Lee *et al.*, 2013; Legg *et al.,* 2014a). In Africa, two major categories exist, namely the cassava-colonising and the non-cassava-colonising *B. tabaci* (Berry *et al.,* 2004; Esterhuizen *et al.*, 2013; Legg *et al.,* 2014a; Wosula *et al*., 2017). Available literatures and *mtCOI* sequence data suggest that sub-Saharan Africa 1 – 5 (SSA1 – 5) putative species of *B. tabaci* have been identified from cassava in Africa (Legg *et al.,* 2002; Berry *et al.*, 2004; Sseruwagi *et al.,* 2006; Esterhuizen *et al*., 2013; Legg *et al.,* 2014a; Tajebe *et al.,* 2015a; Manani *et al.,* 2017). For instance, SSA1 is the most widely distributed, and is found across sub-Saharan Africa; SSA2 has been identified in East and West Africa; SSA3 is present in Cameroon and Togo; whereas SSA4 appears to be restricted to Cameroon; and SSA5 is

probably limited to South Africa (Berry *et al.,* 2004; Gnakiné *et al*., 2012; Esterhuizen *et al.*, 2013; Legg *et al.,* 2014a).

Continuous anthropogenic emission of greenhouse gases in the last three decades is the primary driver of global climate change, and it is unequivocal that the earth's climate system is warming up (Intergovernmental Panel on Climate Change IPCC, 2014). Recent levels of anthropogenic emission of greenhouse gases is highest recorded in modern history, and global CO_2 levels are predicted to reach 650 ppm by 2100 (IPCC, 2014). Trends from existing temperature data from 1880 to 2012 suggest that the earth's surface has warmed by 0.85 °C (IPCC, 2014). For most parts of the world, all assessed climate change emission scenarios indicate an increase in surface temperature, although the degree of warming may vary across locations (IPCC, 2014). Statistics from the IPCC's highest emission scenario predict an increase of 2.6 – 4.8 °C in average global temperature by 2100 if emissions continue at current rate (IPCC, 2014). Global climate change has been predicted to affect both natural and agricultural ecosystems, triggering major changes in geographical distribution, abundance and ecological interaction of insect pests across the globe (Gilioli *et al.,* 2014; Sharma, 2014). Analysing how climate change will affect the future distribution and population dynamics of insect pests of agricultural crop is of particular importance to maintaining food production globally, and especially in developing countries where pests and diseases threaten food security.

Temperature is recognised as the major abiotic factor directly affecting development, survival, abundance and distribution of insects (Bale *et al.*, 2002, Bonato *et al*., 2007; Gilioli

et al., 2014). Whiteflies have a range of optimum temperatures where development, survival, and reproduction is maximised, and also threshold temperatures (upper and lower) beyond which the insect cannot successfully complete its life cycle (Qui *et al.,* 2003; Bonato *et al.,* 2007; Manzano and Lenteren, 2009; Legaspi *et al.,* 2011). Insect life-table studies considering a wide range of temperature where all other environmental factors are kept constant provide useful tools for understanding the population dynamics of insects (Bellows *et al.,* 1992; Khadioli *et al.,* 2014a; Khadioli *et al.,* 2014b).

Life-table studies provide essential information on the development, mortality and reproductive performance necessary for phenology modelling and understanding climate change impacts on the insect species (Kroschel *et al.,* 2013; Sporleder *et al.,* 2016). Two major modelling approaches are widely used for phytosanitary risk assessment and predicting the impact of climate change on the distribution and abundance of insect pests (Venette *et al.,* 2010; Kroschel *et al.,* 2013; Khadioli *et al.,* 2014b). The first is deductive modelling: here, the knowledge of climatic preferences of the insect gathered from detailed laboratory studies is used to understand the potential distribution of the insect (Venette *et al.,* 2010). The inductive approach on the other hand depends on statistical analysis of the known distribution (presence or absence data) of a species and long-term meteorological data to assess its climatic preferences (Venette *et al.,* 2010). Deductive approaches are particularly appealing because the information used for the forecast is based on rigorous laboratory experiments on the biology of the insect, and available data on the biology of the insect can be used for validating the models developed (Venette *et al.,* 2010). The ILCYM software used in this study is based on deductive approach and has been extensively used

to study the impact of climate change on distribution and abundance of several insect species (Kroschel *et al.,* 2013; Khadioli *et al*., 2014b; Fand *et al.,* 2015; Mwalusepo *et al.,* 2015; Sporleder *et al.,* 2016).

Increasing number of study addressed the potential impact of climate change on the distribution and abundance of *B. tabaci* (Campo *et al*., 2011; Jarvis *et al.,* 2012; Bellotti *et al.,* 2012; Gilioli *et al.,* 2014; Gamarra *et al.,* 2016a). Most of these studies are based either on biology of MEAM1 or MED species. At the moment, there is a paucity of information on the potential impact of climate change on firstly an endemic African population, and also cassava-colonising population of *B. tabaci*. The objective of the study therefore is to evaluate how climate change will affect the distribution and abundance of *B. tabaci* SSA1-SG3 (a haplotype of *B. tabaci* SSA1). The results of this study will help governments and other stakeholders understand the impact of climate change on the distribution and population dynamics of *B. tabaci* SSA1. Additionally, the findings will also be used for pest risk mapping, climate change adaptation planning and deployment of robust pest management programmes in different cassava-growing agro-ecologies across Africa.

4.3 Material and methods

4.3.1 The modelling software

The Insect Life Cycle Modelling software (ILCYM version 4.0), developed under an interactive web platform offered by the "Shiny" package implemented in R statistical software. ILCYM is an open source pest risk analysis tool developed by the International Potato Centre, Lima Peru (Kroshchel *et al.,* 2013; Sporleder *et al.,* 2016). ILCYM 4.0 is the

latest version, and has four modules: the “project module” for selection or creation of new projects, "modelling module" which facilitates modelling of temperature-dependence life history variables. It has several linear and non-linear models describing temperature-dependence of insects from which models that best describes the effects of temperature on each life stage of the insect is selected for building the phenology model for that insect. The "Compilation module" tracks modelling progress and shows a report of the modelled variables, while the "Simulation module" is used for spatio-temporal analysis, combining validated pest phenology model with climate data for visualisation of estimated risk indices. ILCYM 4.0 is used for both development of temperature-dependent phenological models, and spatio-temporal pest risk assessment and mapping on local, regional or global scales.

4.3.2 Phenology model

The temperature-dependent phenology model used in this study was that reported in Chapter 3 of this thesis. The process involved using several non-linear models available in ILCYM version 4.0 (Sporleder *et al.,* 2016) to analyse temperature-dependent life history processes including: immature developmental rate, development time, mortality, adult senescence rate, oviposition rate and oviposition time of adult female. The “modelling module” tool was used for phenology model building, while the “simulation module” was used for estimating life-table parameters (doubling time, generation time, intrinsic rate of natural increase, net reproductive rate, gross reproduction rate and finite rate of increase) and validation of the established phenology model. The modelling module combines the same shape distribution method with a rate summation and cohort up-dating algorithm for

simulating the population dynamic of insects (Khadioli *et al.,* 2014b). Models that best describes temperature-dependent life history processes were selected based on Akaike information Criteria (AICs) (Akaike, 1978), statistical criteria (coefficient of determination – R^2, R^2 adjusted) and biological aspects (Sporleder *et al.,* 2016; Mujica *et al.,* 2017). The developed phenology model was validated with life history data collected from *B. tabaci* maintained outdoors at the International Institute of Tropical Agriculture, Dar es Salaam, Tanzania. The *B. tabaci* used for the outdoor experiments are from the same colonies as the ones used for the constant temperature experiments.

4.3.3 Climate data

Downscaled baseline climate data (1960 – 1990) representing monthly average mean minimum and maximum temperature of the Worldclim data set (Hijmans *et al.,* 2005) were downloaded from http://www.worldclim.org. The climate data at 1 km^2 spatial resolution were used for spatial mapping for Africa and Tanzania. Future climate data for 2050 scenario based on IPCC's fifth assessment report (IPCC, 2013) were also obtained from Worldclim database.

4.3.4 Spatial mapping

To take diurnal temperature fluctuations in consideration, ILCYM uses a cosine approximation of daily temperature (minimum and maximum) to estimate temperature-dependent pest population parameters each 15 minute time step. For the first half day

prediction, the cosine function used (Kroschel *et al.,* 2013 and Tonnang *et al.,* 2013) is in form of:

$$T_i = \frac{(Max - Min)}{2} \times cos\left(\frac{\pi \times (i - 0.5)}{48}\right) + \frac{(Min - Max)}{2} \quad \text{equation 14}$$

where T_i is the temperature (°C) of the time step i, and i = 1, 2, 3, 4, 5, ……48, Max and Min represents daily minimum and maximum temperatures. Following the same approach, Ti for the second half of the day was estimated by using minimum temperature of the next day as input. Temperature data and geographical coordinates are needed to develop maps for any region of interest. To achieve this, ILCYM extracts minimum and maximum temperature data covering a period of 12 months (January to December) and the associated geographical coordinates from the downloaded data. The downloaded Worldclim data set is in grid format arranged in the longitude/latitude coordinate reference system.

As previously described in chapter 3, life-table parameters were estimated for each Julian day using both the temperature simulations and the established phenology model. The simulation module of ILCYM 4.0 was used for spatial analysis of risk indices. ILCYM calculated three indices of pest risk: establishment risk Index (ERI), generation index (GI) and activity index (AI) (Kroschel *et al.,* 2013; Tonnang *et al.,* 2013).

4.3.4.1 Establishment risk index

The establishment risk index indicates geographical areas with suitable climate that can favour survivorship and establishment of the pest. Meaning ERI characterises the risk of survival and establishment of the pest. It is also used to understand the potential distribution and risk of establishment under the current scenario, and the possible changes in distribution of the pest with climate change. ERI is represented on a scale of 0 to 1 where, 1 indicates areas where all immature stages of *B. tabaci* can survive throughout the year, while ERI less than 1 indicates areas in which survival and establishment is only possibly at certain periods in the year. ERI greater than 0.95 is associated with permanent establishment of the pest. ERI was estimated from the equation:

$$ERI = (1 - xEgg) \times (1 - xfirst\ instar) \times (1 - xsecond\ instar) \times (1 - xthird\ instar) \times (1 - xfourth\ instar) \times (1 - xpupa) \quad \text{equation 15}$$

where $x = \sum \frac{\text{Number of days a specific stage does not survive}}{365}$ equation 16

The values of 'x' for each immature life stage of the insect are derived by summing the ratio of the number of days a single immature stage would not survive by 365 (total number of days in a year) as shown in equation 16.

4.3.4.2 Generation index

Generation index estimates the mean number of generations that can be produced by an insect within a given year. The index is computed from sum of average generation length for each Julian day divided by the number of days per year. It is calculated using the equation:

$$GI = \frac{\sum_{x=1}^{365} 365/T_x}{365} \qquad \text{equation 17}$$

Where T_x is the predicted generation lengths (days) at Julian day x, (x = 1, 2, 3, . . ., 365) and 365 equal the number of Julian days per year. Development time reduces with increase in temperature until optimum physiological condition thus facilitating quick population growth (Bonato *et al.,* 2007; Xie *et al.,* 2011). However, at extreme temperatures, the optimum physiological conditions are exceeded and development rates drops in addition to decline in immature survival, fecundity of adult female and adult longevity (Qui *et al.*, 2003; Bonato *et al.,* 2007). Hence, with high number of generations per year, there is also increased possibilities of lower population increase over time (Kroschel *et al.,* 2013; Tonnang *et al.,* 2013; Fand *et al.,* 2015). For these reasons, generation index alone does not give sufficient information about population growth potential. The estimates of GI are supplemented with estimates of AI to give more conclusive information about pest population growth (Kroschel *et al.,* 2013; Tonnang *et al.,* 2013).

4.3.4.3 Activity index

Activity index is a more reliable estimate of population growth potential. It takes into account immature developmental time and mortality, and fecundity of adult females, hence a reliable estimate of temperature-dependent rate of finite increase within a year. AI is estimated from the equation given in the form of:

$$AI = \log_{10} \prod_{i=1}^{365} \lambda x$$ equation 18

where λx is the finite rate of increase at Julian day x and x=1, 2, 3, 4, 5.....365. For instance, an AI value of four shows a potential population increase by a factor 10^4 (10, 000) per year assuming the growth of the population is not limited by other environmental or biotic constraints (Kroschel *et al.,* 2013; Fand *et al.,* 2015). Furthermore, besides indicating population growth potential, AI also elucidates the severity of the pest problem and the potential pest damage (Fand *et al.,* 2015).

4.4 Results

4.4.1 Changes in *B. tabaci* SSA1-SG3 distribution

The establishment risk index under current scenario well reflected the current distribution of *B. tabaci* species complex across Africa. Under the current scenario, the majority of the cassava-growing countries had suitable climates and a high risk (ERI > 0.95) of *B. tabaci* SS1-SG3 permanent establishment. In non-cassava-growing countries of North Africa, ERI in Algeria is predicted to decrease as more areas will likely become unsuitable for the pest (ERI 0.40 – 0.6).

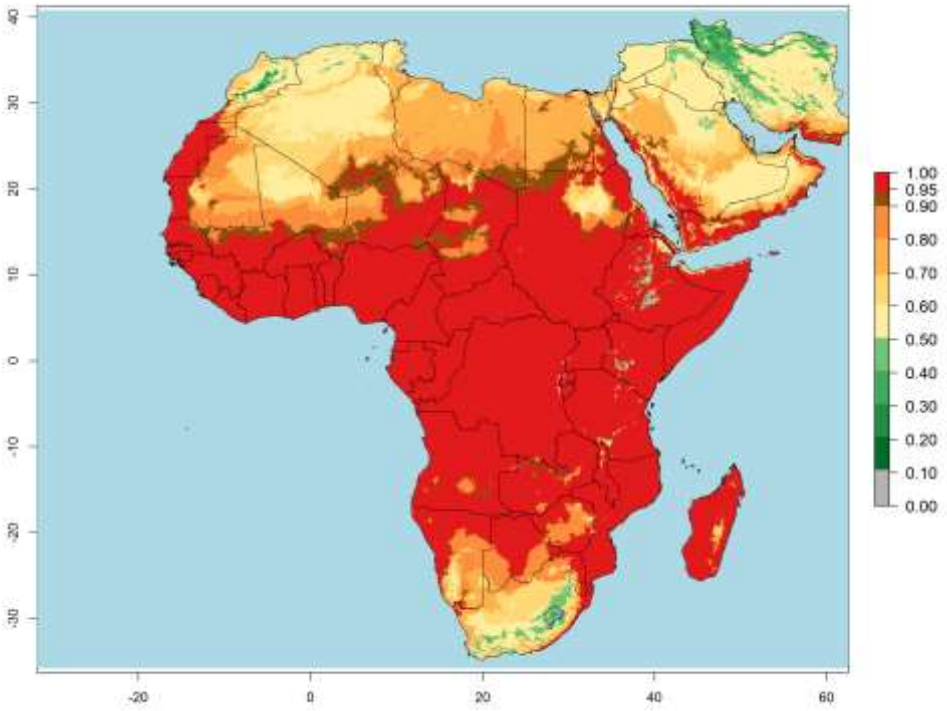

Figure 16: *B. tabaci* SSA1-SG3 establishment risk index in Africa under current scenario

In non-cassava-growing countries of North Africa where *B. tabaci* SSA1 has not been reported, in case of an accidental introduction, a moderate to high risk of establishment is indicated (Figure 16). However, an ERI of 0.4 – 0.5 was estimated for southern regions of South Africa and parts of Morocco (Figure 16). The estimated ERI across Tanzania indicates that almost the whole county has an ERI of 0.95 – 1.0 (Figure 18).

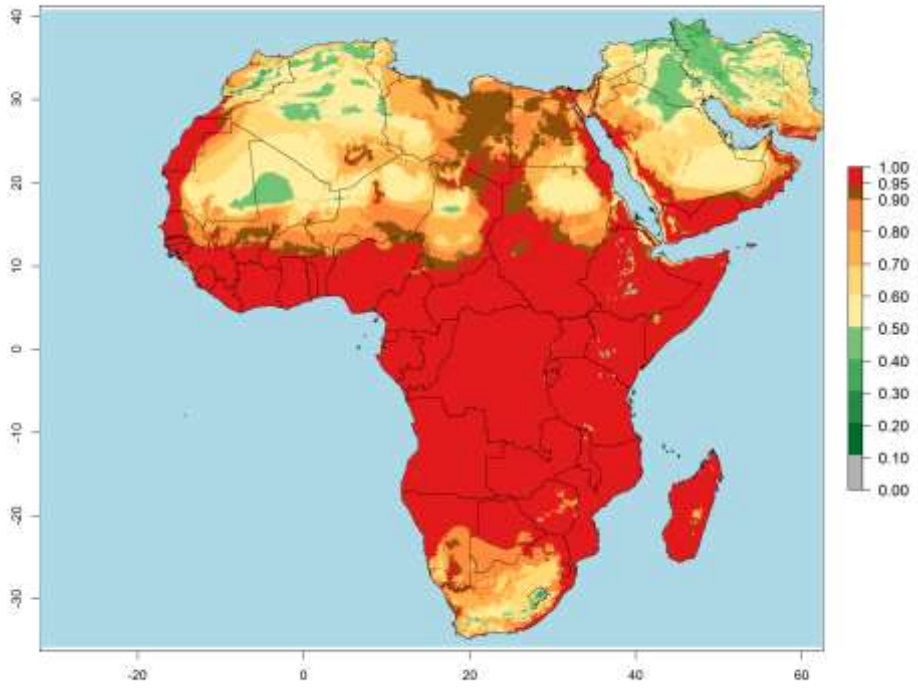

Figure 17: *B. tabaci* SSA1-SG3 establishment risk index in Africa under future scenario (year 2050).

Analysis of future scenario shows that ERI decreased in West Africa (Nigeria, Mali, Niger, Chad, Senegal and Burkina Faso) and Sudan. Nevertheless, vast areas of the cassava-growing countries of West Africa is predicted to have a high risk (ERI > 0.95) of *B. tabaci* SSA1-SG3 establishment (Figure 17). For other parts of North Africa, the ERI of the pest is predicted to increase in the future, and the risk of establishment remains moderate – high (0.6 – 1.0 for most countries). No significant change in ERI was predicted for East Africa since the ERI remains between high (0.95 – 1.0) under both current and future scenario (Figure 17). Overall, a southward range expansion was predicted, bringing *B. tabaci* further south into Southern Africa as indicated by increased ERI in Namibia, Zimbabwe, Botswana and South

Africa, and the portions of areas unsuitable for establishment of the pest under current scenario decreased.

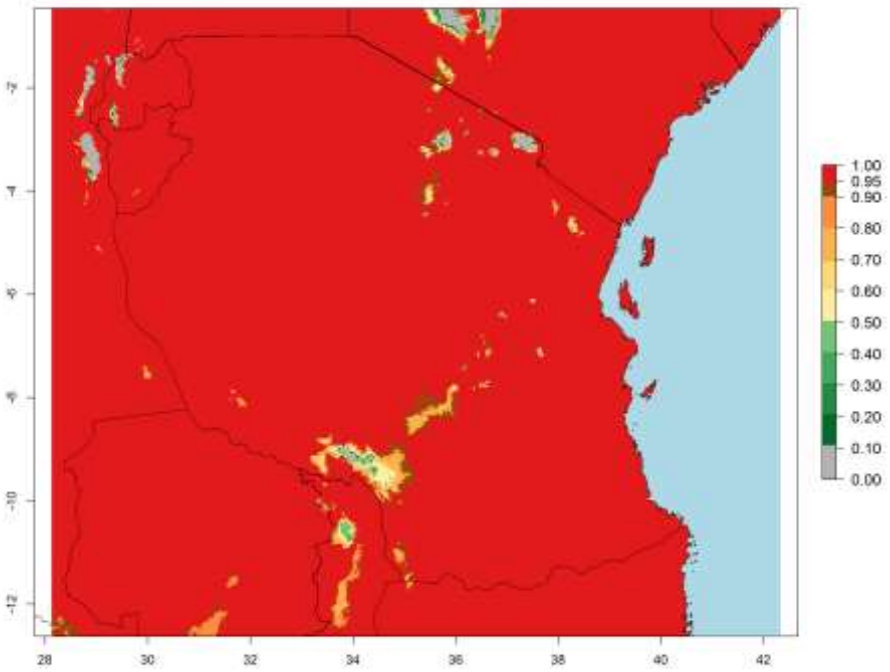

Figure 18: *B. tabaci* SSA1-SG3 establishment risk index in Tanzania under current scenario.

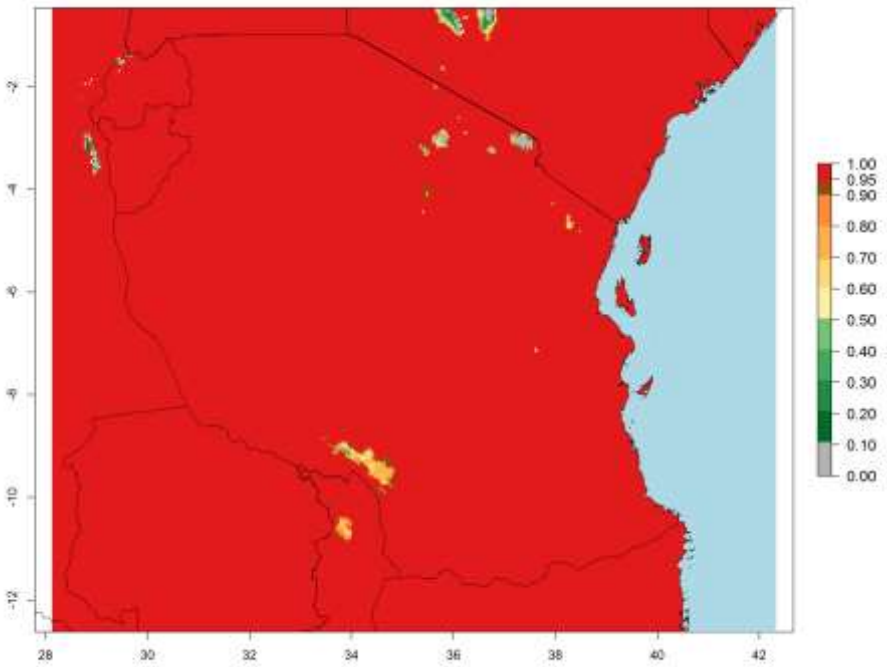

Figure 19: *B. tabaci* SSA1-SG3 establishment risk index in Tanzania under future scenario (year 2050).

4.4.1 Changes in *B. tabaci* SSA1-SG3 abundance

Generation index estimates the mean number of generations that can be produced by an insect within a given year, and the GI map is a pictorial representation of this. The map generated with the current climate data shows that *B. tabaci* SSA1-SG3 is able to complete 6 – 10 generations in most cassava-growing areas across Africa (Figure 20). The GI for the current climate are generally higher for tropical areas than areas with sub-tropical or temperate climate. Under the 2050 scenario, in West and Central Africa, the GI (7 – 10 generations per year) is predicted to increase by 1 – 2 generations (Figure 21).

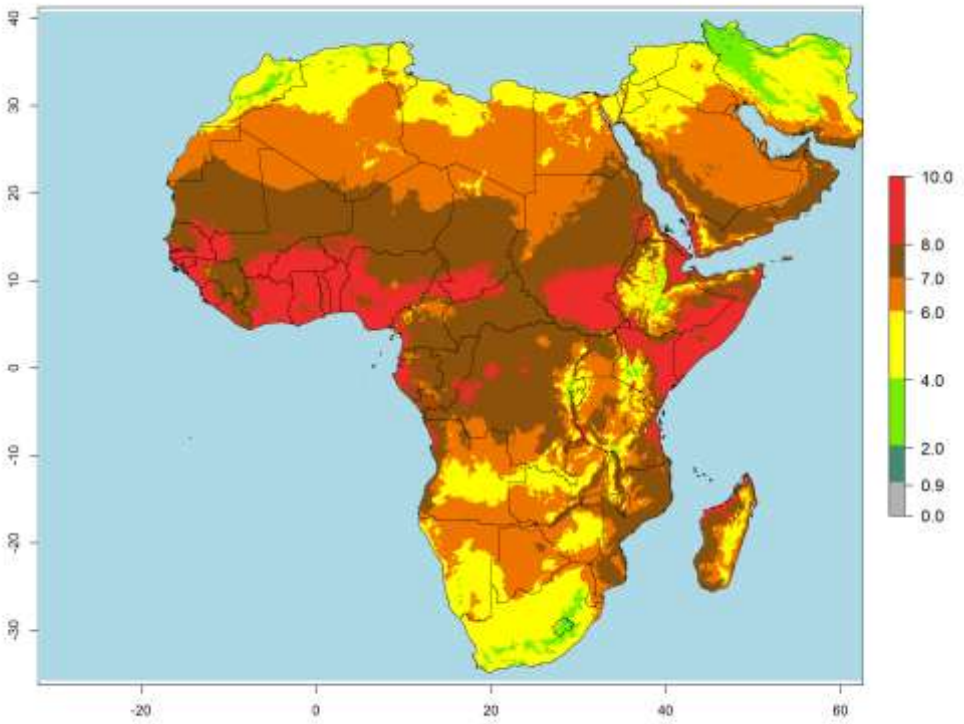

Figure 20: *B. tabaci* SSA1-SG3 generation index in Africa under current scenario.

For North Africa, the GI under the future scenario is lower compared to East and West Africa, but comparable to Southern Africa. These countries are predicted to remain marginally – moderately suitable for *B. tabaci* population increase as only a slight increase in the number of generation is expected in the northern most borders. However, an increase in GI is predicted for some East African countries (Tanzania, Uganda, Rwanda, and Burundi) and Southern African countries (Madagascar, Angola, Zambia, Namibia, Botswana and Mozambique) as 1 – 2 more generations can be completed in parts of these countries under the future scenario (Figure 21). Completion of 1 – 2 generations of *B. tabaci* SSA1-SG3 per year is also predicted for very extensive areas of Sudan, Democratic Republic of Congo and

Mozambique due to climate change. Overall, the number of generations per year is predicted to increase in most cassava-growing countries across Africa.

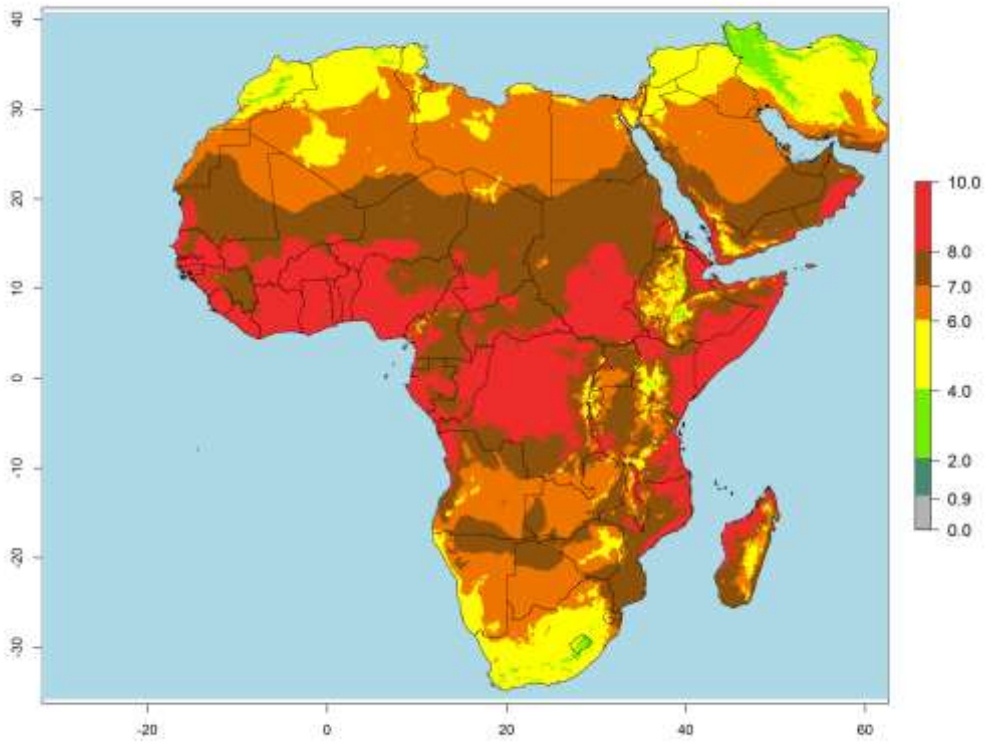

Figure 21: *B. tabaci* SSA1-SG3 generation index in Africa under future scenario (year 2050).

For most parts of Tanzania, climate change is predicted to increase the abundance of *B. tabaci* SSA1-SG3. In Ruvuka, parts of Katavi and Mbeya 2 – 4 more generations is predicted. *B. tabaci* SSA1-SG3 will likely complete an additional generation in areas bordering Mara, Singida, Simiyu, Mwanza and Tabora. Similarly, 2 – 4 more generations is predicted in parts of Tanga, Pwani, Morogoro, lindi and Mtwara. An increase of two or more generations per

year is expected in Iringa, Njombe, Kilimanjaro and Arusha due to increased climatic suitability (Figure 23).

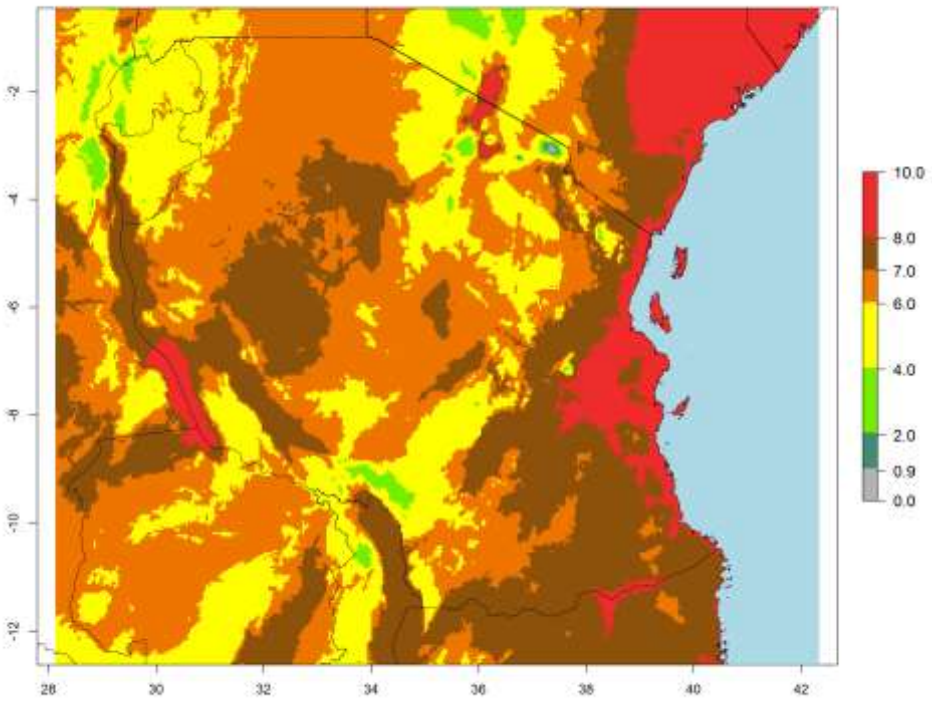

Figure 22: *B. tabaci* SSA1-SG3 generation index in Tanzania under current scenario.

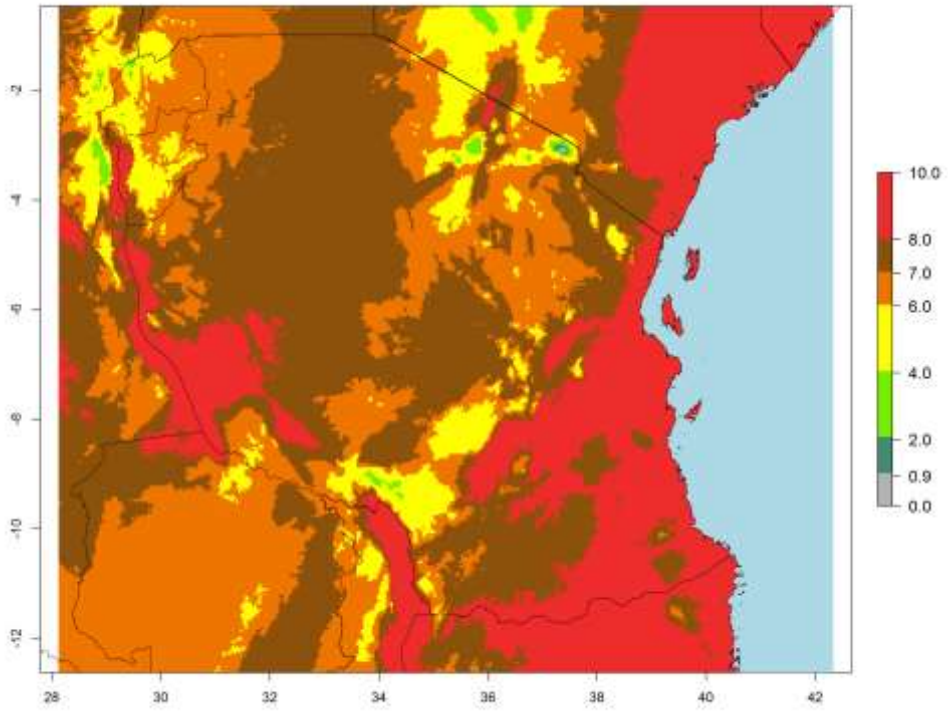

Figure 23: *B. tabaci* SSA1-SG3 generation index in Tanzania under future scenario (year 2050).

The population growth potential based on the AI under the current scenario varied from low (0.9 – 6) in most part of North Africa and extensive areas of some West African countries including Mauritania, Mali, Niger and Chad) to moderate (6 – 8) growth potential in the southern borders of Mali, Niger and Chad (Figure 24). This perfectly reflects the low population growth potential of the cassava-colonising *B. tabaci* SSA1 in the non-cassava-growing regions of North Africa. With climate change, the low population growth potential of *B. tabaci* SSA1 in non-cassava-growing areas of North Africa will worsen as the activity index is predicted to decrease in these countries.

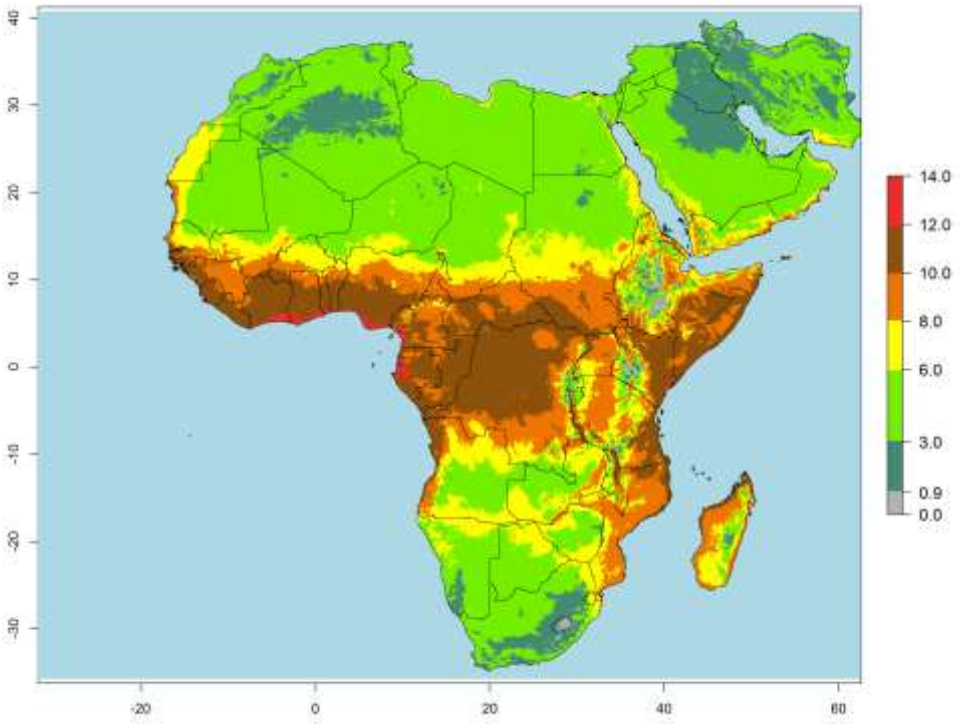

Figure 24: *B. tabaci* SSA1-SG3 activity index in Africa under current scenario.

A similar decrease in population growth potential is expected in West Africa (southern borders of Mali, Niger, Chad; and the northern borders of Burkina Faso, Ghana, Togo, Benin, Ivory Coast, Nigeria and Chad). Since the estimations of AI (measures rate of finite increase) are more reliable than GI (measures number of generations per year based on generation length), climate change will possibly reduce damage from *B. tabaci* in North and West Africa (Figure 25). The population growth potential is also predicted to decrease by a factor of 1 – 2 in Central Africa Republic, southern regions of Sudan; eastern regions of Ethiopia, Kenya and Somalia. An increase in AI by a factor of 1 – 2 is predicted for Cameroon, Gabon, Democratic Republic of Congo, Republic of Congo, Uganda, Burundi, Rwanda and Tanzania

(Figure 25). Climate change is predicted to increase population growth potential for most of the Southern African countries where the AI will likely increase by 2.

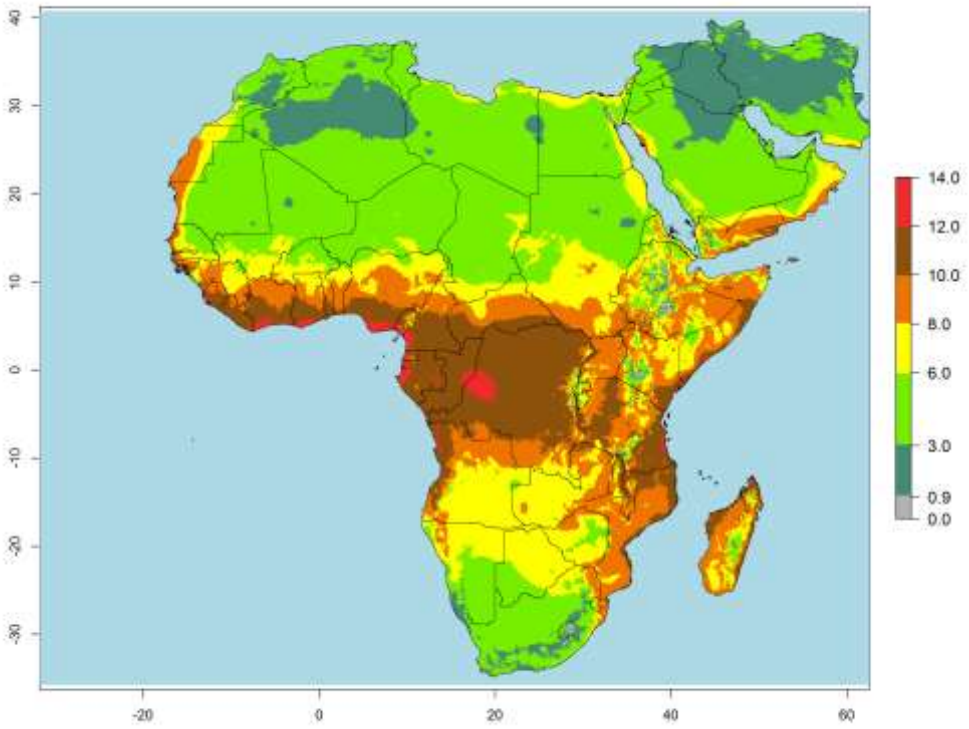

Figure 25: *B. tabaci* SSA1-SG3 activity index in Africa under future scenario (year 2050).

An increase in population based on AI is in the forecast for almost the whole of Tanzania. Highest population of the pest is expected in its current home range (Pwani, Zanzibar). Very high populations of *B. tabaci* SSA1–SG3 is expected in areas around Mara, Singida, Simiyu, Mwanza, Tabora, Tanga, Morogoro, lindi and Mtwara. Whereas the relatively lower population is expected in Njombe, Iringa, Kilimanjaro and Arusha (Figure 27).

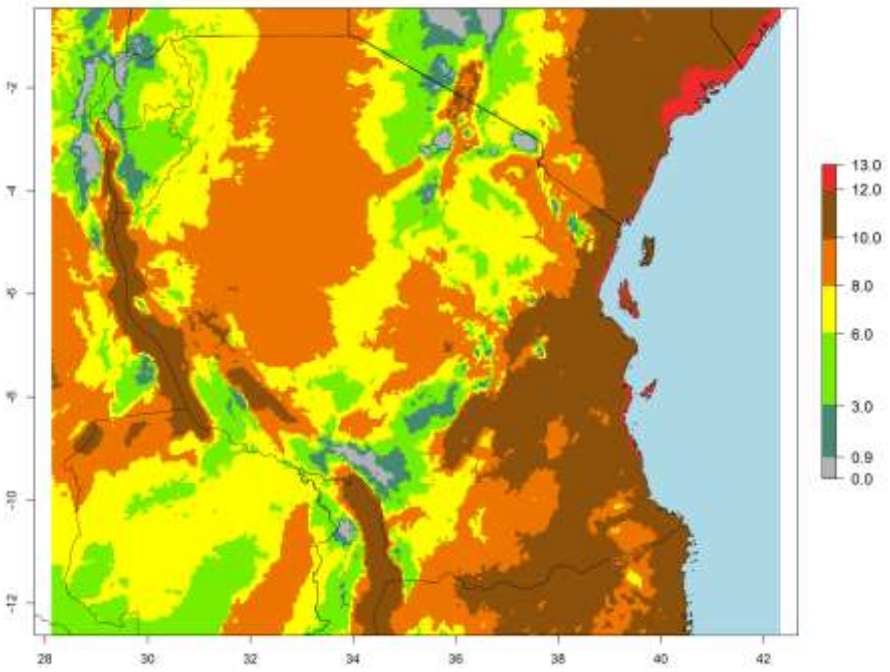

Figure 26: *B. tabaci* SSA1-SG3 activity index in Tanzania under current scenario.

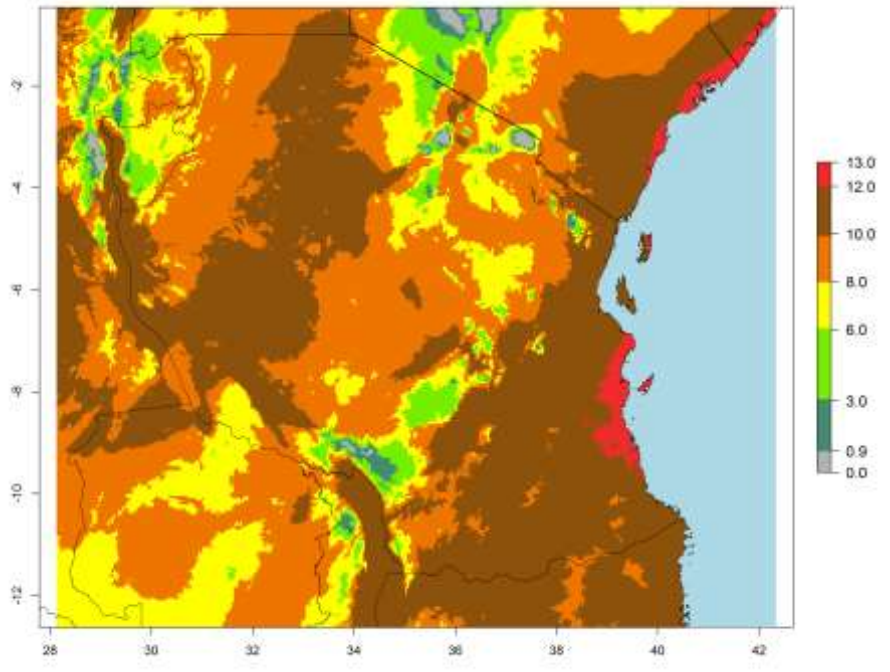

Figure 27: *B. tabaci* SSA1-SG3 activity index in Tanzania under future scenario.

4.5 Discussions

Cassava is an important crop due to its contributions to the livelihood of millions of Africans. Five putative species (SSA1 – 5) have been recognised to colonise cassava across Africa (Legg *et al.,* 2014a). Of these five putative species, *B. tabaci* SSA1 is the most widely occurring (Mugerwa *et al.,* 2012; Legg *et al.,* 2014a; Tajebe *et al.,* 2015a, Manani *et al.,* 2017, Tocko-Marabena *et al.,* 2017; Wosula *et al.,* 2017). Climate change has been predicted to affect the life history, distribution and abundance of many insects (Bale *et al.,* 2002; Bonato *et al.,* 2007; Gilioli *et al.,* 2014) with consequences for the plant viruses they vector. Some studies have investigated the potential impact of climate change on *B. tabaci* but there is no information on how the distribution and abundance of endemic African populations of cassava-colonising whiteflies will be affected by climate change. In this study, we report the first comprehensive predictions on the potential impact of climate change on an endemic African population of cassava-colonising *B. tabaci* SSA1-SG3 (a haplotype of SSA1) based on a phenology model developed considering the detailed life history of the pest, and supported by elaborate field and laboratory experiments.

Our ERI estimate under the current scenario closely captures the distributions of the pest and also indicates areas with the required climatic suitability to support the establishment of *B. tabaci* SSA1. *B. tabaci* SSA1-SG3 has a very high ERI in major cassava-growing countries and could possibly spread or get established in case of an accidental introduction in areas where it does not currently occur. Due to the constantly changing taxonomy of *B. tabaci*, we can only confirm the presence of *B. tabaci* SSA1-SG3 in Tanzania (Tajebe *et al.,* 2015a;

Wosula *et al.,* 2017), Central African Republic (Tocko-Marabena *et al.,* 2017), Madagascar (Wosula *et al.,* 2017), and Uganda (Tocko-Marabena *et al.,* 2017). It is probably also present in Kenya and Mozambique due to their proximity to the current distribution of this haplotype.

The study shows that the distribution for the *B. tabaci* SSA1-SG3 will not change substantially with climate change in cassava-growing areas of East and Central Africa, although a decrease in distribution is indicated for North and West Africa. However, predicted increase in climatic suitability will cause a southward range expansion of *B. tabaci* SSA1-SG3 into more areas of Southern Africa. This represents the major change in the distribution of the pest and can be explained by climatic differences of these regions. Using ecological niche modelling approaches based on presence or absence data, Campo *et al.* (2011), Bellotti *et al.* (2012) and Jarvis *et al.* (2012) also reported a decrease in climatic suitability for *B. tabaci* MEAM1 in West Africa and a high suitability in East and Southern Africa which is consistent with our results for cassava-colonising *B. tabaci* SSA1-SG3. Additionally, Gamarra *et al.*, 2016a used phenology modelling with ILCYM to investigate the potential impact of climate change on the distribution and abundance of *B. tabaci* MEAM1 on sweet potato. Their result, which suggests a decrease in establishment risk in Mauritania, Burkina Faso, and Chad and an increase in the northern regions of South Africa is also comparable with this study.

Based on GI, the estimated risk for *B. tabaci* SSA1-SG3 abundance in cassava-growing areas of West Africa will remain very high. However, a more reliable estimation of population increase (AI) indicates that the population growth potential or the rate of finite increase will reduce in parts of West Africa which is in agreement with the estimated risk for establishment and survival for West Africa. A similar trend has been predicted for parts of Ethiopia, eastern Kenya. This implies that climate change will likely reduce *B. tabaci* SSA1-SG3 damage in cassava-growing areas of West Africa. However, increase in both abundance and the population growth potential across central, southern Africa and most part of East Africa suggests that climate change will cause an increase in pest damage in these locations. Although their predictions are based on ecological niche models which does not fully capture changes in population abundance or population growth potential (relates more to changes in species distribution), Bellotti *et al.* (2012) and Campo *et al.* (2011) also predicted increase in suitability in these countries and suggested that the African rift valley will be an hotspot for *B. tabaci* and the viruses they vector on cassava.

Beyond changes in the suitability (Belloti *et al.,* 2012; Campo *et al.,* 2011, Jarvis *et al.,* 2012), this study also provides a detailed account of how climate change will influence the potential abundance of cassava-colonising whiteflies, and also indicates possible changes in the rate of finite increase or the population growth potential across cassava-growing ecologies in Africa. The risk of establishment in non-cassava agro-ecologies of North Africa is also indicated. Overall, the study agrees with previous studies but the magnitude of decrease in climatic suitability across Africa predicted based on *B. tabaci* MEAM1, a non-

cassava-colonising whitefly (at least in Africa), appears to be more than our findings based on cassava-colonising *B. tabaci* SSA1-SG3.

Although our phenology model is based on the effects of temperature on the biology of the insect, other factors including availability of suitable hosts, natural enemies, human activities and other abiotic factors affects the distribution and abundance of insects. The influence of these variables also need to be considered, particularly how natural enemies will affect the distribution and abundance of whiteflies. This presents an exciting area of research that merits due attention.

Interestingly the areas indicated in this study as whitefly hotspots also coincide with areas experiencing cassava virus disease pandemics of CMD and CBSD suggesting a possible role of climate change in this wide spread disease of viruses vectored by whiteflies. Here we hypothesise that climate change induced increased population of whiteflies is likely responsible for the recent and wide spread cassava virus disease pandemics in East and Central Africa. This also presents an interesting area for further investigation. Potential adaptation options are elaborately discussed in chapter 5 of this thesis.

5. Influence of biotic interactions on the mortality of cassava whitefly, *Bemisia tabaci* (Gennadius)

5.1 Abstract

Ecological life-tables are valuable tools for understanding factors governing insect population dynamics. In this study, age-specific life-tables were constructed for 10 generations of *B. tabaci* on cassava in Dar es Salaam, Tanzania. The experiments ran from May, 2016 to April 2017. Marginal, irreplaceable and key factor analysis were used to assess the effects of biotic and abiotic factors on the mortality of *B. tabaci.* Our results show that the greatest amount of marginal mortality was associated with parasitism in the pupa and fourth instar stages. The highest irreplaceable mortality was associated with egg inviability and parasitism respectively. Our estimate of mortality based on k-values shows that parasitism was the key mortality factors across *B. tabaci* generations and the pupa stage was the key stage that characterised generational mortality. The findings of the study will be useful for planning biological control interventions and management of cassava whiteflies using natural enemies.

Keywords: Mortality, predators, parasitoids, cassava, *B. tabaci*

5.2 Introduction

Cassava has been described as a "super-crop" for its role as food crop, cash crop and industrial raw material. Its production is vital to the well-being of more than 700 million

people globally (FAO, 2013). With increasing appreciation of it food and industrial values, production of cassava has also increased recently (Legg *et al.,* 2014b). Global cassava production is estimated at 268,277,743 tonnes and Tanzania is the sixth largest producer of the crop in Africa (FAO, 2013). Cassava is a resilient crop that can tolerate marginal soils, drought and also elevated CO_2, and has been proposed as an adaptation option to the impact of climate change crop production by smallholder farmers (Jarvis *et al.,* 2012; Legg *et al.,* 2014b).

Viruses and vectors are one of the greatest constraints to cassava production. Among the insect pest of cassava, *B. tabaci* stands out. *B. tabaci* as an economically important pest causing direct damage to a wide range of crops by producing sooty moulds and also transmitting plant viruses. *B. tabaci* is known to vector over 100 plant viruses including at least 11 viruses of cassava driving disease epidemics across cassava production systems globally (Jones, 2003, Legg *et al.,* 2015). Cassava farmers in Africa incur annual losses over 1 billion USD due to damage done by cassava whiteflies and the viruses they transmit (Legg *et al.* 2006).

Although there is progress in understanding the biology and management of *B. tabaci* globally, not much effective control methods have been deployed by smallholder cassava farmers to manage the pest. This is because cassava is largely a subsistence crop and farmers are often unwilling to invest much capital on insecticides or other control methods. However, insecticides are used in the intensive production of vegetables like tomatoes.

Newer *B. tabaci* control methods are being developed and a better understanding of natural enemies and other mortality factors would contribute to developing integrated management for the pest on cassava.

Natural enemies, weather conditions and host-plant attributes are the main components of the agro-ecosystem regulating populations of pest. A major step in developing sound pest management programmes for insect herbivores is to understand how these components of the agro-ecosystem influence host-herbivore-natural enemy interactions (Preiera *et al.,* 2007; Rosado *et al*., 2014). One of the most efficient approach for assessing influence of components of the agroecosystem on mortality of insects is the construction of ecological life-tables. They allow qualitative and quantitative assessment of mortality factors. By identifying and quantifying the causes of mortality over generations of the insect, key mortality factors and the relative importance of each factor can be identified. Life-tables also aid the identification of critical stages where the pest are most vulnerable (Bellows *et al.,* 1992, Miranda *et al.*, 1998; Preiera *et al,* 2007). Till date the only life-table study on *B. tabaci* of cassava was carried out by Asiimwe *et al.* (2007) in Uganda. There are background information on natural enemies of *B. tabaci* in Tanzania (Guastella *et al.*, 2015), and there is need to quantify their contributions to mortality of *B. tabaci* under field conditions for future applications in *B. tabaci* control programmes. This study seeks to identify the mortality factors of *B. tabaci* of cassava, including the key factors and quantify the contribution of each mortality factor.

5.3 Materials and methods

5.3.1 Study site and establishment of cassava in the field

The experiment was conducted on a cassava field established at the International Institute of Tropical Agriculture, Dar es Salaam, Tanzania. Asymptomatic cassava planting materials were supplied by IITA clean-cassava seed programme. Majority of the plants used were tested for *Cassava brown streak virus, Ugandan cassava brown streak virus* and *East African cassava brown streak virus* as described by Lodi *et al.* (1994) with modifications, and Shirima *et al.* (2017) and confirmed virus-free. Cassava stems of variety Albert were planted in plastic pots in the screen house. Two months old plants about 20 cm tall with 10 – 15 leaves were transplanted to the field at a spacing of 1 m by 0.5 m for every generation studied. The field was rain-fed with supplemental surface irrigation in the absence of rain. The experimental plots were insecticide-free throughout the experiment. Weeding was done when necessary.

5.3.2 Insect culture

B. tabaci originally collected from cassava at Bagamoyo, Tanzania was maintained for 8 – 12 generations on cassava plants kept in screened cages in the screen house facilities at IITA-Dar es Salaam Tanzania. More than 34 morphologically indistinguishable species of *B. tabaci* has been reported globally (Boykin *et al.*, 2007; Dinsdale *et al,* 2010; De Barro *et al.*, 2011), and more than one species has be reported to colonise cassava in Tanzania (Mugewa *et al.,* 2013; Legg *et al.,* 2014a; Tejebe *et al.,* 2015a). To facilitate correct identification of species used for the experiments, samples of 15 – 20 adult females *B. tabaci* were collected from

the colony for DNA extraction. Extracted DNA was sent to Commercial Macrogene laboratory USA for sequencing *mtCOI*. The *B. tabaci* were identified as SSA1-SG3. Subsequently, the purity of the *B. tabaci* in the colony was confirmed by routinely sending DNA of *B. tabaci* from the colony for sequencing. *B. tabaci* used for the experiments were collected from these colonies.

5.3.3 Cohort establishment

To ensure sufficient number of eggs were laid, 20 – 30 pairs of adult *B. tabaci* were confined in each plastic clip-cage attached to one of the top three fully expanded cassava leaves. *B. tabaci* has some preference for oviposition on young and fresh leaves. Clip-cages were removed after 24 hours oviposition period to obtain a uniform cohort and the adult *B. tabaci* were removed from the leaves by gently tapping them. In cases where few eggs were laid due to hot weather conditions, more than 30 pairs of *B. tabaci* were subsequently confined per cage. Depending on the number of the eggs on each plant, one or two leaflet(s) of cassava were used. 20 – 30 eggs laid on the abaxial leaf surface were marked per plant with a non-toxic Sharpie® marker, and 10 to 14 plants were used in each generation. More than 120 plants were used for the experiment. All unmarked eggs were carefully removed with the aid of a fine Camel hair brush. Since the marked eggs were not confined in clip-cages, subsequently, other eggs laid by *B. tabaci* on the plot were identified by the creamy colour and removed from the leaves. With this, any selected leaf remained with the specific number of eggs that had all been marked. A ×60 hand lens was used to monitor all

preimaginal stages. Small tags tied around the plants with marked eggs were used to identify the plants for subsequent data collection.

The experiments started late May, 2016 during the raining season and ended in April, 2017 during the raining season. In all, 10 successive generations of *B. tabaci* were monitored daily. A single cohort of individuals was followed through all life stages (egg to adult emergence) and data on hatching, predation, parasitism and other sources of mortality were recorded for each individual.

5.3.4 Identification of mortality factors

The developmental stage and as well as the state of each preimaginal stage was recorded daily and categorised as alive, dead, dislodged, predated or parasitised. A nymph was classified alive based on its appearance, shape, and position of symmetrical bacteriosome. Dead nymphs are often characterised by shrivelled cuticle or a flattened appearance. Dislodgement and inviability and predation were the sources of mortality in the egg stage. We noticed a continuous disappearance of eggs and nymphal stages in which a nymph observed on the previous day disappeared and its mortality could not be accounted for, this was categorised as dislodgement. *B. tabaci* eggs on cassava hatch in 5 – 7 days leaving an empty chorion on leaf surface. Eggs that did not hatch in 11 days were considered inviable.

Predation observed was mainly associated with the activities of sucking predators on first to fourth instar stage. Predators often empty the internal content of the nymphs, leaving

either an empty cuticle or a cuticle with displaced bacteriosome (Asiimwe *et al.,* 2007; Asiimwe *et al.,* 2016). Flattened cuticle with a brownish bacteriosome, also characterised with a hole usually above the location of the bacteriosome indicated the attack of a sucking predator. We verified this by collecting and viewing samples of nymphs attacked at the end of monitoring using a digital microscope (Dino Capture Microscope). Unlike sucking predators that leave a trace of their activities, chewing predators often did not leave a trace of their activities, although a good number of coccinellids were frequently encountered. However, partially eaten nymphs, observed on rare occasions on leaves gave a clue of their activities. Aphelinid parasitoids of the genus *Encarsia* and *Eretmocerus* were responsible for parasitism of immature *B. tabaci.* Although parasitoids can successfully attack all nympal stages, their activities are only obvious at the fourth instar and pupa stages (Naranjo and Ellsworth, 2005). Parasitic activities were noted by the presence of displaced bacteriosome, deformed nymphs, parasiotoid larvae or meconium within the fourth-instar cadavers. A few days after being parasitised, the chacteristics of the parasitoid in immature becomes more conspicuous. Parasitoids were identified using an illustrative guide (James Legg, unpublished) and supplemented with examination of samples under a microscope. Briefly, *Encarsia sophia* parasitised nymphs were identified by the brownish black parasitoid mummy and meconia at the base, while *Encarsia lutea* Girault & Dodd parasitised nymphs recognised transparent/whitish mummy with meconia at the sides. Insect samples were collected from the field for identification and predatory insects found associated with *B. tabaci* nymphs were collected and Identified under a microscope in the laboratory. During cool months of July and August, infection by fungal pathogens were observed as indicted by hyphal growth especially on fourth instars and pupae. Cassava is known to contain high amounts of

cyanogenic glucosides and other secondary metabolites capable of causing mortality of immature *B. tabaci* (Cereda and Mattos, 1996). Even under favourable environmental conditions in the absence of natural enemies, substantial mortality is recorded on cassava (Mugerwa *et al.*, 2012; Boni *et al.*, 2017). In addition, environmental factors like temperature and humidity could also cause desiccation of the immatures. Mortality probably due to host plant effects and/desiccation were collectively grouped as "unknown" sources of mortality since there one can't be easily distinguished from another. To ensure consistency, one worker collected the data for all life stages throughout the study.

5.3.5 Data analysis

5.3.5.1 Marginal mortality

Determination of age-specific mortality rate for each factor was based on observed (apparent) mortality and computed as described by Naranjo and Ellsworth (2005), Asiimwe *et al*. (2007) and Asiimwe *et al.* (2016). Marginal mortality rate refers to mortality from a single factor if the factor acted alone instead of contemporaneously with other existing factors. A mortality factor may be obscured by another factor because these factors could simultaneously cause mortality without acting sequentially (Asiimwe *et al*., 2007). Hence, the use of marginal mortality facilitates separate quantification of contemporaneous factors (Bellows *et al.*, 1992). The simplified version of the standard equations of Naranjo and Ellsworth (2005) were used to calculate marginal mortality rates:

$$M_A = d_A / (1 - d_B), \qquad \text{equation 19}$$

where M_A is the marginal mortality rate due to factor A, d_A is the apparent mortality rate due to factor A, and d_B is the summation of apparent mortalities caused by other competing factors acting concurrently. Marginal mortality rates of egg inviability, nymphal parasitism and unknown were estimated from apparent rates of predation and dislodgment. Marginal rates of mortality of predation was estimated from the apparent rate of mortality caused by dislodgement and marginal rates of mortality for pathogens was calculated from apparent rates of mortality from unknown and predations since these are the two contemporaneous factors that are relevant. Marginal rate of dislodgement was the same as the apparent rate since its effects cannot be obscured by other factors (Table 21, adapted from Naranjo and Ellsworth, 2005 with modifications).

Table 21: Combination of mortality factors used to estimate marginal mortality

Mortality rate (M_A)	apparent rate (d_B)	apparent rate (d_A)	stage
Inviablity	Inviablity	predation + dislodgment	Egg
Parasitism	Parasitism	predation + dislodgment	all nymphal stages
Predation	Predation	dislodgment	all nymphal stages
Pathogens	Pathogens	predation + dislodgment	all nymphal stages
Unknown	Unknown	dislodgment + predation	all nymphal stages

5.3.5.2 Irreplaceable mortality

Irreplaceable mortality is that part of the generational mortality that would not occur, after excluding a mortality factor in question from the life system and allowance is given for the action of other mortality factors (Southwood, 1978; Bellows *et al.,* 1992). The idea is that if one mortality factor was absent earlier in the life cycle of an insect, there are chances that other mortality factors will compensate, causing more mortality later in the life cycle of the insect (Price *et al.*, 2011). Carey (1989) proposed dealing with this problem by computing irreplaceable/indispensable mortality (Price *et al.*, 2011). Irreplaceable mortality for each mortality factor and life stage were computed according to methods originally described by Carey (1989) as adapted by Naranjo and Ellsworth (2005) and Asiimwe *et al.,* (2007). The generation form of the equation used to compute irreplaceable mortality is:

$I_c = D-[1-(1-M_A)(1-M_B)]$, equation 20

and

$D = [1-(1-M_A)(1-M_B)(1-Mc)]$, equation 21

where M_x is the marginal mortality rate for factor or stage A, B or C. I_C is the indispensable or irreplaceable mortality for factor or stage C after eliminating other marginal mortalities for factor or stage C. assumes density-independence

5.3.5.3 Key factor

Insects are exposed to several mortality factors, which are responsible for different mortality in each life stage. The factor that has the highest influences the population fluctuations is called the key factor. Similarly, the stage that influences population fluctuation most is called the key stage (Yamamura, 1999). The method of Varley and Gradwell (1960) was deployed to estimate the key factor and key state and as previously described by Naranjo and Ellsworth (2005). First the partial mortality (k-values) were calculated for each mortality factors using the equation:

$$k = -Ln\,(1-Mx), \qquad \text{equation 22}$$

where *Mx* is the marginal mortality rate for that mortality, k is the difference between natural logarithms of the number entering a life stage and the number dying due to the mortality factor at that life stage. It shows the number dying due to an observed mortality factor. Total mortality (K) was obtained by summing partial mortality, then partial mortality were compared to total mortality graphically to identify the key factor (Varley and Gradwell, 1960).

Figure 28: *B. tabaci* nymph parasitized by *En. sophia*

Figure 29: *B. tabaci* nymph parasitised by *Eretmocerus* spp.

Figure 30: *B. tabaci* nymph parasitized by *En. lutea*

Figure 31: *B. tabaci* nymph attacked by a sucking predator

Figure 32: Empty pupal case after parasitoid emergence

Figure 33: Empty pupal case after *B. tabaci* emergence showing a characteristic "T" slit

5.4 Results

Marginal mortality or mortality from a single factor if the factor acted alone instead of contemporaneously with other existing factors was highest for parasitism in the pupa (0.4177± 0.086) and fourth instar stage (0.3228± 0.073) and least for fungal growth in the second (0.0088) and third instar (0.0260) (Figure 34). When all generations are pooled, the highest marginal mortalities were associated with parasitism (0.8100±0.079), dislodgement (0.5856±0.015) and predation (0.4917±0.027) in descending order. When all mortality factors acting on each life stage are pooled, marginal mortality was highest in the pupa stage (0.7982± 0.061), followed by the fourth instar (0.6710± 0.049), egg (0.4109± 0.050), third instar (0.2803± 0.018), second instar (0.2322± 0.016) and first instar (0.2322± 0.016) stages respectively (Figure 34). Marginal mortality due to each factor varied from one generation to another but was consistently high for parasitism, egg inviability and predation (Figure 35).

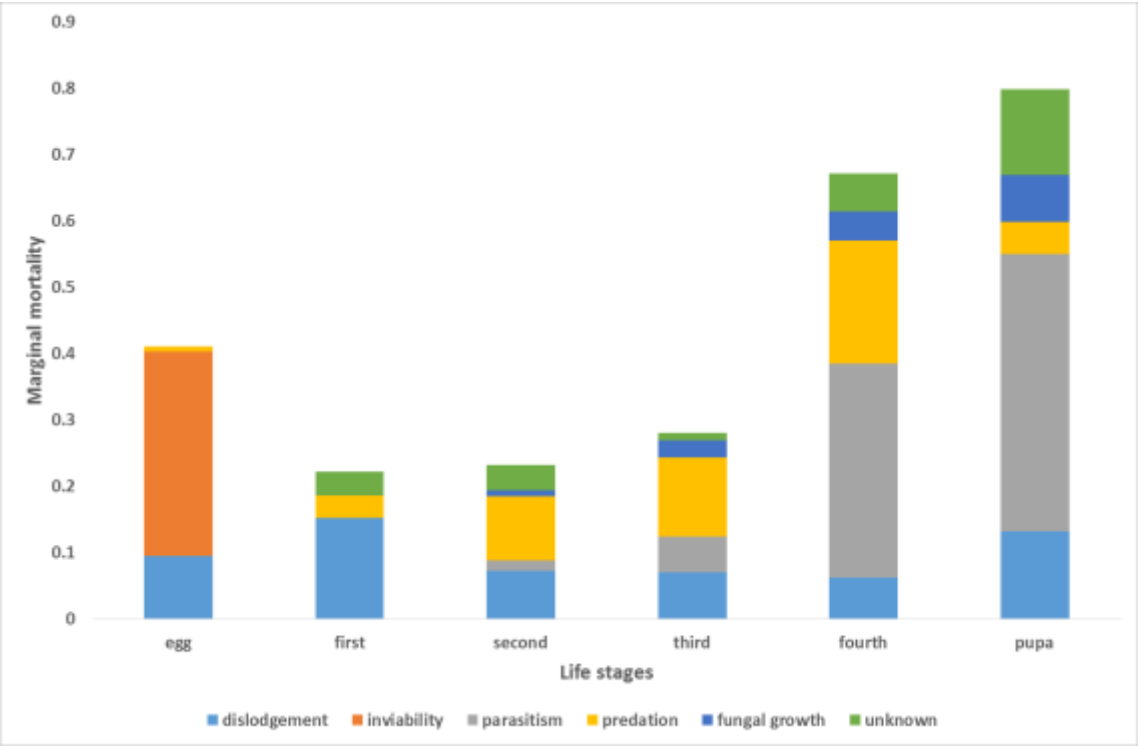

Figure 34: Marginal mortality of *B. tabaci* life stages on cassava in Dar es Salaam, Tanzania

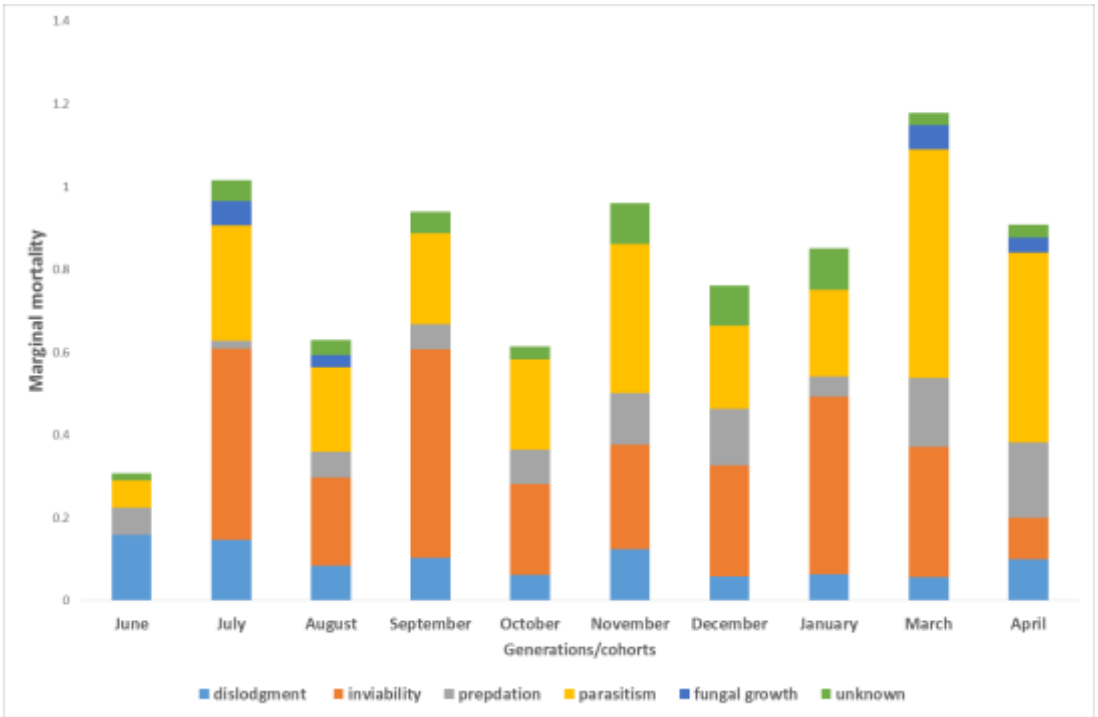

Figure 35: Marginal mortality of *B. tabaci* generations on cassava in Dar es Salaam, Tanzania

When all generations are pooled, irreplaceable mortality was associated with egg inviability (2.486± 0.043), parasitism (1.963± 0.030), predation (1.371± 0.031), dislodgement (1.316± 0.030), fungal growth (1.072± 0.054), unknown death (0.925± 0.037) in decreasing order (Figure 36). For the different life stages, the order was: pupa (1.221± 0.059), fourth instar (0.876± 0.043), egg (0.343± 0.048), third (0.277± 0.015), second (0.199± 0.015), first instar (0.186± 0.027) stages in descending order (Figure 36). Generational irreplaceable mortality also varied across the generations (Figure 37).

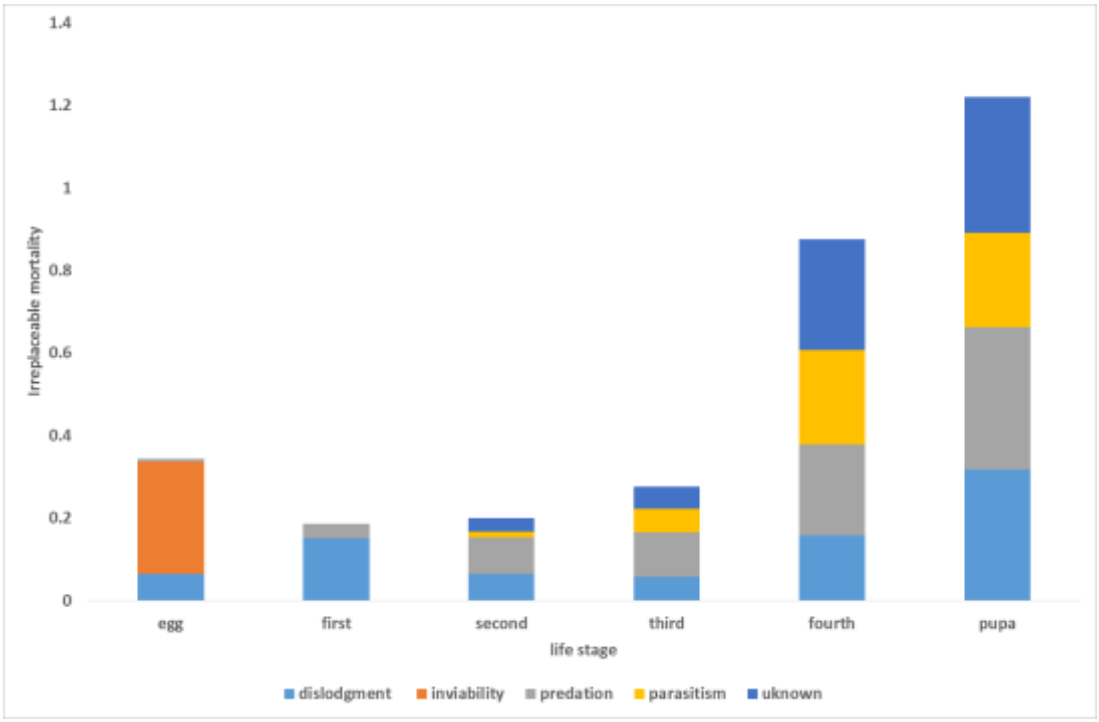

Figure 36: Irreplaceable mortality of life stages of *B. tabaci* on cassava in Dar es Salaam, Tanzania

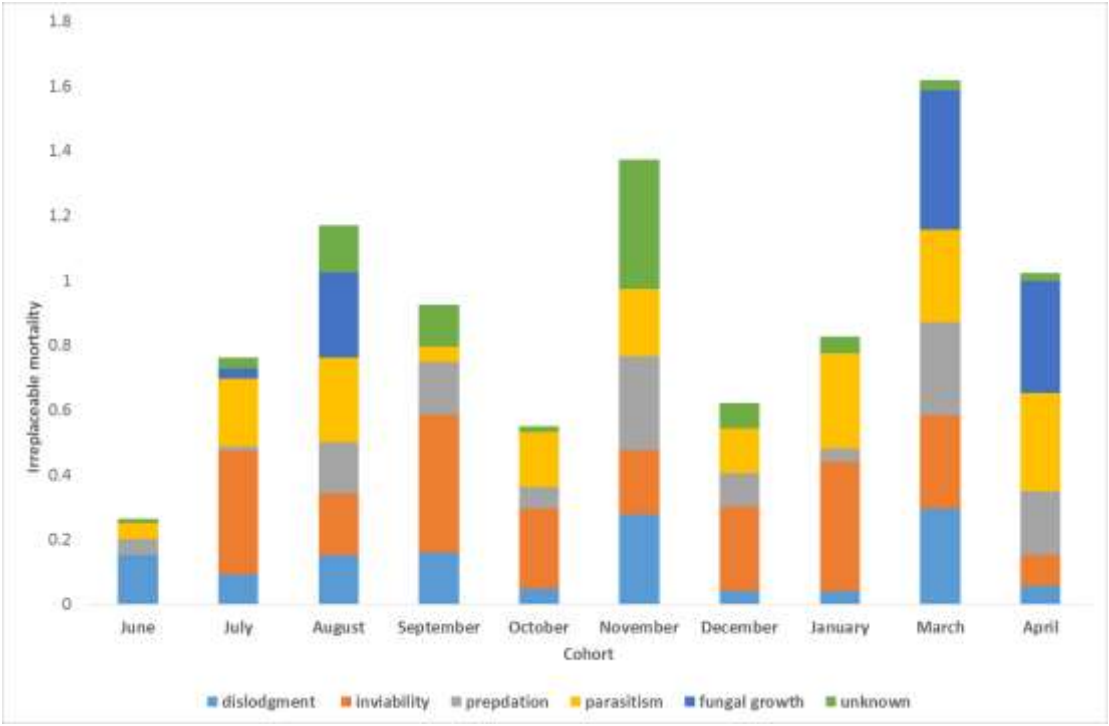

Figure 37: Irreplaceable mortality of cohorts of *B. tabaci* on cassava in Dar es Salaam, Tanzania

Our estimate of mortality based on k-values shows that parasitism was the key mortality factors across *B. tabaci* generations. Mortality rate was in this order from highest to lowest: parasitism (0.398.102±0.074), inviability (0.346±0.071), predation (0.124±0.034), dislodgement (0.102± 0.014), unknown (0.059± 0.012), fungal growth (0.019± 0.008) (Figure 38). Predators and parasitoids were identified during the study. Among the parasitoids of *B. tabaci*, *Encarsia sophia* had the highest parasitism rates. *E. lutea* and *Eretmocerus* spp. has similar occurrence (Table 22). *Serangium* spp. and a predatory thrips were main predators observed. When all generations are pooled, mortality was highest in the pupa and fourth instar stages respectively (Figure 38). Mortality in terms of k-values was least in June while mortality in the month of March was the highest (Figure 39).

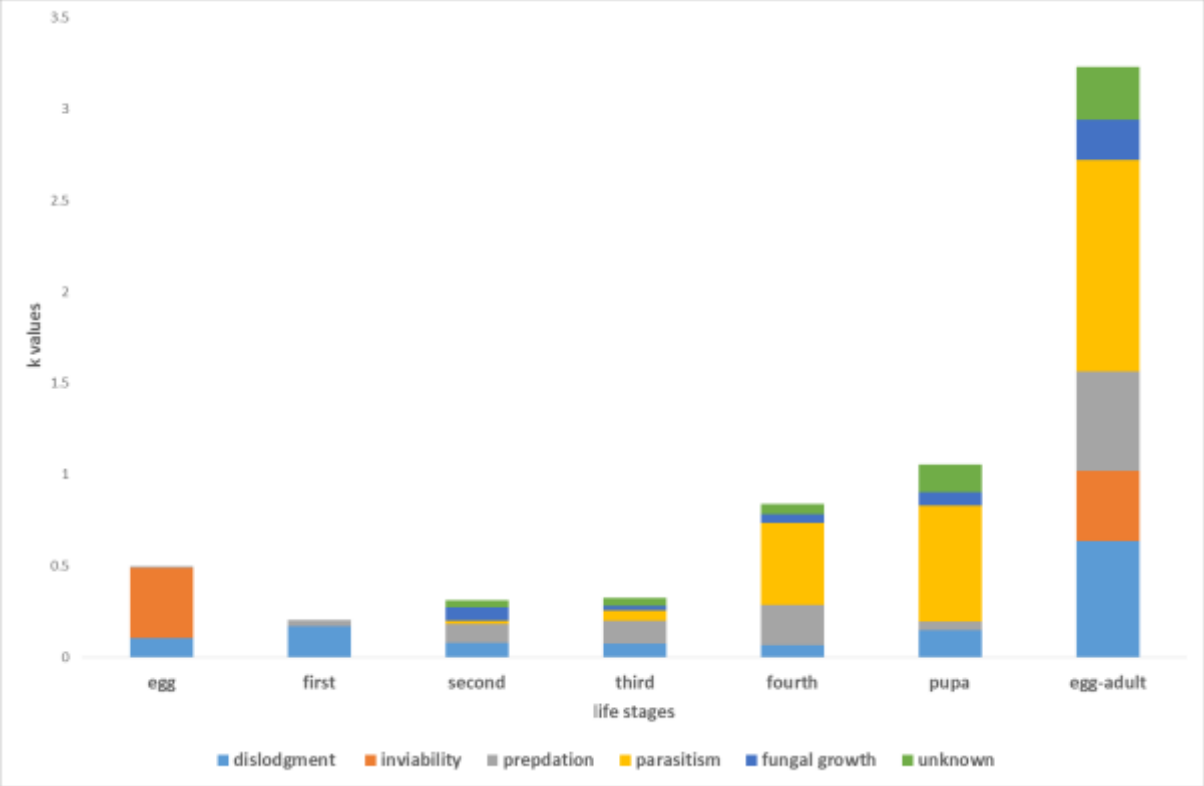

Figure 38: Mortality (k-values) of life stages of *B. tabaci* on cassava in Dar es Salaam, Tanzania

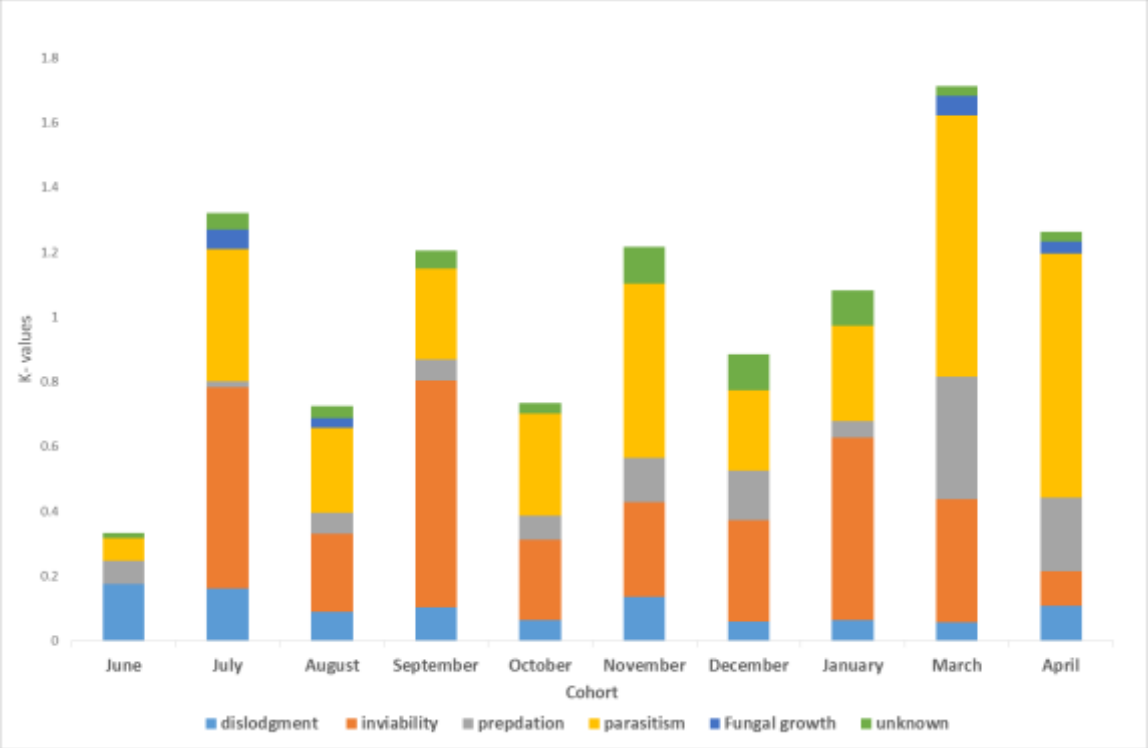

Figure 39: Mortality (k-values) of *B. tabaci* cohorts in Dar es Salaam, Tanzania

Table 22: Distribution of parasitoids identified on cassava whiteflies during experiments in Dar es Salaam

Generations	N	*Encarsia sophia*	*Encarsia lutea*	*Eretmocerus* spp	Unknown parasitoid
September	260	13	1	0	0
October	290	26	3	0	0
November	289	8	15	10	0
December	234	13	4	8	0
January	263	2	12	12	0
March	226	9	0	4	9
April	269	10	2	4	0
Total	1831	81	37	38	9

N = number of *B. tabaci* eggs used to set up the experiments

Note: parasitoid identity was not recorded for the first three months of the experiments, but their occurrence show similar pattern (more *En. sophia*) compared to what was recorded.

5.5 Discussions

Life-tables are valuable tools for understanding factors governing insect population dynamics. In this study, we used a tri-dimensional analysis (key factor, marginal mortality, irreplaceable mortality) to develop and interpret comprehensive life-tables developed for 10 generations of *B. tabaci* on cassava in Dar es Salaam, Tanzania.

Marginal mortality estimates used to separately quantify contemporaneous mortality factors or identify the relative importance of each factor, such that the effect of one factor is not masked by another (Bellows *et al.*, 1992), showed that the highest marginal mortality was associated with parasitism, dislodgement and predation in that order. Meaning the role of parasitoids in causing generational mortality could not be masked by any other mortality factor. This is comparable with the estimates of the key factor analysis that identified parasitism in the nymphal stages as the key factor; inviability in the egg stage and predation across all stages as significant contributors to generational mortality. The pupa and fourth instar stages were also associated with the highest life stage mortalities (as the case for the key factor analysis). This is in agreement with the findings of Asiimwe *et al.* (2007) who reported parasitism, dislodgement and predations (respectively) as the highest sources of marginal mortality of *B. tabaci* on cassava in Uganda. Similarly, Karut and Naranjo (2008) reported parasitism and predation as the primary sources of marginal mortality of *B. tabaci* on cotton in Turkey.

Considering all *B. tabaci* generations, highest irreplaceable mortality was associated with egg inviability, parasitism and predation in that order. Other factors with high irreplaceable mortality are parasitism and predation respectively. In contrast to this study, Karut and Naranjo (2008) reported that the primary source of irreplaceable mortality was parasitism and predation, while Asiimwe *et al.* (2007) reported dislodgement as the primary source of irreplaceable mortality of *B. tabaci.* The difference in our results could be due to the differences in host plants or environment.

Key factor analysis used to identify the factor that had the highest influence on population fluctuations of *B. tabaci* on cassava in Dar es Salaam, Tanzania showed that parasitism in the fourth instar and pupa stages was the key mortality factor, while the pupa stage was the key stage that characterised generational mortality. *En. sophia* and *Er. mundus* have been identified as the primary parasitoids of cassava in Tanzania (Guastella *et al.,* 2015), and they were also frequently encountered during this study. The result is in agreement with previous studies in other countries. For instance, Asiimwe *et al.* (2007) also identified parasitism in the fourth instar stage as the key mortality factor of *B. tabaci* on cassava in Uganda. In contrast, Naranjo and Ellsworth (2005) identified predation in the fourth instar stage as the key mortality factor on cotton in Arizona, while Karut and Naranjo (2008) also reported parasitism as the key mortality factor on cotton in Turkey. Egg inviability and predation were other important mortality factors. Mortality due to egg inviability can both be associated with host plant effects and the influence of abiotic factors (temperature and rain) on the eggs. Cassava is known to produce cyanogenic compounds that could probably affect insect herbivores (Cereda and Mattos, 1996). It is also possible that the eggs could be more vulnerable especially when other abiotic factors acts alongside. Rowley *et al.* 2008 described the effects of predators on immature *B. tabaci* growing on cassava in Uganda. They identified various coccinellids (*Serangium* species), Conwentrizia and syrphid larvae as the main predators of *B. tabaci* on cassava, which was in agreement to our field observations. Parasitism in the pupa stage explained why the pupa stage was the key stage.

6. Adaptation of smallholder farmers to climate change impacts on cassava whiteflies and associated viruses in Tanzania[2]

6.1 Abstract

Survey interviews of 320 farmers in three regions of Tanzania and interviews with 20 international whitefly/virus experts were done with the aim of exploring smallholder farmers' adaptive capacity and identifying adaptation strategies to the impact of climate change on cassava whiteflies and associated viruses. Between January 2016 and January 2017, structured and pre-tested interview schedules were conducted using a multistage sampling technique. Most of the farmers (72.3%) produce cassava primarily for food and rely mainly on their friends (49.4%), and their own farms (49.4%) for cassava planting materials. Adaptive capacity was found to be moderate for most farmers, and some farmers apply simple methods to control cassava viruses (38.1%) and whiteflies (19.7%). Adaptation strategies most recommended by experts were: Integrating pest and disease management programmes, phytosanitation, applying novel vector management techniques and biocontrol of whiteflies. To enhance farms' adaptive capacity most recommended were: capacity building through training of stakeholders, monitoring the pests through surveillance programmes, incorporating pest and disease adaptation planning into agricultural management plans and assessing adaptation needs through stakeholders.

Key words: whiteflies, pest management, climate change adaptation, cassava

[2]Aregbesola OZ, Legg JP, Uzokwe VNE, Adeloye KA, Lund OS, Sigsgaard L, Rapisarda C, 2018. Adaptation of smallholder farmers to climate change impacts on cassava whiteflies and associated viruses in Tanzania. *International Journal of Pest Management* (submitted manuscript).

6.2 Introduction

Cassava is Africa's most important food security crop, and its production sustains about 700 million people globally (FAO, 2013). Pests and diseases are the major constraints to cassava production. The most significant pests and diseases of cassava are the virus diseases, cassava mosaic disease (CMD) and cassava brown streak disease (CBSD). The viruses causing both diseases are transmitted by the whitefly vector, *Bemisia tabaci* (Gennadius) (Dubern, 1994; Maruthi *et al.,* 2005). The continued expansion of cassava virus pandemics driven by super-abundant populations of *B. tabaci* is considered the greatest threat to cassava production in Africa (Legg *et al.,* 2014a). Cassava virus diseases cause more than 47% production losses in severely affected countries and the estimated economic loss for Africa is over 1 billion USD per year (Thresh *et al.,* 1994; Legg *et al.,* 2006; Alabi *et al.,* 2011).

Rosenthal *et al.* (2012) demonstrated a strong positive effect of elevated carbon dioxide (CO_2) levels on cassava yield and concluded that cassava production will likely benefit from the effects of climate change. Based on climate change projections, Jarvis *et al.* (2012) also suggested that cassava is potentially highly resilient to the impact of climate change and could give farmers options for adaptation when other major food crops face challenges. However, climate change effects that would result in increases in pest and disease problems would deprive farmers of the benefits cassava can offer under anticipated future climate change scenarios. Several studies have demonstrated that farmers have some level of adaptive capacity and adaptation strategies to the impact of climate change on agriculture (Howden, 2007; Lobell *et al.,* 2008; Bryan *et al.,* 2009; Deressa *et al.,* 2009; Deressa *et al.,* 2011; Adeloye and Sotomi, 2013; Abdul-Razak and Kruse, 2017).

The response of cassava viruses and their whitefly vector to climate change will vary spatially depending on the prevailing conditions (Bellotti *et al.,* 2012; Jarvis *et al.,* 2012). Gamarra *et al.* (2016) suggested an increase in the population growth of *B. tabaci* for regions in East, Central, and Southern Africa; and considering the year 2050 temperature scenario, most sub-Saharan Africa (SSA) countries are likely to have an increase of 1 – 3 generations of *B. tabaci* per year. Similarly, Campo *et al.* (2011) identified the African rift valley as hotspots for cassava pests and diseases (including *B. tabaci,* CMD and CBSD) considering future climate change. These projected increases in population of *B. tabaci* provide the impetus to explore the adaptive measures likely to be used by farmers for cassava cultivation and pest management. If these can be identified, it should be possible to enhance farmers' adaptive capacity through training and/or awareness raising activities. The present study was conducted to: evaluate cassava farmers' challenges and production characteristics, explore their adaptive capacity and potential adaptation strategies, and investigate opportunities for enhancing their adaptive capacity so that they can respond better to changes in crop damages caused by cassava whiteflies and the viruses that they transmit. The results of this study will help farmers, governments and institutional stakeholders in climate change adaptation planning and developing robust cassava pest management programmes that will be useful for the management of the pests under current and future climate change scenarios. Although the study was implemented in Tanzania, the lessons learnt have implications for other cassava-growing agro-ecologies in SSA.

6.3 Materials and methods

6.3.1 Description of study sites

Farmer surveys were carried out in three locations in the cassava-growing regions of Tanzania: Kakonko (Kigoma Region), Unguja (Zanzibar) and Mkuranga (Pwani Region). The climate is characterised by a long dry spell from May to October, followed by a period of low rainfall. Tanzania experiences a main rainy season from March to June, and a short season from October to December (URT, 2012). The regions selected for this study are part of the major cassava-growing regions of Tanzania and they are also hot spots for cassava mosaic disease and cassava brown streak disease (Legg and Raya, 1998; Ndyetabula *et al.,* 2016).

6.3.2 Measurement of variables

A semi-structured questionnaire was used to collect information on socio-economic characteristics of the famers relating to their age, years of formal education, gender, occupation beside farming, household size etc. Additional information was also collected on challenges and production characteristics of the farmers including: their challenges, reasons for cassava production, sources of cassava planting material, methods used to control cassava whiteflies and viruses, and use of agricultural extension support.

Methods describing how to measure adaptive capacity have been reviewed by Lockwood *et al.* (2015). These include: assessing adaptive capacity from secondary data sources (Adger and Vincent 2005; Brooks *et al.,* 2005; Adger, 2006; Smit and Wandel 2006; Eriksen and Kelly, 2007); futures modelling (Bussey *et al.,* 2012), approaches based on inductive theory

(Pelling *et al.,* 2008; Gupta *et al.,* 2010) and self-assessment (Brown *et al.,* 2010; Raymond and Cleary, 2013). Self-assessment of adaptive capacity is becoming frequently used since it considers essential contextual information and also provides an opportunity for the local stakeholders to shape the assessment. The absence of this facility is a major limitation of the more popular sustainable livelihoods framework (Brown *et al.,* 2010; Park *et al.,* 2012).

In this study, the adaptive capacities of smallholder cassava farmers to the impact of climate change on cassava whiteflies and the viruses they transmit was assessed using a self-assessment approach with dimensions of adaptive capacity modified from Lockwood *et al.* (2015). These included: local network, trust in government, reciprocity (engaging reciprocal action), information behaviour, labour, time, finance and infrastructure, innovation, adaptive management, risk management, and personal resilience. The respondents were asked to assess each dimension of adaptive capacity as related to impact of climate change on cassava diseases for the last five years. The reaction was against a 4-point scale from very useful (4 points), useful (3 points), slightly useful (2 point), and not useful (1 point). The total score per respondent was further classified into three levels of adaptive capacity as follows: low, moderate and high using the mean values of total adaptive capacity score plus/minus the standard deviation.

For the expert survey, the questionnaire intended to collect information on expert opinion on adaptation strategies to the impact of climate change on cassava virus disease pandemics in Africa and ways to enhance adaptive capacity. Climate change adaptation strategies and measures to enhance adaptive capacity were rated on a 4-point scale with 1 =

Not recommended, 2 = Neutral, 3 = Recommended, 4 = Strongly Recommended**.** Questionnaires were pre-tested and updated based on expert advice prior to the actual survey.

6.3.3 Survey

A multi-stage sampling procedure was used in selecting respondents for the study. Three main cassava-growing Regions of Tanzania were purposively selected, namely Kigoma, Pwani and Zanzibar. From each of these Regions, one District was selected. The Districts were Kakonko in Kigoma Region, Mkuranga in Pwani Region, and Unguja in Zanzibar. Four villages were chosen from each District, with 25 respondents per village in Kakonko and Unguja, and 30 respondents per village in Mkuranga, making a total of 320 respondents in all (Figure 40). Out of the 320 questionnaires from the farmers' survey, 318 were suitable for data analysis. The farmers' survey was conducted in the local language (Swahili) for easy comprehension of questions. Questionnaires were administered through face-to-face interviews by trained researchers and extension agents.

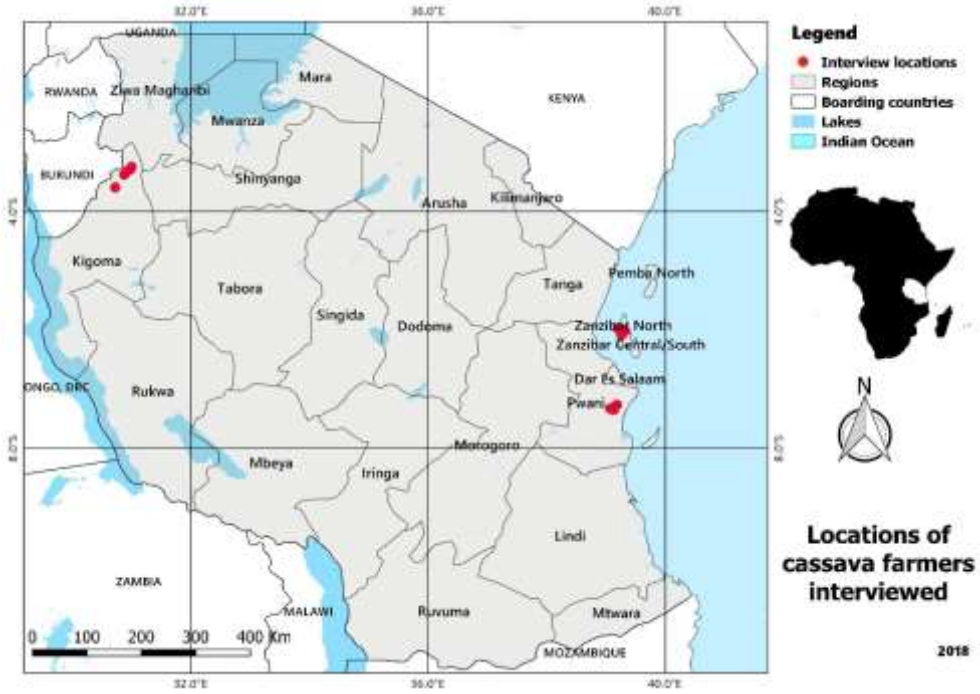

Figure 40. Locations of farmers interviewed

Survey interviews of experts were used to investigate transforming structures and processes that influence farmers' adaptive capacity and also to identify useful adaptation strategies. The expert survey was conducted as both an e-mailed survey and a paper survey. For the expert survey, a database of publications relating to cassava virus diseases and whiteflies, climate change plant disease and insect studies was created. From this database, a list of scientists was compiled based on publication records, and electronic copies of the survey were sent to a total of 80 scientists. Due to the relatively low response rate, the number was augmented by administering a printed copy of the survey to selected experts at the 2nd International Whitefly Symposium held at Arusha, Tanzania. In all, 20 questionnaires were processed for further analysis.

6.3.4 Data analysis

Responses from the questionnaires were encoded and analysed using SPPS® (IBM® SPSS® statistics version 20). Data were summarised with percentages, means and standard deviations.

6.4 Results

6.4.1 Production characteristics of cassava farmers

Cassava farmers surveyed in the three locations had an average age of 44.8 ± 12.8 (s.d.) years; they were semi-literate with an average of 6.2 ± 3.7 years of formal schooling. Average areas under cassava cultivation at the time of the survey were 1.8 ha in Unguja, 1.9 ha in Mkuranga and 2.2 ha in Kakonko. In addition, they have been engaged in cassava cultivation for average of 12.6 years in the three locations with an average of 275.33 USD of annual income (Table 23). Most respondents got their planting materials from their friends and the previous season, and the main reason for cultivating cassava in the study areas was for food (Tables 24 and 25).

Table 23. Production characteristics of cassava farmers

	Locations			
	Kakonko (100)	Mkuranga (118)	Unguja (100)	Total (318)
	Mean	Mean	Mean	Mean
Age (years)	40.4 ± 10.6	45.8 ± 15.3	47.97 ± 10.5	44.8 ±12.8
Formal educ. (years)	7.0 ± 1.9	5.2 ± 3.5	6.7± 4.7	6.2± 3.7
Cassava production experience (years)	6.7 ± 6.7	13.8 ± 9.9	17.0 ± 10.7	12.6±10.1
Area under cassava cultivation (Ha)	2.2 ± 1.7	1.9 ± 0.8	1.8 ± 1.2	2.0 ± 1.3
Income from cassava per year (USD)	195.56 ± 374.9	288.74 ± 329.23	339.88 ± 592.39	275.33 ± 443.68
Off-farm income per year (USD)	158.44 ± 554.39	144.75 ± 288.05	1029.88 ± 2501.00	439.85 ± 1504.17
Grow other crops (%)	100.0	96.0	98.0	98.0
Control whiteflies (%)	0.0	3.5	36.0	19.7
Control cassava viruses (%)	44.0	7.1	64.0	38.1
Get extension support (%)	38.8	18.6	84.8	45.9
Use chemicals to control whiteflies (%)	0.0	0.8	1	0.6

Source: Field Survey, 2016 and 2017, 1 USD = 2258.20 Tsh (Tanzanian shillings)

Table 24. Sources of planting material used by farmers

Locations	N	Friends F (%)	Previous own crop F (%)	Extension service F (%)	Research institute F (%)	Market F (%)
Kakonko	100	57 (57.0)	45 (45.0)	0 (0.0)	5 (5.0)	0 (0.0)
Mkuranga	118	51 (44.3)	62 (53.9)	0 (0.0)	0 (0.0)	3 (2.6)
Unguja	100	49 (49.5)	50 (50.5)	7 (7.0)	35 (35.4)	1 (1.0)
All locations	318	157 (49.4)	157 (49.4)	7 (2.2)	40 (12.6)	4 (1.3)

Source: Field Survey, 2016 and 2017; **F:** Frequency

Table 25. Reasons for growing cassava

Locations	N	Food F (%)	Profit F (%)	Leisure F (%)	Interest F (%)	No choice F (%)
Kakonko	100	60 (61.2)	80 (81.6)	0 (0.0)	0 (0.0)	0 (0.0)
Mkuranga	118	78 (67.8)	35 (30.4)	0 (0.0)	0 (0.0)	2 (1.7)
Unguja	100	92 (93.0)	80 (80.9)	0 (0.0)	2 (2.0)	0 (0.0)
All locations	318	230 (72.3)	195 (61.3)	-	2 (0.6)	2 (0.6)

Source: Field Survey, 2016 and 2017; **F:** Frequency

6.4.2 Challenges faced by farmers in cassava production

Challenges facing cassava farmers at the time of survey were diseases, insect pests, drought, finance, market access, access to planting materials, weeds, transportation and post-harvest

losses in descending order of severity. Diseases was most severe in Kakonko (95.0%), while insect pests (99.1%) and drought (95.7%) were most severe in Mkuranga (Figure 41).

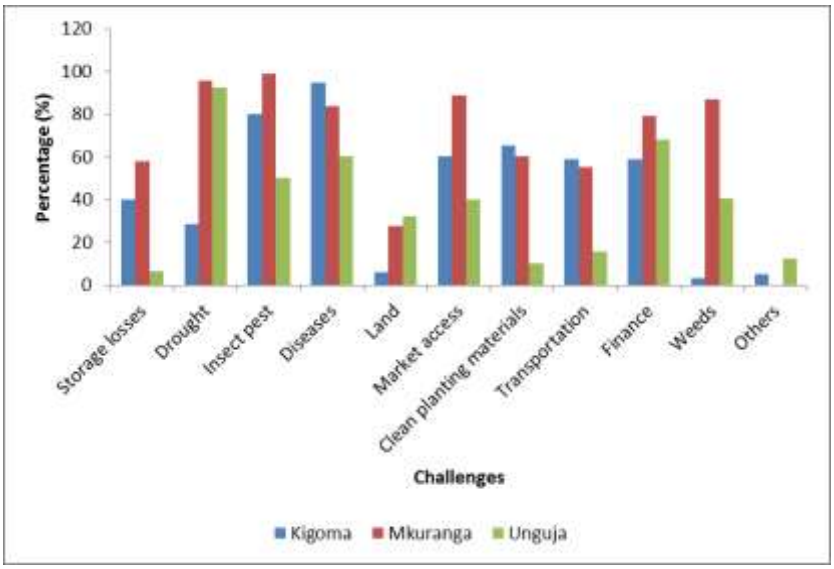

Figure 41. Challenges facing smallholder cassava farmers in Tanzania
Source: Field survey, 2016 and 2017

6.4.3 Current cassava whiteflies and virus control measures employed by the farmers

Most farmers do not control cassava whiteflies and viruses, although there was a higher level of control for viruses than for whiteflies (Table 26). Among the farmers that reported controlling cassava whiteflies and viruses, various approaches were reported. For control of cassava whiteflies, farmers mainly try to apply farm sanitation (weeding) and roguing, while for control of cassava viruses, the farmers use roguing, clean cassava seeds and resistant varieties (Table 26). However, the proportions of farmers applying these control methods

are very low compared to the total number of respondents. Additionally, the farmers do not use chemicals to control cassava whiteflies (Table 23).

Table 26. Whitefly and virus control methods reported by farmers

Whitefly control practices	F (%)	Virus control practices	F (%)
Farm sanitation including. weeding	23 (7.3)	Early planting	1 (0.3)
Improved varieties	3 (0.9)	Planting clean seeds	24 (7.5)
Resistant varieties	3 (0.9)	Improved varieties	3 (0.9)
Tolerant varieties	2 (0.6)	Resistant varieties	16 (5.0)
Roguing	11 (3.5)	Roguing	46 (14.5)
Using ash	1 (0.3)	Using ash	1 (0.3)
No response	5 (1.6)	Weeding	1 (0.3)
No control	270 (84.9)	No response	8 (2.5)
		No control	218 (68.6)

N= 318

6.4.4 Adaptive capacity of the farmers

The results revealed that local networking (3.60) ranked highest in the order of adaptive capacity among its dimensions, followed by adaptive management (3.30) and information behaviour (3.25), while reciprocity (2.56) was ranked lowest (Table 27). The majority of the respondents were within the moderate adaptive capacity range in all three locations (Figure 42).

Table 27. Distribution of cassava farmers by their adaptive capacity

Dimensions of adaptive capacity	Very useful F (%)	Useful F (%)	Slightly useful F (%)	Not useful F (%)	Mean
Local network	225 (70.7)	52 (16.4)	39 (12.3)	2 (0.6)	3.60
Adaptive management	200 (62.9)	56 (17.6)	45 (14.2)	17 (5.3)	3.30
Information behaviour	196 (61.6)	54 (17.0)	60 (18.9)	8 (2.5)	3.25
Innovation	188 (59.1)	67 (21.1)	56 (17.6)	7 (2.2)	3.24
Personal resilience	168 (52.8)	78 (24.5)	65 (20.4)	7 (2.2)	3.16
Labour and time	168 (52.8)	45 (14.2)	65 (20.4)	40 (12.6)	2.96
Finance and infrastructure	165 (51.8)	45 (14.2)	78 (24.5)	30 (9.5)	2.97
Trust in government	156 (49.1)	78 (24.5)	65 (20.4)	19 (7.0)	3.05
Risk management	155 (48.7)	78 (24.5)	69 (21.7)	16 (5.1)	3.11
Reciprocity	132 (41.5)	34 (10.7)	65 (20.4)	87 (27.4)	2.57

Overall mean = 3.09
Standard deviation = 0.15 , N = 318
Source: Field survey, 2016 and 2017

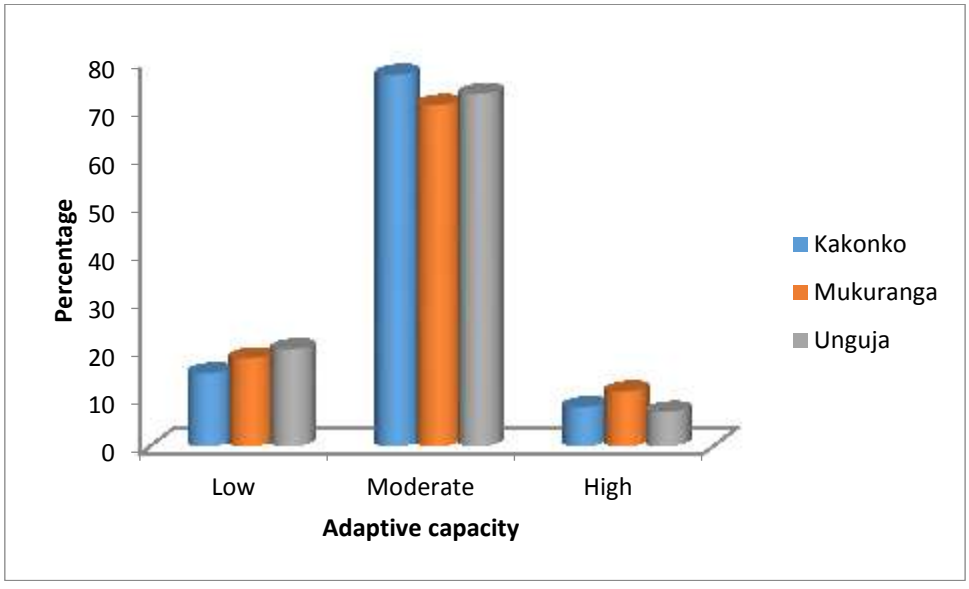

Figure 42. Bar chart showing categories of adaptive capacity
Mean = 58.7; Standard deviation = 7.5
Source: Field survey, 2016 and 2017

6.4.5 Description of experts

The majority (95.0%) of the cassava pest and disease experts surveyed were male, and their most common disciplines were entomology and plant virology (30.0%). Furthermore, they had an average of 19.1 ± 9.4 years of experience as experts in their various fields (Table 28).

Table 28. Distribution of cassava pest and disease experts by selected professional characteristics

Variables	Frequency	Percentages	Mean
Sex			
Male	19	95.0	
Female	1	5.0	
Specialisation			
Entomology	7	35.0	
Plant breeding	2	10.0	
Plant molecular biology	1	5.0	
Plant virology	6	30.0	
Vector entomology	4	20.0	
Years of experience as expert			
Below 10	5	25.0	
11-20	8	40.0	19.1 ± 9.4
Above 20	7	35.0	
Scientific meetings on cassava and climate change attended			
Below 5	18	90.0	
6-10	2	10.0	3.3 ± 2.5
Membership of professional bodies			
Below 5	17	85.0	
6-10	3	15.0	2.4 ± 1.9

N = 20

Source: Field survey, 2016 and 2017

6.4.6 Adaptive strategies to cassava whitefly and viruses

The results showed that integrating pests and diseases management programmes ranked highest as a proposed adaptive strategy to cassava pests and diseases, followed by

phytosanitation, and applying novel vector management techniques, while increasing off-farm income was ranked lowest (Table 29).

Table 29. Distribution of experts by adaptation strategies to cassava whitefly and viruses

Adaptation strategies	NR F (%)	Neutral F (%)	R F (%)	SR F (%)	Mean
Integrating pest and disease management programmes	-	-	7 (35.0)	13 (65.0)	3.25
Phytosanitation	1 (5.0)	2 (10.0)	6 (30.0)	11 (55.0)	3.20
Applying novel vector management techniques	1 (5.0)	3 (15.0)	11 (50.0)	5 (25.0)	3.16
Controlling whiteflies with biocontrol	-	1 (5.0)	11 (55.0)	8 (40.0)	3.11
Diversifying crop production	-	3 (15.0)	9 (45.0)	9 (40.0)	3.05
Controlling whiteflies with resistant varieties	1 (5.0)	-	10 (50.0)	9 (45.0)	2.97
Controlling whiteflies with resistant varieties	1 (5.0)	-	10 (50.0)	9 (45.0)	2.97
Changing planting date	2 (10.0)	5 (25.0)	13 (65.0)	-	2.96
Controlling whiteflies with chemicals	9 (45.0)	6 (30.0)	5 (25.0)	-	2.74
Shifting from cassava to other crops	13 (65.0)	5 (25.0)	1 (5.0)	-	2.60
Increasing off-farm income	3 (15.0)	5 (25.0)	11 (55.0)	1 (5.0)	2.57

N = 20
NR – Not Recommended, R – Recommended, SR – Strongly Recommended

Source: Field survey, 2016 and 2017

6.4.7 Enhancing adaptive capacity to cassava whitefly and viruses

Capacity building through stakeholder training, establishing monitoring networks, and incorporating pest and disease adaptation planning in relation to climate change into agricultural management plans ranked highest in the order of measures to enhance adaptive capacity to cassava pests and diseases in the study area, while improving access to credit and insurance ranked lowest (Table 30).

Table 30. Distribution of respondents by measures to enhance adaptive capacity

Measures to enhance adaptive capacity	NR F (%)	Neutral F (%)	R F (%)	SR F (%)	Mean
Capacity building through training of stakeholders	-	-	6 (30.0)	14 (70.0)	3.60
Establishing monitoring networks	-	-	8 (40.0)	12 (60.0)	3.35
Incorporating pest and disease adaptation planning into agricultural management plans	-	-	8 (40.0)	12 (60.0)	3.35
Assessing adaptation needs through stakeholders	-	2 (10.0)	10 (50.0)	8 (40.0)	3.04
Developing climate change pest/disease models	-	1 (5.0)	12 (60.0)	7 (35.0)	3.02
Developing short range forecasting capacity	-	1 (5.0)	12 (60.0)	7 (35.0)	3.02
Enforcing quarantine and regulations	1 (5.0)	2 (10.0)	10 (50.0)	7 (35.0)	3.02
Improving access to credit and insurance	2 (10.0)	3 (15.0)	12 (60.0)	3 (15.0)	2.85

N = 20

NR – Not Recommended, R – Recommended, SR – Strongly Recommended

Source: Field survey, 2016 and 2017

6.5 Discussion

Studies on the impacts of climate change on agriculture suggest that agricultural systems are vulnerable to climate change (Bale *et al.,* 2002; Morton, 2007; Schlenker and Lobell, 2010; Gilioli *et al.,* 2014). Climate change is also expected to affect cassava whiteflies and the viruses they vector (Campo *et al.,* 2011; Bellotti *et al.,* 2012; Gamarra *et al.,* 2016). In this study, we investigated the challenges of smallholder cassava farmers, identified their production characteristics and adaptive capacity to the anticipated impacts of climate change on cassava whiteflies and viruses. We then used expert judgements to identify adaptation strategies that might be deployed and measures to enhance the adaptive capacity of the farmers to the impact of climate change on cassava whiteflies and the viruses they transmit.

6.5.1 Challenges and production characteristics

As in the study reported here, other authors have also identified the influence of biotic constraints including pests, diseases, weeds and other abiotic factors on cassava production (Fermont *et al.,* 2009; Waddington *et al.,* 2010; Bull *et al.,* 2011). Clean cassava planting materials remains a serious constraint to cassava production in most cassava-producing countries in Africa. Increasing availability and accessibility of clean and resistant planting material will help to improve farmer management of cassava viruses and whiteflies both now and under future climate change conditions. Diversifying crop production is one of the most recommended strategies for adapting to the impacts of climate change on agricultural systems (Howden *et al.,* 2007; Morton, 2007). Our results suggest that the farmers have diversified cropping systems that could make them resilient to the impacts of climate

change on cassava whiteflies and viruses. Deressa *et al.* (2009, 2011) and Bryan *et al.* (2009) stressed the importance of agricultural extension support in adapting to the impacts of climate change on agricultural systems. Access to agricultural extension services is relatively low in two (Mkuranga and Kakonko) of the three study locations, and efforts should be intensified to increase access to quality extension service. Increasing access of African farmers to agricultural information through mobile phone services is likely to augment the work of extension in the years ahead. One example that relates specifically to cassava virus diseases is the on-going development of an artificial intelligence-based phone app that will eventually be freely downloadable by farmers and enable them to instantly identify CMD, CBSD as well as other cassava pest/disease damage conditions (Ramcharan, 2018).

Generally, very few farmers control cassava whiteflies and viruses. This might be related to the small-scale and low input cropping systems employed for cassava production in most cassava-growing areas in SSA. For the control of cassava viruses, planting of clean stem cuttings and the use of resistant varieties are among the best control options (Legg and Fauquet, 2004; Legg *et al.,* 2006; Legg *et al.,* 2015) and our study indicates that many farmers that control cassava viruses depend on these methods. In Tanzania, several varieties have been reported to be resistant to CMD (IITA 2012, 2017) or CBSD (IITA 2012, 2017) and efforts at combining resistance to both CMD and CBSD have been successful (IITA 2017). Additionally, a clean seed system for cassava is currently being developed in Tanzania. This will increase the availability of virus-free cassava planting materials (IITA 2015, 2017). Although roguing is believed to be generally unpopular among farmers due to their unwillingness to lose the yield of infected plants and also the labour involved (Legg *et*

al., 2006), our results suggest that a majority of the famers that control cassava viruses employ roguing. This might be due to more intensive agricultural extension campaigns and increased knowledge on the control of cassava viruses by farmers. Changing planting dates is a frequently recommended strategy for climate change adaptation (Lobell *et al.,* 2008; Bryan *et al.,* 2009; Deressa *et al.,* 2009). This can also be useful for cassava virus management, as periods of peak vector abundance can be avoided. From our study, this approach does not yet appear to be recognised by farmers, since only a few farmers reported changing planting dates to manage cassava viruses. It is possible that farmers can't link any economic benefit of changing planting date with increased productivity. Additionally, it seems likely that the short rainy season in Tanzania ('Vuli') is preferred for cassava cultivation since other crops such as maize are planted in preference during the main rainy season ('Masika'), since their high moisture requirements make them unsuitable for planting during the 'Vuli' season.

Although farmers mostly attempt to control whiteflies by farm sanitation (weeding), the efficacy of this approach for whitefly management is very limited since the whiteflies actual prefer the cassava to the weeds. Whitefly resistant cassava is a very useful tool for managing whiteflies and successes are now been reported in efforts to breed whitefly resistant cassava in East Africa (Omongo *et al.,* 2012). In line with the results of this study, Legg *et al.* (2014b) earlier reported the unpopular nature of the use of insecticides in cassava whitefly management. This might be because cassava is mostly produced at a subsistence level in many parts of SSA, and farmers are typically unwilling to spend money on a crop primarily grown for household consumption. It is likely that this pattern will

change in the future, however, as the on-going process of commercialising the cassava sub-sector gains pace.

6.5.2 Adaptive capacity

Smallholder farmers are known to have some level of adaptive capacity to climate change impacts on their farming enterprise (Howden *et al.,* 2007; Lobell *et al.,* 2008; Bryan *et al.,* 2009; Deressa *et al.,* 2009; Deressa *et al.* 2011; Adeloye and Sotomi, 2013; Abdul-Razak and Kruse, 2017). Similarly, the results of this study suggest that the majority of the respondents fall within the moderate adaptive capacity range. This may be related to the resilience of cassava farmers, many of whom have highly diverse cropping systems. However, it is also possible that there was some level of over estimation in the self-assessment of their adaptive capacity to the impacts of climate change on cassava viruses and whiteflies. It will be necessary, therefore, to aim to further strengthen the adaptive capacity of farmers. Reason for production, gender and source of planting material were associated with adaptive capacity of the farmers (Abdul-Razak and Kruse, 2017). Results on the ranks of the dimension of adaptive capacity to the impacts of climate change on cassava whiteflies and viruses underscores the importance of local networks, information behaviour, adaptive management, innovation and personal resilience in the process of adapting.

6.5.3 Adaptation strategies

Experts suggested that several cassava virus/whitefly control measures would be valuable as part of climate change adaptation strategies. These were ranked (most important first) as: integrating cassava pest and disease management programmes, phytosanitation, using novel whitefly management techniques such as RNA interference, biological control of

whiteflies, and diversifying crop production. The high rank recorded for integrating cassava pest and disease management programmes as a climate change adaptation strategy emphasises the relevance and applicability of the strategy. Climate change is expected to influence the efficacy of methods used to control whiteflies and the viruses they vector, additionally, systematically combining multiple control strategies will give farmers room to choose a combination of effective, affordable and feasible control measures that can be used against cassava whiteflies and viruses. Similarly, Howden *et al.* (2007), Juroszek and von Tiedemann (2011), Fahim *et al.* (2013) and Kroschel *et al.* (2014) also recommended integrated pest management as the best and most economic strategy for adapting to additional pest and disease pressure on cropping systems resulting from climate change. Phytosanitary measures (planting of virus-free materials, roguing and quarantine) are popular and well-known pest management methods useful in the management of cassava viruses and their vectors, and will still be relevant since they are not likely to be affected by climate change. Legg *et al.* (2017) demonstrated the success of community phytosanitation (use of virus-free planting materials coupled with area-wide roguing) for managing CBSD in some regions of Tanzania. Furthermore, Kroschel *et al.* (2014) suggested the reinforcement of phytosanitary regulations related to distribution/movement of cassava plant materials between regions and countries to minimise the spread and distribution of cassava pests due to that could be exacerbated with climate change. In line with the findings of this study, developing robust cropping systems through conservation and augmentation of biological control agents, introduction of novel pest management techniques (e.g. RNA interference) and diversifying crop production will build the basis for adaptation to anticipated increases

in distribution and abundance of cassava pest under climate change scenarios (Kroschel *et al.,* 2014).

6.5.4 Measures to enhance adaptive capacity

Capacity building through training of stakeholders, incorporating pest and disease adaptation planning into general agricultural management plans, establishing monitoring networks, and assessing adaptation needs through stakeholders emerged as principal measures that can be deployed to enhance the adaptive capacity of smallholder farmers to the impact of climate change and the viruses they vector. The role of governments and institutions in enhancing the adaptive capacity of farmers to the impacts of climate change on cassava viruses and whiteflies is crucial. Legg *et al.* (2014b) argued that training farmers on the importance of *Bemisia* species and equipping research and extension personnel with relevant and up-to-date information on the management of *B. tabaci* and the viruses they transmit, as well as publishing informative materials to support training programmes will significantly reduce pest pressure. It is well known that climate change affects several sectors in every country, making it necessary to prioritise the allocation of available resources among competing adaptation options (Lobell *et al.*, 2008). This will require the mainstreaming of climate change adaptation plans into existing agricultural and other policies targeted at improving resilience to risk and promoting sustainable development (Howden *et al.,* 2007). The distributions and abundance of cassava pests are predicted to change with climate change (Campo *et al.,* 2011; Bellotti *et al.,* 2012; Jarvis *et al.,* 2012). Furthermore, the ecology and biological characteristics of both whiteflies and the viruses

they transmit are also changing (Legg and Thresh, 2000; Legg *et al.,* 2014c; Nduguru *et al.,* 2016). Monitoring cassava whiteflies and viruses is necessary for tracking changes at regional and national levels, and also estimating the success of regional pest management initiatives implemented to adapt to climate change. Surveillance programmes can also facilitate the early detection and eradication of cassava viruses or *B. tabaci* spp. if they move into territories in which they were previously absent. Surveillance data may also provide the basis for evaluating cost-benefit and management decisions (Kalaris *et al.,* 2014). Whiteflies and whitefly-transmitted viruses affecting cassava vary greatly in their abundance/incidence between regions and countries. Assessing adaptation needs to these pests/diseases will therefore require cooperation among farmers, research institutions and the government, in order to target adaptation initiatives as effectively as possible. There is an increasing capacity in modelling and forecasting climate change impacts on insect pests of importance to African agriculture (Tonnang *et al.,* 2009; Khadioli *et al.,* 2014ab; Tonnang *et al.,* 2015; Mwalusepo *et al.,* 2015; Ngowi *et al.,* 2017). Newer initiatives are now focused on expanding pest models for African populations of the cassava whitefly (chapter 6) which will provide very useful country and regional level whitefly risk maps that will meaningfully aid detailed and targeted adaptation planning.

7. General discussions

Previous studies have described temperature-dependence and climate change impacts on non-cassava-colonising *B. tabaci* MEAM1 and MED (Wang and Tsai, 1996; Qui *et al*., 2003; Yang and Chi, 2006; Bayhan *et al*., 2006; Bonato *et al.,* 2007; Campos *et al.,* 2011; Tsueda *et al*., 2011; Xie *et al*., 2011; Bellotti *et al.,* 2012; Jarvis *et al.,* 2012; Guo *et al*., 2013; Han *et al.,* 2013; Gamarra *et al.,* 2016a; Gilioli *et al.,* 2014).

For the first time, laboratory (constant temperatures) and field experiments were combined to describe temperature-dependent effects on the life history traits of an African population of cassava-colonising *B. tabaci*. Among new facts and information established by the study are life-table parameters, thermal thresholds, and an overall phenology model for *B. tabaci* SSA1-SG3. The information on the life history traits included immature development time and survival, longevity of adult males and females, fecundity of adult females under both field and laboratory conditions. The study confirms that cassava-colonising African population of *B. tabaci* SSA1-SG3 differs from non-cassava types (MED and MEAM1) in terms of the influence of temperature on their life history. The findings are reliable considering the proper identification of the whitefly before experimentation and the

thorough approach of data collection. The study on life history also provided the needed information for modelling the impacts of climate change on cassava-colonising *B. tabaci*, directly contributing to the achievement of the overall objective of the PhD study.

For the first time, the study described potential impact of climate change on the distribution and abundance of a cassava-colonising African population of *B. tabaci*, thus answering the most important overall question raised by the study. Lastly, for the first time, a life-table study showing key factors responsible for the mortality of cassava-colonising *B. tabaci* in Tanzania, and the relative importance of each factor was conducted. These contributions to the knowledge on the biology of the pest described in the study will find relevance in designing management programmes for the pest both now and under future climate change scenarios.

In addition to the evident interactions between chapter 1 and all other chapters, and also chapter 3 and 4, some other interesting connections in the study are here summarised. In terms of the overall trend, findings from chapter 3 are congruent with literature reports (chapter 2). The review of literature on whiteflies suggest that, impact of climate change on whiteflies will show some location specificity, which was confirmed in chapter 4. The predicted increase in abundance of *B. tabaci* in parts of East and Southern Africa as reported in chapter 4, supports the argument that spatial variations in suitability changes can be expected due to differences in climate and local topography (chapter 2). Chapter 4 predicted potential changes in distribution and abundance of *B. tabaci* while chapter 6

complements this by identifying possible adaptation strategies and measures that can be used to enhance the adaptive capacity of the farmers (in Tanzania) to the impacts identified in chapter 4.

One of the limitations of the study is that, although *B. tabaci* SS1-SG3 was used for the experiments, *B. tabaci* SSA1-SG1 is the CMD pandemic associated *B. tabaci* on cassava in East Africa (Tajebe *et al.,* 2015a). Significant cassava virus problems are also found in areas where *B. tabaci* SS1-SG1 is not prevalent. Furthermore, *B. tabaci* SSA1-SG1 is not present in coastal Tanzania where the experiments were conducted (Tajebe *et al.,* 2015a). For quarantine and ethical reasons, *B. tabaci* SSA1-SG1 could not be used for the experiments in IITA-facility at Dar es Salaam (Coastal Tanzania). At least 5 putative species of *B. tabaci* colonise cassava in Africa (Legg *et al.,* 2014a), but for practical reasons *B. tabaci* SSA1-SG3 was used for the experiments. This does not weaken the conclusions of the study. Given that *B. tabaci* SSA1 is the most prevalent cassava-colonising whitefly in Africa, and *B. tabaci* SSA1-SG3 is equally widespread, estimates of changes in its distribution and abundance due to climate change can sufficiently represent other cassava-colonising *B. tabaci*. Future studies can incorporate other cassava whitefly endemic in each region.

In this study, the primary concentration was on the influence of temperature on life history and biological characteristics of *B. tabaci*. However, several abiotic factors associated with climate change also influence the biology of *B. tabaci*. Temperature was chosen as the test abiotic factor due to its established importance and influence on insects. It is generally

agreed that temperature is the most important abiotic factor influencing the reproductive performance, developmental characteristics, survival, distribution and abundance of insects (Bale *et al.,* 2002). This limitation (concentrating on temperature alone) was augmented by reviewing the impact of other abiotic factors on whiteflies as discussed in chapter 2.

Setting up the experiments on development and survival was initially problematic. Effects of static electricity used to make the insect clip-cages caused high insect mortality. The problem was solved by confining the insects to clip-cages for only 24 hours before the clip-cages were removed. For this reason it was not easy to collect the whitefly for determining their sex on emerging into adults. The problems with mortality due to static electricity was avoided during the experiments on longevity and fecundity of *B. tabaci* by designing insect clip-cages made of glass. With the glass clip-cages, mortality due to static electricity was completely eliminated.

Like *B. tabaci* SSA1, *B. tabaci* SSA1-SG3 is also strongly associated with cassava in East, Central and Southern Africa. For instance, *B. tabaci* SSA1-SG3 has been reported from Tanzania (Legg *et al.,* 2014a; Tajebe *et al.,* 2015a; Wosula *et al.,* 2017), Kenya (Mugerwa *et al.,* 2012, Boykin *et al.,* 2018), Uganda (Tocko-Marabena *et al.,* 2017), Central African Republic (Tocko-Marabena *et al.,* 2017), Zambia (Legg *et al.,* 2014a), Malawi (Legg *et al.,* 2014a), South Africa (Legg *et al.,* 2014a) and Madagascar (Wosula *et al.,* 2017). There is a possibility of the occurrence of *B. tabaci* SSA1-SG3 in countries close to where it has been identified but yet to be reported. The widespread distribution of *B. tabaci* SSA1-SG3 further strengthens the conclusion of this study and provides an opportunity for generalisation of

the findings of this study across cassava-growing ecologies in Africa. Furthermore, a recent study on the taxonomy of African populations of *B. tabaci* (Boykin *et al.,* 2018) recommends retaining intermediates names at the putative species level (e.g MEAM1, MED, SSA1, SSA2) until differences in biological characteristics of identified sub-species are confirmed with more molecular markers and biological experiments.

7.1 How will climate change affect whiteflies and the viruses that they vector?

A review of the potential impact of climate change on whiteflies and vectored plant viruses was undertaken considering the impacts on life history, population dynamics, distribution and, efficacy of management practices and effects on vectored plant viruses (chapter 2). The study suggests that as temperature increases within a range that permits the optimum biochemical, behavioural and physiological functioning of the whiteflies, immature developmental time and adult longevity decreases. Similar trends have been reported for other insects like *Aphis spiraecola* Patch (Wang and Tsai, 2000), *Busseola fusca* Fuller and *Sesamia calamistis* Hampson (Khadioli *et al.,* 2014a), *Chilo partellus* Swinhoe (Khadioli *et al.,* 2014b), *Helicoverpa armigera* Hübner (Mironidis and Savopoulou-Soultani, 2008) and *Plutella xylostella* L (Liu *et al.,* 2002). This can be explained by the metabolic theory of ecology (Brown *et al.,* 2004) which simply posits that organisms living in warmer environments tend toward higher metabolic rates compared to those living in cooler environments. Life history of insects including whiteflies are tightly linked to environmental temperatures, and over a broad range of temperatures, enzyme catalysed reactions show

some form of temperature-dependence and become faster with increasing temperature (Harrison *et al.,* 2012). Additionally, with increasing temperature, a greater proportion of the enzymes and their substrates gain velocities producing Gibbs-free energy values higher than their activation energies. Within a limited range of temperatures, all enzyme-linked physiological processes benefit from higher temperatures. Obviously, as temperature becomes high enough (when membranes, and proteins starts to disintegrate), fitness and performance of insects reaches a peak and then declines precipitously. A decrease in fecundity with temperature might be a survival strategy used by the whitefly to concentrate resources on its own survival rather than producing offspring with reduced chances of survival. While shortened immature development time at higher temperatures can increase population growth potential and more generations can be completed per year (Harrison *et al.,* 2012), reduced fecundity and longevity at higher temperatures may limit population growth potential depending on the thermal sensitivity and thermal tolerance of the whitefly.

In chapter 2, elevated CO_2 resulted in lengthening of development time, whereas adult longevity and fecundity were unaffected. At elevated CO_2, several studies have reported profound effects on host plant nutrition resulting in a shift of C:N ratio favouring the accumulation of carbon based compounds like starch or phenolics (Trip *et al.,* 1992; Coviella and Trumble, 2000; Stiling and Cornelissen, 2007). Elevated CO_2 improves photosynthetic efficiency and increases plant growth. This is referred to as the nitrogen dilution effect, and these host plants are considered poor quality hosts. Consequently, the nutrition of insects growing on them is severely affected due to the lower levels of nitrogen available for the

biosynthesis of essential proteins and enzymes required for life processes (Docherty *et al.,* 1996). Slower growth rates may have additional implications since the whitefly may spend longer periods in a vulnerable stage, which may increase exposure to natural enemies (Awamack and Leather, 2002). Results of this study are consistent with reports for *Rhynchaenus fagi* Fabricius on European Beech (Docherty *et al.,* 1996), *Lymantria dispar* L. (Lindroth *et al.,* 2007), where elevated CO_2 lengthened developmental time but had no effect on fecundity. More comprehensive metadata analyses on the effects of elevated CO_2 on insect herbivores covering all insect guilds show that the performance of most feeding guilds, except the phloem feeders, are negatively affected at elevated CO_2 (Coviella and Trumble, 2000; Stiling and Cornelissen, 2007; Robinson *et al.,* 2012).

From review of whitefly literature, impact of climate change on whiteflies distribution and population dynamics tends to show some latitudinal patterns. Increase in population and distribution is mostly predicted for temperate zones and at high altitude in tropical zones where the temperature is not limiting (Gilioli *et al.,* 2014; EFSA, 2015; Gamarra *et al.,* 2016a, c; Zidon *et al.,* 2016), whereas whitefly populations are predicted to reduce in some tropical locations (Bellotti *et al.,* 2012; Jarvis *et al.,* 2012; Gamarra *et al.,* 2016a, c) depending on the thermal physiology of the whitefly involved and the habitat temperature. Similarly, latitudinal patterns have been reported for other insect taxa (Addo-Bediako *et al.,* 2000; Deutsch *et al.,* 2008; Youngsteadt *et al.,* 2016), and there may be within region variabilities due to differences in topography or altitudinal gradients (Shah *et al.,* 2017). Species thermal physiology and spatio-temporal climatic variability are essential to determining species distribution on earth (Khaliq *et al.,* 2014). A possible explanation for the latitudinal pattern is

the climate variability hypothesis, which states that the breadth of thermal tolerance range of a taxa is positively related to the level of climatic variability experienced with increasing latitude. Meaning that climates with higher variabilities select for organisms with broader thermal tolerance profiles, while the converse is true for less variable or stable climates (Gutiérrez-Pesquera *et al.,* 2016; Shah *et al.,* 2017).

Increased resistance to viruses and reduced coat protein and/disease severity reported for whitefly transmitted viruses (Huang *et al.,* 2013; Guo *et al.,* 2016) appears to be common for other non-whitefly transmitted viruses (Malmström and Field, 1997; Zhang *et al.,* 2015). In almost all cases, elevated CO_2 mediated changes in C:N ratios and its resultant impacts on plant secondary metabolites including plant defense systems have been implicated for these observations. Poleward expansion of diseases caused by whitefly transmitted viruses here predicted, can be attributed to increased climatic suitability for plant viruses and expansion of cropping areas due to the warming. Similarly, epidemics of disease caused by *Potato yellow vein virus* and *Potato leaf roll virus* (adapted to warmer regions) have been predicted to spread to higher latitudes/elevations and to mountainous areas of the tropics and subtropics previously unsuitable due to cold conditions (Jones, 2016). These patterns are similar to those predicted for vectors of plant viruses and there is a high possibility of climate change induced modifications in the distribution of vectors influencing the distribution of plant viruses (Canto *et al.,* 2009).

7.2 Life history and temperature-dependent phenology model of cassava-colonising populations of *Bemisia tabaci*

Insect temperature-dependence models have been successfully used to describe the relationship between temperature and life history of whiteflies. For instance, according to Bonato *et al.* (2007) and Han *et al.* (2011), the relationship between development rates of *B. tabaci* MED was well described by Logan model (Logan *et al.,* 1976), Taylor model (Taylor, 1982) and the Weibull function (Kim *et al.,* 2001). Similarly, Wang and Tsai (1996) used Sharpe and DeMichele model (Sharpe and DeMichele, 1977); Navas Camberos *et al.* (2001) used Stinner model (Stinner *et al.,* 1974) to describe the relationship between temperature and development rates of *B. tabaci* MEAM1. Insect temperature-dependence models have also been applied to other non-*B. tabaci* whiteflies. Legaspi *et al.* (2008) used the Berie 1 model (Briere *et al.,* 1999) to describe effects of temperature on development of the whitefly, *S. simplex*. In this study, all available temperature-dependence models in ILCYM were simultaneously tested on each life stage of *B. tabaci* SSA1-SG3 and the best were selected as described in the method section of chapter 3 (based on Adj R^2, AIC and biological considerations).

For fitting a temperature-development function to each stage, pooling the data would reduce the number of data points, hence the number of degrees-of-freedom in the regression. There was no gain in model precision because of the reduction in degrees-of-freedom. Therefore, the study used the estimated median development times from each replication to fit the functions.

All life history traits of whiteflies are important in determining the distribution and the abundance hence correct estimation is very essential. Repeated trials (two to five) of the development and survival of *B. tabaci* SSA-SG3 and relatively large overall sample size provided a very reliable estimation of temperature-dependent effects on these traits, and majority of the experimental data points were within the 95% confidence interval. Similarly, experiments on longevity and reproduction consistently measured these traits as the sample sizes used were higher than that used for a lot of other studies on impact of temperature on whiteflies. Consequently, results of temperature-dependent effects on life history of *B. tabaci* SSA1-SG3 was within biologically reasonable range and comparable to previous studies on whiteflies.

Even though data used for phenology model building were based on constant temperature experiments, reliability of the estimates were checked by validating the model with temperature data that included daily natural diurnal temperature variations. Furthermore, future climate data used for predicting changes in distribution and abundance of the pests in ILCYM takes diurnal variations in temperature into account, thus avoids any misleading conclusions.

The ecological significance of decrease in developmental duration with temperature increase is that, more generations can be completed per year which will have additional implications for the population densities of the whiteflies. That developmental time

increases above the optimum condition emphasises the importance of thermal tolerance and thermal sensitivity of the species which may limit the anticipated population explosion above optimum temperatures. Furthermore, the relatively lower development rate of the *B. tabaci* SSA1-SG3 compared to MEAM1 and MED suggests that the species may not be as fit as these highly invasive species which account for their wide adaptability to hundreds of host plants (Oliveira *et al.,* 2001).

A number of factors including predators and parasitoid accounted wide difference between survival under field and laboratory conditions. The high mortality observed might be related to the fitness of this species and also negative host plant effects. This suggests that species interactions involving the host (cassava), whiteflies, and natural enemies (predators, parasitoid and pathogens) will significantly influence the distribution and abundance of the species with climate change. A preliminary assessment of these interactions reviewed in chapter 2 of this thesis, suggests that moderate to good efficacy of natural enemies can be anticipated with climate change. Considering the great importance of these interactions, there is need for further research to quantitatively explain the clear interactions between these species under future climate change.

The study suggests that whiteflies are not congruent in their life-table profiles, as they differ in their thermal thresholds (minimum, optimum and maximum), thermal sensitivity and thermal tolerance, which are critical to predicting the optimum temperature for their propagation. The multidimensional variability in life history of members of the *B. tabaci* species complex repeatedly emphasised in almost every aspect of this study can be

attributed to three primary reasons. First is the differential performance of *B. tabaci* on diverse host plants, second is the genetic variability among members of the *B. tabaci* species complex. A third important factor is climatic variability. Several studies have confirmed that *B. tabaci* performance differs from one host plant to another (Coudriet *et al.,* 1985, Bethke *et al.,* 1991; Tsai and Wang, 1996; Nava-Camberos *et al.,* 2001; Zang *et al.,* 2006). In some cases, differences in performance among varieties of the same host have also been recorded (Nava-Camberos *et al.,* 2001; Boni *et al.,* 2017). This is directly related to host suitability and preference. Some hosts are probably better able to support the nutrition of *B. tabaci* because of the availability of their nutrient with relatively less toxic secondary metabolites, or *B. tabaci* finds it easier to metabolise or degrade them (Awamack and Leather, 2002). It's also very possible that plants differ in their ability to elicit effective defense, thus, plants that are better able to do this may succeed in reducing the performance of the host herbivore.

Differential performance of members of the *B. tabaci* species complex is also widely reported (Muniz and Nombela, 2001; Omondi *et al.,* 2005; Zang *et al.,* 2006; Chaubey *et al.,* 2015). Genetic differences could be the primary reason for the differential performance. Another biologically significant reason can be possible differences in mechanisms of host colonisation used by the species. For instance, there is evidence that *B. tabaci* MEAM1 is able to manipulate host plant defense strategies to increase its performance and increase plant susceptibility (Kempema *et al.,* 2007; Zarate *et al.,* 2007; Walling, 2008). It remains a question to what extent other *B. tabaci* species deploy similar or more sophisticated host defense strategies, this requires further research attention.

Environmental factors, especially temperature have long been established to affect insect performance (Bale *et al.,* 2002). Insects grow and reproduce within a range of temperature characterised by a lower threshold – below which the insect cannot survive, an optimum temperature that best supports the insect and a maximum temperature –above which death occurs. Differences in insect performance with temperature have been explained in terms of its metabolic and physiology activities.

7.3 Potential impact of climate change on the distribution and abundance of cassava-colonising *Bemisia tabaci* (Gennadius) in Africa

More than a dozen models haven been used to assess pest risk/climate change impacts on insect pests (Vennette *et al.,* 2010). New additions are the Physiologically Based Demographic Model (PBDM) of Gilioli *et al.* (2014), and ILCYM used in this study. Popular among these modelling tools are MaxEnt, CLIMEX and BIOCLIM. ILCYM though relatively new, is gaining popularity and has been applied to model both the temperature-dependence and impact of climate change on several insect pests. ILCYM favourably competes with other popular models, and has been used in several research projects (Kroschel *et al.,* 2013; Khadioli *et al*., 2014a, Khadioli 2014b; Fand *et al.,* 2014, Fand *et al.,* 2015; Mwalusepo *et al.,* 2015; Sporleder *et al.,* 2016, Mujica *et al.,* 2017; Ngowi *et al.,* 2017).

A review of the climate of Africa shows that the areas in North Africa and parts of West Africa predicted to experience both a decline in the distribution and population growth potential of *B. tabaci* SSA1-SG3 is characterised by warm desert climate. These countries

cover a wide expanse of the Sahara desert, which is considered among the hottest places on earth (Wikipedia, 2018ab). The same eco-climatic reason also perfectly explains the predicted decline in population growth potential of *B. tabaci* SSA1-SG3 in South Sudan; eastern regions of Ethiopia, Kenya and Somalia. Additionally, IPCC's fifth assessment projections of temperature change for Africa shows that in comparison to the 20th century, mean annual temperature may rise more than 2 °C by the end of the century considering the SRES A1B and A2 scenarios (Niang *et al.,* 2014). Small temperature increase (due to climate change) in tropical environments could have adverse impacts on the performance of ectotherms, since some of these species are already living in hot habitats with temperatures close to their optimum (Zeh *et al.,* 2012; Woodin *et al.,* 2013).

The estimated risk indices agree with an increase in the number of generations and population growth potential in most parts of East and Southern Africa. For East Africa, the climate is generally tropical, however, topographical variabilities across the region, especially its extensive high elevations, tend to reduce the average temperature (Low and Marcus, 1998). This reduced average temperature, which is generally within optimal developmental range (20 – 28°C), possibly explains why the population growth potential and abundance of *B. tabaci* SSA1-SG3 is still able to increase. This also applies to Southern Africa, where there is a transition to a semi-tropical or temperate climate (Wikipedia, 2018a), which increases the climatic suitability of the region for *B. tabaci* SSA1-SG3 range expansion and population growth under the future scenario.

Except for a decrease in climatic suitability in Central Africa (which does not agree with this study), a very similar pattern of a decrease in the establishment risk of *B. afer* (also cassava-colonising) under the 2050 scenario is also predicted for West Africa (Gamarra *et al.,* 2016b). Additionally, the establishment risk of *B. afer* in East and Southern Africa is similarly predicted to continue to remain very high or increase (Gamarra *et al.,* 2016b). An increase in generation index and population growth potential of *B. afer* is also predicted for East and Southern Africa (Gamarra *et al.,* 2016b).

Maps generated in the study included locations where *B. tabaci* SSA1-SG3 has not been reported. This can be explained in the sense that, the maps are risk maps (based on the three risk indices) showing potential risk posed by *B. tabaci* SSA1-SG3 in each country represented on the map under both current and future scenarios. Additionally, *B. tabaci* SSA1-SG3 is a haplotype (of SSA1, the most widely occurring) and other members of *B. tabaci* SSA1, and closely related SSA species exist in many of those locations showing high generation and activity index, thus confirming the suitability of those ecologies for *B. tabaci* SSA1-SG3 population growth. Furthermore, while ERI well indicated the risk of establishment under current and future scenarios, the estimated moderate–high risk areas indicated by AI and GI well reflects the cassava-growing ecologies in Africa.

The findings on the impact of climate change on cassava-colonising *B. tabaci* have implications for vectored cassava viruses in Africa. Jeremiah *et al*. (2015) suggest that climate change is the likely cause of increasing geographical coverage and consequent

damage of CBSD in Tanzania. The current areas experiencing the dual pandemics of CMD and CBSD also surprisingly correspond with the areas predicted to have increased population growth and abundance with climate change, meaning more virus damage should be expected in these areas. This proposition is supported by the predictions of Campo *et al.* (2011) that suggest an increased climatic suitability for both CMD and CBSD in East and Central Africa. This potential threat to food security calls for some action to adapt.

7.4 Influence of biotic interactions on the mortality of cassava whitefly, *Bemisia tabaci* (Gennadius)

Understanding the population dynamics of insect pests and the importance of biotic factors in regulating their populations is essential to the development of effective pest management strategies (Varley *et al.,* 1973). Age-specific life-tables are often used to study changes in insect populations, as well as evaluate the contributions of different biotic and abiotic factors to the overall population dynamics (Varley *et al.,* 1973; Southwood and Henderson, 2000).

For the first time, age-specific life-tables were developed for cassava-colonising *B. tabaci* in Tanzania. The study identified factors contributing to the mortality of *B. tabaci* on cassava in Tanzania, and the relative importance of each factor. Parasitism, predation and dislodgement were respectively identified as important factors. This will find direct usefulness in the biological control of *B. tabaci* on cassava in Tanzania. Parasitoids and

predators will be very valuable parts of biological control for *B. tabaci* on cassava in Tanzania. However, at the moment commercial biological control for *B. tabaci* on cassava is not available in Tanzania. More research efforts are required to bring these solutions to famers. This could be in form of commercialising biological control, which will make the products available to farmers.

7.5 Adaptation by smallholder farmers to climate change impacts on cassava whiteflies and associated viruses in Tanzania

Literature and chapter 4 of this study suggest that climate change will increase whiteflies and virus problems in East Africa, including Tanzania. Even though studies on adaptation to the impact of climate change on crop pests and diseases exist (Howden *et al.,* 2007; Juroszek and von Tiedemann, 2011; Fahim *et al.,* 2013; Kroschel *et al.,* 2014), they are not common. The study here reported specifically explored possible adaptation strategies to the impact of climate change on whiteflies and viruses of cassava. The study provided useful information on proportion of cassava farmers controlling cassava whiteflies and viruses in the study area, their sources of planting materials and the methods used to manage the pests. Additionally, adaptive capacity, adaptation strategies and measures that can be used to enhance the adaptive capacity of farmers to the impact of climate change on cassava whiteflies and the viruses they transmit were also identified.

The study would have benefited from interviewing more farmers or covering more areas in Tanzania. However, the intensity of cassava cultivation varies across the regions of Tanzania,

and it was preferable to interview farmers in regions currently facing serious cassava whiteflies and virus problems. This was particularly useful since reliable information were gathered while labour, time and money were optimally utilised. Despite efforts to get more international cassava whiteflies/virus experts to respond to the interview, only 20 responded. Given the extensive experience of the experts interviewed, their number was not a limitation as their thorough contributions helped identify and rank possible adaptation strategies and measures to enhance adaptive capacity of the farmers to the impact of climate change on cassava whiteflies and viruses.

Understanding current production characteristics and adaptive capacity of the farmers to the impact of climate change on cassava whiteflies and virus problems, identifying adaptation strategies and measures necessary for enhancing adaptive capacity of cassava farmers are key for maintaining sustained cassava production as well as ensuring food security in the face of climate change. This will require addressing relevant identified vulnerabilities, cooperation of stakeholders, and ensuring that adaptation initiatives are complementary to agricultural and climate change plans. The findings will strengthen climate change adaptations, and general cassava whiteflies and virus management in Tanzania, and other cassava-growing countries.

8. Conclusions and recommendations

The study investigated the potential impact of climate change on cassava-colonising *B. tabaci* SSA1-SG3. Literatures on how climate change can affect whiteflies and the viruses they vectored were first reviewed, then the effects of temperature on the reproductive performance and developmental characteristics of *B. tabaci* SSA1-SG3 colonising-cassava were studied. Data collected on life history of *B. tabaci* SSA1-SG3 from both constant temperature and field experiments were used for phenology modelling. The established phenology model was then used to evaluate temperature-dependence, and the potential impact of climate change on cassava-colonising *B. tabaci*. The study was finalised by identifying possible adaptation options to the potential impact of climate change on cassava whiteflies and associated viruses.

In chapter 2, a review on how climate change can affect whiteflies and the viruses they vector was conducted. The study highlighted the dynamism of the interactions between the

vectors, transmitted viruses and host plant species. It was possible to conclude that, climate change will affect life history of whiteflies, and the impacts of climate change on whiteflies and the viruses they vector will vary widely depending on thermal profile of the whiteflies, host plants and local climatic conditions.

In chapter 3, the life history and temperature-dependent phenology model of cassava-colonising population of *B. tabaci* were investigated. The study confirms that temperature affects the life history traits of cassava-colonising *B. tabaci* SSA1-SG3, and that *B. tabaci* SSA1-SG3 differs from *B. tabaci* MEAM1 and MED in the response of its life history parameters to temperature. The established phenology model demonstrates the influence of temperature on the growth potential of cassava-colonising *B. tabaci* and can be used to explain its population dynamics. Future efforts could be geared toward developing similar temperature-dependent phenology models for both *B. tabaci* and one of its parasitoid, like *En. sophia* or a natural enemy like *S. japonicum.*

The study on the potential impact of climate change on the distribution and abundance of cassava-colonising *B. tabaci* SSA1-SG3 showed that climate change will differentially affect the distribution and abundance of cassava-colonising whiteflies across Africa. The study concludes that while a reduction in *B. tabaci* problems is predicted for the cassava-growing areas of West Africa, cassava-colonising *B. tabaci* and viruses they vector will likely cause more problems in East and Central Africa. With a southward range expansion of *B. tabaci* SSA1-SG3 into wider areas of Southern Africa, cassava virus problems will also likely increase.

This calls for climate change adaptation planning and development of more robust whiteflies and cassava virus management programmes in affected countries to ensure sustained livelihood and food security of millions of Africans depending on this crop.

The influence of biotic interactions on the mortality of cassava whitefly, *Bemisia tabaci* was discussed in chapter 5. Life-table approach was used to assess the factors causing mortality of *B. tabaci* on cassava in Dar es Salaam (Tanzania). From the study, it was possible to conclude that parasitism and predation are the primary cause of nymphal mortality respectively, while egg inviability and dislodgement were the primary cause of mortality in the egg stage respectively. It was also possible to conclude that the highest generational mortality is associated with fourth and pupa instars respectively.

In chapter 6, adaptation of smallholder farmers to climate change impacts on cassava whiteflies and associated viruses in Tanzania was investigated. Relatively few farmers attempt managing cassava whiteflies and virus problems on their farms based on their knowledge and resources. Considering their production characteristics and adaptive capacity, it was possible to conclude that, the farmers can moderately adapt with climate change driven increase in whiteflies and virus problems on their farms. It was also possible to conclude that training of all stakeholders and providing needed information and resources would help enhance the adaptive capacity of the farmers. Lastly, integrating pest and disease management programmes, phytosanitation, applying novel vector management

techniques, biocontrol of whiteflies and other strategies could help farmers adapt to increased cassava whiteflies and virus problems on their farms.

Based on findings of this study, directions for future research are summarised below. The study on the potential impact of climatic change on the distribution and abundance of cassava-colonising whiteflies suggest a possible role of climate change in the cassava virus disease pandemics in East and Central Africa (predicted *B. tabaci* hotspots corresponds with areas experiencing the cassava virus disease pandemics). Future research effort should devote some effort in this direction to elucidate the possible role of climate change on the pandemics of cassava viruses in East and Central Africa. Furthermore, future research initiative addressing the potential impact of climate change on trophic interactions of cassava whiteflies, viruses and their natural enemies will also significantly contribute to knowledge on the possible impact of climate change on cassava whiteflies.

9. References

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