# Genetic diversity and structure of the superabundant whitefly populations, vectors of viruses causing diseases of cassava in three East African countries (Malawi, Tanzania, and Uganda)

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**UNIVERSITÉ DE LA RÉUNION**

Ecole Doctorale Sciences, Technologies et Santé (EDSTS-542)

UMR PVBMT Peuplement Végétaux et Bioagresseurs en Milieu Tropical CIRAD – Université de La Réunion

**THESE**

Présentée à l'Université de La Réunion pour obtenir le

**DIPLOME DE DOCTORAT EN SCIENCES**

**Discipline : Biologie des Populations**

# Diversité et structuration génétique des populations émergentes d'aleurodes vecteurs de maladies sur manioc en Afrique de l'Est (Malawi, Tanzanie, et Uganda)

Par

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Soutenue publiquement le 05 juillet sur le campus du Tampon, devant le jury suivant :

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# DEDICATION

***To my father, who have dedicated years of his life to make sure that I had access to education. Gone but never forgotten "to Allah we belong and truly to Him we shall return".***

# ACKNOWLEDGEMENT

**I would like to begin by thanking the Almighty God for enabling me to achieve my higher degree, I do believe my efforts alone without him could not have accomplished this.**

**My sincere gratitude goes to my supervisor Dr. Helene Delatte for being supportive throughout my studies. You played two major roles: as my supervisor you were very resourceful in giving me constructive ideas and comments. More than that you have been like a mother/sister especially during the time of my pregnancy until I delivered. Sincere thanks from me and my beloved husband, we thank you so much Helene.**

**Without forgetting Lulu, you saved my days, thanks for sharing experience and assisting me with laboratory work.**

**I would also like to further extend my gratitude to my cosupervisors Prof. J. Colvin and Prof. M. Gowda for positive inputs. Furthermore, to my theses committee team Dr. C. Omongo and Dr. S. Brunschot who gave me constructive comments during my study.**

**Additionally, I would also like to thank the CIRAD staffs, especially those who work at 3P. You have shown me a good cooperation throughout the time I was here, the language was not a barrier to our cooperation, thank you so much. These thanks also go to my PhD colleagues Cathleen, Alizee, Karim, Pauline and the list is too long thank you all.**

**I would also like to thank my parents for their undying support. My father for being close with me since I started school until death came upon him 13 years ago "to Allah we belong and truly to Him we shall return". To my mum and my sister for taking care my daughters Fatma and Navil as well to my brothers, sister in-laws and uncles for being close to me.**

**Special thanks to my beloved husband Bakari Jiriwa. Despite being away from him, I felt like I was around him, thanks for your patience and for believing in me, taking care of our daughters, and helping my family as well. These thanks also go to my mother in-law and sister in-law for taking care of my little daughter Navil.**

**My research would not be possible without the money. Extended thanks go to all people who developed the African cassava whitefly project led by Prof. J. Colvin. Special thanks to our project donor Bill and Melinda Gates Foundation.**

**Finally, I want to thank my employer, the ministry of agriculture, under Tanzania Agriculture Research Institute (TARI) for giving me a study leave to pursue this course. I would also like to take this opportunity to thank my colleagues from TARI Ukiriguru for keeping me updated on important information.**

**Asanteni wote**

# RÉSUMÉ


**Diversité et structuration génétique des populations émergentes d'aleurodes vecteurs de maladies sur manioc en Afrique de l'Est (Malawi, Tanzania, et Uganda)**

Des pullulations d'aleurodes du complexe d'espèces cryptiques de *Bemisia tabaci* ont été associées à la propagation de deux maladies frappant le manioc en Afrique orientale: la maladie de la mosaïque du manioc (CMD) et, plus récemment (2000), la maladie de la striure brune du manioc (CBSD). Parmi les espèces d'aleurodes de ce complexe, l'espèce SSA2 a été associée à la première épidémie de CMD au cours des années 1990 en Ouganda. Cependant, SSA2 aurait été remplacée par SSA1 dans les années 2000, provoquant une recrudescence de CMD et de CBSD, participant à leur propagation dans plusieurs pays voisins. L'hypothèse défendue à ce jour expliquant la propagation de ces maladies vers le sud et l'ouest de l'Afrique incrimine cette nouvelle espèce considérée comme émergente et même invasive dans certains de ces pays.

Dans ma thèse, j'ai utilisé des données écologiques et des approches moléculaires (marqueurs mitochondriaux et nucléaires) afin de mieux comprendre les facteurs à l'origine des pullulations de vecteurs en Afrique de l'Est. Nous avons ainsi analysé : i) l'abondance, la diversité et la répartition des espèces (géographiques et plantes hôtes) sur un transect au travers trois pays : Ouganda, Tanzanie et Malawi, ii) la diversité génétique et la structure des populations actuelles des espèces de *B. tabaci,* iii) des échantillons de collections des années 90 (dans les zones forte incidence de CMD) qui ont été comparées aux populations actuelles (2017). Cette étude très large nous a permis d'avoir une image d'une situation plus complexe qu'attendue, en effet, l'espèce SSA1 a été détectée comme à l'origine de certaines des pullulations observées mais, également d'autres espèces, notamment IO et SSA1-SG3 ont aussi montrées cette capacité. Les foyers observés ne sont donc pas liés à une seule espèce en Afrique de l'Est.

De plus, nous avons montré que la communauté d'espèces et sa diversité génétique diffèrent d'un pays à l'autre, impliquant différentes situations épidémiologiques. L'analyse des anciens échantillons n'a pas mis en évidence l'implication d'une nouvelle espèce ni l'émergence d'une nouvelle population en 20 ans, bien qu'un changement de la dynamique au sein des groupes génétiques d'aleurode ait été observée. Nos résultats ont apporté de nouvelles connaissances sur les populations très abondantes sur manioc en Afrique orientale et permettrons de proposer des mesures de contrôle ciblées pour les populations locales.



**Mots clés** : *Bemisia tabaci,* mtCOI, microsatellite markers, Manioc, Afrique de l'Est.

# ABSTRACT


**Genetic diversity and structure of the superabundant whitefly populations, vectors of viruses causing diseases of cassava in three East African countries (Malawi, Tanzania, and Uganda)**

High populations of the whitefly, *Bemisia tabaci* Gennadius, a cryptic species complex have been associated with the vectoring and spread of viruses causing two diseases of cassava in East Africa: the cassava mosaic disease (CMD) and cassava brown streak disease (CBSD). Among the *B. tabaci* species, sub-Saharan Africa 2 (SSA2) was the vector associated with an epidemic of CMD since the 1990s in Uganda. However, this species is now replaced by the sub–Sahara Africa 1 (SSA1) and led to development of another epidemic by CBSD since the mid 2000s. The spread of both diseases toward South and West Africa is feared with this new supposed invader.

In my thesis I have used ecological data and molecular approaches (mitochondrial and nuclear markers) to better understand the factors driving the presence of the superabundant whitefly populations on cassava in East Africa. We have analyzed: i) species abundance, diversity and distribution (geographic and host plants) along a transect survey over three East African countries: Uganda, Tanzania, Malawi, ii) the genetic diversity and structure of current populations of B. *tabaci* species, and iii) comparing genetic changes between the old and new populations collected in 1997 and 2017, respectively. This study involved a large number of samples ($n$ = 3563) provided insights of a more complex picture than expected. SSA1 was found to be the source of some observed outbreaks although SSA1–SG3 and IO species, have also shown this capability. The observed outbreaks are therefore not just related to a single species in East Africa.

In addition, we showed that the species community and its genetic diversity differ from one country to another, involving different epidemiological situations, without any clear pattern of invasion detected between the countries. Analysis of old samples did not show the involvement of a new species or the emergence of a new population in 20 years, although the dynamics within the whitefly genetic groups was observed over time. Our results contributed new knowledge on the super abundant populations on cassava in Eastern Africa and will facilitate the development of targeted control measures for these local populations.



**Key words:** *Bemisia tabaci*, mtCOI, microsatellite markers, cassava, East Africa, genetic clusters

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# ABBREVIATION

| | |
|---|---|
| ACMV | African cassava mosaic virus |
| AFLP | Amplified fragment length polymorphism |
| AnSL | Africa non–silver leafing |
| ASL | Africa silver leafing |
| *B. afer* | *Bemisia afer* |
| *B. tabaci* | *Bemisia tabaci* |
| CBSD | Cassava brown streak disease |
| CBSV | Cassava brown streak virus |
| CdTV | Chino del tomate virus |
| CMD | Cassava mosaic disease |
| CMV | Cassava mosaic virus |
| DNA | Deoxyribonucleic acid |
| DRC | Democratic Republic of Congo |
| EA | East Africa |
| EACMV | East Africa cassava mosaic virus |
| EACMV-UG | East Africa cassava mosaic virus Uganda variant |
| EST | Esterase |
| FAO | Food and agriculture organization |
| IO | Indian Ocean |
| ITS | Internal transcribed spencer |
| HWE | Hardy-Weinberg equilibrium |
| MCMC | Marcov chain monte Calo algarithm |
| MEAM1 | Middle East-Asia Minor-1 |
| Med | Mediterranean |
| Ms | Former name of IO |
| mtCOI | Mitochondrial cytochrome oxidase 1 |
| NextRAD | Next restriction site associated DNA |
| PCR | Polymerase chain reaction |
| PHV | Pepper huasteco virus |
| PCA | Principle component analysis |
| PYLCV | Pepper yellow leaf curl virus |
| RAPD | Random amplified of polymorphic DNA |
| RCA | Central Africa Republic |
| rDNA | Ribosomal deoxyribonuceic acid |
| SCAR | Sequence characterized amplified regions |
| SG | Subgroup |
| SNPs | Single nucleotide polymorphism |
| SSA | Sub-Sahara Africa |
| ssDNA | Single stranded DNA |
| ssRNA | Single stranded ribonucleic acid |
| SWIO | Southwest Indian Ocean |

| | |
|---|---|
| ToCMoV | Tomato chrolotic mottle virus |
| ToCV | Tomato chrolosis virus |
| TYLCV | Tomato yellow leaf curl virus |
| Ug | Uganda |
| Ugsp | Uganda sweetpotato |
| US | United states |
| ZHJ | *B. tabaci* species originated from China |

**Units**

| | |
|---|---|
| ~ | Approximately |
| oC | Degree celcius |
| $ | Dollars |
| % | Percent |
| N | Number |
| Km | Kilometre |
| Min | Minute |
| S | Second |
| µl | Microlitre |
| ± | Plus or minus |

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GENERAL INTRODUCTION

Crop protection plays a key role in safeguarding global crop production against losses, thereby helping to meet the increasing demand for food caused by a growing human population (Oerke and Dehne 2004). Crop diseases, insect pests and weeds are among the factors causing extensive losses in the yield and quality of many cultivated crops.

In this era of climatic change, cassava is considered as one of the most important food security crops particularly in sub–Sahara Africa (SSA) due to its ability of tolerating drought. Its starchy roots are a major source of calories for more than 800 million people around the world. Despite its importance, the crop is affected by two groups of viruses cassava mosaic begomoviruses (CMBs) and cassava brown streak ipomoviruses (CBSIs), which cause cassava mosaic disease (CMD) and cassava brown streak disease (CBSD), respectively. CMBs and CBSIs are transmitted by the whitefly species *Bemisia tabaci* (Legg and Ogwal 1998, Maruthi et al. 2017). Masinde et al. (2016) observed the maximum yield losses attributed by CMD and CBSD were 56.7% and 74.0% respectively from Migori county in Kenya. Severe epidemics of CMD and CBSD have been facilitated by the rapid increase in whitefly populations (*B. tabaci*) (Legg and Ogwal 1998, Legg 1999, Legg et al. 2002, Maruthi et al. 2017).

*B. tabaci* affects plants by feeding, excretion of honey dew which is a substrate for sooty mold fungi, however by far the largest impact is caused by the transmission of viruses. It transmits over 300 plant viruses including CMBs and CBSIs (Hendrix et al. 1992, Navas-Castillo et al. 2000, Navas-Castillo et al. 2011, Navas-Castillo et al. 2014, Legg et al. 2015). The whitefly *B. tabaci* has been considered a complex of over 40 morphologically indistinguishable cryptic species. Species differentiation within this complex was based on the use of molecular markers due to their cryptic status. The core region of the mitochondrial cytochrome oxydase I gene (mtCOI) has been used as a species barcode. The *B. tabaci* species were found to differ in genetic composition, insecticide resistance, host plant utilization, ability to induce physiological disorders, virus transmission capacities, ability to host different communities of secondary endosymbiont and their differential geographical distribution (De Barro et al. 2011, Mugerwa et al. 2018).

Furthermore, some *B. tabaci* species are not able to hybridise (Maruthi et al. 2004, Omondi et al. 2005b, Liu et al. 2007, Wang et al. 2010, Xu et al. 2010, Tsueda and Tsuchida 2011, Saleh et al. 2012).

Two of these species have invaded a large part of the World: Middle East Asia minor I (MEAM1) and Mediterranean (MED), while others are continental restricted including sub–Sahara Africa (SSA1 to SSA13, except SSA2 that can also be found in Southern Europe (Banks et al. 1998, Hadjistylli et al. 2015). The first five SSA (SSA1 – SSA5) species prefer cassava plants for feeding and reproduction (Wang et al. 2011, Barbosa et al. 2014, Laarif et al. 2015, Wosula et al. 2017, Mugerwa et al. 2018). The SSA2 species was previously, associated with CMD epidemic on cassava in Uganda during the initial outbreak (1990s) (Legg et al. 2002). Nevertheless, in current studies the increase in abundance of whitefly population was by SSA1 with its two subgroups (SG1 and SG2) in all CMD and CBSD affected regions in Africa (Legg et al. 2002, Maruthi et al. 2005, Sseruwagi et al. 2005, Mugerwa et al. 2012, Legg et al. 2014b, Tajebe et al. 2015a). The distribution of whiteflies in Africa varied with SSA1 found throughout but dominated in east Africa (Ghosh et al. 2015, Tajebe et al. 2015a, Wosula et al. 2017, Mugerwa et al. 2018).

In this study, I used two molecular markers, the sequencing of the mtCOI barcoding region and a set of nuclear markers, to understand 1) *B. tabaci* species diversity according to host species and countrywide distribution in East Africa, 2) the genetic diversity and population gene flows within species from different countries, 3) to understand the population and species dynamics, and potential genetic diversity changes over time by comparing whitefly samples collected during the initial whitefly outbreak (1997) and the current outbreak of 2017 in Uganda.

# Chapter 1


Figure 1. 1: Examples of cassava products. Sources Dada (2010), www.farmsteadmarket.com, https://www.medicalnewstoday.com, https://www.poukouhalalfood.com.

# Chapter 1: literature review

## 1.1. Importance of cassava as a staple food in sub–Sahara Africa, with focus on East Africa

Cassava is a woody shrub, considered as an important staple food crop in many countries of tropical and subtropical areas (Legg et al. 2006). Cassava originates from South America, it was introduced in Africa by the Portuguese during the 16th century on the west coast of Africa (Jones 1959) and later was introduced in East Africa via Madagascar and Zanzibar (Fauquet and Fargette 1990). This crop is produced in 102 countries with a majority of them found in Asia and Africa (FAOstat 2017). Its adaptation to marginal land makes it affordable for most subsistence farmers in Africa, because of the low cost of production. Cassava's ability to tolerate drought makes it a food security crop (Jarvis et al. 2012, Reincke et al. 2018) and feeds more than 800 million people, majoriy of them are from sub–Sahara Africa (FAOstat 2017).

Cassava is valued for its different usages (Fig. 1.1): the roots are used as a source of carbohydrate, leaves as a leaf vegetable nutritionally important in fibre, vitamin A and B, protein and essential amino acids, while the stem as a source of fuel as well as planting material for the next season (Zhu et al. 2015). The roots can be harvested in piecemeal manner which provides food throughout the year as fresh meal, or it can be dried and processed into flour. The cassava flour can be sold in local markets or processed into value added food products such as in bakery (Hillocks et al. 2002).

Nigeria, Democratic Republic of Congo, Thailand, Indonesia, Brazil, Ghana, Angola, Cambodia, Viet Nam and Mozambique are among the 10 largest cassava producers in the world. Majority of these countries are from Southeast Asia and West Africa (FAOstat 2017). In Asia, cassava is mainly used for starch production or to feed animals, while in Africa cassava is used for human consumption (Howeler et al. 2013, Parmar et al. 2017). Africa produces 57% of the global cassava production with more than 20% coming from Nigeria alone (Bennett 2015, FAOstat 2017).

In East Africa, Tanzania is the leading producer. The crop is grown in different agroecological zones, but the main production areas include the Lake Zone (Mwanza Mara and

Figure 1. 2: Adults *B. tabaci*, photo: A. Franck, CIRAD, UMR PVBMT©.

Shinyanga), Coast regions (Lindi, Mtwara, Tanga, Zanzibar), Kigoma and Ruvuma areas. Being the third most important crop in the country, it contributes to 7.8% of the total calories in Tanzanian diet after maize and rice (Cochrane and D'Souza 2015).

Uganda is the second largest cassava producer in East Africa, and the crop also ranks second in importance after plantain (Haggblade and Dewina 2010). Per capita consumption the crop accounts for about 11% of calories intake (Haggblade and Dewina 2010). Cassava is grown in all regions of Uganda normally in mixed farming systems and about 9% of farmers grow the crop as a cash crop (Otim-Nape and Zziwa 1990).

Malawi is the largest cassava producer in Southern African zone. The crop ranks second after maize and as being drought resistance, it gained popularity following drought intervention in late and mid 1990s when maize was reduced by half of its normal production (Kambewa 2010, Minot 2010). The crop feeds 30 to 40% of Malawian population (Chipeta and Bokosi 2013) and also contributes to 7% of calories intake per capita consumption (Minot 2010).

Despite increases in cultivated land, significant reductions in cassava yields have been reported (FAOstat 2017). Cassava yield has the potential to reach up to 80.0 tonnes per ha under optimal conditions, however, the World average yield is only 12.2 tonnes, with much of the low productivity coming from sub–Saharan Africa (Howeler et al. 2013). Several factors attribute to this loss among them are poor soil fertility, early water stress, altitude, poor agriculture practices, inadequate extension services, poor processing as well as pests and diseases (Legg 1999, Moyo et al. 2004, Fermont et al. 2009, Patil et al. 2015, Reincke et al. 2018). Among the diseases, CMD and CBSD are the most prominent together with the insect pest whiteflies.

## 1.2. Whiteflies

Whiteflies are sap sucking insects. The name whitefly is derived from their white appearance due to the deposition of fine white powdery wax over their four wings and body (Fig.1.2). Whiteflies are not true flies, they are in the same order of insect as scales, aphids and mealy bugs of the order Hemiptera.

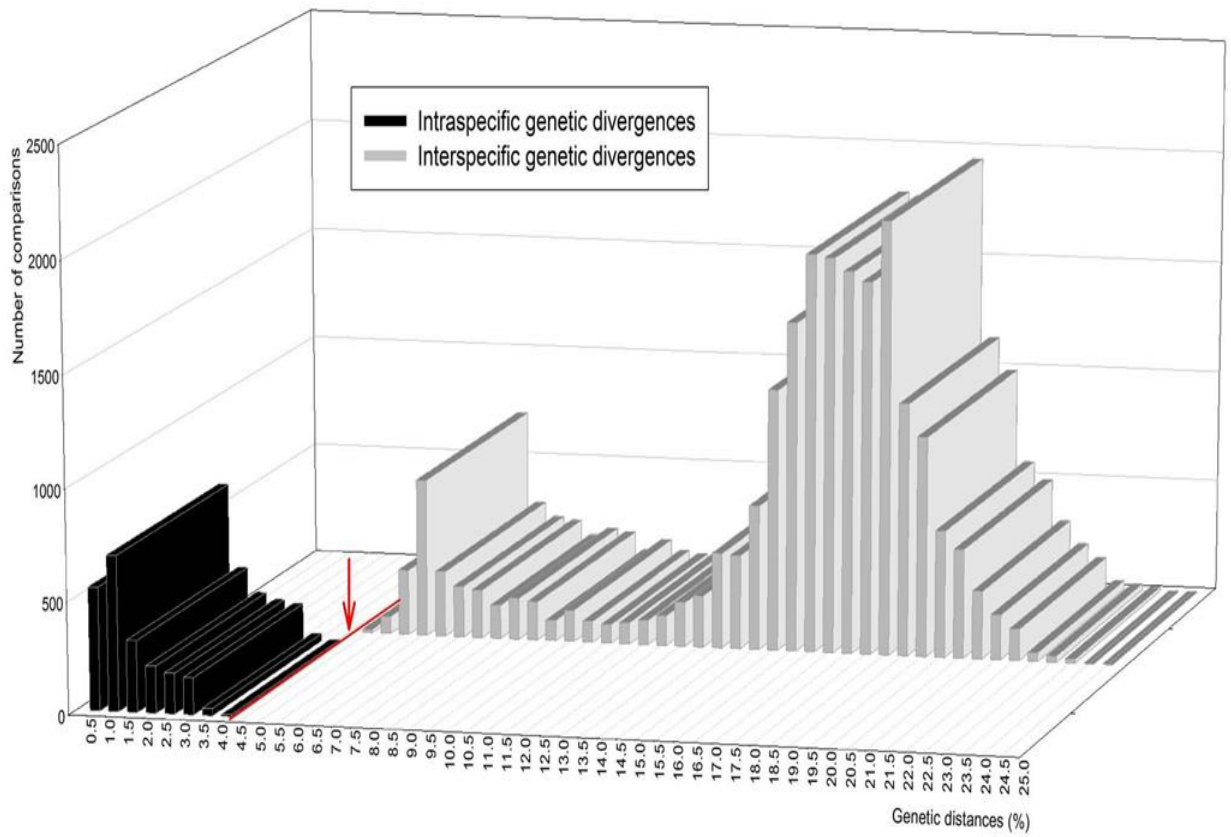


Figure 1. 3: Distribution of genetic divergences based on the Kimura-2 parameter analysis for taxonomic levels as described by Lee et al., (2013).

They belong to the Aleyrodidae family which is further divided into two sub families: Aleurodicinae which include, *Aspidiotus destructor* (Mackie) and *Aleurodicus dispersus* (Russell) and Aleyrodinae. More than 1550 species of whiteflies have been classified (Ko 2001, Martin 2003). Aleyrodinae ranks the largest sub family with around 140 genera, among them one of economic importance pest and vector known as *B. tabaci*.

### 1.3. *Bemisia tabaci* classification

The first *B. tabaci* specimen was found in Greece (1897), it was collected on tobacco and was described as a new genus, *Bemisia inconspicua* as a "type" species (Quaintance and Baker 1914, Gill 1990). It's only in 1957 that this species, along with a dozen other species of whiteflies, were put synonimized (grouping of species) in the same taxon: *Bemisia tabaci* (Russell 1957).

The classification of whiteflies is based on the morphology of the last larval stage or pupa than on adults, which differ very little morphologically (Gill 1990). The observation of a large morphological variability of the last larval stage, related to the physical characteristics of the host plant, led the taxonomists to synonymize numerous species. Nevertheless, the subsequent variations reported in pupal morphology depended on host plant (Russell 1948), leaf surface character (Mound 1963), atmosphere (temperature) as well as surrounding environment (Sundararaj and David 1992).

Due to that discrepancy some populations were not differentiated. Other factors were considered in classifying populations which were based on life history (Costa and Brown 1991, Viscarret et al. 2003), induction of physiological disorders (Costa and Brown 1991, Cohen et al. 1992), mating behaviour (Bethke et al. 1991), or insecticide resistance (Dittrich et al. 1990, Costa and Brown 1991). This is the period where the concept of biotypes or races was introduced (Brown et al. 1995a). As a result, several studies considered *B. tabaci* as a species complex (Perring et al. 1993, Bellows Jr et al. 1994, Oliveira et al. 2001, De Barro et al. 2011, De Barro 2012, Lee et al. 2013).

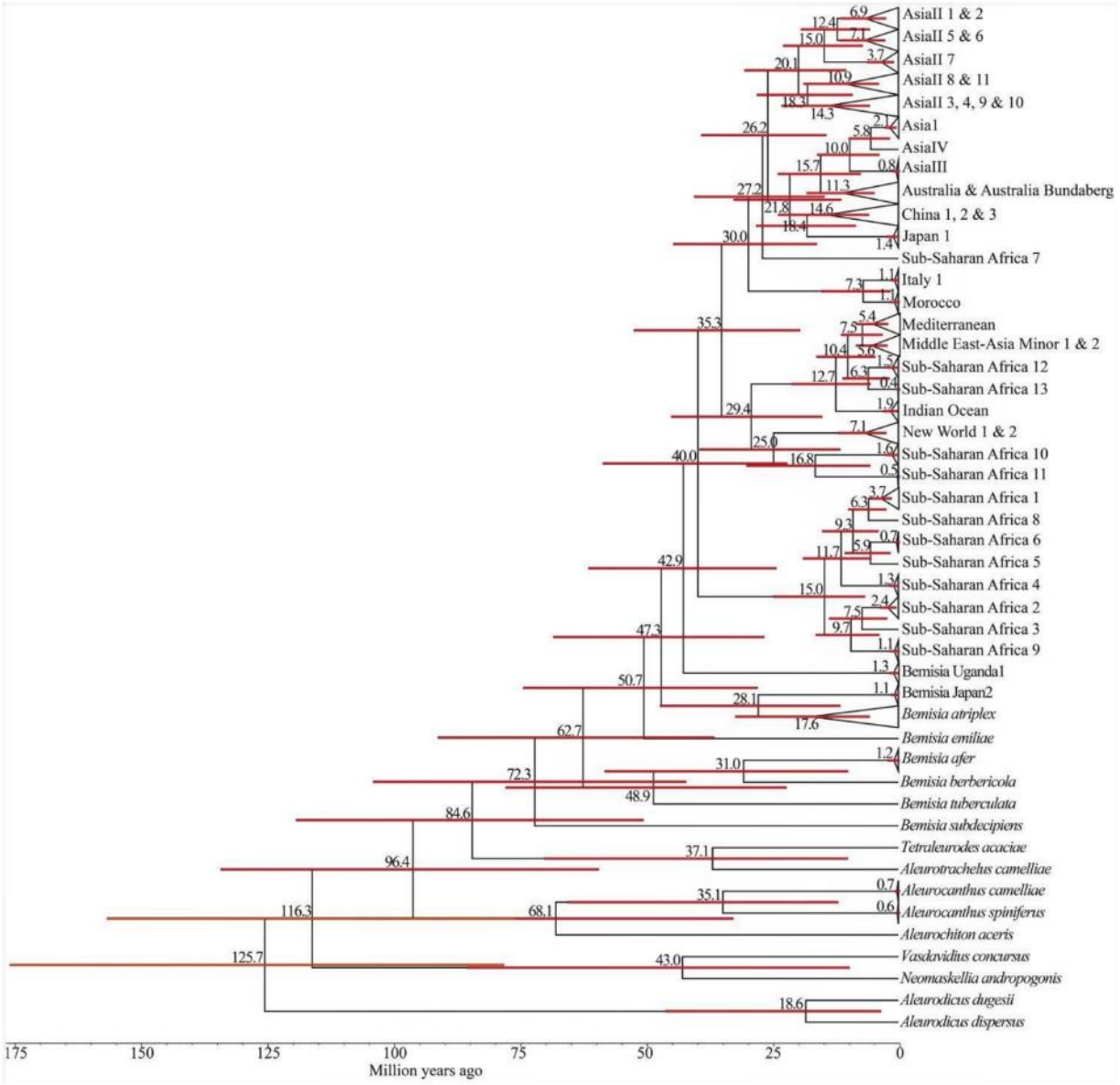


Figure 1. 4: Different *B. tabaci* species obtained through mtCOI sequences according to Mugerwa et al., (2018).

Different approaches have been used to study population diversity and differentiation within each of the species complex, but the first true taxonomic differentiation between *B. tabaci* species was performed with the help of molecular tools. Those tools included several molecular markers such as polymerase chain reaction (PCR) amplified fragment length polymorphism (AFLP), or AFLP-PCR, the technique of PCR–restriction fragment length polymorphism (PCR-RFLP), microsatellite markers, Rad-seq, or sequencing of mitochondrial markers (Cytochrome oxidase 1, mtCOI) (Costa and Brown 1991, Wool et al. 1991, De Barro et al. 2003, De Barro et al. 2005, Sseruwagi et al. 2005, Delatte et al. 2006, Ma et al. 2007, Hadjistylli et al. 2016, Wosula et al. 2017).

Using mtCOI, 11 major *B. tabaci* genetic groups with 24 potential species were described with 3.5% of nucleotides of divergence between the morpho-species (Boykin et al. 2007, Dinsdale et al. 2010). The number of cryptic species increased from 24 to 28 (De Barro et al (2011), to 31 (Lee et al., 2013) and currently believed to be over 40 (Mugerwa et al., 2018). Lee et al., (2013) observed that the 31 species revealed an average of intraspecific genetic divergence of 1.2% (0.2 to 3.9%) and an average of interspecific genetic divergence of 15.7% (4.2 to 24.1%). These authors therefore proposed to raise the "threshold bar" samples of 3.5% of the species within the complex to 4% (Fig. 1.3).

Several species have been identified in SSA (see section 1.9) (Fig. 1.4). Although some *B. tabaci* species such as MEAM1 and Med live in sympatry, biologically, they cannot reproduce (De Barro et al. 2000, Saleh et al. 2012). Lack of hybridization between other *B. tabaci* species were also reported previously (Maruthi et al. 2004, Omondi et al. 2005b, Liu et al. 2007, Wang et al. 2010, Xu et al. 2010, Tsueda and Tsuchida 2011, Saleh et al. 2012).

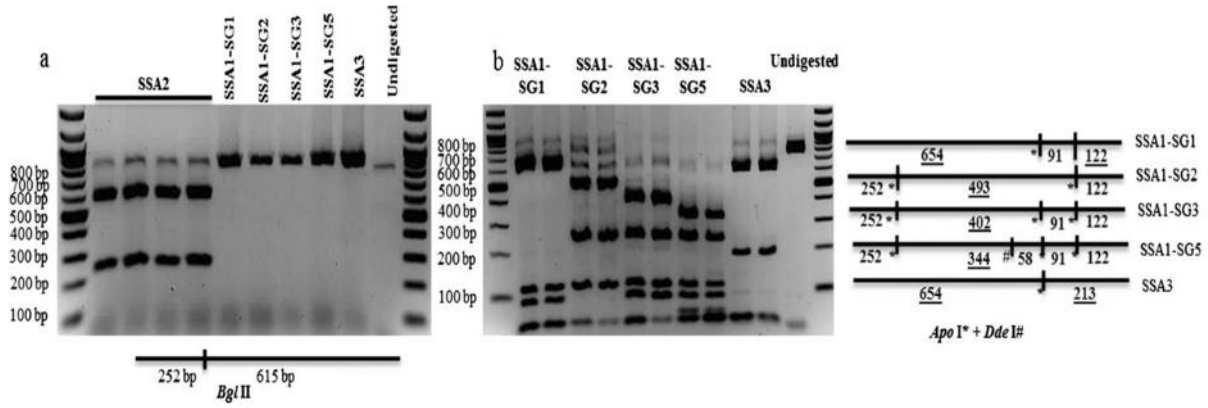


Figure 1. 5: Detection of cassava whitefly populations based on RFLP (Ghosh et al. 2015).

## 1.5. Molecular tools used for molecular taxonomic issues

### (a) Amplified fragment length polymorphism (AFLP)

This method relies on the presence or absence of polymorphism within restriction enzyme sites. For example, the procedure was used to differentiate fall army worms strains collected from corn and forage grasses at Louisiana State (McMichael and Prowell 1999). Variation of Med and MEAM1 species was accessed using AFLP from populations in Brazil and China Cervera (2000). The AFLP technique was also used to study genetic relationship among *B. tabaci* species, as well as differentiating MEAM I and Med in China (Guo et al. 2012).

### (b) Restriction fragment length polymorphism (RFLP)

In this technique polymorphism is determined by variation on the length of DNA fragment produced by restriction enzymes (Fig. 1.5). For instance, the method used to identify molecular phylogeny and evolutionary relationships among four mosquito (Diptera: *Culicidae*) species from India (Sharma et al. 2013). Similar approach was used to understand the genetic diversity of *B. tabaci* collected from DRC, Malawi, Tanzania and Uganda (Ghosh 2015). The RFLP technique was used in other studies to understand genetic diversity of different *B. tabaci* species (Bosco et al. 2006, Shoorcheh et al. 2008, Rocha et al. 2011, Queiroz et al. 2016).

### (c) Random amplified of polymorphic DNA (RAPD)

The RAPD technique uses a single primer for amplification. The technique was applied in molecular ecology for studying taxonomic identity, kinship relationships, analyse mixed genome samples or create specific probes (Hadrys et al. 1992). In insects, RAPDs have widely been used for example to study aphid polymorphism (Black et al. 1992) and many other species. Studies using this marker were also, conducted on whiteflies, revealing first distinction between “biotype B” (former name of MEAM1) and non-B biotypes within the Brazilian *B. tabaci* populations (Lima et al. 2000, Lima et al. 2002). RAPD was also used to differentiate the cassava *B. tabaci* species from non–cassava species from *B. tabaci* collected in the major cassava growing area in Africa (Abdullahi et al. 2003). Other studies also, reported the genetic variation within *B. tabaci* by using similar procedures (De Barro and Driver 1997, Guirao et al. 1997, Horowitz et al. 2003, Delatte et al. 2005).

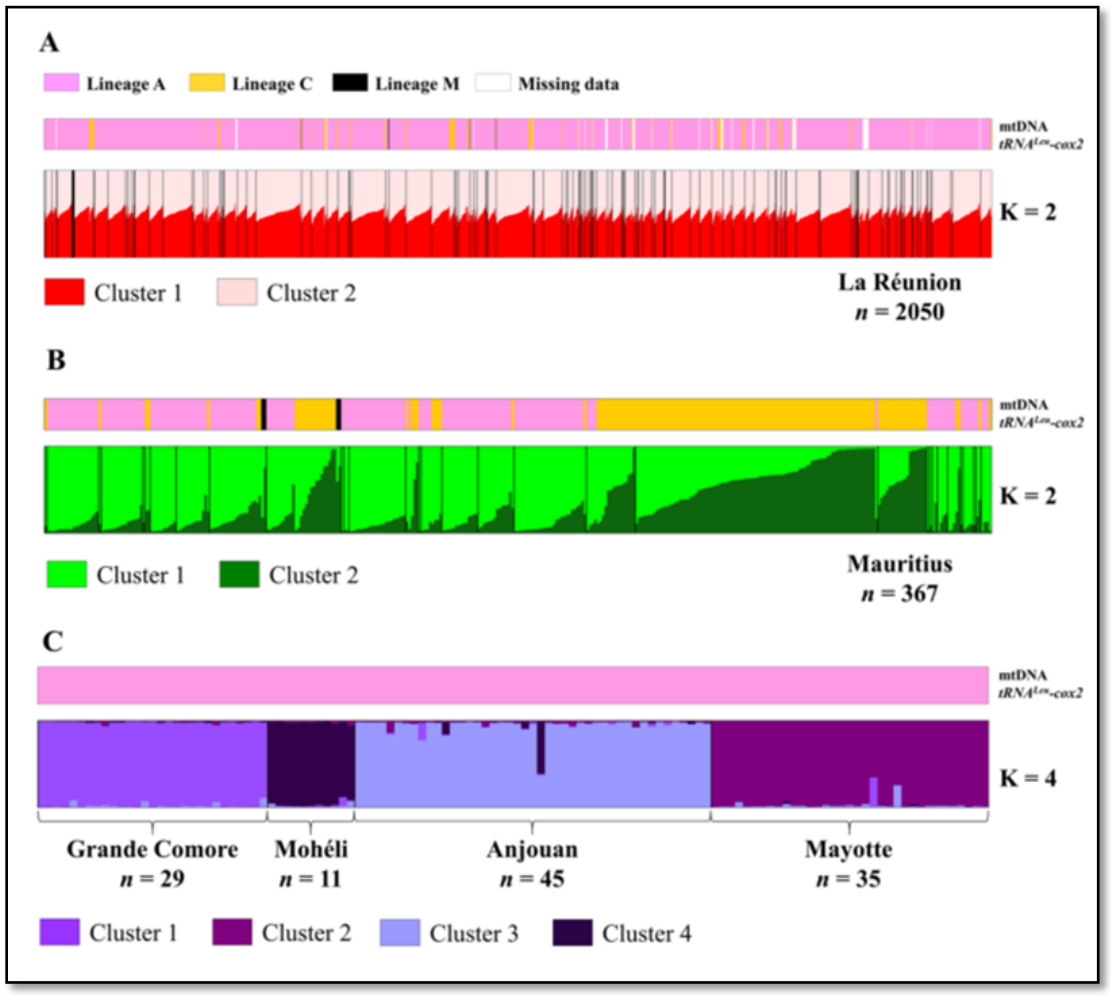


Figure 1. 6: Different structure patterns of honey bee collected from the Southern West of Indian Ocean archipelago, described by Teacher et al. (2017).

**(d) Sequence characterized amplified regions (SCAR)**

A locus specific marker is another PCR based tool. The primer can be designed following sequence analysis of RAPD or AFLP fragments (Agustí et al. 2000, Khasdan et al. 2005). Donkers–Venne (2000) developed a SCAR marker that were able to distinguish three species of major agriculture pest of *Meloidogyne incognita*, *M. javanica* and *M. arenaria* (Donkers-Venne et al. 2000). Correspondingly, two primer sets of SCAR was developed to study different *B. tabaci* populations (Ko et al. 2007). Further, the SCAR technique was used to understand the dynamic of species complex of MEAM1 and Med *B. tabaci* population in Israel (Khasdan et al. 2005, Queiroz et al. 2016) and India (Shankarappa et al. 2007)

## 1.6. Other nuclear markers for population studies

**(a) Microsatellite markers**

These are tandem repeat motifs ranging from two to six base pairs occurring within the nuclear genome of organism. They are widely distributed consisting of coding and non–coding regions (Zane et al. 2002, Kalia et al. 2011). Being highly polymorphic, with high resolution power, chromosome specific and codominant, they are useful to study population genetics (Queller et al. 1993, Tenzer et al. 1999, De Barro 2005, Parida et al. 2006, Kalia et al. 2011, Georgescu et al. 2014). The application of microsatellite markers showed great potential in various population genetic studies.

For example, 12 microsatellite loci developed from melon fly (*Bactrocera cucurbitae)* species revealed the existence of genetic structure and little gene flow among *B. cucurbitae* collected from Asia (Wu et al. 2009, Wu et al. 2011). Similar procedures were utilized in Reunion island (Jacquard et al. 2013) or as a worldwide scale (Virgilio et al. 2010) showing parental invasion routes and population groups specific to different regions. Indeed, the application of microsatellite markers were used in many different insect population genetic studies including, for example, honey bees (Fig. 1.6) (Rasolofoarivao et al. 2015, Techer et al. 2016, Techer et al. 2017b, Techer et al. 2017a), thrips (Wu et al. 2014) and flat black beetle (*Cryptolestes ferrugineus*) (Wu et al. (2016).

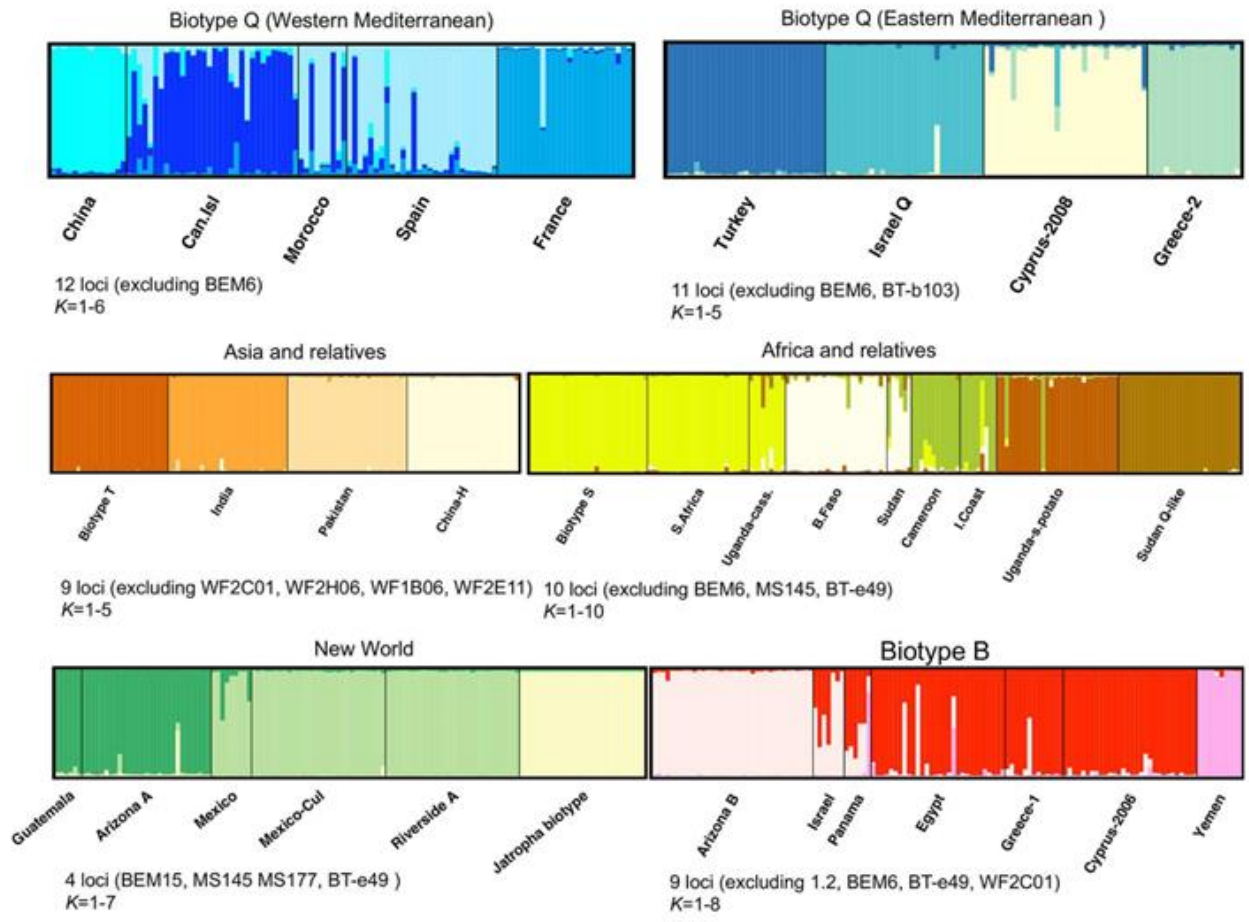


Figure 1. 7: Bayesian clustering analysis presenting different *B. tabaci* species collected from different agroecological zones, different genetic clusters are seeing within the same species described by Hadjistylli et al. (2016).

De Barro (2003, 2005) initiated the use of this technique on *B. tabaci* populations. Those markers are being used to address many questions at the population levels such as retracing invasion routes, gene flow or hybridization between populations, deciphering species boundaries on close species, genetic diversity, inbreeding of populations but also, testing for population structure based on ecological factors (seasonal, host plants, elevation, geographic distance). Currently, several *B. tabaci* microsatellites markers have been used to understand the genetic parten of *B. tabaci* populations including MEAM1 and Med (De Barro et al. 2003, Delatte et al. 2006, Dalmon et al. 2008)

In the southern west Indian Ocean (SWIO), the genetic structure, distribution and geographical range of the indigenous IO species was revealed in the islands of Reunion, Madagascar, Mauritius, Comoros and Seychelles (Delatte et al. 2006, Thierry et al. 2011, Thierry et al. 2015).

Another combined study using 13 microsatellites loci and mtCOI analysed a worldwide set of populations (Hadjistylli et al. (2016). In this study, *B. tabaci* populations used were collected from 50 different countries worldwide. The results showed that the microsatellites markers used were able to resolve distinct genetic groups according to the geographical location (Fig. 1.7). Furthermore, the genetic structure between *B. tabaci* populations collected from greenhouses in southern France was studied by using seven microsatellite loci by Dalmon et al. (2008). In another study, the microsatellite analyses were able to separate MEAM I and Med structure from the *B. tabaci* samples collected from different host plants in Tunisia (Saleh et al. 2012) or in China Med (Chu et al. 2011). Another study revealed a high level of genetic differentiation to the same Med Q1 species sampled around the Mediterranean basin (Gauthier et al. 2014). A similar approach was used, with six microsatellite markers combined with the sequencing of the barcoding region of the mtCOI in Greece, revealing a substructure population of Med Q in two genetic clusters Tsagkarakou et al.(2007).

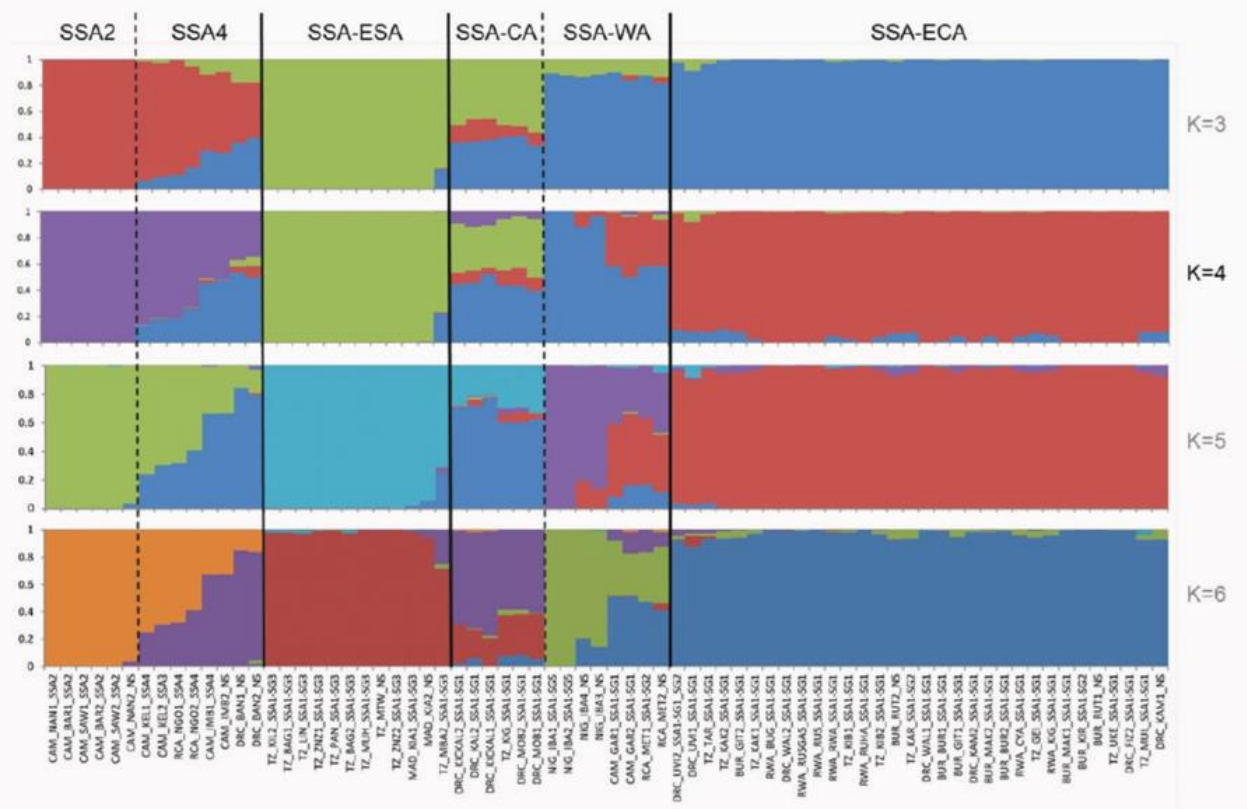


Figure 1. 8: Population structure of *B. tabaci* showing hybridization between SSA1 and its sub-groups SG1 and SG2 (Wosula et al. (2017).

**(b) Restriction site associated DNA markers (RADseq)**

RADseq is a popular technique based on next generation sequencing (NGS). RADseq has been recently used in the new era of NGS techniques in genome-scale research for assessing population structure, hybridization, demographic history, phylogeography and migration (Lowry et al. 2017). RADseq are similar to microsatellite markers but generated by specific restriction enzymes. The restriction fragments are ligated to an adapter and the fragment of a selected size range are sequencing using NGS. The technique utilizes multiple loci to decipher population genetic analysis (McCormack et al. 2013).

A first study using this technique on whiteflies (Wosula et al. 2017) has shown its ability to cluster *B. tabaci* populations collected in eight cassava growing regions in Africa into six phylogenetic groups. Indeed, the study revealed the hybridization between SSA1 subgroups (SG1 and SG2) from DRC, Tanzania, Rwanda and Burundi. Additionally, sub structuring of SSA1 within and between countries was highlighted (Fig. 1.8) (Wosula et al. 2017).

## 1.7. Biology of *B. tabaci*

### 1.7.1. *B. tabaci* developmental stages

*B. tabaci* is an haplodiploid insect (haploid arrhenotoky), females are diploid, produced from fertilized eggs while, males are haploid developed from unfertilized eggs (Byrne and Bellows Jr 1991) Adult female whiteflies are slightly larger than males, and their sizes differ according to species or host usage (Delatte et al. 2009). Female whiteflies live for up to 60 days while the life span for male whitefly ranged between 9 to 17 days in laboratory conditions (Gill 1990, Gangwar and Gangwar 2018). Mating takes place on the host plant and occurs several times during the life of the adult (Liu et al. 2007).

*B. tabaci* undergoes six life stages including the egg, four nymph stages and the adult (Fig. 1.9). The duration from egg to adult *B. tabaci* is influenced by several factors, among them are host plants for example sweet pepper is less preferred by MEAM1 (Iida et al. 2009, Tsueda and Tsuchida 2011), on the contrary, MEAM1 developed quicker on a wide host range than indigenous species of China (ZHJ2 and ZHJ2) (Table 1.1) (Zang et al. 2006, Xu et al. 2011).

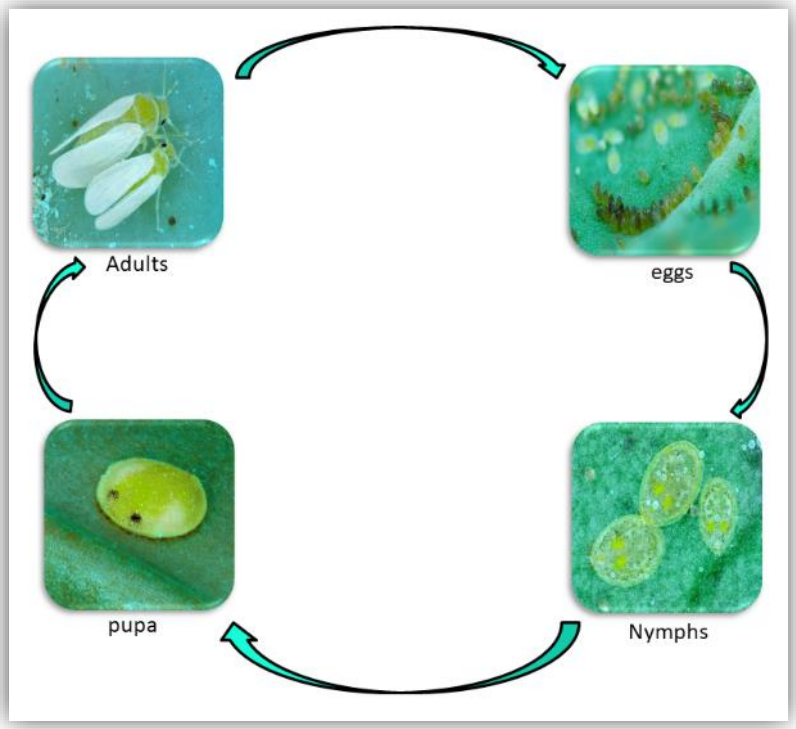


Figure 1. 9: Different developmental stages of *B. tabaci* MEAM1 on cabbage leaves (photos are from A Franck, CIRAD UMR PVBMT©).

Table 1. 1: Survival and development from egg to adult of two *B. tabaci* putative species on eight different host plants. Table extracted from Xu et al., (2011).

| | | % survival from egg to adult[2] | | Development time from egg to adult in days[3] | |
|---|---|---|---|---|---|
| Host plants | Whitefly species[1] | No. replicates (No. initial whiteflies) | Mean ± SEM | No. replicates (No. whiteflies) | Mean ± SEM |
| Cotton | B | 10 (503) | 91.1 ± 0.8 b (a)[4] | 10 (457) | 24.7 ± 0.5 a (a)[4] |
| | ZHJ2 | 10 (339) | 87.3 ± 0.6 b (b) | 10 (296) | 25.3 ± 0.5 c (a) |
| Squash | B | 10 (647) | 95.3 ± 0.7 a (a) | 10 (620) | 22.4 ± 0.3 b (b) |
| | ZHJ2 | 7 (136) | 95.5 ± 1.4 a (a) | 7 (129) | 28.0 ± 0.5 a (a) |
| Tomato | B | 10 (277) | 92.6 ± 1.7 ab (a) | 10 (257) | 24.2 ± 0.2 a (b) |
| | ZHJ2 | 6 (163) | 26.7 ± 3.6 c (b) | 6 (44) | 27.2 ± 0.4 ab (a) |
| Tobacco | B | 10 (294) | 81.0 ± 2.1 c (a) | 10 (238) | 22.6 ± 0.3 b (b) |
| | ZHJ2 | 10 (309) | 16.3 ± 1.9 d (b) | 10 (49) | 25.9 ± 0.3 bc (a) |
| Sweet potato | B | 3 (67) | 88.8 ± 1.4 b (a) | 3 (60) | 22.5 ± 0.5 b (a) |
| | ZHJ2 | 6 (173) | 85.8 ± 1.4 b (a) | 6 (148) | 22.6 ± 0.2 d (a) |
| Kidney bean | B | 10 (366) | 57.8 ± 2.1 d (b) | 10 (208) | 21.0 ± 0.3 c (a) |
| | ZHJ2 | 10 (801) | 92.7 ± 1.4 a (a) | 10 (752) | 20.6 ± 0.4 e (a) |
| Pepper (Caifeng 1) | B | 10 (276) | 0.0 ± 0.0 e (b) | –[5] | – |
| | ZHJ2 | 10 (306) | 7.6 ± 1.0 e (a) | 10 (25) | 31.1 ± 0.8 |
| Pepper (Hangjiao 1) | B | 10 (255) | 0.0 ± 0.0 e (b) | – | – |
| | ZHJ2 | 10 (365) | 25.0 + 2.4 c (a) | 10 (112) | 26.7 + 0.4 |

Other factors that influence the larva developmental stages are temperature and humidity (Gerling et al. 1986). Bonato (2007) revealed the impact of temperature on developmental time, with low temperature a minimum of 20 days and the maximum of 56 days at 30°C and 17°C, respectively, recorded for Med Q1 reared on tomato.

The female *B. tabaci* lays eggs on the abaxial part of the upper leaves of the host plant. The Female whitefly can oviposit more than 300 eggs during its life time (Gangwar and Gangwar 2018), but this number depends on several factors including species of *B. tabaci,* temperature and host plants. At 21 $^{o}$C MED Q1 can lay an average of 105.3 eggs (Bonato et al. 2007). Delatte et al. (2009) revealed a range of 74 – 170 eggs laid on tomato leaves by MEAM1 at 30 $^{o}$C.

Four instar stages occur on whiteflies life cycle, the 1$^{st}$, 2$^{nd}$, 3$^{rd}$ and the 4$^{th}$ instar stages. The duration between each of the four instar stages depend on temperature and species, however, the first three instar stages share a similar duration range. The duration range of 2.4 – 6.4 days at 25 $^{o}$C was recorded from first, second and third instar by (Sharaf and Batta 1985) on *B. tabaci* population reared on eggplant, Lantana shrubs, tobacco and tomato, while at 15 $^{o}$C, the number of days raised from 7 – 9.5. Further, on similar stages (Bonato et al. 2007) noted a minimum range of 3.2 – 3.3 days on Med species reared on tomato.

The duration of the 4$^{th}$ instar stage has a wide range of values. An average of a maximum duration of 8.2 days was recorded on tomato and a shorter duration of 5.9 on eggplants. These data were recorded on MEAM1 species following a study conducted to understand the effect of host plant on development and reproduction (Kakimoto et al. 2007). Meanwhile, a negative correlation between temperature and duration of fourth instar was revealed, such as a duration range of 3.02 to 6.36 days for MEAM1 at 30 and 20 $^{o}$C, respectively (Delatte et al. 2009).

At pupa stage no nutrients are taken any more. Some studies include this stage as the 4$^{th}$ instar (Sharaf and Batta 1985). However, Delatte et al. (2009) considered as unique stage, authors revealed variation in duration, this variation depends on temperature and the *B. tabaci* species. It was observed minimum duration of 2.3 and 2.36 days at 30 $^{o}$C for IO and MEAM1 *B. tabaci* species respectively, whereas at 20 $^{o}$C a maximum of 4.68 and 4.79 days was observed for the two species.

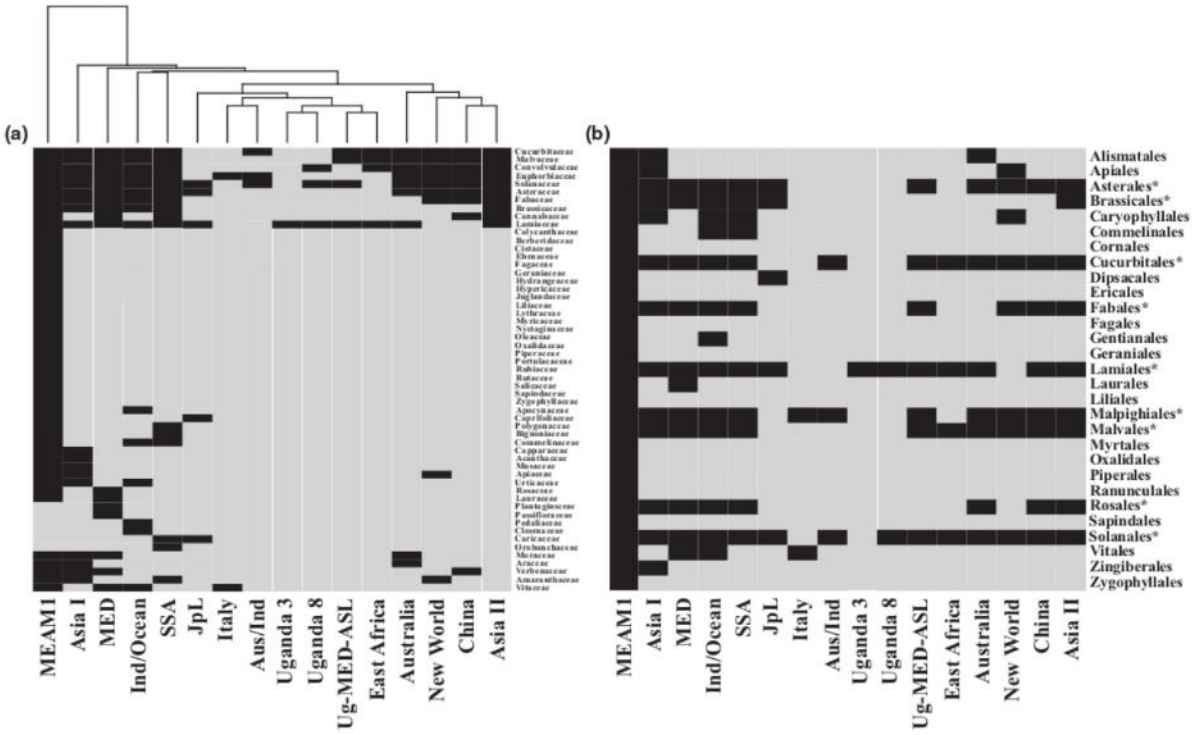


Figure 1. 10: *B. tabaci* species host range (a) according to botanical families (b) according to plant order showing nine orders with asterisks are commonly shared by most of *B. tabaci* species as described in Malka et al. (2018).

### 1.7.2. *B. tabaci* host plants utilization

*B. tabaci* has been described as a polyphagous species with more than 1000 host plants belonging to 74 families (Mound and Hashley 1978, Brown et al. 1995a, Simmons et al. 2008, Malka et al. 2018). The most frequently reported host plants belong to the families: Malvacea, Euphobiacea, Solanaceae, Leguminosae, Convolvulaceae and Cucurbitaceae (Brown et al. 1995a, Simmons et al. 2008, Malka et al. 2018).

Although *B. tabaci* is described as having a wide host range, because it's a complex of cryptic species, not all species of the complex equally utilized all those plants (Malka et al. 2018). MEAM1 species is reported to have the widest host range including vegetable crops such as cabbage, squash, kidney beans, pepper, tomato, cowpea, cassava, soybean, cucurbits as well as cash crops like cotton and tobacco and ornamental including poinsettia (Muñiz 2000, Simmons et al. 2008, Malka et al. 2018). The polyphagy of MEAM1 was further demonstrated when it colonized the medicinal plants such as feverfew (*Tanacetum parthenium),* St. John's wort (*Hypericum perforatum* L.), purple coneflower species (*Echinacea pallida* and *E. purpurea* L.) and common valerian (*Valeriana officinalis* L.) in south California (Simmons et al. 2000).

Both MEAM1 and Med Q1 are polyphagous species, however, the two species differ on their host plant usage. A study conducted in Tunisia to understand the regional co- occurrence of distinct *B. tabaci* species in relation to the role of host plants, revealed that the Med was closely associated with ornamentals while MEAM1 was associated with vegetables crops (Laarif et al. 2015). The occurrence of MEAM1 and Med into different host plants were also observed in Uganda (Sseruwagi et al. 2005), as well as in West Africa (Gnankine et al. 2013b).

In a recent review on host plant species, families and orders shared by 16 species of the *B. tabaci,* 31% of the plant orders were commonly shared by different *B. tabaci* species (Malka et al. 2018) (Fig. 1.10). Further analyses revealed the existence of common detoxification machinery that was shared by the high performer groups of *B. tabaci* species which allowed them to adapt a wide range of host plants and new environments.

Despite the common belief that species within *B. tabaci* complex of cryptic species are polyphagous, a few exceptions are found.

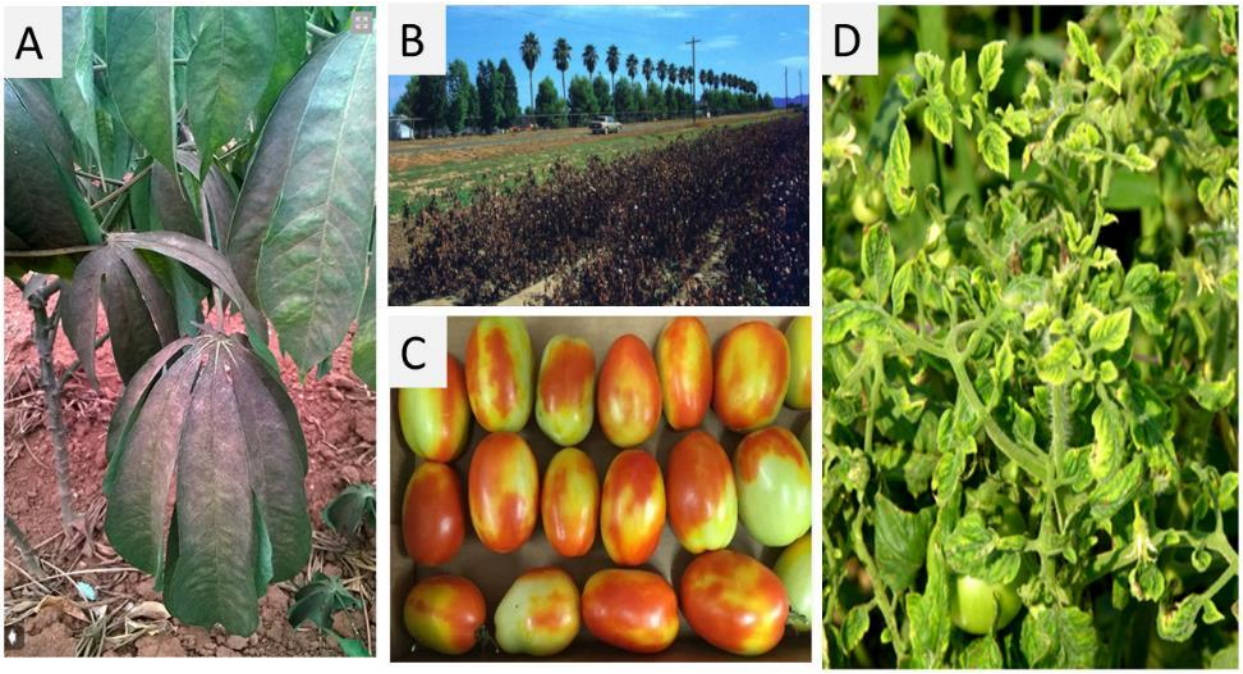


Figure 1. 11: *B. tabaci* effect (A) sooty mold on cassava leaves, (B) cotton field infested with whitefly, (C) unregular ripening on tomato, (D) tomato plant infected with tomato yellow leaf curl begomovirus transmitted by whitefly, photo source: A) NRI library, B) Toscano et al. (1998), C) http://blogs.ifas.ufl.edu/pestalert/2017/02/10/whitefly-alert/ , D) https://www.lsuagcenter.com.

A mono-phagous population was reported from jatropha in Puerto Rico (Bird and Maramorosch 1978, Bird and Brown 1998). The SSA species including SSA1 to 5 were formerly known as cassava restricted species (Abdullahi et al. 2003, Berry et al. 2004, Omondi et al. 2005a, Legg et al. 2014b) but, lately, the SSA1 were found on a wider variety of plants and crops (Sseruwagi et al. 2006, Tajebe et al. 2015a, Tocko-Marabena et al. 2017, Mugerwa et al. 2018).

## 1.8. Whitefly impact on agriculture

Since, 1926 *B. tabaci* has been reported as one of the most destructive pest and plant virus vector of agriculture. However, attention to the species emerged around the 1980s after severe crops yield losses were reported together with increased whitefly numbers (Brown et al. 1995a, Perring 2001, Legg et al. 2002, Liu et al. 2012, Legg et al. 2014b). The effects caused by *B. tabaci* populations vary depending on host plants, season or climatic condition and the damages can be both direct and indirect (Fig. 1.11).

*B. tabaci* is a phloem sucking insect, both adults and immature nymphs feed directly from the host plant. The process involves taking up potential nutrients including potassium, resulting in leaves turning to yellow, which then interfere in the photosynthesis process and eventually weaken the plants, leading to reduction in plant vigour, quality and yield (Uchida 2000, Polston et al. 2014, Gangwar and Gangwar 2018).

Several studies were performed to understand the relationships between MEAM1 and development of physiological disorders on tomato (Schuster et al. 1990, Schuster 2001) that were specifically observed for this species (Fig 1.11). Indeed, high abundances of MEAM1 on tomato were positively linked to cause irregular ripening and incomplete external colour on tomato, resulting in streaking as well as white spongy like tissue internally (Fig. 1.11) (Schuster 2001, McCormack et al. 2013).

Similarly, a study conducted in Imperial Valley (California, USA) showing an increase in abundance of invasive MEAM1 *B. tabaci* population had led to losses of more than US$ 2 billion in 1991, due to the effects observed on melon and on cotton, affecting the quantity and quality of cotton (Toscano et al. 1998).

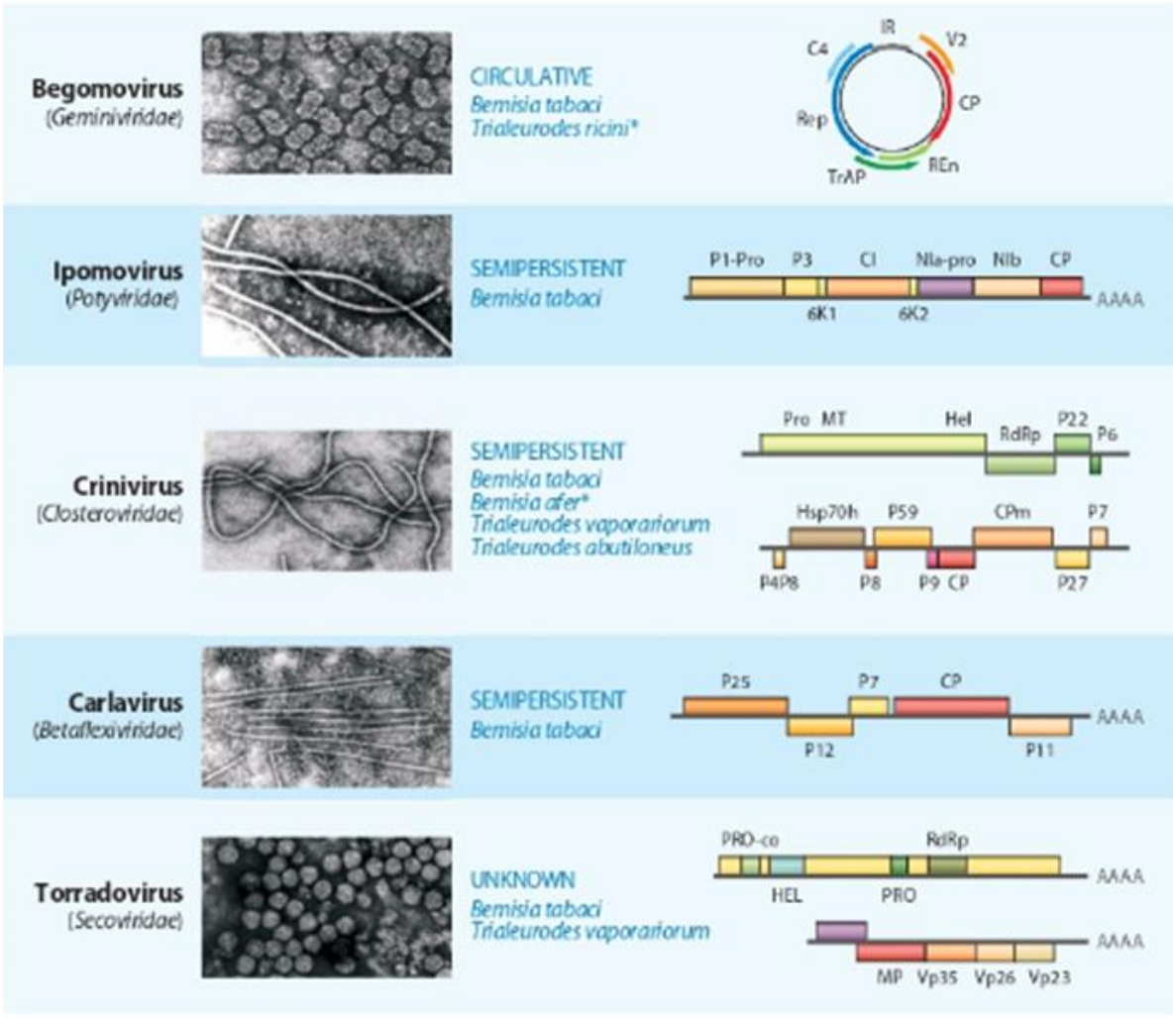


Figure 1. 12: Diagram of the main groups of plant viruses transmitted by whiteflies, according to the structure of their viral particles, their mode of transmission and their genomic organization. Described by Navas-Castillo et al (2011).

Whiteflies also excrete honeydew on the plant leaf. The excreted honeydew favours the growth of sooty mold fungus which covers the leaf surface, as a result it interferes with photosynthesis process (Davidson et al. 1994). The sticky excretory waste can also stick to cotton lint together making difficult to gin as well reduce the cotton quality. Over 40% loss of production was reported on melon because of sooty mold in Guatemala (Dávila 1999).

Instars of MEAM1 species have been reported to induce plant physiological disorders commonly known as squash silver leafing (SSL) disorder on *Cucurbita* species (Yokomi et al. 1990, Costa and Brown 1991, Hoelmer et al. 1991, Brown et al. 1995a, Jiménez et al. 1995)**.** Infected plant leaves appeared silver, normally at the upper part. The damage to the plants includes deformation of palisade cells a primary site for photosynthesis, severe infection by MEAM1 on pumpkin caused 40 to 50% chlorophyll reduction on pumpkin (Jiménez et al. 1995). The studies reported the ability of MEAM1 in induction of silver leafing in other countries (Delatte et al. 2005, Sseruwagi et al. 2005, Lourenção et al. 2011, Vyskočilová et al. 2018). Delatte et al. (2005) was also, observed the capability of IO species in induction of such a disorder.

The biggest impact caused by whitefly is by the spread of over 400 viral plant pathogens, belonging to different genera: *Begomovirus, Ipomovirus, Crinivirus, Closteroviridae, Carlavirus* and *Torradovirus* (Jones 2003, Navas-Castillo et al. 2011, Navas-Castillo et al. 2014, Polston et al. 2014). These viruses are all transmitted by the *B. tabaci* complex of species by different modes (Fig. 1.12).

Those viruses were reported to cause severe damages to vegetable, legume, fibre crops and ornamental crops (Legg 1999, Livieratos et al. 1999, Usharani et al. 2005). Among all, begomoviruses are economically most significant (Oliveira et al. 2001) They include: Cassava mosaic begomoviruses (CMBs), *Tomato yellow leaf curl virus* (TYLCV), *Tomato chlorotic mottle virus* (ToCMoV), *Pepper yellow leaf curl virus* (PYLCV), *Chino del tomate virus* (CdTV), *Pepper huasteco virus* (PHV) and several others (Polston et al. 1999, Navas-Castillo et al. 2011, Albuquerque et al. 2012, Silva et al. 2014).

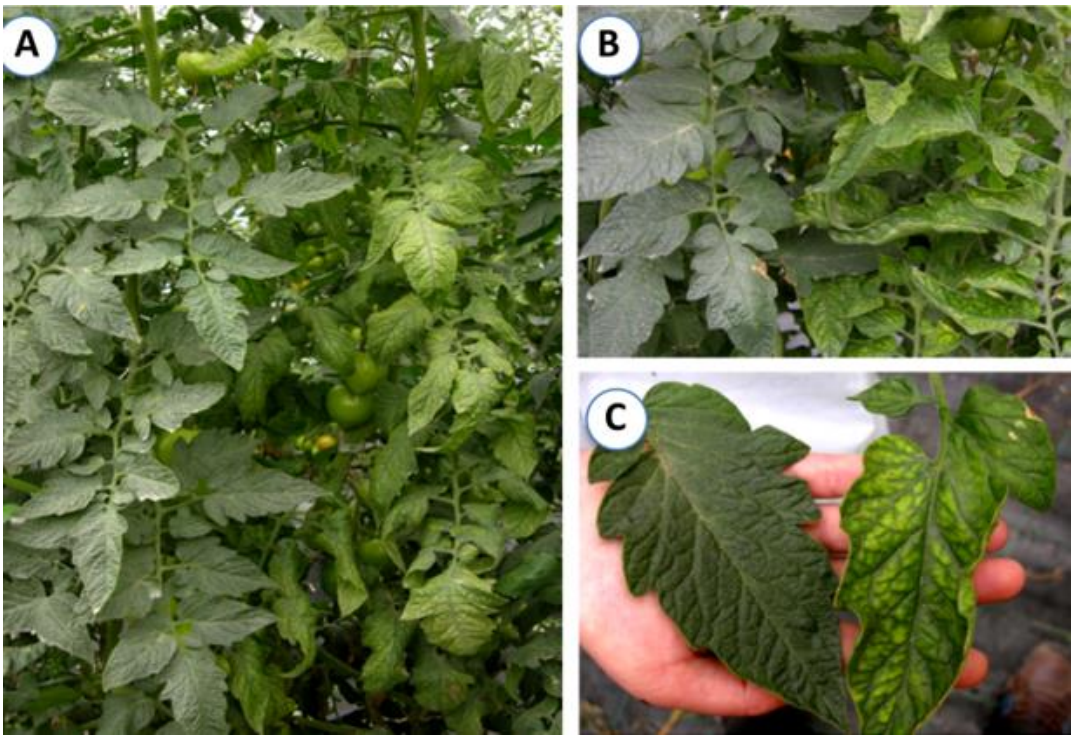


Figure 1. 13: ToCV leaf symptoms in comparison to healthy plants (left) and ToCV-infected plants (right). Interveinal yellowing, necrotic flecking, rolling and thickening of the leaf blade are shown on entire plants (A), leaves (B) and leaflets (C), illustration from Navas-Castillo et al. (2014).

TYLCV is among the most devastating disease affecting tomato production. This virus most probably originates from Iran where the highest TYLCV genetic diversity was found. It then invaded the Middle Eastern basin including Israel, where it was first described by (Cohen and Harpaz 1964), Americas and spread further worldwide (Lefeuvre et al. 2010)

The infected tomato plants show the symptoms of severe stunting, leaf necrosis, leaf curling, leaf size reduction and reduction in fruit production (Fig. 1.10). This virus was reported in different countries including Caribbean islands, Japan, Spain, Australia, North and Southern America (Polston et al. 1999, Navas-Castillo et al. 2000, Idris et al. 2007, Sugiyama et al. 2008) (Polston et al. 1999, Navas-Castillo et al. 2000, Delatte et al. 2007, Idris et al. 2007, Sugiyama et al. 2008, Van Brunschot et al. 2010). Yield losses can reach 100% in severe infected fields of tropical and subtropical regions (Picó et al. 1996, Lapidot et al. 2000).

The *Tomato chlorosis virus* (ToCV) belongs to the family *Closteroviridae*, genus *Crinivirus* had been also reported to damage tomato in different countries (Orílio and Navas-Castillo 2009, Hirota et al. 2010, Navas-Castillo et al. 2011, Polston et al. 2014). High whitefly abundance in Malaga Spain facilitated the severe spread of ToCV (Navas-Castillo et al. 2000). The infected tomato showed symptoms including interveinal yellowing, necrotic flecking, rolling and thickening of leaves (Fig. 1.13). As a result, yield reduction, delay fruit ripening as well as induce early senescence (Navas-Castillo et al. 2014). Zhao et al. (2013) showed 5 – 80% ToCV disease incidence in China. Apart from transmitting diseases on tomato, the whitefly species vectored ToCV on sweet pepper (Lozano et al. 2004, Wintermantel and Wisler 2006).

Whitefly also involved in the transmission of plant virus including: Carlavirus example *Cowpea mild mottle virus* (CpMMV) affecting soy bean (Zanardo et al. 2014), Torradovirus example *Tomato torrado virus* (ToTV) affecting tomato (Amari et al. 2017) and Polerovirus example *Pepper whitefly borne vein yellow virus* (PeWBVYV) causing damage to pepper (Ghosh et al. 2019)


Figure 1. 14: Symptoms expression (a) leaf chlorosis and distortion following infection with CMD (b) Leaf chlorosis after CBSD infection (c) brown root necrotic following infection with CBSD, photo A and B were taken in Tanzania following a field survey conducted in February 2016 and C is from the NRI library.

In Africa, two major cassava viruses threaten the most important staple food in sub–Sahara Africa. Cassava viral epidemics were observed following upsurges *B. tabaci* populations in East Africa (Legg and Ogwal 1998, Legg et al. 2002, Legg et al. 2014b).

The CMD in Africa is primarily caused by single stranded DNA viruses known of which *Africa cassava mosaic virus* (ACMV), *East Africa cassava mosaic virus* (EACMV–Ug) and *South Africa cassava mosaic virus* (SACMV) are most common (Legg 1999, Neuenschwander et al. 2002). The viruses belong to the family *Geminiviridae*, genus *Begomovirus*. All those viruses are vectored by *B. tabaci* (Legg et al. 2002, Sseruwagi et al. 2005). The SSA species (SSA1 – SSA5) were previously associated to colonize cassava, however, they are also reported on non-cassava species (Sseruwagi et al. 2006) and caused high yield losses on cassava (Legg et al. 2001, Legg and Fauquet 2004).

At least nine CMBs are reported from Africa (Owor et al. 2004, Legg et al. 2006, Legg et al. 2014b). Infected cassava crops harbour mild to severe mosaic and leaf deformation symptoms (Fig. 1.14a). Subsequent significant yield loss was observed in different studies, a range of 15 to 24% losses were reported in Uganda Thresh et al.(1994), whereas up to 90% yield loss was reported in Kenya (Hahn et al. 1980, Masinde et al. 2016).

Variation between single and dual infection of of ACMV and EACMV were induced high yield reduction (by 82% in dual infection, while 12% in single infection) (Owor et al. 2004). On average CMD causes yield loss of 47% in susceptible varieties grown in the major cassava growing area of Africa (Legg et al. 2006). CBSD is caused by another cassava virus also vectored by *B. tabaci*, it is a linear ssRNA which belongs to the family *Potyviridae*, and *Ipomovirus* genus (Monger et al. 2001, Mbanzibwa et al. 2011), affecting cassava in East Africa. Two ipomoviruses are known to affect cassava; *Cassava brown streak virus* (CBSV) and the *Ugandan cassava brown streak virus* (UCBSV) which are together called cassava brown streak ipomoviruses (CBSIs) (Maruthi et al. 2005, Legg et al. 2011, Mohammed et al. 2012).

CBSIs infected cassava exhibit diverse leaf symptoms, including stem yellowing streaks, necrotic vein banding on leaf and most importantly the damage to roots by causing root necrosis (Fig. 1.14b and 1.14c). A recent survey reported about 750 million US$ annual losses in Tanzania, Uganda, Kenya and Malawi due to CBSD Hillocks and Maruthi (2015) (Masinde et al. 2016) revealed a maximum of 77.5% yield loss due to CBSD in Migory county in Kenya.

## 1.9. *Bemisia tabaci* distribution

### 1.9.1 Worldwide distribution of *B. tabaci* invasive species

*B. tabaci* was regarded as one among 100 World's invasive alien species classified by the International Union for the Conservation of nature and Natural Resources (Lowe et al. 2000). The complex of species of *B. tabaci* is globally distributed on all continents and countries (Perring 2001), only a very few *B. tabaci*-free countries are listed, it includes the United Kingdom and Finland (Cuthbertson and Vänninen 2015).

Among this species, MEAM1 and Med are most invasive. MEAM1 originates from the Middle East, North Africa, Mediterranean, and Asia Minor regions (Kirk et al. 2000, Brown et al. 2007, De Barro et al. 2011). It was first identified in the late 1980s after severe outbreaks in the Southwestern United States (Price et al. 1987, Costa and Brown 1991, Dennehy et al. 2005, Hsieh et al. 2007).

Several factors have been associated with its spread including movement of infected planting materials, agricultural practices including mono-cropping, introduction of new crops and improper use of pesticides (De Barro 1995, Varma et al. 2011, Barbosa et al. 2014). It is highly polyphagous nature (Oliveira et al. 2001) and has better fitness than other indigenous species (Delatte et al. 2009).

Because of its capacity to adapt to different environmental conditions, MEAM1 can be found in tropical, subtropical as well as temperate climates (Brown et al. 1995a, Gueguen et al. 2010). This has enabled its rapid spread throughout Americas (Costa et al. 1993, Brown et al. 1995a, Viscarret et al. 2003). The presence of *B. tabaci* MEAM1 was documented in Mexico, Caribbean basin, United States and Brazil Costa et al. (1993).

The Med Q1 is the second most invasive species after MEAM1, it is originating from the Mediterranean basin. Compared to MEAM1, Med Q shows resistance to different insecticide molecules (Dennehy et al. 2005, Roditakis et al. 2009, Horowitz and Ishaaya 2014). Med was considered as invasive in the late 2000s as it was establishing in countries where MEAM1 was first invaded and become the new invasive species. The Med Q had been reported to expand its occurrence from herbs and ornamental in greenhouses to open agricultural fields in the United States (McKenzie and Osborne 2017). Currently, the distribution of Med Q had been reported globally, including Japan (Ueda and Brown 2006), Israel (Horowitz et al. 2003), China (Chu et al. 2006, Ahmed et al. 2009, Chu et al. 2011), Mexico (Martinez-Carrillo and Brown 2007), Guatemala (Bethke et al. 2009), Italy (Parrella et al. 2012) and several countries in Africa and the Indian Ocean (Table 1.2). In some places both Med Q and MEAM1 were reported to occur in sympatry, nevertheless, the two species cannot interbreed (Bedford et al. 1994, De Barro and Hart 2000, Saleh et al. 2012).

Both Med and MEAM1 are present in Africa together with other species including the host specific cryptic group SSA. Nevertheless, the SSA2 species was reported in the southern Europe including France and Spain (Banks et al. 1998, Hadjistylli et al. 2015). The SSA are distributed in different parts of Africa (Esterhuizen et al. 2013, Gnankine et al. 2013b, Legg et al. 2014b, Tocko-Marabena et al. 2017, Mugerwa et al. 2018).

### 1.9.2. *B. tabaci* distribution in sub–Sahara Africa

Several cryptic genetic groups of *B. tabaci* are found in sub–Sahara Africa (Table 1.2). Those species are divided into two major groups, the cassava and non-cassava colonizing groups (Burban et al. 1992, Berry et al. 2004).

#### 1.9.2.1. The cassava colonizing group

The SSA is commonly observed on cassava, five genetic groups were earlier reported on this crop including SSA1 to SSA5. The occurrence of SSA1 colonizing non–cassava crops was reported, but however with a preference for cassava (Sseruwagi et al. 2006). The distribution of these genetic groups or species varies between the countries with the SSA1 found in several African countries.

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Table 1. 2: *B. tabaci* species identified on cassava and other plant hosts from sub-Sahara Africa

| Species identified | Country/ies identified | Host plant | References |
|---|---|---|---|
| **SSA1 (former ug1/ sub-Sahara I / SSAF1/AnSL1)** | | | |
| SSA1 | Benin, Togo | *Manihot esculenta* | (Berry et al. 2004, Mouton et al. 2012) |
| SSA1 (SG1, SG2, SG1/2, SG3) | Burundi, DRC, Kenya, Rwanda, Tanzania and Uganda | *Manihot esculenta* | (Legg et al. 2002, Legg et al. 2014b) |
| SSA1 | Uganda | *Manihot esculenta* | (Sseruwagi et al. 2005, Sseruwagi et al. 2006) |
| SSA1 (SG1 & SG2) | Kenya, Tanzania, Uganda | *Manihot esculenta* | (Mugerwa et al. 2012, Mugerwa et al. 2018, Mugerwa et al. 2019) |
| SSA1 | | *Manihot esculenta* | Berry et al.(2004) |
| SSA1 (SG1, SG2, SG3) | Burundi, Cameroon, RCA, DRC, Madagascar, Nigeria, Tanzania, Rwanda | *Manihot esculenta* | Wosula et al.(2017) |
| SSA1 (SG1, SG2 & SG5) | RCA | *Manihot esculenta, Arachis hypogaea L, Solanum lycopersicum, Solanum melongena, Ipomea batatas, Gossypium spp. and Sida acuta* | Tocko-Marabena et al.(2017) |
| SSA1 | Benin, Togo | *Manihot esculenta* | Mouton et al.(2012) |
| SSA1 | Benin, Togo | *Manihot esculenta* | Gnankine et al.(2013b) |
| SSA1 | South Africa | *Solanum lycopersicum, Manihot esculenta* | Esterhuizen et al.(2013) |
| SSA1 (SG1, SG2, SG3, SG5) | Malawi, Nigeria, Tanzania, Uganda | *Manihot esculenta, Cucurbita pepo, Ipomea batatas, Lamiaceae weed, Leonotis nepetifolia, Abelmoschus esculentus, Solanum lycopersicum, Gossypium spp, Helianthus* | (Ghosh et al. 2015, Tajebe et al. 2015b) |
| **SSA2 (former ug2/sub-Sahara II/AnSL2)** | Uganda | *Manihot esculenta* | (Lima et al. 2002, Legg et al. 2014b) |
| | Tanzania, Mozambique, Zambia, South Africa, Swaziland | *Manihot esculenta, Capsicum, Brassica oleracea var. capitate* | Berry et al. (2004) |
| | Uganda | *Manihot esculenta* | (Sseruwagi et al. 2005, Sseruwagi et al. 2006) |
| | Uganda | *Manihot esculenta, Euphobia heterophylla, Commelina benghalensis* | Mugerwa et al.(2018) |
| | RCA | *Manihot esculenta* | Tocko-Marabena et al.(2017) |
| | Benin, Togo | *Manihot esculenta* | Gnankine et al.(2013b) |
| | Cameroon | *Manihot esculenta* | Wosula et al.(2017) |
| **SSA3 (former sub-Sahara III)** | Cameroon | *Abelmoschus esculentus* | Berry et al.(2004) |
| | DRC | *Manihot esculenta* | Legg et al.(2014b) |
| | RCA | *Arachis hypogaea L, Solanum lycopersicum, Solanum melongena, Manihot esculenta, Gossypiumsp.* | Tocko-Marabena et al.(2017) |
| | Nigeria | *Manihot esculenta* | (Ghosh et al. 2015) |
| | Cameroon | *Manihot esculenta* | Wosula et al.(2017) |
| **SSA 4 (former sub-Sahara IV)** | Cameroon | *Manihot esculenta, Abelmoschus esculentus* | (Berry et al. 2004, Wosula et al. 2017) |
| **SSA5 (former sub-sahara V)** | Ivory Coast | *Manihot esculenta* | Berry et al.(2004) |
| | South Africa | *Manihot esculenta, Ipomea batatas, Solanum lycopersicum, Cucurbita spp, Malva parviflora* | Esterhuizen et al.(2013) |

| | | | |
|---|---|---|---|
| **Mediterranean Q1, Q2, Q3 (former ASL/biotype Q/Ug4/Ug5)** | | | |
| | Ivory Coast, Cameroon, Zimbabwe | *Manihot esculenta, Abelmoschus esculentus* | Berry et al. (2004) |
| Med | Uganda | *Cucurbita sp, Nicotiana tabacum, Gossypium spp,* | (Sseruwagi et al. 2005, Sseruwagi et al. 2006, Mugerwa et al. 2018, Vyskočilová et al. 2018) |
| | | *Solanum melongena, Leonotis leonurus* | Ally et al., submitted |
| | | *Crocus sativus, Commelia benghalensis, Manihot esculenta, Commelina benghalensis, Pavonia urens, Cleome gynandra Vernonia amygdalina* | |
| Med | RCA | *Manihot esculenta, Cucurbita, Gossypium spp, Splanum melongena, Solunum lycopersicum* | Tocko-Marabena et al. (2017) |
| Med | Tanzania | *Leonotis nepetifolia, Cucurbita, Ipomea batata* | Tajebe et al. (2015a) |
| Med Q1, Q3 | Burkina Faso, Benin, Togo | *Solanum lycopersicum, Gossypium spp, Lantana camara, Cucurbita sp, Nicotiana tabacum* | (Gnankine et al. 2013a, Gnankine et al. 2013b) |
| Med Q | South Africa | *Solanum lycopersicum* | Esterhuizen et al. (2013) |
| Med Q1 & Q3 | Bukinafaso, Cameroon | *Not identified* | Gueguen et al. (2010) |
| Med Q1 | Senegal | *Lycopersicon esculentum, Capsicum annuum, Capsicum, Abelmoschus esculentus, Cucurbita, Solanum macrocarpon, Solanum melongena,* | Delatte et al. (2015) |
| Med Q1 | Uganda | *Ipomea batata* | Malka et al. (2018) |
| Med Q2 | Reunion | *Solanum melongena, Euphorbia pulcherrima, Phaseolus vulgaris Cucurbita pepo* | Mouton et al. (2012) |
| Med ASL | Burkina Faso, Cameroon, Ivory Coast | *Not identified* | Gueguen et al. (2010) |
| Med ASL | Burkina Faso, Benin, Togo | *Solanum lycopersicum, Gossypium spp, Lantana camara, Cucurbita sp, Nicotiana tabacum* | (Gnankine et al. 2013a, Gnankine et al. 2013b) |
| Med ASL | Uganda | *Ipomea batata, Cucurbita pepo* | (Malka et al. 2018, Vyskočilová et al. 2018) |
| **MEAM1 (former B biotype/ Ug6)** | | | |
| MEAM1 | Uganda | *Pavonia urens, Vernonia amygdalina, Abelmoschus esculentus* | (Sseruwagi et al. 2005, Sseruwagi et al. 2006, Mugerwa et al. 2018) |
| MEAM1 | RCA | *Solanum lycopersicum* | Tocko-Marabena et al. (2017) |
| MEAM1 | South Africa | *Solanum lycopersicum* | Esterhuizen et al. (2013) |
| MEAM1 | Reunion island | *Not identified* | Gueguen et al. (2010) |
| MEAM1 | Senegal | *Lycopersicon esculentum, Capsicum annuum, Solanum macrocarpon, Solanum melongena, Capsicum, Abelmoschus esculentus, Cucurbita* | Delatte et al. (2015) |
| MEAM1 | Reunion, Mayote, Mauritius | *Solanum lycopersicum, Gossypium spp, Crocus sativus, Solanum melongena, B. oleracea var. capitate* | (Delatte et al. 2005, Delatte et al. 2011) |

| | | | |
|---|---|---|---|
| **IO (former Ms)** | Uganda | *Manihot esculenta, Phaseolus vulgalis, Commelia benghalensis, Gossypium spp, Abelmoschus esculentus, Euphobia heterophylla* | (Sseruwagi et al. 2005, Sseruwagi et al. 2006, Mugerwa et al. 2012, Mugerwa et al. 2018) Legg et al. (2014b) |
| | Tanzania | *Manihot esculenta, Leonotis nepetifolia, Solanum lycopersicum* | Tajebe et al. (2015b) |
| | Reunion, Mauritius, Madagasca, Seyshelles, Mayotte | *Euphobia pulcherrima, Solanum lycopersicum, Phaseola vulgalis, Jatropha curcas, Manihot esculenta, Lantana camara, Cucurbita pepo* | (Delatte et al. 2005, Delatte et al. 2011) |
| | Grand Comore | *Abelmoschus esculentus, Gossypium spp, Brassica oleracea var. capitate Cucumis sativus, Solanum melongena, Solanum melongena,* | |
| | RCA | *Solanum lycopersicum* | Tocko-Marabena et al. (2017) |
| **EA1** | Tanzania | *Leonotis nepetifolia, Cucurbita, Abelmoschus esculentus Manihot esculenta,* | (Legg et al. 2014b, Tajebe et al. 2015a) |
| **SSA9, SSA10, SSA11, SSA12 & SSA13** | Uganda | *Manihot esculenta, Pavonia urens, Commelina benghalensis, Euphobia heterophylla, Vernonia amygdalina* | Mugerwa et al. (2018) |
| **Uganda 1 (former Ugsp)** | Uganda | *Pavonia urens, Euphobia heterophylla, Cleome gynandra, Vernonia amygdalina, Commelina benghalensis, I. batata* | (Legg et al. 2002, Sseruwagi et al. 2005, Mugerwa et al. 2018) |

Abbreviations: SSA and SSAF (sub–Sahara Africa), –SG (subgroup), Med (Mediterranean), IO (Indian ocean), EA (East Africa), MEAM 1 (Middle East Asia Minor 1), DRC (Democratic Republic of Congo), CAR (Central Africa Republic)

Following severe CMD epidemics in Uganda in the 1990s, (Legg et al. 2002) revealed the presence of two genetic groups on cassava and named them as Ug1 and Ug2 currently known as SSA1 and SSA2, respectively (Legg et al. 2002, Dinsdale et al. 2010). The first whitefly upsurge in the 1990s was linked to the high abundance of SSA2 (Legg et al. 2002). The presence of both SSA1 and SSA2 in Uganda was also reported by (Sseruwagi et al. 2005). Mugerwa et al. (2012); (2018) also, revealed the occurrence of SSA1 (SG1 and SG2) on cassava in Uganda. Similarly, two major cryptic groups of SSA1 (SG1 and SG2) were reported in Uganda (Ghosh et al. 2015), Burundi, Rwanda and Madagascar (Wosula et al. 2017, Legg et al. 2014b).

Furthermore, extensive surveys linked to population dynamics, to understand whitefly abundances increase, were conducted during 1997 to 2010 in East and Central African regions including the countries of Burundi, Kenya, Rwanda, Tanzania and Uganda (Legg et al. 2014b). This study revealed the occurrence of cassava associated species of SSA2 in those countries, however, an abrupt reduction of SSA2 was observed over the years (Fig. 1.15). The SSA1 populations were further clustered into mitochondrial haplotype subgroups called: SSA–SG1, SSA1–SG2, SSA1–SG3, SSA1–SG4 and SSA–SG1/2 (Legg et al. 2014b). In Tanzania, SSA1 (-SG1, -SG2, -SG3) was reported (Ghosh et al. 2015, Tajebe et al. 2015a, Wosula et al. 2017), whereas, SSA1 (-SG1 and -SG2) as well as SSA2 were reported in Kenya (Mugerwa et al. 2012, Manani et al. 2017).

The occurrence of SSA3 and SSA4 were reported in Cameroon (Berry et al. 2004, De la Rúa et al. 2006, Wosula et al. 2017), SSA1, SSA2 and SSA3 in Central Africa Republic (CAR) (Tocko-Marabena et al. 2017), SSA1 and SSA5 in South Africa (Esterhuizen et al. 2013) and SSA1 in Nigeria (Berry et al. 2004, Esterhuizen et al. 2013, Wosula et al. 2017) (Tocko-Marabena et al. 2017). (De la Rúa et al. 2006) found the presence of SSA2 and SSA4 in Ghana, and SSA1 and SSA2 in Benin and Togo (Gnankine et al. 2013b).

#### 1.9.2.2. Non–cassava colonizing group

This group contains *B. tabaci* species of Med, (Med Q1, Q2, Q3 and Med ASL), MEAM1, IO, Uganda sweetpotato (Ugsp), SSA11, SSA12, SSA13 and EA1.

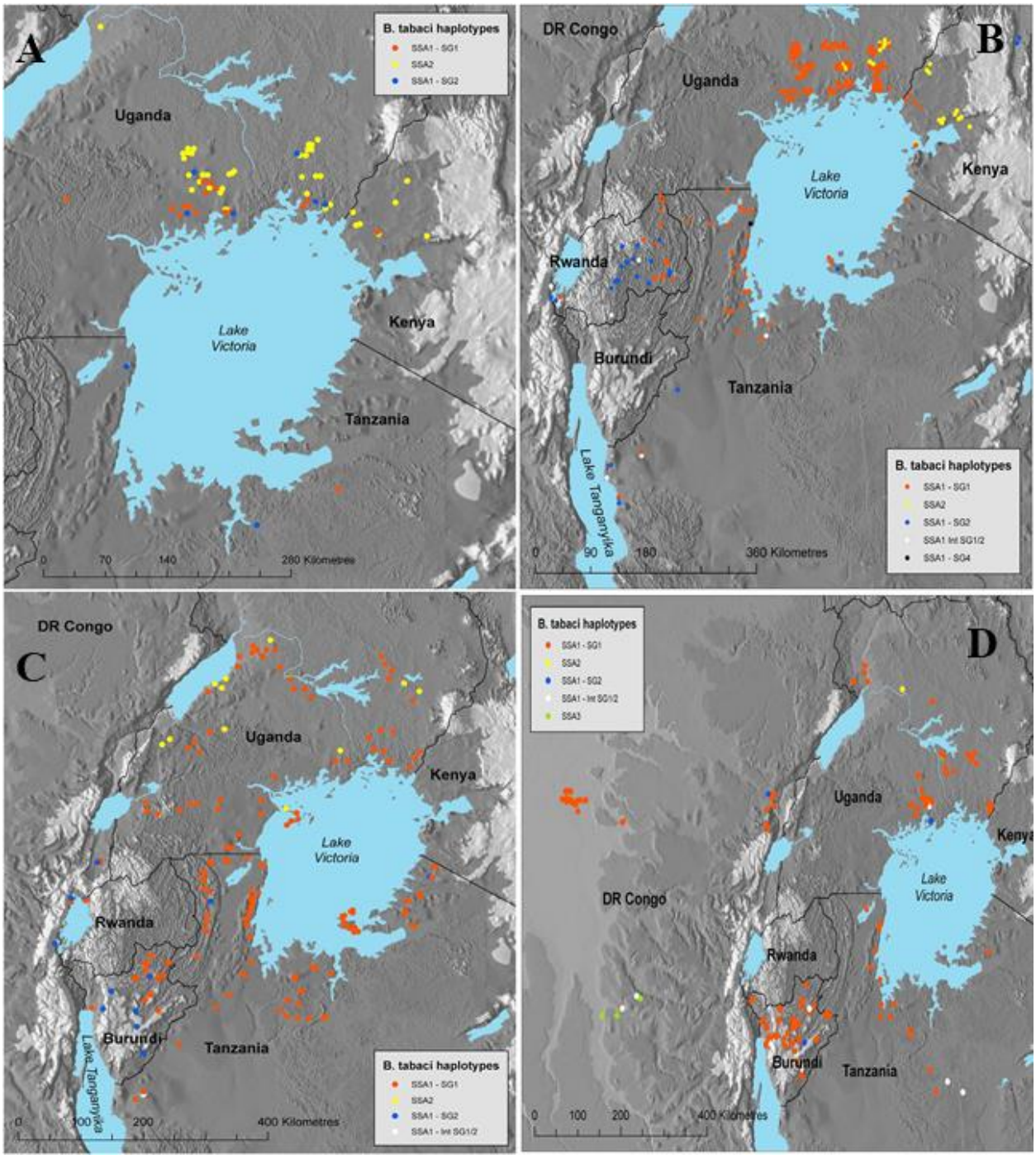


Figure 1. 15: Geographical distribution of *B. tabaci*, with increased SSA1 and reduction of SSA2 presented by yellow dots during (A) 1997 – 1999 (B) 2000 – 2001 (C) 2002 – 2003 (D) 2004 – 2010 (Legg et al. 2014b).

Those species are commonly reported on different vegetables, cash crops or ornamental crops including tomato, pumpkin, cabbage, eggplant, okra, poinsettia, watermelon, sweetpotatoes, sunflower, or cotton, among many others. Nevertheless, some species including IO and Med were also reported on cassava (Legg et al. 2014b, Tajebe et al. 2015a, Tocko-Marabena et al. 2017). Ugsp was solely reported in Uganda (Legg et al. 2002, Maruthi et al. 2004, Sseruwagi et al. 2005, Mugerwa et al. 2018) while EA1 only from Tanzania (Legg et al. 2014b, Tajebe et al. 2015a).

An integrative approach involving combined experimental evidences of (i) differences in reproductive compatibility, (ii) hybrid verification using a specific nuclear DNA marker and hybrid fertility confirmation and (iii) high-throughput sequencing-derived mitogenomes, discovered two cryptic species within Med: Med from the Mediterranean basin (that are further divided in the literature as Med Q1, Q2, Q3, but fully hybridise) and the Med ASL from SSA (Vyskočilová et al. 2018). *B. tabaci* samples collected from Burkina Faso, Benin and Ghana were analysed by (Gnankine et al. 2013b) and revealed the occurrence of both Med ASL and Med Q (Q1 and Q3). Nevertheless, the distribution varied between countries. Burkina Faso was dominated by Med Q which further divided into Med Q1 and Med Q3, while in Benin and Togo Med ASL was prevailing. Additionally, the presence of both Med ASL and Med Q1 were reported in Burkina Faso, Ivory Coast, Cameroon (De la Rúa et al. 2006, Gueguen et al. 2010).

Other countries where Med species was identified included: South Africa (Esterhuizen et al. 2013), Senegal (Delatte et al. 2015), CAR (Tocko-Marabena et al. 2017) Tanzania and Uganda (Sseruwagi et al. 2005, Sseruwagi et al. 2006, Legg et al. 2014b, Tajebe et al. 2015a, Mugerwa et al. 2018).

MEAM1 has been reported in different countries of Africa including Senegal (Delatte et al. 2015), in CAR Tocko-Marabena (2017), in South Africa (Brown et al. 1995b, Esterhuizen et al. 2013), in the SWIO island of Reunion (Delatte et al. 2005) Tanzania and Uganda (Sseruwagi et al. 2005, Sseruwagi et al. 2006, Legg et al. 2014b, Tajebe et al. 2015a, Mugerwa et al. 2018).

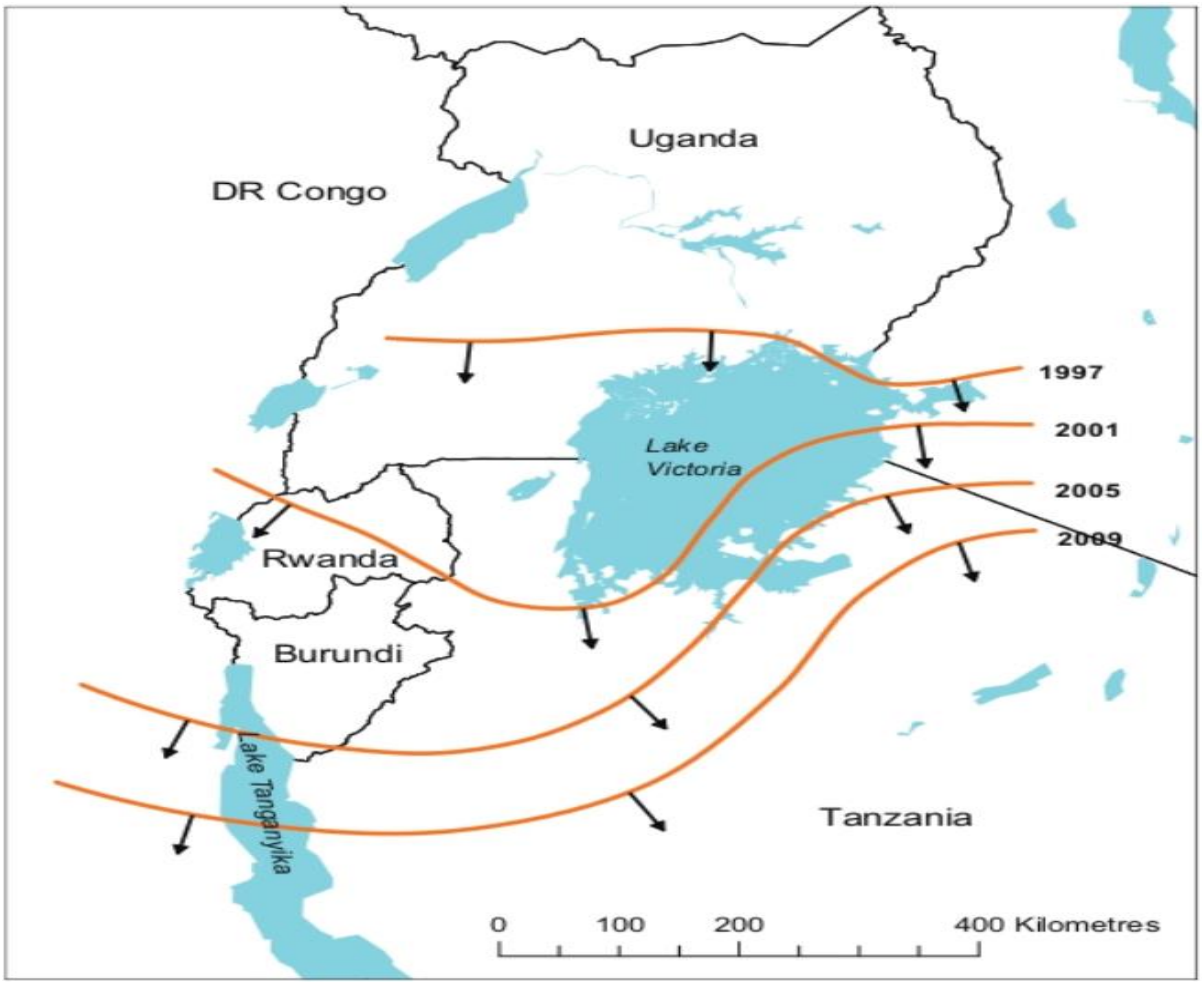


Figure 1. 16: Pattern of spread of the pandemic of severe cassava mosaic disease through East and Central Africa between 1997 and 2009. Arrows indicate the direction of spread of the pandemic 'front' as described by Legg et al. (2014b).

The IO is an indigenous species from the SWIO islands of Reunion, Mauritius, Madagascar, Comoros and Seychelles but most probably originating from mainland Africa (Delatte et al. 2005, Delatte et al. 2011). In Tanzania the species was reported in East, Central and Northern regions (Tajebe et al. 2015a), while, in Kenya it was found in the coastal part (Mugerwa et al. 2012). Sseruwagi et al. (2005) found the occurrence of the species in Uganda formerly identified as Ug7 (Sseruwagi et al. 2005, Boykin et al. 2018). Moreover, the IO was also found in law number in Central Africa Republic (Tocko-Marabena et al. 2017).

### 1.10.1. History of the CMD pandemic from the initial outbreak in 1920s

The first initial outbreak of CMD was recorded in the 1920s and 1930s in Uganda. To combat this disease the production of resistant cassava varieties was initiated (Thresh et al. 1997). Since then, several studies were conducted aiming at the understanding of the aetiology of the causative agent Resistant varieties allowed to diminish the viral symptoms and increase yield. Unfortunately, re-emergence of the CMD occured in the late 1980s and early 1990s in Central Uganda and resulted in serious damages to cassava crop that led some farmers to stop growing cassava. During this new wave of high incidence of CMD, it was reported a tremendous increase of whitefly vector populations facilitating the spread of the disease (Legg et al. 1998).

A few years later, in the late 1990s the CMD Uganda outbreak became a regional pandemic which spread beyond the borders of Uganda into Kenya, Tanzania, Rwanda and the Eastern parts of DRC (Fig. 1.16). Finally, in the 2000s a so- called “continental pandemic” of this virus has been observed. It spread over a much greater area to countries including: DRC, Gabon and Angola (Legg et al. 2002, Legg et al. 2011, Legg et al. 2014a). It is believed that the increased whitefly populations observed in the second outbreak in the 1990s and in the latest in the 2000s are among the major factors that are responsible of the disease spread beyond the Ugandan borders (Legg et al. 2002, Colvin et al. 2004, Tajebe et al. 2015a).

### 1.10.2. Factors driving the whitefly upsurges in East Africa, partly responsible of the spread of CMD

Population of insects are fluctuating according to seasons over the years. From time to time outbreaks or population upsurges (rapid increase of an insect population in a specific locality) can be observed. These outbreaks can change dramatically from generation to generation, such generational dynamic might occur within a growing season or over period of years, also, it can be in a restricted area or widespread Berryman (1987). The outbreaking process can be triggered by environmental conditions, host range and/or natural predators.

For example, a study conducted in Japan to understand the emergence and spread of outbreaking population of a native mirid bug species, *Stenotus rubrovittatus* concluded that this population increase was not related to the arrival of a new species or population. They instead realized that when this bug species was given suitable environmental conditions, local populations may have the potential to outbreak even without invasion of populations from other areas (Kobayashi et al. 2011).

During the past decades, outbreaks of *B. tabaci* have been found more often in many regions of sub-Saharan Africa, and crops colonized by *B. tabaci* have suffered major yield reduction (Thresh et al. 1997, Colvin et al. 2004, Legg and Fauquet 2004, Legg et al. 2011). Indeed, numbers of *B. tabaci* have increased more than 200-fold since the 1990s in many parts of East and Central Africa (Legg et al. 2002, Legg et al. 2014a, Tajebe et al. 2015a, Tocko-Marabena et al. 2017). Synergistic interactions between CMD infected cassava cultivars and *B. tabaci* were considered among the factors explaining the abundance of whitefly populations (Colvin et al. 1999). However, more recent studies demonstrated the presence of higher numbers of *B. tabaci* on improved symptomless varieties than local susceptible ones (Omongo et al. 2012). Several biotic and abiotic factors have been mentioned for these outbreaks (Legg et al. 2014a, Macfadyen et al. 2017).

### 1.10.21. Biological factors

Polyphagy: SSA1 was previously reported to colonize cassava (Legg et al. 2002, Berry et al. 2004, Mugerwa et al. 2018) and it is now found on other plants such as *Manihot glaziovii, Jatropha gossypifolia, Euphorbia heterophylla, Aspilia africana,* and *Abelmoschus esculentus.* Those plants can act as an alternative host for whitefly.

**Host plant preference**: Species adaptation to host plant play a great role on increasing the whitefly abundance, for instance SSA1 are well adapted to cassava. Further, leaf morphology such as wider leaf compare to narrow leaf can provide habitat for large number of whitefly population as well as providing a space for development (Macfadyen et al. 2018).

**Whitefly symbiotic bacteria**: Members of the complex of the whitefly species complex harbour eight endosymbionts, the obligatory primary endosymbiont *Portiera aleyrodidarum* plays a key role of supplying essential nutrients which are absent in arthropods. The occurance other secondary symbionts varies between *B. tabaci* species and played different roles for instance the presence of *Rickettsia* sp. nr. *Bellii* caused higher whitefly fecundity as well as increased female ratio (Himler et al. 2011).

### 1.10.22. Abiotic factors (temperature and rainfall)

Temperature and rainfall regimes are major environmental factors that affect *B. tabaci* population dynamics (Fargette and Thresh 1994). Generally, *B. tabaci* species cannot tolerate temperatures below 17 $^{o}$C and high amounts of rainfall (Vetten and Allen 1983, Fargette and Thresh 1994, Barbosa et al. 2014).

Drought can also have a direct link with increase of whitefly population when irrigated crops are present in the ecosystem. For example, in India, drought impacted the growth of whitefly host plants in the natural ecosystem, as a result high whitefly abundance where reported on cotton (Sundaramurthy 1992). Improper use of pesticides resulted into development of resistance mechanisms in *B. tabaci* species such as MEAM1 and Med (Elbert and Nauen 2000, Palumbo et al. 2001, Horowitz et al. 2005).

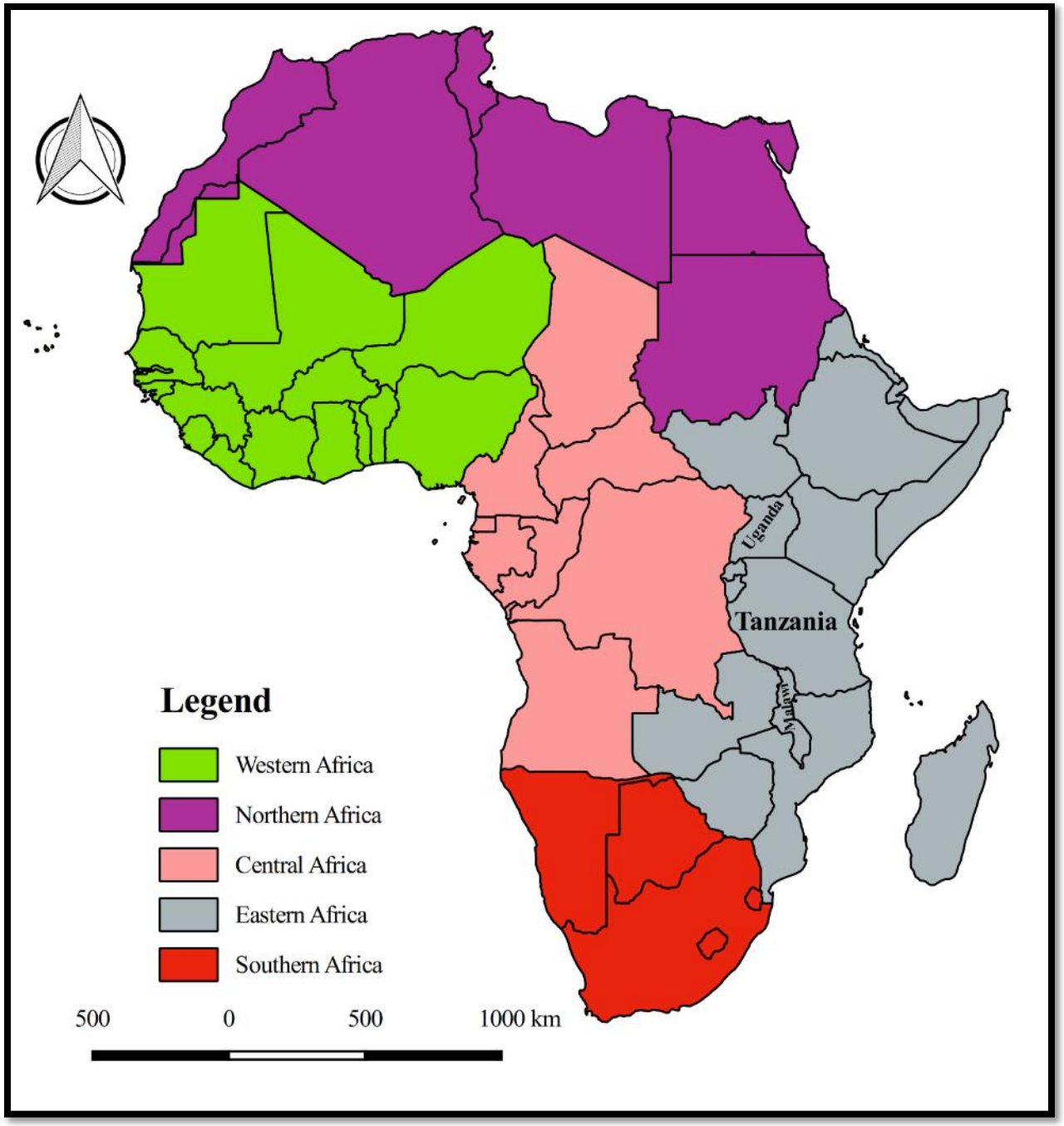


Figure 1. 17: African map showing five regions as described by United Nations geoscheme for Africa

The application of pesticide also, causes the destruction of natural enemies including predators and parasitoïds consuming whiteflies, as a result high whitefly abundance could arise (Bacci et al. 2007, Solangi and Lohar 2007, Macfadyen et al. 2018). However, pesticides are scarcely applied on cassava crops.

## 1.11. Study area: East Africa countries geography, demography, land use and agroecological zones

Africa is the second largest continent in the world. It covers an area of 30.3 million $km^2$ with 25% of its area is a desert. According to the United Nations geoscheme for Africa, the continent is divided into five main regions including Western Africa (15 countries), Northern Africa (seven countries), Central Africa (nine countries), Eastern Africa (18 countries) and Southern Africa (5 countries) (Fig. 1.17). The economies of many African countries depend on agriculture, approximately 30 to 60% of its population relies on it. Wide agriculture system exists in Africa, this include crop production as well as animal husbandry. This study was conducted in three countries of East Africa (Malawi, Tanzania and Uganda) (Fig. 1. 17).

The Eastern part of Africa consists of 18 regions, among them are Malawi, Tanzania and Uganda. Although there are variations in climatic conditions within the three countries, all countries are dominated by tropical savanna climate**.** Tanzania shows highest weather diversity with all climatic condition from Uganda and Malawi (Table 1.3).

Malawi is a landlocked country located southern of Tanzania with an area of 118,480 $km^2$ (Fig. 1.17), Lake Malawi covered one third of the country area. The country is divided into three regions with 28 districts. Its population was estimated to be 18.6 million people in 2017 with 80% living in rural area. The country bordered by Zambia to the northwest, Tanzania to the northeast and Mozambique to the east, south and west. The economy of Malawi depends on agriculture which account one third of its gross domestic product (GDP).

Table 1. 3: Different climatic conditions experienced in Tanzania, Malawi and Uganda, the order is in accordance with the dominance per country (https://en.climate-data.org/).

| Malawi | Tanzania | Uganda |
|---|---|---|
| Tropical savanna climate | Tropical savanna climate | Tropical savanna climate |
| Hot-summer Mediterranean climate | Warm-summer Mediterranean climate | Tropical monsoon climate |
| Warm-summer Mediterranean climate | Hot semi-arid climates | Tropical rainforest climate |
| Humid subtropical climate | Tropical monsoon climate | Oceanic climate |
| Hot semi-arid climates | Hot-summer Mediterranean climate | Subtropical highland oceanic climate |
| Oceanic climate | Subtropical highland oceanic climate | Hot semi-arid climates |
| Subtropical highland oceanic climate | Oceanic climate | |
| | Humid subtropical climate | |
| | Tropical rainforest climate | |

The most exported crops in Malawi are tobacco, tea, sugar cane, coffee and cassava (Masanjala 2006, Kambewa 2010). Maize is the most important food crop, other food crops grown include, beans, rice, groundnuts, sorghum, sunflower, millet, and pigeon pea (Benson et al. 2016). Agriculture in Malawi is conducted in four different aggro ecological zones which are tropical cool semi-arid, tropical cool sub humid, tropical warm semiarid and tropical warm sub humid**.** Malawi receives estimated annual rainfall ranging between 800 to 1400 mm, with large part experience a unimodal rain fall regime. The precipitation season occur from November to April. The country altitude varies ranging from 30 to 3000 meter above sea level (masl), however large part is above 600 masl Minot (2010).

Tanzania is situated just south of the equator consisted of 945,087 km² including three major island of Pemba and Unguja (Zanzibar) and Mafia (Fig. 1.18). The current estimated population has reached 60,525,260. It is bordered by Kenya and Uganda in the North, West by Burundi, Rwanda and Democratic republic of Congo, Southwest by Malawi, south by Mozambique and Zambia. The country also surrounded by water bodies including the major one: Indian Ocean, Lake Victoria, Lake Tanganyika and Lake Malawi. Agriculture is the dominant activity for the economy contributing for 24.5 of the national GDP. Besides, agriculture the economy of Tanzania is also depends on minerals, tourism and fisheries. Agriculture is a mainstay for 75 to 80% of Tanzania population. Despite having a rich base of land 44 million equivalent to 46% of its land territory, only 32% used for agriculture (Malozo 2014). Tanzania climate is characterized by a wide range of agroecological zones including arid, semiarid, plateau, coast and highlands. Tanzania experience an average annual precipitation of 1150 mm, with two rainfall regimes. Bimodal pattern where some parts including the Northern Coast and Zanzibar, Eastern highland and Lake Victoria basin receiving heavy rainfall (masika) between March to May and short rainfall (vuli) between October to December. A unimodal rainfall pattern comprised of southern, central, western, and south-eastern parts of the country receiving rainfall between December to April (Hamisi 2013). The country had a wide crop diversity, major cash crops grown in Tanzania includes coffee, sisal, cashew nuts, tea, cotton and tobacco. Other food crops grown include maize, rice, wheat, cassava, sweet potato, Irish potato, sorghum.

Uganda is a landlocked country which lies within the Nile basin (Fig. 1.18). The country has a total area of 41,038 $km^2$ with an estimated population of 44,270,563 people. Agriculture is the most important activity providing an employment for 72% of its population. Coffee is the main export crop accounting for 16% of its total export, other cash crops grown in Uganda includes tea, cotton and tobacco. It also depends on minerals including gold which account for 10% of its export. The main food crops grown in different agroecological zones of Uganda includes plantains, cassava, sweet potatoes, millet, sorghum, maize, beans, and groundnuts. The agroecological zones of Uganda is characterized by Lake Victoria crescent, pastoral rangelands, savanna grassland, highland and north eastern dryland. Temperature and altitude vary across the region. The country experiences two rainfall regimes. The annual rainfall ranging from 500 mm in the northeast and 1300 mm in the southwest (Haggblade and Dewina 2010). The altitude ranges between 500 to 3500 masl.

## 1.12. Study objectives

Cassava feeds millions of people and majority of them living in sub–Sahara Africa. Its ability to adapt to adversely environments makes it a useful crop in this period of climate change along with increasing human population. Despite its importance the crop is threatened by two major viral diseases such as CMD and CBSD. *B. tabaci* has been conclusively proven as the vector CMVs, but also new data on the mechanism of transmission suggesting that CBSVs, like other ipomoviruses, are also transmitted semi-persistently by this insect (Legg et al. 2011). *B. tabaci* populations have increased more than 200-fold in recent years in many parts of East and Central Africa in crops, in particular on cassava (Legg et al. 2011). However, despite many studies focusing on that aspect, there is still a lack of information on whitefly species colonizing cassava, more specifically on their dynamics (link to species identification) according to host plants in East African countries, and their genetic diversity, which are very important factors for understanding these outbreaks.

The main objective of this study was to better understand the global population genetic analysis of superabundant *B. tabaci*, its population dynamics and factors leading to outbreak.in Malawi, Tanzania and Uganda. The hypothesis was if the current *B. tabaci* outbreak (2017) in Uganda was due to the onset of a new invasive population or species of *B. tabaci* that later invaded neighbour countries such as Tanzania and spread further to Malawi.

This was achieved through further study on the following specific objectives and each objective considered as a chapter.

1) What has changed in the outbreaking populations of the severe crop pest whitefly species in cassava in two decades?
2) Whitefly species distribution in Tanzania and Uganda: their genetic diversity and structuring according to agroecological zones, host plant utilization and population dynamic status.
3) The whitefly, *Bemisia tabaci*, species distribution and genetic diversity in Malawi.

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# Chapter 2

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# Chapter 2: What has changed in the outbreaking populations of the severe crop pest whitefly species in cassava in two decades?

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**Abstract**

High populations of African cassava whitefly (*Bemisia tabaci*) have been associated with epidemics of two viral diseases in Eastern Africa. We investigated population dynamics and genetic patterns by comparing whiteflies collected on cassava in 1997, during the first whitefly upsurges in Uganda, with collections made in 2017 from the same locations. Nuclear markers and mtCOI barcoding sequences were used on 662 samples. The composition of the SSA1 population changed significantly over the 20-years period with the SSA1-SG2 percentage increasing from 0.9 to 48.6%. SSA1-SG1 and SSA1-SG2 clearly interbreed, confirming that they are a single biological species called SSA1. The whitefly species composition changed: in 1997, SSA1, SSA2 and *B. afer* were present; in 2017, no SSA2 was found. These data and those of other publications do not support the 'invader' hypothesis. Our evidence shows that no new species or new population were found in 20 years, instead, the distribution of already present genetic clusters composing SSA1 species have changed over time and that this may be in response to several factors including the introduction of new cassava varieties or climate changes. The practical implications are that cassava genotypes possessing both whitefly and disease resistances are needed urgently.

## Introduction

Crop protection involves practices to manage the plant diseases, weeds and pests that damage agricultural crops and forestry. It plays a key role in safeguarding global crop production against losses, thereby helping to meet the increasing demand for food caused by a growing human population (Oerke and Dehne 2004). Cassava (*Manihot esculenta* Crantz) is an important root crop, which is drought tolerant and able to grow under suboptimal conditions such as low soil fertility (Jarvis et al. 2012). It provides food for about 800 million people worldwide (Howeler et al. 2013). Cassava has proven to be an invaluable food security crop, particularly to smallholder farmers in Sub-Saharan African countries (Manyong 2000). Cassava production, however, has been decreasing, particularly in East Africa, despite the increasing area under cultivation Faostat (2014). The main cause of this trend is two major viral diseases, cassava mosaic disease (CMD) and cassava brown streak disease (CBSD). These are both transmitted by their whitefly vector, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) (Legg et al. 2002).

CMD in Africa is caused by eight species of single-stranded DNA cassava mosaic begomoviruses (CMBs) (family Geminiviridae: genus *Begomovirus*) (Hong et al. 1993, Zhou et al. 1997, Dutt et al. 2005) and CBSD by two cassava brown streak ipomoviruses (CBSIs) (family Potyviridae: genus *Ipomovirus*) (Lister 1959, Hillocks et al. 1996, Monger et al. 2001). In addition to being transmitted by *B. tabaci*, both CMBs and CBSIs are spread by farmers, through the use of virus-infected stem cuttings. The two diseases can occur singly or in dual infections in cassava and the damage can be severe. Yield losses of about 47% from CMD infected fields were recorded in eastern and central African cassava-growing areas (Legg et al. 2006), while in other fields losses of up to 70% were reported due to CBSD (Hillocks et al. 2008).

*B. tabaci* is a group of at least 35 morphologically indistinguishable species. Members of the different species are found on more than 500 plant-host species in 74 families, which includes crops that are crucial to food security, such as cassava (Boykin et al. 2007, Dinsdale et al. 2010, De Barro et al. 2011). These pests affect plants by direct phloem feeding by nymphs and adults on crop foliage or production of honeydew, which encourages the growth of sooty mould fungus on leaves (Davidson et al. 1994, Legg and Fauquet 2004).

However, by far the greatest impact is caused by the spread of >350 plant viruses including CMBs and CBSIs (Colvin et al. 2004, Maruthi et al. 2005, Polston et al. 2014). Epidemics of CMD and CBSD have been reported in several parts of Eastern and Southern Africa since the early 1990s and these were associated with unusually high numbers of whiteflies on cassava (Legg and Ogwal 1998, Holt and Colvin 2001, Colvin et al. 2004). The presence of these 'superabundant' populations has been responsible for the rapid spread and development of two disease epidemics (Legg et al. 2014b), but the reason(s) for their upsurges remain uncertain (Legg et al. 2014a).

Five putative species of *B. tabaci* (described by their mtCO1 marker) have been found colonising cassava in sub-Saharan Africa (SSA) and these were named serially SSA1 to SSA5 (Berry et al. 2004, Sseruwagi et al. 2006, Legg et al. 2014b), with several sub-groups reported for some species. The SSA1 (Boykin et al. 2007) species is widely distributed in Africa; SSA2 is mostly found in the Eastern, Southern and Central areas of Africa as well as in the South of Spain; while SSA3 and SSA4 have been reported in Cameroon and the Central African Republic. SSA5 has only been described in the Ivory Coast and South Africa (Berry et al. 2004, De la Rúa et al. 2006, Sseruwagi et al. 2006, Legg et al. 2014b). SSA2 was hypothesised to be an invasive species associated with the CMD epidemic in Uganda in the 1990s but has subsequently been rarely found (Mugerwa et al. 2012, Wosula et al. 2017). In addition, phylogenetically distinct populations have been described within the SSA1 species, known as SSA1 sub-groups 1 and 2 (SSA1-SG1 and SSA1-SG2, respectively), which were also associated with the CMD and CBSD epidemics (Mbanzibwa et al. 2011, Legg et al. 2014a).

Analysis of genotypes and genetic diversity of *B. tabaci* species is of crucial importance as it can facilitate selection of appropriate management control measures (Mugerwa et al. 2012). Analysing the nuclear genetic diversity of whitefly populations had been performed in the past using several types of markers, among which neutral-codominant markers such as microsatellites gave reliable results.

Those markers allowed to distinguish *B tabaci* species and populations within those species, including Med Q1 and ASl (Mouton et al. 2015), Med and MEAM1(Dalmon et al. 2008, Saleh et al. 2012, Thierry et al. 2015), Med Q1/Q2(Gauthier et al. 2014), or between a wide range of species worldwide (Hadjistylli et al. 2016). Nevertheless, those markers had not been commonly used to untangle population structure among SSA species in Sub-Sahara Africa.

The objectives of the current study, therefore, were to understand: (i) whitefly species distributions in cassava fields in Uganda in 1997 during the initial stages of the CMD epidemic and compare these with the high whitefly populations still present in 2017; (ii) the genetic pattern (diversity and genetic structuring) of population dynamics over two decades in rapidly evolving *B. tabaci* species. To meet these objectives, we estimated the genetic diversity and population structuring of the whitefly species by sequencing the partial mitochondrial cytochrome oxidase I (mtCOI) barcoding region and 13 nuclear markers from specimens collected in 1997 and 2017 from the same geographical location.

## Material and methods

**Whitefly collection.** Live adult whiteflies were collected from cassava plants during a survey of 13 fields from seven districts (Mityana, Mpigi, Wakisa, Kalungu, Masaka, Rakai and Gomba) in Uganda in February 2017 (Table 2.1, Fig. 2.1). The fields were separated by about 20 km (except for three that were <10 km apart) and their GPS coordinates were recorded. QGIS v.2.18.17 online software (https://qgis.org) was used to map the site locations (Fig. 2.1). Whiteflies were collected with a mouth aspirator and then preserved in Eppendorf tubes containing absolute ethanol. In the same geographical location adult whiteflies and cassava leaves with eggs, nymphs and pupa were collected (Table 2.1, Fig. 2.1, within 2–3 km radius) in February 1997 and stored at −80°C. No GPS coordinates were recorded in 1997 but the names of sites/villages and recorded distances were used to approximately match the old and new sites.

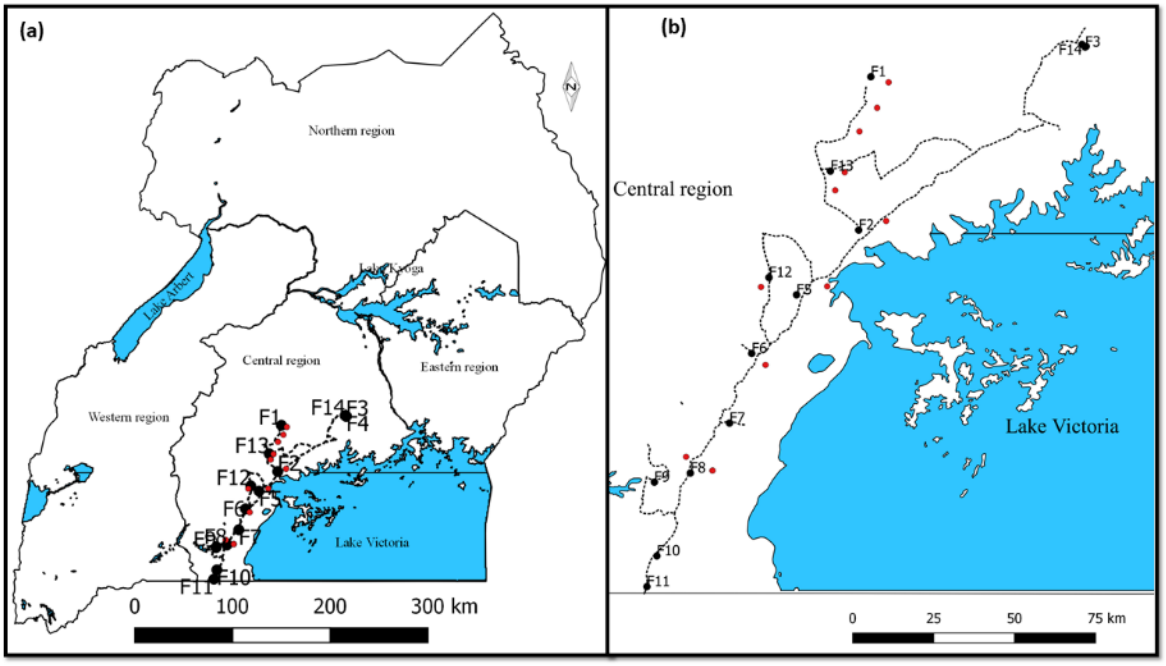


Figure 2. 1: Geographical locations of sampling surveys conducted in (a) Uganda as a whole and (b) part of the central region in which sampling was conducted. Red and black circles are sample sites for whitefly collections made in February 1997 and February 2017.

Table 2. 1**.** Location and information of adult whiteflies collected in Uganda.

| FN | Village name | DN | SY | CA | CV | WC | CMS | CBS | X | Y |
|---|---|---|---|---|---|---|---|---|---|---|
| **F1** | Mityana I | Mityana | 1997 | – | | – | 2 | – | * | * |
| **F1** | Kireku | Mityana | 2017 | 7 | Gomboka | 100 | 3 | 1 | N00.43564 | E032.04041 |
| **F2** | Masaka 25 | Mpigi | 1997 | – | | 100 | 3 | – | * | * |
| **F2** | Kalagala | Mpigi | 2017 | 6 | Akena | 100 | 1 | 3 | N00.00979 | E032.00677 |
| **F3** | NaCCRI | Wakiso | 2017 | 2.5 | NASE 3 | 1 | 1 | 1 | N00.51831 | E032.63553 |
| **F5** | Kampala-Masaka 55 km | Kalungu | 1997 | – | | 100 | 1 | – | * | * |
| **F5** | Kyanagolo | Kalungu | 2017 | 4 | TME 14 | 1 | 4 | 3 | S00.16989 | E031.83412 |
| **F6** | After Nkosi 15 km | Masaka | 1997 | – | | – | 1 | – | * | * |
| **F6** | Masaka | Masaka | 2017 | 6 | Unknown | 10 | 3 | 3 | S00.33294 | E031.70984 |
| **F7** | Kalisizo | Rakai | 2017 | 6 | Unknown | 100 | 2 | 2 | S00.52627 | E031.64813 |
| **F8** | Masaka 50 km | Rakai | 1997 | – | | – | 1 | – | * | * |
| **F8** | Kiwesi | Rakai | 2017 | 3 | TME 204 | 10 | 2 | 2 | S00.66515 | E031.53927 |
| **F9** | Rutula | Rakai | 2017 | 4 | TME 14 | 10 | 1 | 1 | S00.69034 | E031.43948 |
| **F10** | Nabigasa | Rakai | 2017 | 7 | Kalandila | 100 | 3 | 1 | S00.89538 | E031.44637 |
| **F11** | Agasamvu | Rakai | 2017 | 6 | TME 14 | 500 | 4 | 2 | S00.98063 | E031.41873 |
| **F12** | After Nkosi | Kalungu | 1997 | – | | 100 | 1 | – | * | * |
| **F12** | Ntale | Kalungu | 2017 | 3 | TME 14 | 500 | 1 | 1 | S00.12179 | E031.75773 |
| **F13** | Mityana II | Gomba | 1997 | – | | – | 2 | – | * | * |
| **F13** | Wasinda | Gomba | 2017 | 5 | NASE 3 | 100 | 1 | 1 | N00.17379 | E031.92822 |
| **F14** | NaCRRI Valley | Wakiso | 2017 | 8 | NAROCAS 2 | 100 | 3 | 1 | N00.52556 | E032.62680 |

Field number (FN), village name, district where sample population was collected (DN), year of sampling (SY), samples were made in February 1997 and February 2017), cassava age (CA), cassava variety (VA), CMD and CBSD severity symptoms scores and GPS coordinates. *Exact GPS coordinates are not available for the 1997 survey; sites were referenced as distances from Kampala on different roads

**Determination of whitefly population.** The number of adult whiteflies on the top five leaves of five plants selected randomly in each cassava field was recorded as described by Sseruwagi *et al*. (Sseruwagi et al. 2004) in the 2017 sampling. The number of whiteflies per plant was estimated according to the following system: "1" = 1–9 adults per plant, "10" = 10–49, "50" = 50–99, "100" = 100–499 and "500" = >500.

**Assessment of CMD and CBSD symptom severity.** The symptom severity for CMD and CBSD were recorded for each sampled field. The severity was assessed by using a disease scale 1–5 according to Sseruwagi *et al*. (2004), where 1 = no disease symptoms and 5 = the most severe symptoms. Five plants were randomly assessed in each field in 2017.

**DNA extraction of *B. tabaci*.** Leica MZ8 stereomicroscope 100X (Leica Microsystems, Nanterre, France) was used for selection, at most 35 adult female whiteflies were selected from each field. A total of 662 samples were successfully extracted for DNA in this study (108 eggs, 78 nymphs, 28 pupae and 2 adult whiteflies from the 1997 collection, and 446 adults from the 2017 collection). Two methods of DNA extraction were utilised. The non-destructive method was used for 2017 samples at 3P, CIRAD UMR PVBMT in Reunion Island, as described in Delatte et al. (2011) and the destructive method of Ghosh *et al*. (Ghosh et al. 2015) for 1997 collections at Natural Resource Institute (NRI), University of Greenwich, England.

**Mitochondrial DNA amplification and sequencing.** A total of 662 individuals were successfully PCR-amplified and sequenced for mtCOI by using a primer pair designed by Mugerwa *et al*. (2018) (2195Bt 5′-TGRTTTTTTGGTCATCCRGAAGT-3′ and C012/Bt-sh2 5′-TTTACTGCACTTTCTGCC-3′). The PCR reaction mixture was prepared with a final volume of 20 µl, containing 10 µl of Type-it (2x) PCR master mix (Qiagen, France), 7 µl of pure HPLC water CHROMASOLV (Sigma-Aldrich, France), 1 µl of each primer (forward and reverse) and 1 µl of DNA template. Initial denaturation of DNA template occurred at 95°C for 15 min followed by 40 cycles of denaturation at 95°C for 30 s, primer annealing at 52°C for 30 s, extension at 72°C for 1 min and final extension at 72°C for 10 min. Plates were sent to the Macrogen Europe laboratory for sequencing.

**Sequence analysis**. Sequences were manually edited and aligned using the Geneious R10 software (Kearse et al. 2012). The number and distribution of haplotypes within our sequences were achieved through DnaSP v.6 software (Rozas et al. 2003). The selected sequences together with reference sequences from the literature were aligned using ClustalW (Thompson et al. 1994) before being subjected to Jmodeltest 2.1.10 (Posada 2008). The phylogenetic tree was computed using MrBayes (Ronquist and Huelsenbeck 2003) at GTR + G (the closest to the selected model under MrBayes). Four Markov chains were conducted simultaneously for 1 100 000 generations starting from random initial trees and sampled every 200 generations. Variation in the ML scores was examined graphically and 10% of the trees generated prior to stabilization of ML scores were discarded.

**Microsatellite PCR amplification and genotyping–Microsatellite design**. Two pools of extracted DNA of 25 individuals (each tube) of *B. tabaci* from laboratory colonies of SSA2, SSA1-SG1, SSA1-SG2, SSA1-SG3 and SSA3 were made and sent to GenoScreen$_{VR}$ (Genoscreen, Lille, France). Each pool contained 10.2 ng of DNA. The company developed a microsatellite-enriched library using a 454GS-FLX Titanium pyrosequencing (Malausa et al. 2011) tool. The enriched library was then constructed as described by Atiama et al (Atiama et al. 2016). Total DNA was enriched by probes with the following motifs: TG, TC, AAC, AGG, ACAT, ACG, AAG and ACTC. About 534,451 reads were obtained with average fragment length of 247 bp. A first filter of quality was applied to discard short fragments (<40 bp) and low-intensity fragments, which removed 38% of the sequences.

The software QDD (Meglécz et al. 2009) was run on the remaining sequences to identify microsatellite motifs in 73,060 raw sequences, among which 160 primers were designed. The objective was to obtain primers that would cross-amplify between all the pooled species and other whiteflies from the same complex of species with different sizes. From these, 41 primers were selected that could amplify various fragment lengths (100–260 bp) and had different repeat motifs (from di nucleotides to tetra nucleotide motifs). Those primers were tested by PCR individually, on four female specimens of the following species or whitefly genotype groups (-SG): SSA1-SG1, SSA1-SG2, SSA1-SG3, SSA2, SSA3, MEAM1, Med and IO.

The amplified DNA was loaded on agarose gels and sorted. Among all those tested primers we kept nine primers that were (i) amplifying for all species or genotype groups with good signal intensity, and (ii) giving polymorphisms between individuals within species and between species/genotypes. These nine primers were fluorescently labelled (forward primer; Applied Biosystems, Waltham, MA, USA) and tested in simplex and multiplex PCR mixes on several field samples of the different whitefly species named above. Only five of them were retained in the present study, the other four were discarded due to the high number of null alleles observed in different populations and species within the species complex tested.

**Amplification and genotyping of old and recent field populations from Uganda**. PCR for genotyping was conducted using 13 microsatellite loci, which were combined in three multiplex primer reactions. Five of the markers were newly developed for this study (Table 2.2). All markers were selected based on their ability to amplify different species within *B. tabaci* complex.

A PCR mix of 15 µl was prepared with 7.5 µl of 2x multiplex PCR master mix (Type-it, QIAGEN), 4.5 µl of HPLC water and 0.1 µl of each primer followed by addition of 2 µl of template DNA. The volume was slightly changed in Mix 2, in which 0.2 µl of WF1GO3 and P5 primers were used. All PCR programs were as follows: initial denaturation 95°C (15 min) followed by 40 cycles, 95°C (30 s), 55°C (180 s), 72°C (1 min) and at 60°C (15 min) for denaturation, primer annealing, extension and final extension, respectively, except for Mix 3 for which the annealing temperature was increased from 55°C to 56°C. Prior to genotyping, the amplified PCR products were diluted in different ratios according to the band intensity obtained for each mix. The final mix consisted of 10.8 µl of formamide, 0.2 µl of Applied Biosystems LIZ size marker and 1 µl of diluted amplified DNA. The mix was run in an Applied Biosystems 3130XL DNA sequencer machine. Genotypic data were retrieved visualised and scored manually using Gene mapper v.4.0 software.

**Population structure analysis**. The Bayesian cluster approach with Structure v.2.3.4 (Pritchard et al. 2000) was used to assess genetic population structure between individuals.

Table 2. 2: Characteristics of loci used for nuclear analysis.

| LN | Reference | Sequence name | Motif | NuA | FL | %MS | NA | Range (bp) |
|---|---|---|---|---|---|---|---|---|
| **MS145** | Dalmon et al., 2008 | F: CCTACCCATGAGAGCGGTAA<br>R: TCAACAAACGCGTTCTTCAC | (AC)9 | 0.24 | PET | 11 | 29 | 124–278 |
| **P59** | Delatte et al., 2006 | F: CGGCGTTTCTCGTTTTCTT<br>R: TTTGCCAACTGAAGCACATCAATCA | (T)44(G)18 | 0.17 | 6-FAM | 0.8 | 16 | 152–216 |
| **P7** | Delatte et al., 2006 | F: AGGGTGTCAGGTCAGGTAGC<br>R: TTTGCGTAATAGAAAA | 8(GT) | 0.16 | VIC | 6.1 | 40 | 105–261 |
| **WF2H06** | Hadjistylli et al., 2014 | F: TATTCGCCAATCGATTCCTT<br>R: CGGCGGAAATTTCGATAAA | (TTTG)11 | 0.12 | NED | 6.8 | 24 | 102–208 |
| **P62** | Delatte et al., 2006 | F: CTTCCTTAGCACGGCAGAAT<br>R: TTTGGCGCAATTTTTAGCGTCTGT | (GT)8 | 0.1 | 6-FAM | 5.4 | 49 | 112–296 |
| **WF1G03** | Hadjistylli et al., 2014 | F: CTCCAAAATGGGACTTGAAC<br>R: GTAGAAGCCACACATACTAGCAC | (GTTT)8 | 0.07 | PET | 4.5 | 29 | 100–292 |
| **WF1D04** | Hadjistylli et al., 2014 | F: GTTGTTAGGTTACAGGGTTTGTC<br>R: GTCTTTACTTCTTTTCCTCCG | (CAAA)16 | 0.06 | VIC | 1.2 | 19 | 100–182 |
| **P5** | Delatte et al., 2006 | F: ATTAGCCTTGCTTGGGTCCT<br>R: TTTGCAAAAACAAAAGCATGTGTCAAA | (GT)8 | 0.16 | NED | 15.5 | 52 | 100–282 |
| **CIRSSA2** | This study | F: ACAATGCATGTTGATTGTGAA<br>R: TGAAAATGTCTACGGCCAGA | (AG)6 | 0.01 | VIC | 0.3 | 5 | 100–108 |
| **CIRSSA6** | This study | F: CATATCGGTCATTATCCGCA<br>R: CATCAGGCTGGAAAGACGAG | (TC)6 | 0.11 | VIC | 0.2 | 8 | 125–173 |
| **CIRSSA7** | This study | F: TGGCGATCCTCTTCTTGTTT<br>R: AAGAAGCAGCAGTTCATCCG | (TC)5 | 0.13 | PET | 0.6 | 8 | 134–152 |
| **CIRSSA13** | This study | F: AGTGCTGAAGGTCCACCGTA<br>R: GGGATTTCCAGGGGTTAAGA | (CT)6 | 0.03 | NED | 1.4 | 7 | 203–225 |
| **CIRSSA41** | This study | F: TGGGTGCATGGTTCTTACAG<br>R: TATCCGGTCGACAAACACAA | (CT)6 | 0.56 | 6-FAM | 57 | 15 | 210–267 |

Locus name (LN), source reference, sequence name, microsatellite repeat motif, null allele frequency in the whole dataset (NuA), fluorochromes used for PCR product detection (FL), percentage of missing data in the whole dataset (%MS), number of alleles counted per locus in the whole dataset (NA), allele size range (Range, bp). Loci CIRSSA2, CIRSSA6, CIRSSA7, CIRSSA13 and CIRSSA41 are described here for the first time. The MS, NA, range and null allele columns were obtained on the SSA1 and SSA2 populations sampled ($n$ = 643)

The method assigns individuals to different clusters (a series of K to be set). Each K is the number of estimated population clusters characterised by posterior probabilities. Structure 2.3.4 was set at 100,000 burn in length with run length of 1,000,000 MCMC, this step was repeated three times and K was set to range from 1 to 20. The dataset was arranged according to mtCOI results and field numbers. The best number of clusters (K) was estimated by means of ΔK as described by Evanno *et al.* (Evanno et al. 2005) using the online program Structure Harvester (Earl 2012). An online program CLUMPAK (Clustering Markov Packager Across) (Kopelman et al. 2015) was used to summarise the best K posterior probabilities and to reconstruct the bar plots using Clumpp (Jakobsson and Rosenberg 2007) and Distruct (Rosenberg 2004) software.

As null alleles were still recorded in our datasets, we then ran two Bayesian analyses using 12 microsatellite loci with and without the recessive alleles option, as explained by Falush *et al.* (Falush et al. 2007). Both datasets were executed using burn-in length of 100,000 and MCMC run length of 1,000,000, repeated three times, and an assumed number of population (*K*) values between 1 and 20. Similar results were obtained from both analyses (Fig. 2a, b), showing robust analyses regardless of null alleles.

**Population genetic analyses**. The basic population parameters were analysed by using a set of programs within Genetix v.4.05.2, such as the number of alleles per population, expected heterozygosity and observed heterozygosity (according to the method of Nei (Nei 1978) and correlation within individuals following the method of Weir and Cockerham (Weir and Cockerham 1984). Deviation from Hardy-Weinberg equilibrium was tested using MCMC (run length of 1,000,000) implemented in Arlequin v.3.5.2.2 (Excoffier et al. 2005) following the method utilized by Guo and Thomson (Guo and Thompson 1992). GENEPOP v.4.2 (Rousset 2008) was used to test genotypic disequilibrium by Fisher's method (Fisher 1935). The effect of null alleles on inferring population structure was studied, as described by Falush *et al* (Falush et al. 2007). Allelic richness using rarefaction was estimated by FSTAT v.2.9.3.2 (Goudet 2002). Genetic differentiation among year, between populations within year was inferred by AMOVA by Arlequin. PCA and DAPC were also used to determine the genetic clusters among individuals using R software (Lê et al. 2008) v. 3.4.2 with the Adegenet package (Jombart 2008).

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Recent genetic bottleneck signature was also tested in population of 2017 using the genetic software Bottelneck 1.2.02 (Piry et al. 1999). The software measures the temporary excess of heterozygosity that results from a decrease of the effective population size and proposes tests to detect this anomaly (Cornuet and Luikart 1996, Luikart and Cornuet 1998). Deviations from expected heterozygosity were computed through 1000 permutations, using both the stepwise mutation model (SMM) and the two-phased model of mutation (TPM). One-tailed Wilcoxon sign-rank tests were used to determine whether a population exhibits significant heterozygosity deficit or excess.

## Results

**Whitefly abundance and CMD and CBSD symptoms.** Whitefly abundance varied between fields from <10 to over 500 adults per plant. Fields with over 100 adult whiteflies per plant were considered superabundant populations. Based on this criterion, eight (61.5%) of the 13 fields visited in 2017 had superabundant whitefly populations, among which two fields did not show CMD and CBSD symptoms (Table 1). The distribution of CMD within fields was higher (69.2%) than that of CBSD (46.2%) with a maximum leaf severity score of 4 detected in two fields. Moreover, 38.5% of the fields were dually infected with both viruses. Furthermore, during the 1997 survey, three fields (42.9%) had superabundant whitefly populations (Table 2.1) and one of these had plants exhibiting severe CMD symptoms. Three fields had plants with CMD symptoms, despite a low whitefly number (<10 per plant). No CBSD symptoms in any plants were recorded during 1997.

**Phylogenetic analysis. T**he partial mtCOI gene of 665 whiteflies was sequenced, of which 219 were from the 1997 collection (110 eggs, 79 nymphs, 28 pupae and 2 adults) and the remaining 446 were all adults from the 2017 collection. After manual checking and editing for errors, the mtCOI sequences were trimmed to different lengths: 700 bp ($n$ = 251), 657 bp ($n$ = 219), 500 bp ($n$ = 112) and 300 bp ($n$ = 80) depending on the sequence quality obtained. Despite the shorter sizes of some sequences (300 bp), it was possible to differentiate between putative species and SSA1 sub-groups, as well as to use the shorter sequences as species tags in further analysis.

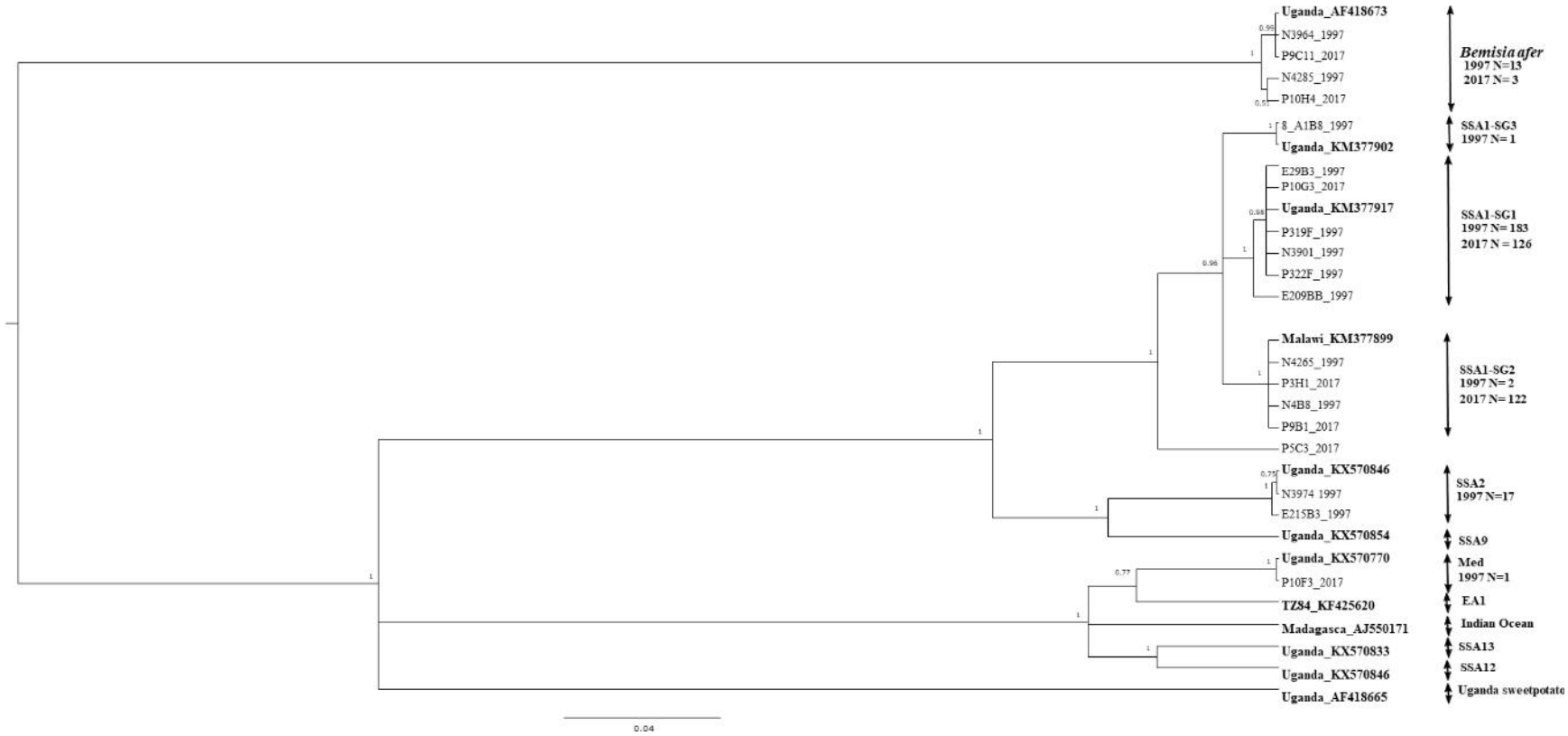



Figure 2. 2: Posterior probability phylogenetic tree generated by MrBayes by the Markov chain Monte Carlo method for all the different mtDNA COI haplotype sequences (651bp) of 1997 and 2017 ($n$ = 14) together with reference sequences ($n$ = 12, in bold) obtained from GenBank for comparison.

To increase robustness of the phylogenetic tree, a total of 470 sequences that were at least 651 bp long, together with an additional 12 sequences from the GenBank, were used. Bayesian phylogenetic analysis used to generate the tree divided our sequences into four main clusters (SSA1(-SG1 -SG2 and -SG3), SSA2, Mediterranean (Med) and *Bemisia afer*) supported by high posterior probability values (>0.9) (data not shown). The specific group of haplotypes within SSA1 named SSA1- SG1 were found to be dominant with 183 individuals (84%), followed by SSA2 (*n* = 22, 10%), whereas others belonged to the other haplotype groups named SSA1-SG2 (*n* = 2, 0.9%) and SSA1-SG3 (*n* = 1, 0.5%), and to *B. afer* individuals (*n* = 10, 4.6%) from the 1997 collection (Supplementary Fig. S 2.1). The 2017 samples revealed both SSA1-SG1 (*n* = 126, 50.2%) and SSA1-SG2 (*n* = 122, 48.6%) as the dominant groups over all observed genetic clusters. The other species characterised were Med and *B. afer*, which together represented 1.2% of the total (Supplementary Fig. S 2.2).

Haplotype diversity results revealed 12 haplotypes from *B. tabaci* species within the combined dataset of longest sequences (651 bp), comprising 470 (Table 2.3) individuals (219 and 251 from 1997 and 2017 respectively); however, only two of these were observed in both 1997 and 2017 (Fig. 2.2). Ten haplotypes were observed in 1997, among which five were observed for SSA1-SG1, with the largest group containing 176 individuals (84.2%) represented as P319F in the phylogenetic tree (Fig. 2.2). This haplotype shared 100% identity with the previously identified sequence of KM377899 (Maruthi et al. 2004) and KX570785 (Mugerwa et al. 2018), both from Uganda. The remaining four SSA1-SG1 haplotypes contained nine individuals (4.3%). Two haplotypes were observed for SSA1-SG2. Apart from SSA1, two haplotypes were found for SSA2 (*n* = 22, 10.5%) from 1997 collected samples. In 2017, five haplotypes were found from *B. tabaci* species, including one haplotype for SSA1-SG1 (*n* = 126, 50.6%) represented as P10G3 (Fig. 2.2). These individuals shared 100% identity with the majority of SSA1-SG1 found in 1997. In addition, three SSA1-SG2 haplotypes were observed, among which 117 individuals (47%) shared 100% identity with the KM377899 (Maruthi et al. 2004) and KX570790 (Mugerwa et al. 2018) reference sequences recognised in Malawi and Uganda obtained from GenBank, and the other two SSA1-SG2 haplotypes contained five individuals (2%). One haplotype (*n* = 1, 0.4%) of the Med species was found.

Table 2. 3: *B. tabaci* haplotype distribution within fields F1–F14 (Table 1) sampled 1997 or 2017

| Field no. | Year | Species status | NA (mtCOI) | SP code (mtCOI) | SR | AN |
|---|---|---|---|---|---|---|
| | 1997 | Nymph | 2 | SSA2 | **N3974** | **MK360171** |
| | 1997 | Nymph (20), pupa (12) | 32 | SSA1-SG1 | N4155 | Same haplotype as MK360162 |
| | 1997 | Nymph | 1 | SSA1-SG1 | **N3901** | **MK360172** |
| | 1997 | Nymph (7), Egg (1) | 6 | *B. afer* | **N3964** | **MK360160** |
| F1 | 1997 | Nymph | 1 | SSA1-SG2 | **N4265** | **MK360170** |
| | 1997 | Nymph | 2 | *B. afer* | **N4285** | **MK360169** |
| | 2017 | Adult | 19 | SSA1-SG1 | P9G3 | Same haplotype as MK360164 |
| | 2017 | Adults | 13 | SSA1-SG2 | **P3H1** | **MK360168** |
| | 2017 | Adult | 2 | SSA1-SG2 | **P9B1** | **MK360167** |
| | 1997 | Egg | 18 | SSA2 | E213B3 | Same haplotype as MK360171 |
| | 1997 | Eggs | 2 | SSA2 | **E215B3** | **MK360174** |
| | 1997 | Egg | 1 | SSA1-SG1 | **E29B3** | **MK360176** |
| F2 | 1997 | Egg | 1 | *B. afer* | E14B3 | Same haplotype as MK360160 |
| | 2017 | Adult | 15 | SSA1-SG1 | P9D4 | Same haplotype as MK360164 |
| | 2017 | Adult | 17 | SSA1-SG2 | P3H9 | Same haplotype as MK360168 |
| | 2017 | Adult | 2 | SSA1-SG2 | P9B3 | Same haplotype as MK360167 |
| | 2017 | Adult | 11 | SSA1-SG1 | P9D4 | Same haplotype as MK360164 |
| F3 | 2017 | Adults | 3 | SSA1-SG2 | P9G5 | Same haplotype as MK360168 |
| | 1997 | Eggs | 17 | SSA1-SG1 | E208BB | Same haplotype as MK360162 |
| F5 | 1997 | Eggs | 1 | SSA1-SG1 | E233BC | Same haplotype as MK360176 |
| | 2017 | Adult | 5 | SSA1-SG1 | P9E7 | Same haplotype as MK360164 |
| | 2017 | Adults | 9 | SSA1-SG2 | P9C8 | Same haplotype as MK360168 |
| | 1997 | Eggs | 22 | SSA1-SG1 | E31B6 | Same haplotype as MK360164 |
| F6 | 1997 | Eggs | 1 | SSA1-SG1 | E27B6 | Same haplotype as MK360172 |
| | 2017 | Adult | 5 | SSA1-SG1 | P9B9 | Same haplotype as MK360164 |
| | 2017 | Adults | 5 | SSA1-SG2 | P9G8 | Same haplotype as MK360168 |
| | 2017 | Adult | 3 | SSA1-SG1 | P9B10 | Same haplotype as MK360164 |
| F7 | 2017 | Adult | 11 | SSA1-SG2 | P9G10 | Same haplotype as MK360168 |
| | 2017 | Adults | 1 | *B. afer* | **P9C11** | **MK360166** |
| | 1997 | Eggs | 28 | SSA1-SG1 | E96B8 | Same haplotype as MK360162 |
| | 1997 | Egg | 2 | SSA1-SG1 | E111B8 | Same haplotype as MK360176 |
| F8 | 1997 | Nymph | 1 | SSA1-SG2 | **N4B8** | **MK360173** |
| | 1997 | Adult | 1 | SSA1-SG3 | **A1B8** | **MK360177** |
| | 2017 | Adult | 7 | SSA1-SG1 | P10D1 | Same haplotype as MK360164 |
| | 2017 | Adult | 4 | SSA1-SG2 | P10F2 | Same haplotype as MK360168 |
| | 2017 | Adult | 5 | SSA1-SG1 | P10A3 | Same haplotype as MK360164 |
| F9 | 2017 | Adult | 10 | SSA1-SG2 | P10B3 | Same haplotype as MK360168 |
| | 2017 | Adult | 4 | SSA1-SG1 | **P10G3** | **MK360164** |
| | 2017 | Adult | 8 | SSA1-SG2 | P10E3 | Same haplotype as MK360168 |
| F10 | 2017 | Adult | 1 | *B. afer* | **P10H4** | **MK360163** |
| | 2017 | Adult | 1 | Med | **P10F3** | **MK360165** |
| | 2017 | Adult | 5 | SSA1-SG1 | P10B6 | Same haplotype as MK360164 |
| F11 | 2017 | Adult | 9 | SSA1-SG2 | P10F5 | Same haplotype as MK360168 |
| | 1997 | Egg (17), adult (1) | 18 | SSA1-SG1 | E205BB | Same haplotype as MK360162 |
| F12 | 1997 | Egg | 1 | SSA1-SG1 | **E209BB** | **MK360175** |
| | 2017 | Adult | 12 | SSA1-SG1 | P10C8 | Same haplotype as MK360164 |
| | 2017 | Adult | 10 | SSA1-SG2 | P10C7 | Same haplotype as MK360168 |
| | 1997 | Nymph (43), pupa (15) | 59 | SSA1-SG1 | **P319F** | **MK360162** |
| | 1997 | Pupa | 1 | SSA1-SG1 | **P322F** | **MK360161** |
| F13 | 1997 | Nymph | 1 | *B. afer* | N4326 | Same haplotype as MK360160 |
| | 2017 | Adult | 13 | SSA1-SG1 | P10G9 | Same haplotype as MK360164 |
| | 2017 | Adult | 15 | SSA1-SG2 | P10C10 | Same haplotype as MK360168 |
| F14 | 2017 | Adult | 22 | SSA1-SG1 | P8C10 | Same haplotype as MK360164 |
| | 2017 | Adult | 4 | SSA1-SG2 | P10A11 | Same haplotype as MK360168 |
| Total | | | 470 | | | |

Species status, numbers in parenthesis represent number of individuals at each stage; total number of individuals amplified for mtCOI (Ni); species code according to mtCOI barcoding (SP code); Individual code for selected representative among similar mtCOI haplotype sequences (SR), where bold individuals were used in the construction of the phylogenetic tree (Fig. 2b) and sequences were submitted to GenBank; and AN refers to the accession number given by GenBank.

Apart from 12 haplotypes of *B. tabaci* species, two other *B. afer* haplotypes were also observed. All the new haplotypes were submitted to GenBank and were assigned accession numbers from MK360160 to MK360177 (Table 2.3).

**Nuclear genetic analysis.** A total of 594 out of 662 individuals (407 and 203 from the 2017 and 1997 samples, respectively) were successfully genotyped. All loci were checked with Microchecker (Chakraborty et al. 1992) and no PCR artefacts linked to large allele drop-out or stuttering were detected. All individuals and loci with missing data greater than 20% and/or 25% of null alleles were discarded from the dataset, meaning that 68 individuals and one loci (CIRSSA41) were removed. The number of alleles per locus from the 13 microsatellite markers over the whole dataset ranged from 5 to 52. The highest polymorphism observed was for the P5 locus and the lowest was for the CIRSSA2 locus. The mean null allele frequency for all loci and populations was 0.128 but ranged from 0.01 to 0.56 (from CIRSSA6 to CIRSSA41, respectively) (Table 2.3).

The population genetic diversity indices were calculated in SSA1 and SSA2 species separately. The results from SSA1 species showed the mean alleles richness over all loci, per field, ranged from 4.22 ($n$ = 14; 2017) to 6.66 ($n$ = 57; 1997) with the highest mean values observed in the 1997 collection (Supplementary Table S1 online). None of our collected samples, analysed per population, showed deviation from Hardy–Weinberg equilibrium, using the exact test of Markov Chain of Monte Carlo (MCMC) (Supplementary Table S1). Three out of 66 pairs of loci across all populations showed deviation from genotypic disequilibrium after Bonferroni correction.

Genetic structuring and population differentiation. Bayesian clustering analysis revealed three major genetic clusters from the SSA1 population with an optimal number of clusters of $K$ = 3 (estimated by means of $\Delta K$, as described by Evanno *et al.* (Evanno et al. 2005) (Supplementary Fig. 2.4a, b). The first two genetic clusters at K3, in Fig. 2.3b, dominated the 1997 *B. tabaci* samples. Individuals of the two mtCO1 sub-groups SSA1-SG1 and SSA1-SG2 were not differentiated and belonged to the same genetic clusters (Fig. 2.3b).

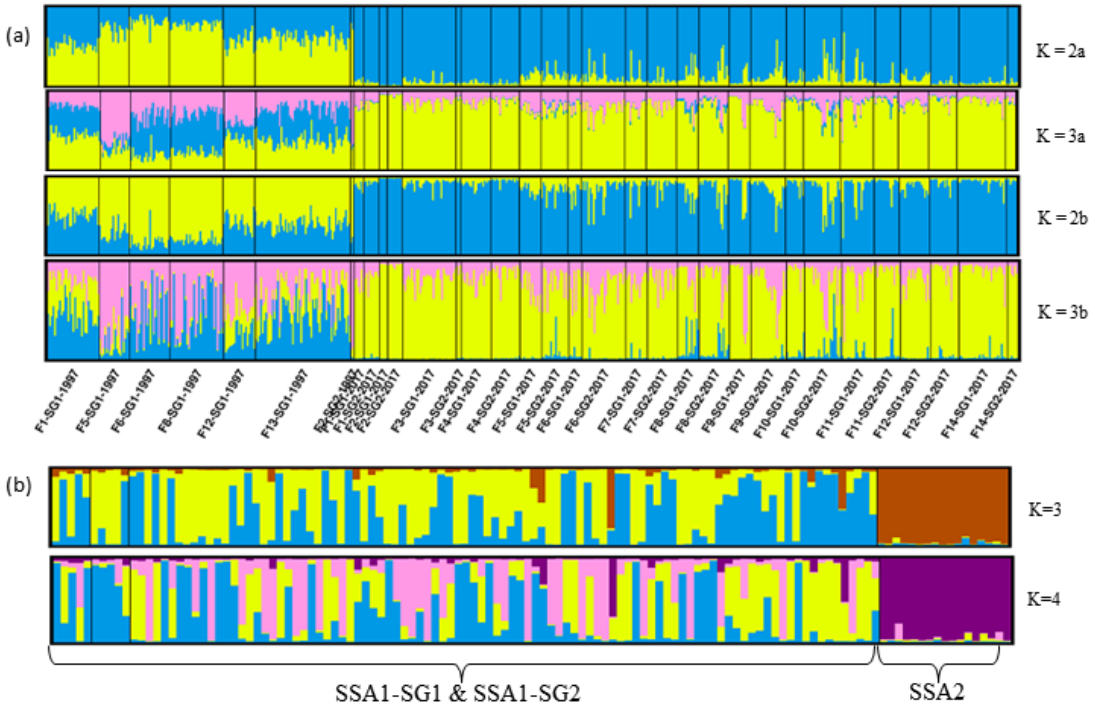



Figure 2. 3:**.** STRUCTURE bar plots for SSA1 and SSA2 populations collected from Uganda **(a)** for 33 populations of SSA1 arranged by subgroup, site and year at *K* = 2 and 3, e.g., K2(a) and K3(a) with recessive allele option turned on, and K2(b) and K3(b) without the option turned on. **(b)** For 102 randomly selected SSA1-SG1 and SSA1-SG2) together with 17 individuals of SSA2 at *K* = 3 and 4. The black line within SSA1 separates individuals of SSA1-SG1 and SSA1-SG2 for 2017 and SSA1-SG1 for 1997.

The third genetic cluster, denoted by yellow colour, dominated the 2017 collections except for some individuals of the two other genetic clusters found within the 2017 samples at $K = 3$. Conversely, a few individuals assigned to the pink genetic clusters were also found in 2017 collections. We can also observe a proportion of individuals with less than 50% of posterior probability assigned to one genetic cluster, which were perceived to be part of several genetic clusters. These individuals could be assigned as individuals with gene flow between genetic clusters.

Although there were few samples of the SSA2 population (17 individuals), another Bayesian analysis was run together with SSA1 individuals to understand the genetic pattern between the two-putative species. To decrease the effect of unbalanced samples, 102 samples of SSA1 together with 17 samples of SSA2 were randomly chosen, and similar results were obtained showing some level of shared genetic background, as expected for closely related species (Fig. 2.3b).

Individuals with 70% posterior probability from the Bayesian analysis dataset were selected and used to perform a principal component analysis (PCA), subsequently the analysis split the dataset into three clusters/ellipses similar to the previously identified genetic clusters of Bayesian analysis (Fig. 2.4). The 2017 samples were aggregated in one ellipse. In contrast, the majority of 1997 individuals belonged to the other two ellipses. However, some individuals from the two collections were mixed within clusters. A discriminant analysis of principal components (DAPC) was performed and the best BIC value was found at $K = 3$, as the best $K$ number of assumed populations. Accordingly, the DAPC spread the dataset into three clusters; two were dominated by 1997 collections, whereas the third cluster was represented by the 2017 samples.

The AMOVA carried out on our SSA1 samples to test for population differentiation between years, using only sites that were sampled in 1997 and 2017 (ie. 6 sites were considered for each year) showed a very low, but significant variation (Table 2.4).

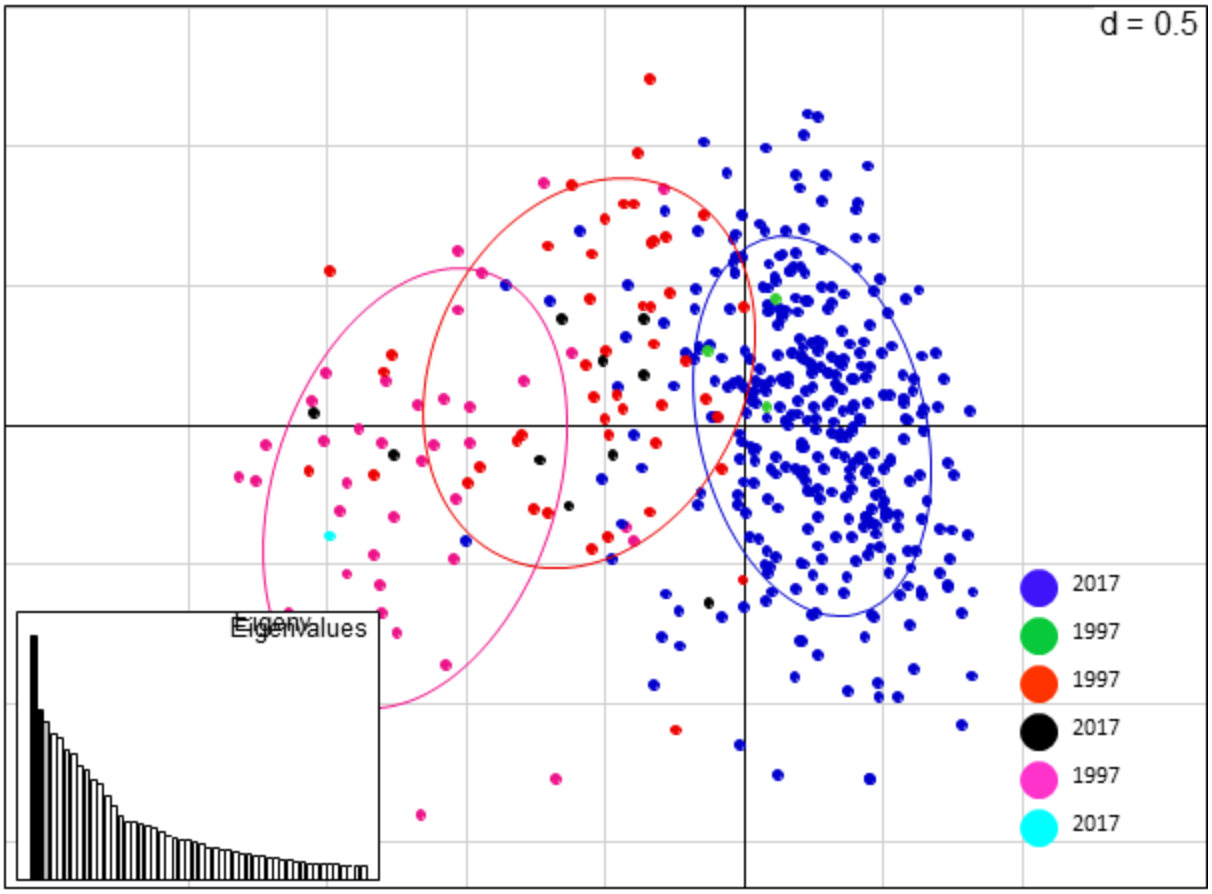



Figure 2. 4**:** Principal component analysis of *B. tabaci* populations from Uganda. Colours show the genetic clusters found with the Bayesian analysis of structure at $K = 3$. Each dot represents one individual. The blue cluster is dominated by the 2017 population, whereas the pink and orange clusters are dominated by the 1997 population. In each cluster there are few individuals of different years mixing within clusters.

Table 2. 4: Analysis of molecular variance (AMOVA average over loci) from Ugandan populations of *B. tabaci*, comparing SSA1 populations between sampling year, * indicates significant variation among populations within species and within individuals.

| Source of variation | Sum of square | Sum of component Variation | Percentage of Variation | Fixation indices |
|---|---|---|---|---|
| Among years | 76.16 | 0.1931 | 4.99843 | FCT : 0.05* |
| Among population within years | 88.96 | 0.09658 | 2.50012 | FSC : 0.03* |
| Within individuals | 2374.86 | 3.5735 | 92.50145 | FST : 0.07* |
| Total | 2539.98 | 3.86318 | | |

Further analysis of differentiation between groups was performed through analysis of the population pairwise matrix of genetic distances Fst between sites, subgroups and years. Results revealed a few significant differences between SSA1-SG1 and SSA1-SG2 of the 2017 samples for only 31 comparisons. Most of the populations of 1997 were significantly different from the ones of 2017, except for field 5 (Supplementary Table 2.2).

The bottelneck analyses performed on the 2017 dataset showed that all populations had undergone a significant bottleneck (One-tailed Wilcoxon sign-rank tests, $P<0.05$) in the recent past with the SMM model (Supplementary Table 2.3).

## Discussion

We used two different molecular markers to identify population genetic variations within the African *B. tabaci* colonizing cassava in Uganda, to compare 2017 populations with those of the 1997 outbreak. Our results reveal that SSA1 was the dominant species in Uganda both in 1997 and 2017 and that its subgroups SG1 and SG2 can interbreed. Populations within SSA1 were found to be structured into three genetic clusters, irrespective of subgroups, which varied in abundance between 1997 and 2017. The SSA2 individuals were clustered separately. The main results obtained here are showing that the genetic composition of SSA1 whitefly species has changed rapidly over the 20 years period, which is contrasting with the previous invader hypothesis.

Out of the 13 cassava fields visited in 2017, we observed 8 fields with >100 mean adult whiteflies per plant, which were defined as having superabundant populations. Within those eight fields, 63% ($n$ = 5) showed CMD symptoms and 50% showed symptoms of CBSD. The association between the two diseases and *B. tabaci* population on cassava has been reported by Colvin *et al*. and Legg *et al*. (Colvin et al. 2004, Legg et al. 2011). In the remaining five fields with <50 mean adult whiteflies per plant, up to 60% CMD and CBSD symptoms were observed. The improved cassava varieties TME14 and TME 204 were grown in these fields.

Despite the relatively low number of whiteflies observed in the field located at Kynagolo (1–9 mean adult whiteflies per plant) planted with TME 14 and the field at Masaka (10–49 mean adult whiteflies per plant) planted with an unknown variety, both had average CMD and CBSD symptom severity (Table 2.1).

Regardless of the superabundant whitefly population in two fields (Ntale and Wasinda), no CMD and CBSD symptoms were observed, which may be related to the type of variety grown (NASE3, an improved cassava variety, which might be tolerant to CMD and CBSD).

The average age of cassava field with high whitefly abundance (100 and above) was 6 months, which contrasts with the age recently shown by Kalyebi (Kalyebi et al. 2018) of 2–3 months. These observed discrepancies might be linked to the surveyed cassava varieties, which might be more whitefly susceptible in our case, or the very small amount of field samples in our study ($n$ = 8). Furthermore, our study revealed whitefly abundance increased toward the southern part of Uganda, with a maximum population of >500 whiteflies per plant in 2017. This result corresponds to the previous studies conducted in Uganda during the 1990s (Legg 1999, Ntawuruhunga and Legg 2007).

Despite all efforts made to combat CMD and CBSD diseases since the first outbreaks of whitefly populations reported in the 1990s (Otim-Nape et al. 1996, Legg and Ogwal 1998, Legg 1999) in Uganda, most of the cassava varieties grown in the 2017 surveyed fields (TME 14, TME 204 and NAROCAS II) were infected with both diseases. Development of whiteflies on cassava is the result of synergistic interaction of several factors including viruses, bacterial symbionts and cassava genotypes (Ghosh et al. 2018), all of which require more research attention. In order to combat these problems effectively, research and development efforts need to be focussed on creating cassava varieties that combine both virus- and whitefly-resistance traits.

SSA1-SG1 was present at all sites in 1997 and 2017 (Table 2). The presence of SSA1-SG1 in different regions of Central and Eastern Africa, including Uganda, has been reported in several studies. Interestingly, a balanced distribution of SSA1-SG1 and SSA1-SG2 was found in 2017 compared with the very low proportions of SSA1-SG2 in 1997 (0.9% in 1997 vs 48.6% in 2017).

Recent studies describing the SSA1 sub-groups found similar results in Uganda (Sseruwagi et al. 2005, Mugerwa et al. 2012, Legg et al. 2014a).

The proportion of SSA2 was low (10%) in 1997 and we did not detect it at all in 2017. Legg *et al.* (Legg et al. 2014b) also reported a drastic decline in SSA2 from 63.9% for 1997–1999 sampling to 1.4% by 2009–2010. The reduction of SSA2 in favour of SSA1-SG1 and SSA1-SG2 in Uganda has also been reported in two recent studies (Mugerwa et al. 2012, Ghosh et al. 2015). The reason for the decrease of SSA2 in eastern Africa is unknown but could be associated with less suitable environmental conditions, such as the use of improved cassava varieties following the CMD epidemic, which might have impacted the abundance of SSA1. In addition, it might be related to biological consequences of mating interruption between the two species, where copulation events occur between individuals of the two species but without viable progeny. Consequences of this behaviour is observed with a decreasing success of mating of the species in lower abundance (Liu et al. 2007, De Barro et al. 2011).

Analysis of mitochondrial DNA placed SSA1-SG1 and SSA1-SG2 in different haplotype groups within SSA1; however, nuclear analyses based on several methods revealed substantive gene flow between these two haplotypes. The ability of these two groups to interbreed and exchange genetic material resulted in there being no significant genetic differentiation between the individuals of both groups. The homogenisation of this group from potentially two different maternal lineages probably resulted in the maintenance and increase of SSA1-SG2 over the years. Similar results were observed from a genomic approach, showing no differences between SSA1-SG2 and SSA1-SG1 from Burundi, Tanzania, Rwanda or the Democratic Republic of Congo (Wosula et al. 2017). These results collectively indicate that SSA1-SG2 and SSA1-SG1 should not be considered as different entities, but only as different mitochondrial haplotypes within the SSA1 species.

Nuclear analyses from 1997 sampling also revealed that SSA2 individuals analysed were considered as a separate group to SSA1; however, with a signal of low shared background between both groups. This weak signal could be explain by the fact that both species are closely related ones.

Similar results were seen in the recent genomic analysis by Wosula *et al. (Wosula et al. 2017)* and had been observed in La Réunion between the invasive Middle East Asia minor 1 (MEAM1) and indigenous Indian Ocean (IO) species (Delatte et al. 2006). High abundant SSA1 populations and low abundant SSA2 populations in sympatry might have created conditions favouring mating between those groups, which could have resulted in few cases of mating success between both cryptic species.

Our study also revealed no new populations between 1997 and 2017, but a significant genetic difference between the two collection periods. This is clearly shown in the Bayesian analysis structure (Fig. 2.3b) with the dominance of one cluster at K3 for 2017 SSA1 populations, whereas the two other genetic clusters characterised the 1997 SSA1 populations. Despite the variations in distribution of genetic clusters, we also observed mixed genetic patterns within populations between the years.

The Bayesian analyses, DAPC (BIC criteria) and PCA all showed structuring of SSA1 putative species into three genetic clusters that can interbreed. However, despite the gene flow patterns between several individuals, this structuring into three genetic clusters was stable between 1997 and 2017 and the individuals did not completely homogenise into a single population, with significant differentiation observed between populations of both years. Although the reasons for this are not entirely clear, mating preferences or other specific loose barriers to hybridisation may act to support this pattern. Presence of different symbiont communities could also be a factor. Indeed, some symbionts are known to play such a role in other insects (O'Neill et al. 1992, Kikuchi 2009) as well as whiteflies, where a specific bacterial community (*Arsenophonus* and/or *Cardinium*) had been partly implicated in manipulating reproduction of MEAM I and IO species (Thierry et al. 2011). SSA1 supports a high bacterial diversity (Ghosh et al. 2015, Tajebe et al. 2015); however, no link has yet been established between the complex bacterial community and hybridisation barriers. Further studies should be conducted to better understand the roles of endosymbionts in different *B. tabaci* species.

Despite the moderate null allele frequencies detected in our dataset, our results remained consistent through the four different analyses.

All analyses produced similar patterns, which indicates the robustness of our results. All results obtained here categorically reject the hypothesis that new outbreaks of whiteflies in Uganda in the 1990s were due to the arrival of a new population or species of whiteflies (Legg et al. 2014b). Nevertheless, frequency of specific genetic clusters significantly changed over the studied 20-year period within the SSA1 species, with 2017 populations having a strong signature of a recent bottleneck event. It is possible that the most abundant genetic cluster comprising SSA1-SG1 and SSA1-SG2 might have overcome or displaced the previous most abundant genetic clusters. Correspondingly, three new hypotheses might be raised to explain the observed results: (i) the previous "old" dominant genetic clusters might be less fit for new cassava cultivars released in Uganda, (ii) environmental change occurred within the studied 20-year period and the SSA1-SG1 and SSA1-SG2 cluster was preferably adapted to it and (iii) the re-emergence of CBSD in Uganda in the early 2000s (Alicai et al. 2007). Confirming these hypotheses will require further experiments.

The strategy of using disease-resistant cultivars has not proved effective in combating CMD and CBSD. Some 'improved' varieties such as TME 14 and TME 204 became susceptible in Uganda (Howeler et al. 2013) and many virus-resistant cassava varieties are highly susceptible to whiteflies (Omongo et al. 2012). The intensification of cassava production to meet the high demand for food under increasing human population in the era of climate change might be impossible without the concomitant control of *B. tabaci* populations and development of virus-resistant crop varieties. This can only be achieved by a better understanding of the main viral vectors, which will facilitate design and selection of appropriate disease management and control measures.

## Acknowledgements

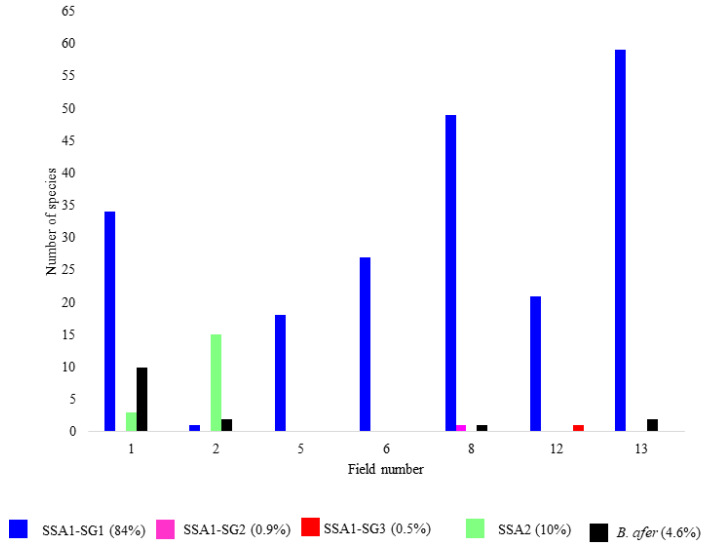
We would like to thank all farmers from Uganda that allowed us to sample whiteflies in their cassava fields for their warm welcome during the survey. We also would like to thank the field team of National Crops Resources Research Institute (NaCRRI) for their help in the survey and E. Chapier for technical assistance in screening the microsatellite primers of the bank.

This work was supported by the Natural Resources Institute, University of Greenwich, from a grant provided by the Bill & Melinda Gates foundation (Grant Agreement OPP1058938), and by CIRAD and the European Agricultural Fund for Rural Development (EAFRD). The authors acknowledge the Plant protection Plateform (3P, IBISA). We would like to thank both anonymous referees for the remarks that helped us to greatly improve this manuscript.

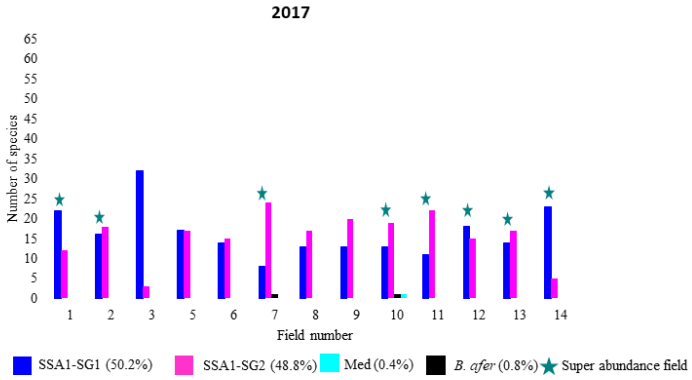
**Authors' contributions**

H.D, J.C and M.N.M. designed experiment, H.M.A, H.D, M.N.M., J.C and C.A.O conducted field sampling and data collection. H.M.A, H.E.H, H.D. and C.S performed laboratory analysis. H.M.A, H.D and C.S carried out data analysis. H.M.A and H.D drafted manuscript. M.N.M., J.C and C.A.O edited manuscript.

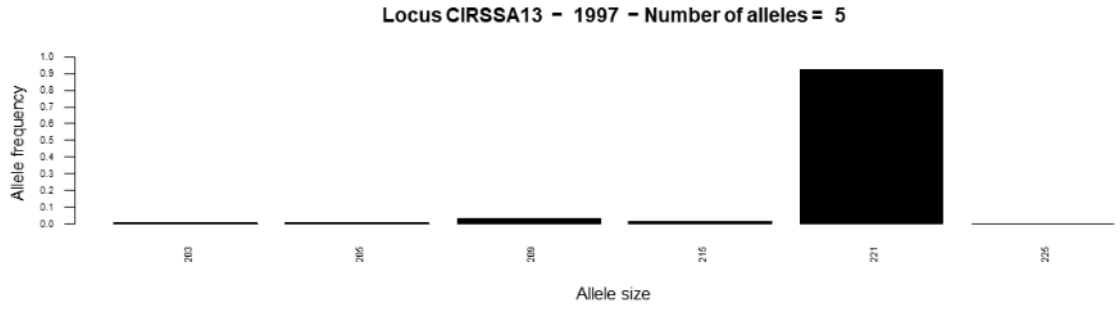
**Supplementary information:**




**Supp Figure 2.1:** Species distribution per field for samples collected in Uganda 1997




**Supp Figure 2.2:** Species distribution per field for samples collected in Uganda 2017


Locus CIRSSA13 – 1997 – Number of alleles = 5
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0.3
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0.7
0.8
0.9
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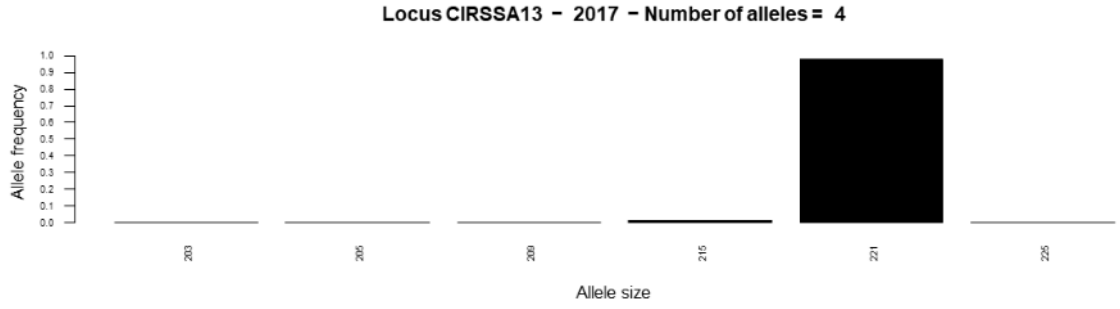
203
205
209
215
221
225
Allele size


Locus CIRSSA13 – 2017 – Number of alleles = 4
Allele frequency
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0.3
0.4
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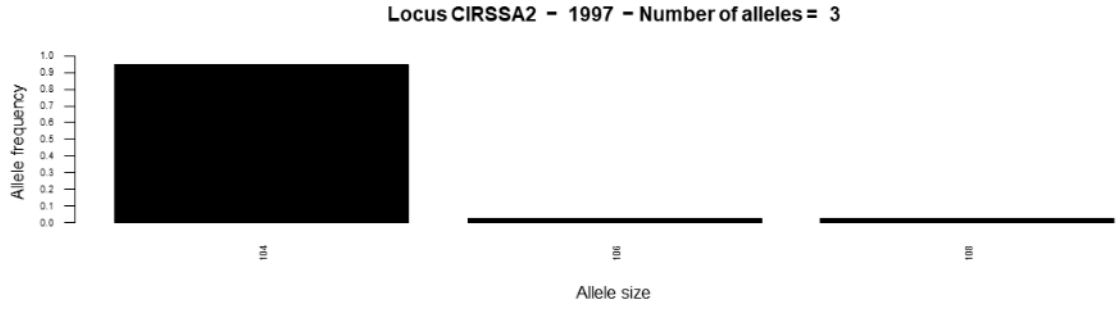
0.7
0.8
0.9
1.0
203
205
209
215
221
225
Allele size


Locus CIRSSA2 – 1997 – Number of alleles = 3
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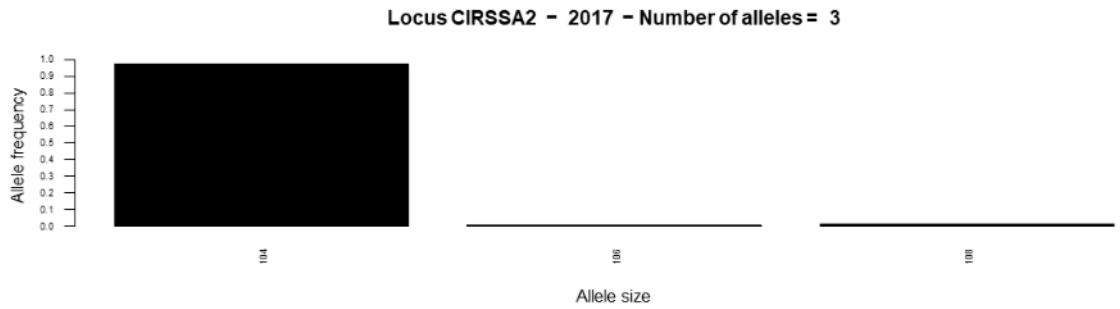
0.6
0.7
0.8
0.9
1.0
104
106
108
Allele size


Locus CIRSSA2 – 2017 – Number of alleles = 3
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0.5
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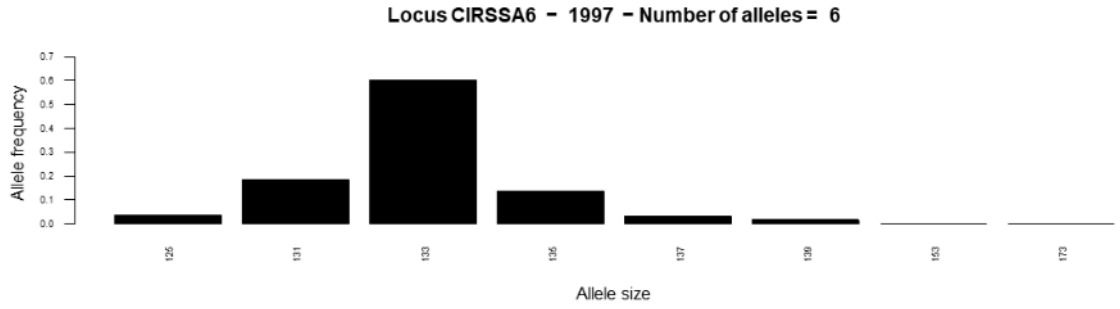
0.7
0.8
0.9
1.0
104
106
108
Allele size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Allele frequency
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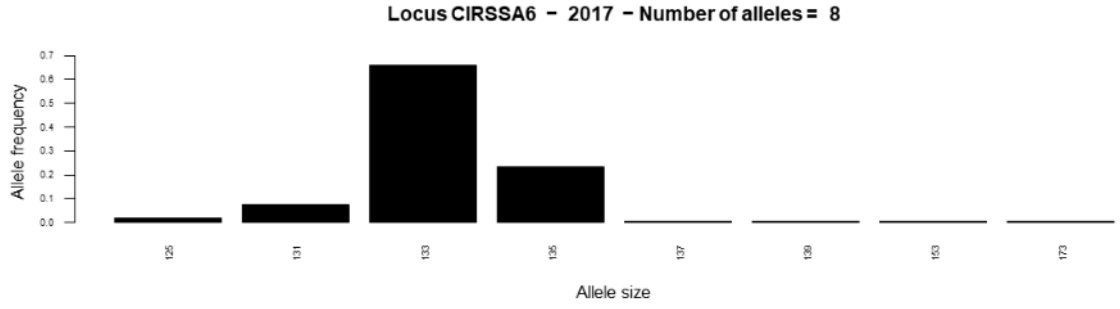
0.4
0.5
0.6
0.7
125
131
133
135
137
139
153
173
Allele size


Locus CIRSSA6 – 2017 – Number of alleles = 8
Allele frequency
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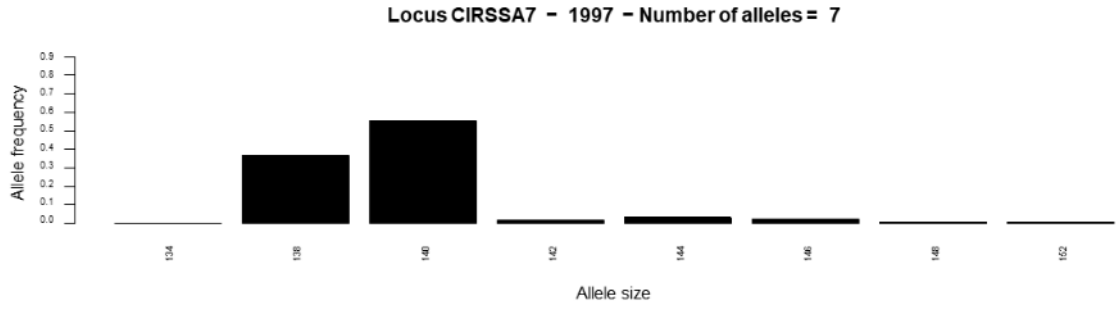
0.7
125
131
133
135
137
139
153
173
Allele size


Locus CIRSSA7 – 1997 – Number of alleles = 7
Allele frequency
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0.2
0.3
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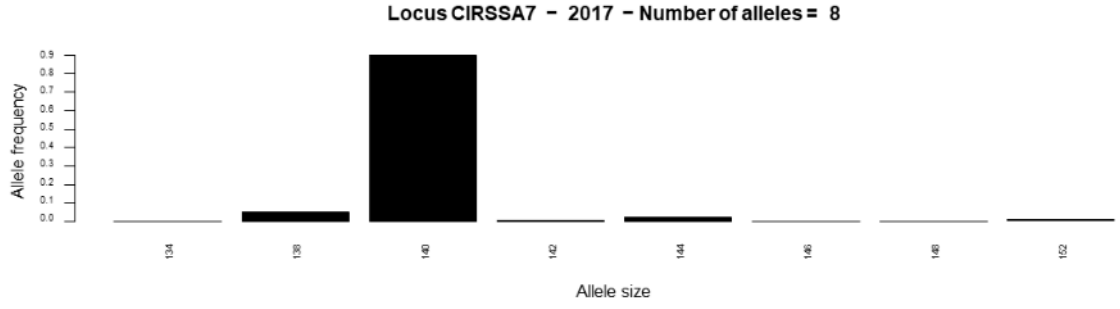
0.6
0.7
0.8
0.9
134
138
140
142
144
146
148
152
Allele size


Locus CIRSSA7 – 2017 – Number of alleles = 8
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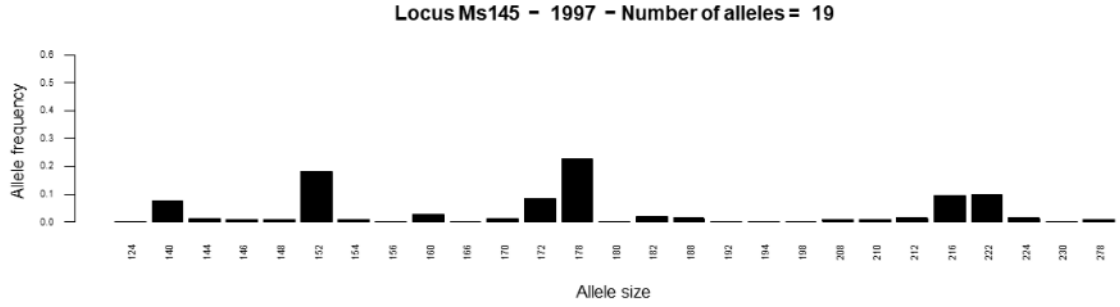
0.8
0.9
134
138
140
142
144
146
148
152
Allele size


Locus Ms145 - 1997 - Number of alleles = 19
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0.5
0.6
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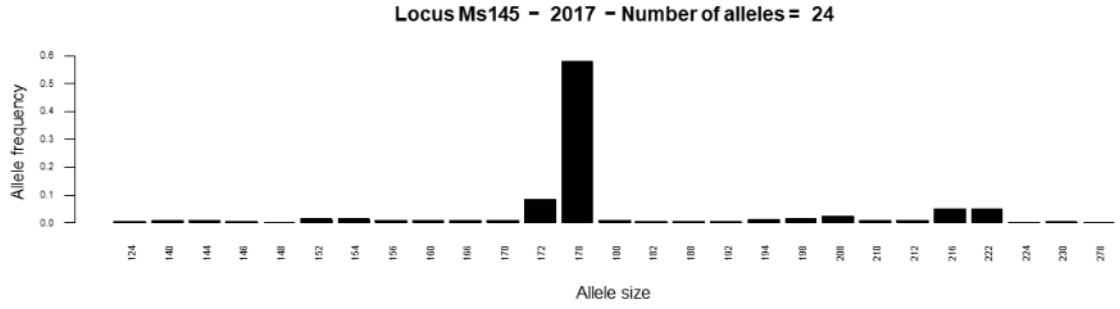
Allele size


Locus Ms145 - 2017 - Number of alleles = 24
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0.6
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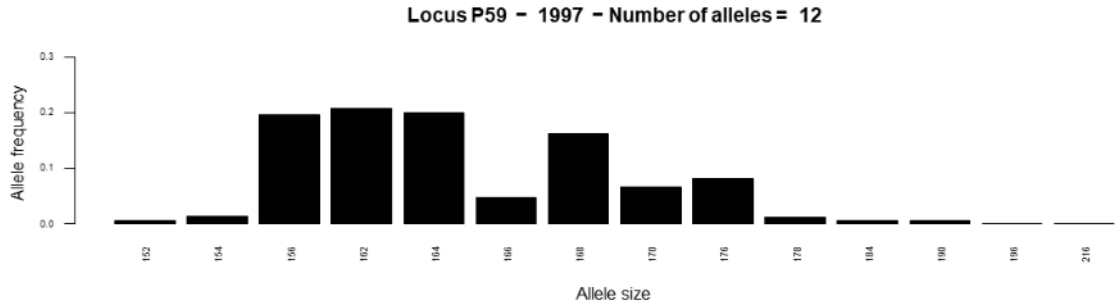
Allele size


Locus P59 - 1997 - Number of alleles = 12
Allele frequency
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0.3
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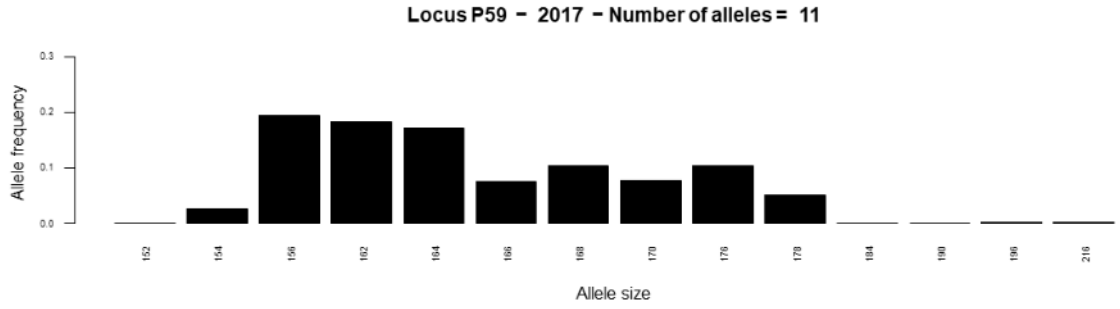
Allele size


Locus P59 - 2017 - Number of alleles = 11
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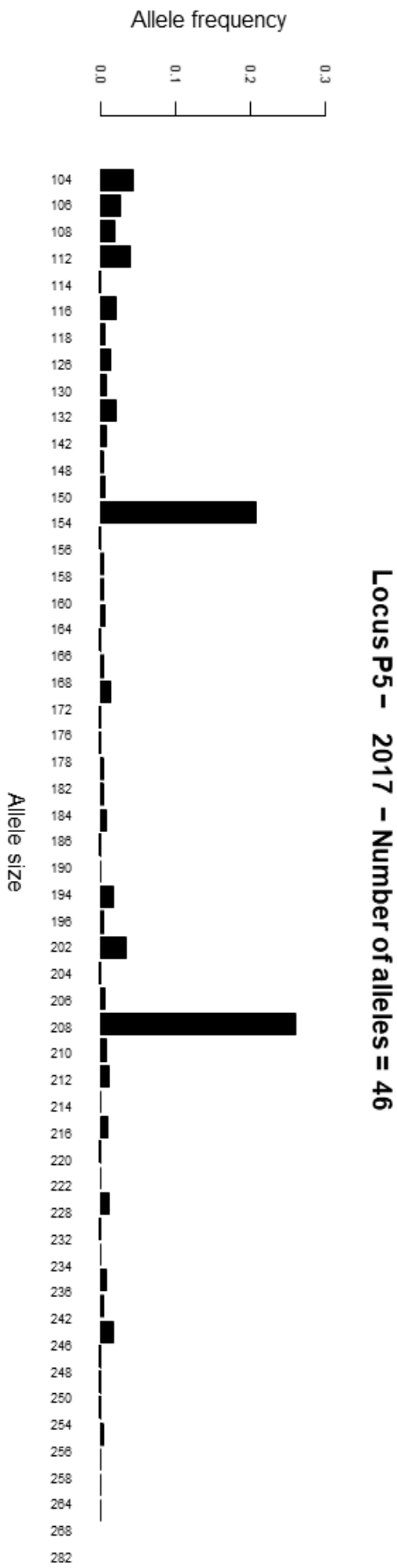
Allele size


Allele frequency
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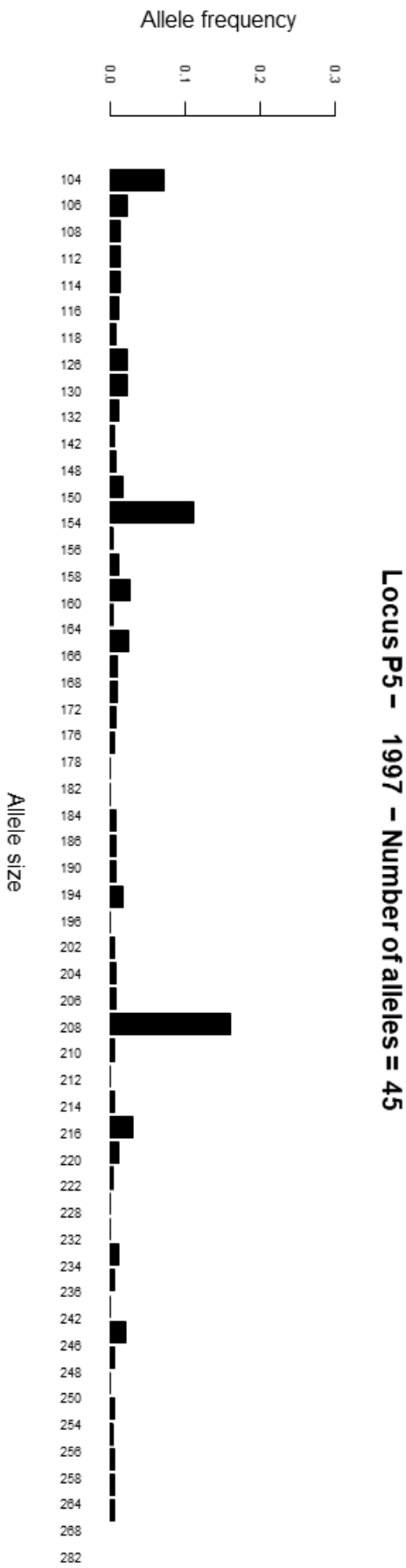
212
214
216
220
222
228
232
234
236
242
246
248
250
254
256
258
264
268
282
Allele size
Locus P5 – 2017 – Number of alleles = 46


Allele frequency
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0.3
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108
112
114
116
118
126
130
132
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154
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212
214
216
220
222
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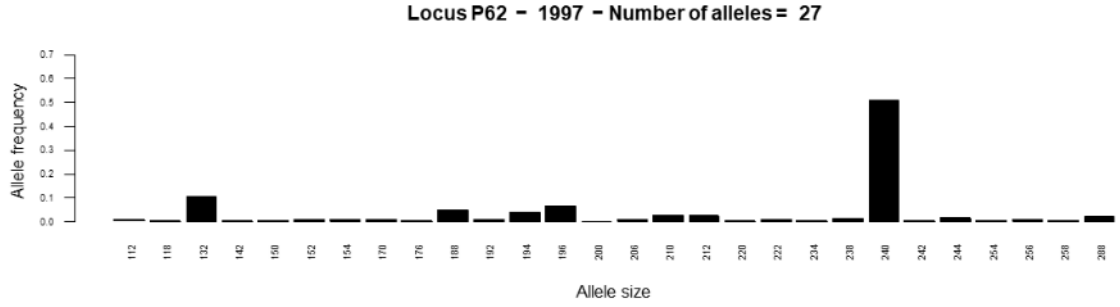
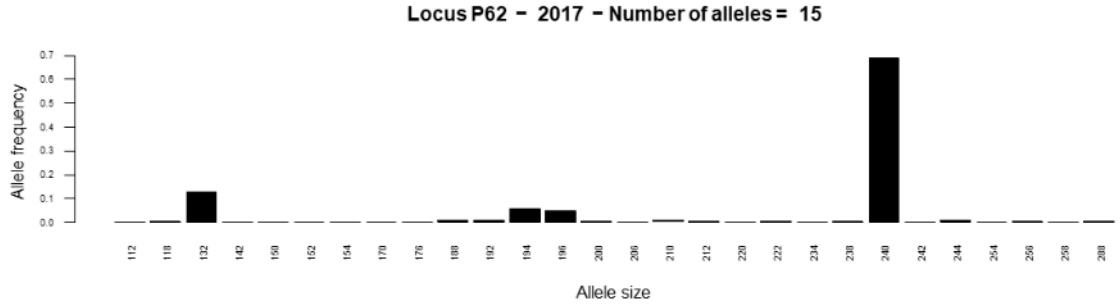
Allele size
Locus P5 – 1997 – Number of alleles = 45


Locus P62 - 1997 - Number of alleles = 27
Allele frequency
Allele size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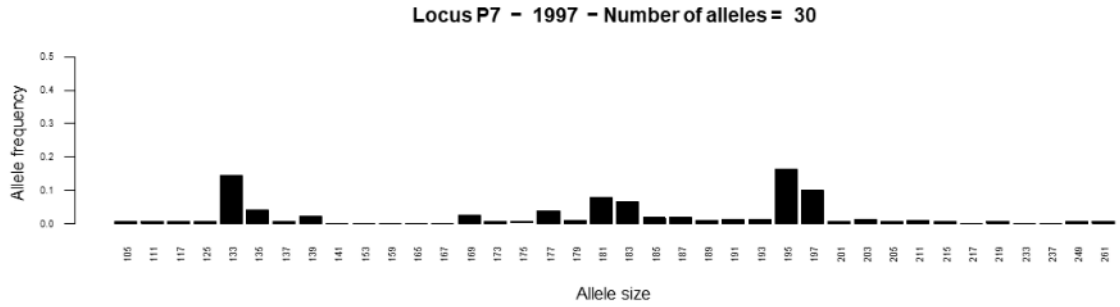
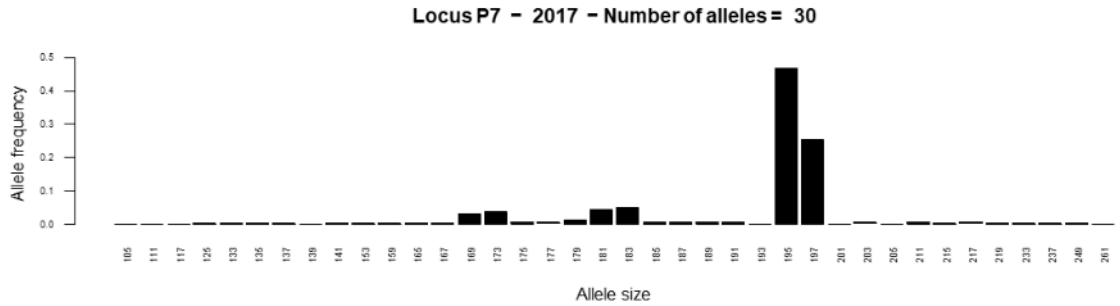
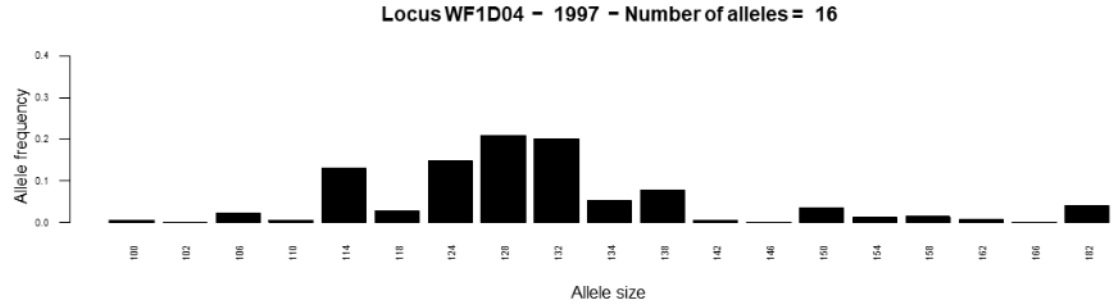
Allele frequency
Allele size


Locus P7 - 1997 - Number of alleles = 30
Allele frequency
Allele size


Locus P7 - 2017 - Number of alleles = 30
Allele frequency
Allele size


Locus WF1D04 - 1997 - Number of alleles = 16
Allele frequency
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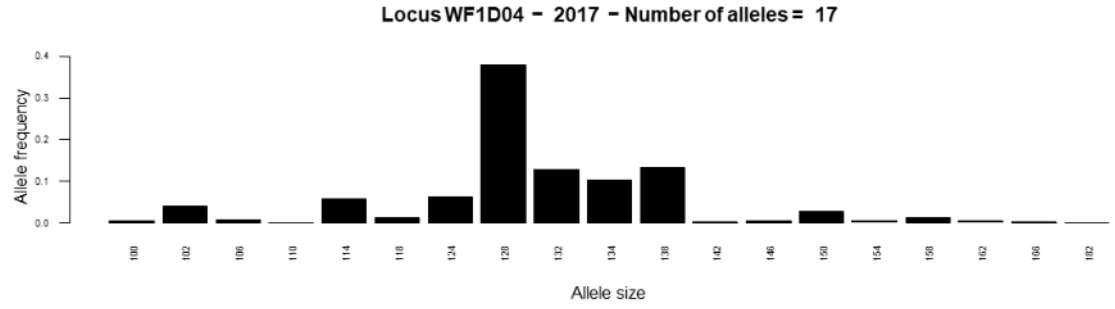
0.4
100 102 106 110 114 118 124 128 132 134 138 142 146 150 154 158 162 166 182
Allele size


Locus WF1D04 - 2017 - Number of alleles = 17
Allele frequency
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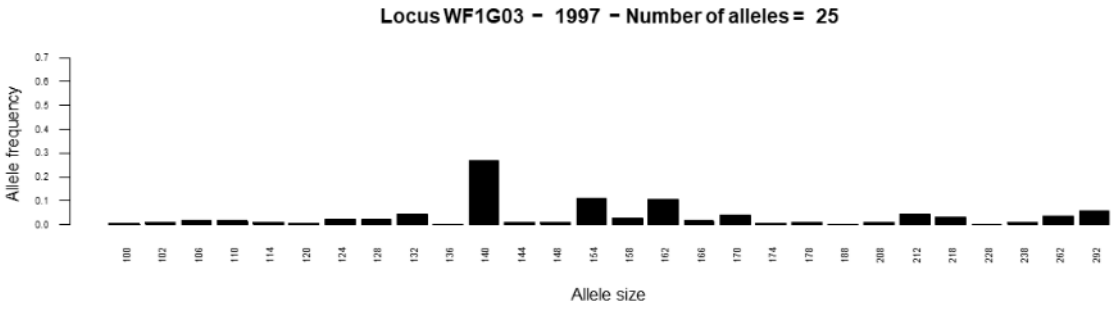
Allele size


Locus WF1G03 - 1997 - Number of alleles = 25
Allele frequency
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0.2
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0.6
0.7
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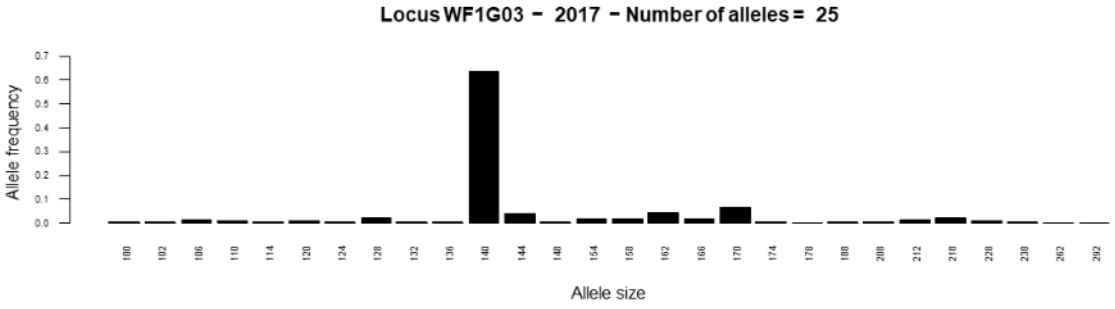
Allele size


Locus WF1G03 - 2017 - Number of alleles = 25
Allele frequency
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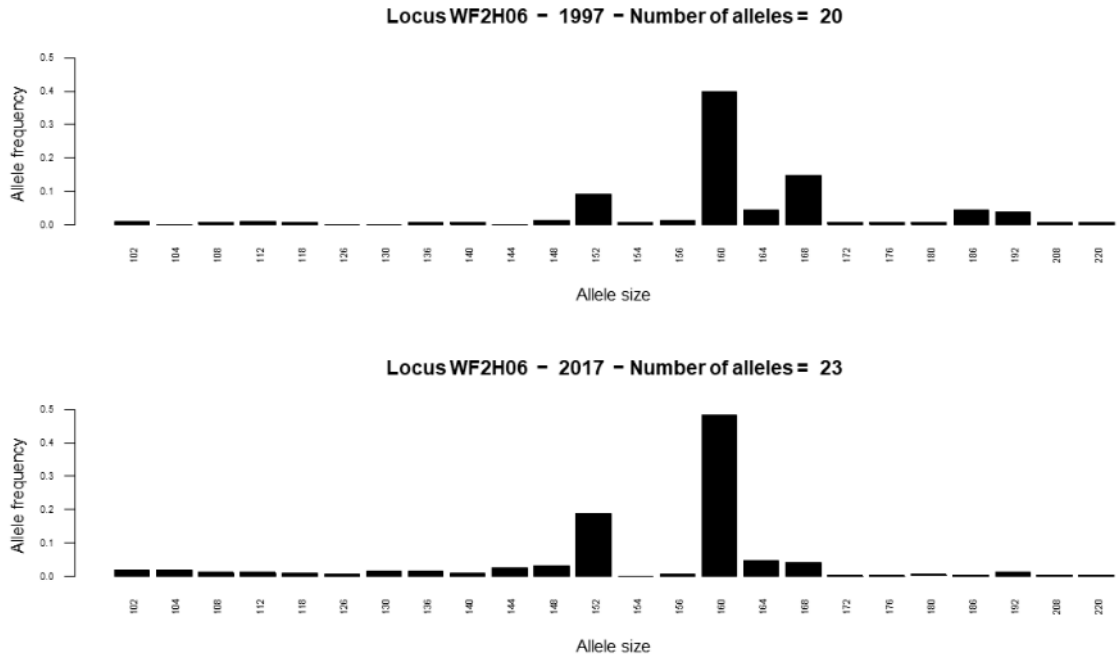
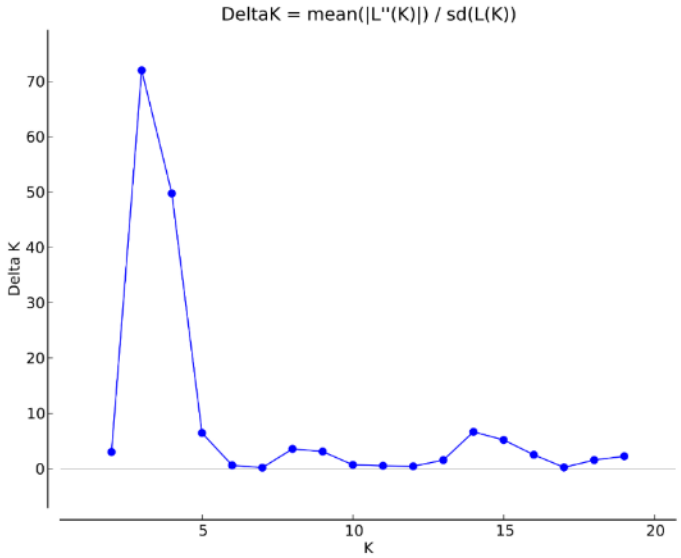
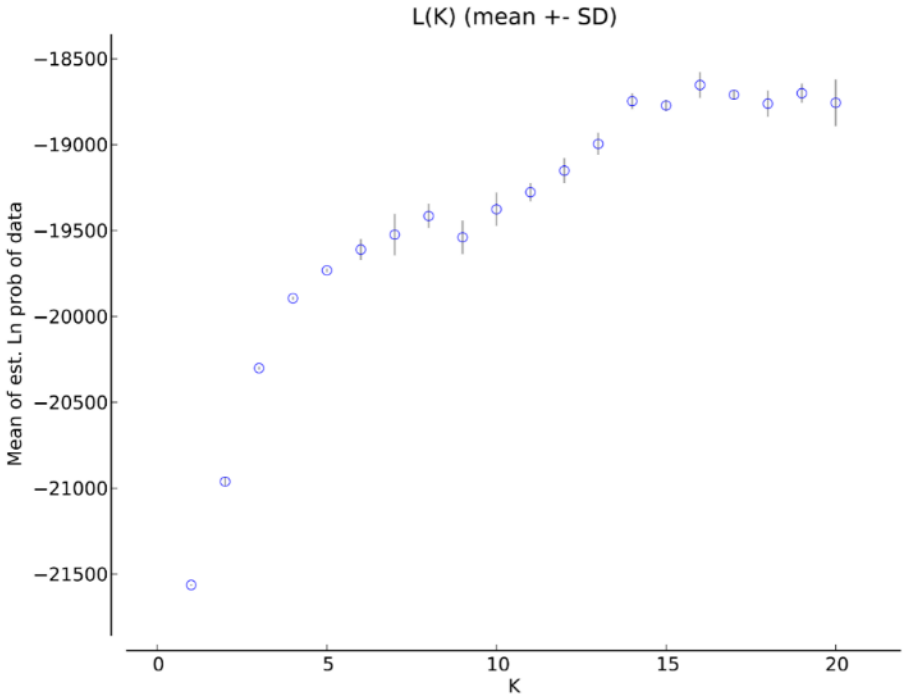
0.1
0.2
0.3
0.4
0.5
0.6
0.7
100 102 106 110 114 120 124 128 132 136 140 144 148 154 158 162 166 170 174 178 188 208 212 218 228 238 262 292
Allele size



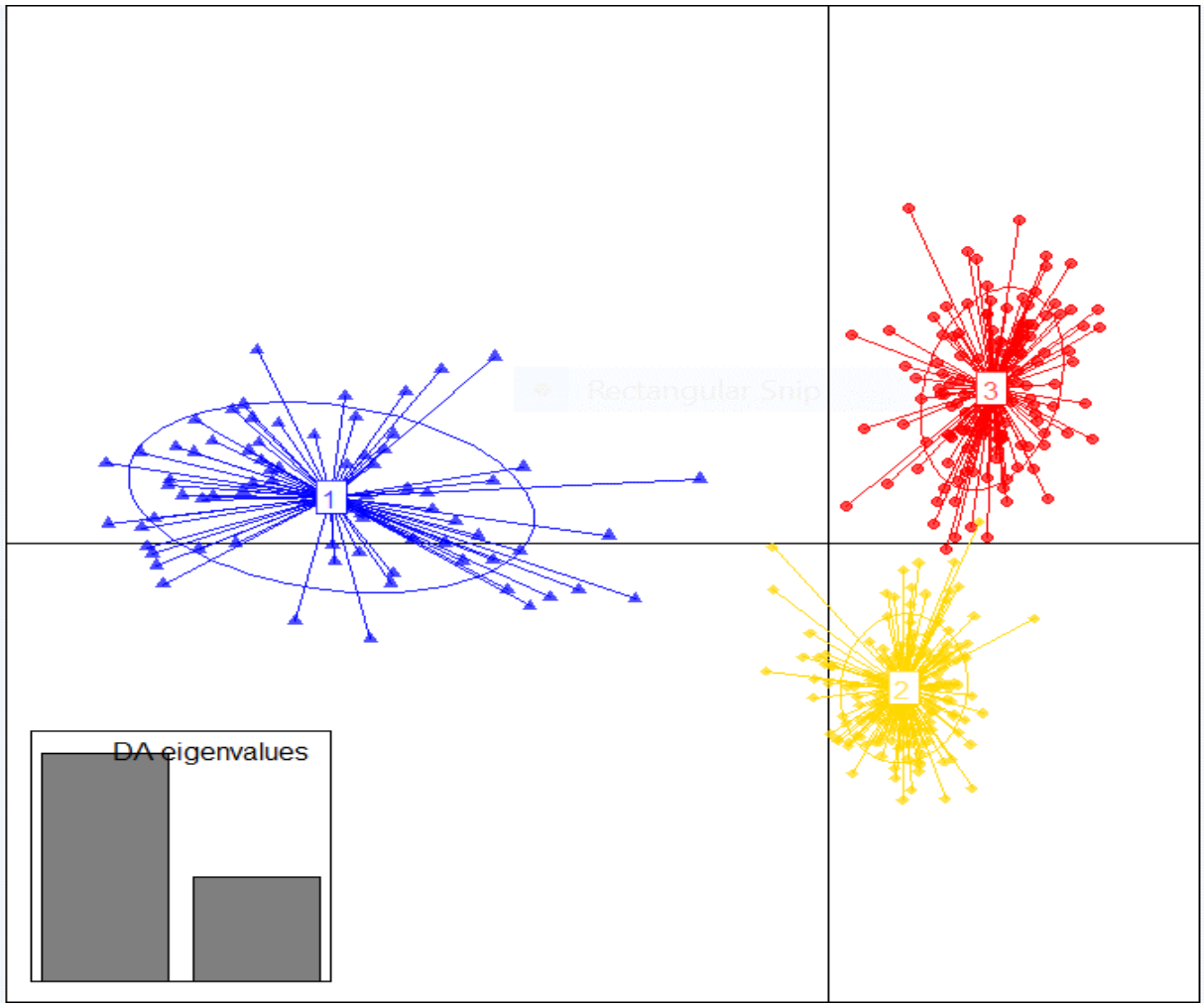

**Supplementary Fig. 2.3**: Histogram presenting the frequency of allele distribution per each microsatellite locus used and in each sampling year.




**Supplementary Figure 2.4a:** Plot showing the number of genetic clusters K against the ΔK estimator derived from STRUCTURE HARVESTER using Evano et al. (2005) method.




**Supplementary Figure 2.4b:** Plot showing the number of likely genetic clusters (K) against the estimated Ln probability of data.




**Supplementary Figure 2.5**: DAPC analysis of *B. tabaci* population collected from Uganda, Presented at K=3, Cluster one and two contained 2017 population while cluster three contained 1997 population.

**Supplementary Table 2.1:** Population genetic diversity indices within *B. tabaci* collected in 1997 and 2017.

| Population/Fno. | n | NA | CI | He (sd) | Hn.b. | Ho (sd) | Fis | Ar |
|---|---|---|---|---|---|---|---|---|
| **SSA1SG1/G2** | | | | | | | | |
| F1-2017 | 35 | 8.67 | 0.15-0.26 | 0.54(0.3) | 0.55(0.3) | 0.44(0.25) | 0.19 | 1.55 |
| F1-1997 | 32 | 8.75 | 0.41-0.52 | 0.66(0.24) | 0.67(0.25) | 0.33(0.24) | 0.5 | 1.67 |
| F2-2017 | 35 | 8.08 | 0.20-0.32 | 0.53(0.3) | 0.54(0.3) | 0.4(0.23) | 0.27 | 1.54 |
| F2-1997 | 1 | – | – | – | – | – | – | – |
| F3-2017 | 35 | 7.42 | 0.12-0.25 | 0.48(0.27) | 0.49(0.27) | 0.39(0.25) | 0.21 | 1.49 |
| F5-2017 | 35 | 8.58 | 0.11-0.22 | 0.54(0.3) | 0.55(0.31) | 0.44(0.27) | 0.2 | 1.55 |
| F5-1997 | 18 | 6.92 | 0.36-0.52 | 0.62(0.27) | 0.64(0.28) | 0.32(0.32) | 0.5 | 1.64 |
| F6-2017 | 30 | 7.75 | 0.26-0.41 | 0.56(0.28) | 0.57(0.28) | 0.35(0.21) | 0.38 | 1.57 |
| F6-1997 | 24 | 7.83 | 0.37-0.44 | 0.67(0.22) | 0.69(0.23) | 0.39(0.22) | 0.44 | 1.69 |
| F7-2017 | 34 | 8.58 | 0.22-0.35 | 0.57(0.27) | 0.58(0.27) | 0.41(0.21) | 0.29 | 1.58 |
| F8-2017 | 31 | 8 | 0.21-0.30 | 0.52(0.26) | 0.53(0.26) | 0.39(0.22) | 0.27 | 1.53 |
| F8-1997 | 34 | 8.92 | 0.39-0.56 | 0.66(0.26) | 0.67(0.26) | 0.35(0.23) | 0.48 | 1.67 |
| F9-2017 | 34 | 8.5 | 0.18-0.35 | 0.56(0.24) | 0.57(0.25) | 0.4(0.24) | 0.3 | 1.57 |
| F10-2017 | 33 | 8.17 | 0.25-0.36 | 0.55(0.28) | 0.56(0.28) | 0.39(0.21) | 0.31 | 1.56 |
| F11-2017 | 35 | 8.83 | 0.31-0.40 | 0.57(0.26) | 0.58(0.26) | 0.38(0.22) | 0.36 | 1.58 |
| F12-2017 | 35 | 8.25 | 0.22-0.32 | 0.53(0.26) | 0.54(0.27) | 0.39(0.19) | 0.29 | 1.54 |
| F12-1997 | 19 | 7.17 | 0.49-0.64 | 0.63(0.27) | 0.64(0.28) | 0.3(0.26) | 0.55 | 1.64 |
| F13-2017 | 35 | 8.08 | 0.19-0.36 | 0.51(0.29) | 0.52(0.3) | 0.39(0.23) | 0.25 | 1.52 |
| F13-1997 | 57 | 11.67 | 0.35-0.44 | 0.65(0.27) | 0.66(0.27) | 0.39(0.25) | 0.41 | 1.66 |
| F14-2017 | 35 | 7.83 | 0.17-0.30 | 0.51(0.27) | 0.52(0.27) | 0.39(0.23) | 0.25 | 1.52 |
| **SSA2** | | | | | | | | |
| F1-1997 | 3.00 | 2.50 | 0.41-0.62 | 0.43(0.22) | 0.52(0.27) | 0.22(0.26) | 0.62 | 2.50 |
| F2-1997 | 12.00 | 4.92 | 0.36-O.55) | 0.60(0.24) | 0.63(0.25) | 0.30(0.28) | 0.54 | 3.08 |

Population and field number where individuals collected (population/Fn), number of individuals sampled (n), mean number of alleles per population (NA), confidence interval (CI), expected heterozygosity (He), observed heterozygosity (Ho), fixation indices (Fis) presented together with p value from Hardy- Weinberg equilibrium test (* significant at $p < 0.05$) and Ar = allele richness and – no enough samples

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# Chapter 3

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# Chapter 3: *B. tabaci* species distribution in Tanzania and Uganda: their genetic diversity and structuring according to agroecological zones, host plant utilization and population dynamic status

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**Abstract**

*B. tabaci* outbreak is an increasing concern in sub–Sahara Africa, because of the damage it causes to major staple food crop: cassava. The insect had been rapidly spread the cassava mosaic and cassava brown streak virus diseases (CMD and CBSD) in major sub–Sahara Africa cassava growing regions. The purpose of this research was to investigate the spread of the outbreaking cassava *B. tabaci* populations from the origin in Uganda to the neighbouring Tanzania. Using the mtCOI barcording sequences and microsatellite markers, we analysed the genetic diversity and population structure of *B. tabaci* (*n* = 1983 and 661) on different host plants (*n* = 43) and agroecological zones from the two couontries. The results revealed several new and important findings; (i) genetic variation for the dominant species IO in Tanzania and SSA1 (SG1 and SG2) in Uganda, (ii) the SSA12, SSA13 and Ugsp only found in Uganda while SSA1–SG3 observed only in the coastal parts of Tanzania, (iii) the population genetic structure between the two countries appeared to differ, (iv) SSA1–SG1 and SSA1–SG2 can hybridize, (v) traces of gene flow between SSA1–SG1/SG2 and –SG3 and, finally (vi) the IO was found on several host plants including cassava. These results confirm that the local Tanzanian populations were capable developing into an outbreaking populations that they were not necessarily spread from the original Ugandan populations.

**Keywords:** *B. tabaci*, mtCOI, microsatellite marker, genetic clusters, host plant

## Introduction

Population outbreaks can be due to the introduction of a new species to a certain area or growth of native populations in favourable conditions (Kobayashi et al. 2011). An outbreaking population is characterized by the rapid change in population density from generation to generation. This change can occur within a growing season or over a period of years (Berryman 1987). Climatic conditions, host range usage shift and natural enemies are among factors that can trigger those outbreaks (Kobayashi et al. 2011). A modelling study suggested that a severe drought could induce mosquito outbreaks in wetland areas (Chase and Knight 2003). The effects of an insect outbreak include severe consequences, such as the spread of diseases in humans (i.e. malaria and dengue, vectored by mosquitoes) or plants (i.e pathogens transmitted by insects or direct effect by sap spoliation) (Navas-Castillo et al. 2000, Legg et al. 2006, Hillocks and Maruthi 2015).

Among the known insect pest vectors, *Bemisia tabaci* is one of the devastating species with capability to transmit plant viruses which affect agricultural crops (Maruthi et al. 2005, Polston et al. 2014). *B. tabaci* occurred in both tropical and subtropical area Worldwide (Oliveira et al. 2001). It is a species complex morphologically indistinguishable with more than 40 cryptic species (Dinsdale et al. 2010, De Barro et al. 2011, Lee et al. 2013, Mugerwa et al. 2018). The mtCOI barcoding sequencing with an initial threshold of 3.5% between species was used to differentiate the many species within the *B. tabaci* group (Boykin et al. 2007, Dinsdale et al. 2010, De Barro et al. 2011). This was proposed to be extended to 4.0% subsequently (Lee et al. 2013).

*B. tabaci* is polyphagous found on >1000 different plants belonging to over 80 plant families including Malpighiales, Solanales, Malvales and Fabales (Mound 1963, Byrne and Bellows Jr 1991, Secker et al. 1998, Oliveira et al. 2001, Li et al. 2011).Several whitefly species have been identified in sub–Sahara Africa including: cassava colonizing groups sub–Sahara Africa 1–5 (SSA1 to SSA5) and non–cassava colonizing groups such as Med (Q1, Q2 and Q3), Med ASL, MEAM1, Indian ocean (IO), East Africa 1 (EA1) and Uganda sweetpotato (Ugsp) (Burban et al. 1992, Berry et al. 2004, Sseruwagi et al. 2005, Sseruwagi et al. 2006, Mugerwa et al. 2012, Legg et al. 2014b, Tajebe et al. 2015a, Tocko-Marabena et al. 2017, Mugerwa et al. 2018). Recently, five new *B. tabaci* species were identified in Uganda SSA9 to SSA13 (Mugerwa et al. 2018), two of these SSA9 and SSA10 were found predominantly on cassava.

The distribution of those species varies between countries. SSA1 had found throughout the SSA regions but dominating in East Africa (Gnankine et al. 2013b, Legg et al. 2014b, Tocko-Marabena et al. 2017, Wosula et al. 2017, Mugerwa et al. 2018). The other SSA species: SSA2 to SSA4 were reported in West and Central Africa regions (Berry et al. 2004, Gnankine et al. 2013b, Ghosh et al. 2015, Tocko-Marabena et al. 2017, Wosula et al. 2017), while SSA5 was found in Ivory Coast and South Africa (Berry et al. 2004, Esterhuizen et al. 2013). The Ugsp has been solely reported from Uganda (Sseruwagi et al. 2005, Mugerwa et al. 2018). The IO had a wide range of distribution, it was found from the Indian Ocean islands, through East Africa up to the Central Africa (Delatte et al. 2005, Sseruwagi et al. 2005, Mugerwa et al. 2012, Tajebe et al. 2015a, Tocko-Marabena et al. 2017). Other species like Med (Q1, Q2 and Q3), Med ASL and MEAM1 were also reported (Sseruwagi et al. 2005, Gueguen et al. 2010, Esterhuizen et al. 2013, Gnankine et al. 2013a, Gnankine et al. 2013b, Delatte et al. 2015, Mugerwa et al. 2018).

Over the past decades, *B. tabaci* outbreaks have been reported in many regions of sub–Sahara Africa (SSA) and the crops colonized suffering major yield reduction including cassava (Legg et al. 2002, Colvin et al. 2004, Tajebe et al. 2015a, Tocko-Marabena et al. 2017). The abundance of *B. tabaci* has increased more than 200-fold in recent years in many parts of East and Central Africa on cassava and other associated crops (Legg et al. 2002, Legg et al. 2014a, Tajebe et al. 2015a, Tocko-Marabena et al. 2017). These increases have resulted in pandemics of cassava mosaic virus disease (CMD) and cassava brown streak virus disease (CBSD) in major cassava growing regions within SSA (Legg et al. 2001, Legg et al. 2002, Sseruwagi et al. 2005, Legg et al. 2006, Legg et al. 2014b, Tajebe et al. 2015a, Tocko-Marabena et al. 2017).

Reemergence of CMD in Uganda during the late 1980s is thought to be the results of several combined factors including i) the recombination of two viruses: the *African cassava mosaic virus* (ACMV) with *East Africa cassava mosaic virus* (EACMV) that produced EACMV-Uganda variant (EACMV–Ug); and ii) the subsequent high abundance of whiteflies, which ensured rapid spread of the severe CMD pandemic to the neighboring countries (Otim-Nape et al. 1997, Legg et al. 2002, Colvin et al. 2004).

Understanding whitefly species distribution, their genetic diversity and structure is of great importance as it can facilitate the selection of appropriate management control measures. We tested the hypothesis that the *B. tabaci* outbreaks seen in Tanzania were a result of invasion from Ugandan populations. The objectives of this study were to understand the whitefly outbreaks on cassava by comparing Tanzanian and Ugandan populations from different sites, host plants and agroecological zones by population genetics approach.

## Material and methods

### Study area

This study was conducted in two East African countries: Tanzania and Uganda. The two countries dominated by tropical savanna, however they have different agroecological zones. Tanzania is characterised by arid, semiarid land, plateau, highland and coast zone with an estimated annual rainfall of 1150 mm. Tanzania rainfall is governed by two rain pattern: Bimodal pattern including the area in the Northern coast and Zanzibar, Eastern highland and Lake Victoria basin receiving heavy rainfall (masika) between March to May and short rainfall (vuli) between October to December and a unimodal rainfall pattern occurs at Southern, Central, Western, and South-eastern parts of the country receiving rainfall between December to April (Hamisi 2013). Elevation ranging from the sea to the peak of Mount Kilimanjaro (5895 m). Uganda is characterized by Lake Victoria crescent, pastoral rangelands, savanna grassland, highland and north eastern dryland. Uganda experiences two rainfall regime such as unimodal in the Northern part whereas bimodal in the regions near equator with major rainy season in March to May and shorter season in September to November (Kisembe et al. 2018). The estimated annual rainfall is 952 mm. The altitude ranges between 500 to 3500 masl.

### Sample collection

Major surveys were conducted from 20$^{th}$ to 28 of February 2016 in Tanzania, and 8$^{th}$ to 13$^{th}$ of February 2017 in Uganda. Whitefly samples were collected from a toal of 27 fields from Tanzania in the Northern (Arusha and Manyara), Central (Dodoma), Eastern (Morogoro), and Coastal mainland regions (Pwani and Dar es Salaam) as well as the Zanzibar Island (Unguja).

From Uganda, samples were collected from 14 fields from the Central region in seven districts (Mityana, Mpigi, Wakiso, Kalungu, Masaka, Rakai, and Gomba) (Table 3 1. Adult whiteflies were collected in a mixed cropping system in each site on all available plant species including weeds found surrounding cassava fields up to at a range of 5-10 meters. The survey was conducted along the main roads at ~50 Km intervals depending on the availability of cassava fields. A geographical positioning system (GPS) was used to record the coordinates in each field, and a map of sample positions was created in QGIS 2.18 (https://qgis.org; (Fig. 3.1).

Where possible up to a maximum of 50 adult whiteflies were collected from a total of 43 different host plants and these included: cassava (*Manihot esculenta*) as main crop, other crops were tomato (*Solanum lycopersicum*), eggplant (*Solanum melongena*), pumpkin (*Cucurbita moschata*), okra (*Abelmoschus esculentus*), watermelon (*Citrullus lanatus*), sweetpotato (*Ipomoea batatas*), cowpeas (*Vigna unguiculata*), green gram (*Vigna radiata*), cabbage (*Brassica oleracea*), groundnut (*Arachis hypogaea*), zucchini (*Cucurbita pepo*), sunflower (*Helianthus annuus*), beans (*Phaseolus vulgaris*) and different weeds of Malvaceae, Cleomaceae, Asteraceae, Solanaceae, Lamiaceae, Euphhobiaceae, Nyctaginaceae, and Brassicaceae (Table 3.1). Samples were collected by using a mouth aspirator and stored in eppendorf tubes containing absolute ethanol prior to laboratory analysis. Each adult whitefly sample collected consisted of individuals sampled at the same time, the same site and on the same host species (Table 3.1).

**Adult *Bemisia tabaci* abundance, CMD and CBSD severity**

Five cassava plants were randomly selected per field, the number of *B. tabaci* adults were counted on the uppermost five young plant leaves of each selected plant according to (Sseruwagi et al. 2004b). We classified the whitefly abundance into two classes: all host plants within a field with less than 100 whitefly counts as “less abundant” and all fields with at least one host plant above 100 as “super abundant”. Whitelfy counts were made on cassava plant species in the collection site. The presence of silver leaf symptoms on *C. moschata* were recorded when present together with adult whitefly sampling on this host. The CMD and CBSD symptoms were visually scored on cassava using the scale 1–5 where, 1 indicates no disease symptoms and 5 severe disease symptoms, as explained by (Mahungu et al. 1994).

Table 3. 1: Host plants and location of sampled adult *B. tabaci* in Tanzania and evidence of disease on cassava

| Region | F/N | CD | Common name | Plant order | Family Name | *Scientific name* | CV | MAP | Latitude | Longtude | WC | CMD | CBSD | SL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F1 | 2/20/2016 | Tomato | Solanales | Solanaceae | *Solanum lycopersicum* | | 2 | S3°26.640' | E36°12.167' | 1 | NA | NA | |
| | F1 | 2/20/2016 | Eggplant | Solanales | Solanaceae | *Solanum melongena* | | 2 | | | 1 | NA | NA | |
| | F1 | 2/20/2016 | Sweetpotato | Solanales | Convolvulaceae | *Ipomea batata* | | 0.5 | | | 1 | NA | NA | |
| | F1 | 2/20/2016 | Fish poison | Fabales | Fabaceae | *Tephrosia vogelii* | | | | | 1 | NA | NA | |
| Arusha | F1 | 2/20/2016 | Kale | Brassicales | Brassicaceae | *Brassica oleracea* | | 0.75 | | | 1 | NA | NA | |
| | F1 | 2/20/2016 | Beans | Fabales | Fabaceae | *Phaseolus vulgaris* | | 1 | | | 1 | NA | NA | |
| | F2 | 2/20/2016 | Wireweed | Malvales | Malvaceae | *Sida acuta* | | | | | 1 | NA | NA | |
| | F2 | 2/20/2016 | Moon flower | Solanales | Solanaceae | *Datura stramonium* | | | | | 1 | NA | NA | |
| | F3 | 2/20/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Wild cassava | | S04°06.404' | E035°45.694' | 1 | 2 | 1 | |
| | F3 | 2/20/2016 | Pumpkin | Cucurbitales | Cucurbitaceae | *Cucurbita* | | | | | 1 | NA | NA | NO |
| | F3 | 2/20/2016 | Wireweed | Malvales | Malvaceae | *Sida acuta* | | | | | 1 | NA | NA | |
| | F3 | 2/20/2016 | Eggplant | Solanales | Solanaceae | *Solanum melongena* | | | | | 1 | NA | NA | |
| Manyara | F3 | 2/20/2016 | Fire plant | Malpighiales | Euphorbiaceae | *Euphorbiaceae sp* | | | | | 1 | NA | NA | |
| | F4 | 2/20/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Kigami | 7 | S04°06.765' | E035°40.296' | 1 | 2 | 1 | |
| | F4 | 2/20/2016 | Fish poison | Fabales | Fabaceae | *Tephrosia vogelii* | | | | | 1 | NA | NA | |
| | F4 | 2/20/2016 | Groundnut | Fabales | Fabaceae | *Arachis hypogaea* | | | | | 1 | NA | NA | |
| | F4 | 2/20/2016 | Bristly starbur | Asterales | Asteraceae | *acanthospermum hispidum* | | | | | 1 | NA | NA | |
| | F5 | 2/21/2016 | Cowpea | Fabales | Fabaceae | *Vigna unguiculata* | | | S04°55.515' | E035°48.562' | 1 | NA | NA | |
| | F5 | 2/21/2016 | Sweetpotato | Solanales | Convolvulaceae | *Ipomea batata* | | | | | 1 | NA | NA | |
| | F5 | 2/21/2016 | Pumpkin | Cucurbitales | Cucurbitaceae | *Cucurbita* | | | | | 1 | NA | NA | YES |
| | F6 | 2/21/2016 | Cassava | Malpighiales | Euphhobiaceae | *Manihot esculenta* | Kaniki | 13 | S05°04.536' | E035°47.593' | 1 | 3 | 1 | |
| | F6 | 2/21/2016 | Groundnut | Fabales | Fabaceae | *Arachis hypogaea* | | | | | 1 | NA | NA | |
| | F6 | 2/21/2016 | Dicotyledone weed | | | | | | | | 1 | NA | NA | |
| | F6 | 2/20/2016 | Sesame | Lamiales | Pedaliaceae | *Sesamum indicum* | | | | | 1 | NA | NA | |
| | F7 | 2/21/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Unknown | 5 | S05°50.783' | E035°45.450' | 1 | 3 | 1 | |
| | F7 | 2/21/2016 | Sesame | Lamiales | Pedaliaceae | *Sesamum indicum* | | | | | 10 | NA | NA | – |
| | F7 | 2/21/2016 | Spider flower | Brassicales | Cleomaceae | *Cleome viscosa* | | | | | 1 | NA | NA | |
| | F7 | 2/20/2017 | Cucumber | Cucurbitales | Cucurbitaceae | *Cucumis sativus* | | | | | 1 | NA | NA | |
| | F7 | 2/21/2016 | Sweetpotato | Solanales | Convolvulaceae | *Ipomea batata* | | | | | 1 | NA | NA | |
| | F7 | 2/21/2016 | Pink morning glory | Solanales | Convolvulaceae | *Ipomea carnea* | | | | | 1 | NA | NA | |
| Dodoma | F8 | 2/21/2016 | Watermelon | Solanales | Convolvulaceae | *Citrullus lanatus* | | | S06°07.461' | E035°48.471' | 1 | NA | NA | |
| | F8 | 2/21/2016 | Azanza | Malvales | Malvaceae | *Thespesia garckeana* | | | | | 1 | NA | NA | |
| | F8 | 2/21/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Unknown | 2 | | | 1 | 2 | 1 | |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F8 | 2/21/2016 | Bristly starbur | Asterales | Asteraceae | *Acanthospermum hispidum* | | | | | 1 | NA | NA | |
| | F8 | 2/21/2016 | Cowpea | Fabales | Fabaceae | *Vigna unguiculata* | | | | | 1 | NA | NA | |
| | F8 | 2/21/2016 | Groundnut | Fabales | Fabaceae | *Arachis hypogaea* | | | | | 1 | NA | NA | |
| | F8 | 2/21/2016 | Tomato | Solanales | Solanaceae | *Solanum lycopersicum* | | | | | NA | NA | NA | |
| | F8 | 2/21/2016 | Okra | Malvales | Malvaceae | *Abelmoschus esculentus* | | | | | 1 | NA | NA | |
| | F8 | 2/21/2016 | Morning glorry | Solanales | Convolvulaceae | *Ipomea sp* | | | | | 1 | NA | NA | |
| | F8 | 2/21/2016 | Greengram | Fabales | Fabaceae | *Vigna radiata* | | | | | 1 | NA | NA | |
| | F9 | 2/22/2016 | Groundnut | Fabales | Fabaceae | *Arachis hypogaea* | | | S06°07.497' | E036°12.121' | 10 | NA | NA | |
| | F9 | 2/22/2016 | Cowpea | Fabales | Fabaceae | *Vigna unguiculata* | | | | | 10 | NA | NA | |
| | F9 | 2/22/2016 | Sunflower | Asterales | Asteraceae | *Helianthus* | | | | | 10 | NA | NA | |
| | F9 | 2/22/2016 | Morning glorry | Solanales | Convolvulaceae | *Ipomea sp* | | | | | 10 | NA | NA | |
| | F9 | 2/22/2016 | Wireweed | Malvales | Malvaceae | *Sida acuta* | | | | | 10 | NA | NA | |
| | F10 | 2/22/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | unknown | 11 | S06°02.759' | E036°35.372' | 1 | 1 | 1 | |
| | F10 | 2/22/2016 | Sunflower | Asterales | Asteraceae | *Helianthus* | | | | | 1 | NA | NA | |
| | F10 | 2/22/2016 | Watermelon | Solanales | Convolvulaceae | *Citrullus lanatus* | | | | | 1 | NA | NA | |
| | F10 | 2/22/2016 | Okra | Malvales | Malvaceae | *Abelmoschus esculentus* | | | | | 1 | NA | NA | |
| | F10 | 2/22/2016 | Cowpea | Fabales | Fabaceae | *Vigna unguiculata* | | | | | 1 | NA | NA | |
| | F10 | 2/22/2016 | Pumpkin | Cucurbitales | Cucurbitaceae | *Cucurbita* | | | | | 1 | NA | NA | NO |
| | F10 | 2/22/2016 | Dockeweed | Caryophyllales | polygonaceae | *Oxygonum sp* | | | | | 1 | NA | NA | |
| | F11 | 2/22/2016 | Spider flower | Brassicales | Cleomaceae | *Cleome viscosa* | | | S06°08.243' | E036°56.220' | 1 | NA | NA | |
| | F11 | 2/22/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Kaniki | 11 | | | 1 | 2 | 1 | |
| | F11 | 2/22/2016 | Rattlepods | Fabales | Fabaceae | *Crotalaria sp* | | | | | 1 | NA | NA | |
| | F11 | 2/22/2016 | Pumpkin | Cucurbitales | Cucurbitaceae | *Cucurbita* | | | | | 1 | NA | NA | YES |
| | F11 | 2/22/2016 | Moon flower | Solanales | Solanaceae | *Datura stramonium* | | | | | 1 | NA | NA | |
| | F11 | 2/22/2016 | Fire plant | Malpighiales | Euphorbiaceae | *Euphorbiaceae sp* | | | | | 10 | NA | NA | |
| | F11 | 2/22/2016 | Cowpea | Fabales | Fabaceae | *Vigna unguiculata* | | | | | 1 | NA | NA | |
| | F11 | 2/22/2016 | Azanza | Malvales | Malvaceae | *Thespesia garckeana* | | | | | 1 | NA | NA | |
| | F11 | 2/22/2016 | Sweetpotato | Solanales | Convolvulaceae | *Ipomea batata* | | | | | 1 | NA | NA | |
| | F12 | 2/22/2016 | Spider flower | Brassicales | Cleomaceae | *Cleome viscosa* | | | S06°22.700 | E37°19.733' | 10 | NA | NA | |
| | F12 | 2/22/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Unknown | 2 | | | 100 | 2 | 2 | |
| | F12 | 2/22/2016 | Erect boerhavia | Caryophyllales | Nyctaginaceae | *Boerhavia erecta* | | | | | 1 | NA | NA | |
| Morogoro | F12 | 2/22/2016 | Wireweed | Malvales | Malvaceae | *Sida acuta* | | | | | 10 | NA | NA | |
| | F13 | 2/22/2016 | Cowpea | Fabales | Fabaceae | *Vigna unguiculata* | | 2 | S06°40.550' | E37°37.517 | 1 | NA | NA | |
| | F13 | 2/22/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Shinatenga | 3 | | | 10 | 1 | 1 | |
| | F13 | 2/22/2016 | Pumpkin | Cucurbitales | Cucurbitaceae | *Cucurbita* | | 1.5 | | | 100 | NA | NA | YES |
| | F13 | 2/22/2016 | Sunflower | Asterales | Asteraceae | *Helianthus* | | | | | 1 | NA | NA | |
| | F13 | 2/22/2016 | Okra | Malvales | Malvaceae | *Abelmoschus esculentus* | | | | | 10 | NA | NA | |
| | F13 | 2/22/2016 | Erect boerhavia | Caryophyllales | Nyctaginaceae | *Boerhavia erecta* | | | | | 10 | NA | NA | |
| | F14 | 2/23/2016 | Woody vines | Fabales | Fabaceae | *Cissus sp* | | | S06°40.670' | E37°58.846' | 10 | NA | NA | |
| | F14 | 2/23/2016 | Erect boerhavia | Caryophyllales | Nyctaginaceae | *Boerhavia erecta* | | | | | 10 | NA | NA | |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F14 | 2/23/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Kikombe | 3 | | | 100 | 3 | 2 | |
| | F14 | 2/23/2016 | Cowpea | Fabales | Fabaceae | *Vigna unguiculata* | | 3 | | | 500 | NA | NA | |
| | F14 | 2/23/2016 | Wireweed | Malvales | Malvaceae | *Sida acuta* | | | | | 100 | NA | NA | |
| | F14 | 2/23/2016 | Fish poison | Fabales | Fabaceae | *Tephrosia vogelii* | | | | | 100 | NA | NA | |
| | F14 | 2/23/2016 | Bristly starbur | Asterales | Asteraceae | *Acanthospermum hispidum* | | | | | 10 | NA | NA | |
| | F14 | 2/23/2016 | Okra | Malvales | Malvaceae | *Abelmoschus esculentus* | | | | | 1 | NA | NA | |
| | F14 | 2/23/2016 | Pumpkin | Cucurbitales | Cucurbitaceae | *Cucurbita* | | | | | 10 | NA | NA | YES |
| | F15 | 2/23/2016 | Okra | Malvales | Malvaceae | *Abelmoschus esculentus* | | | S06°38.470' | E38°23.393' | 1 | NA | NA | |
| | F15 | 2/23/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Ndope | 9 | | | 100 | 1 | 1 | |
| | F15 | 2/23/2016 | Pumpkin | Cucurbitales | Cucurbitaceae | *Cucurbita* | | | | | 10 | NA | NA | NO |
| Pwani | F15 | 2/23/2016 | Wireweed | Malvales | Malvaceae | *Sida acuta* | | | | | 10 | NA | NA | |
| | F15 | 2/23/2016 | Bush weed | | | | | | | | 10 | NA | NA | |
| | F15 | 2/23/2016 | Cowpea | Fabales | Fabaceae | *Vigna unguiculata* | | | | | 10 | NA | NA | |
| | F16 | 2/23/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Unknown | 4 | S06°43.502' | E39°06.782' | 100 | 4 | 3 | |
| | F16 | 2/23/2016 | Watermelon | Solanales | Convolvulaceae | *Citrullus lanatus* | | | | | 10 | NA | NA | |
| | F17 | 2/23/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Ndope | 9 | S06°47.333' | E39°06.784' | 10 | 3 | 1 | |
| | F17 | 2/23/2016 | Spider flower | Brassicales | Cleomaceae | *Cleome viscosa* | | | | | 1 | NA | NA | |
| DSM | F17 | 2/23/2016 | Pumpkin | Cucurbitales | Cucurbitaceae | *Cucurbita* | | | | | 10 | NA | NA | YES |
| | F17 | 2/23/2016 | Erect boerhavia | Caryophyllales | Nyctaginaceae | *Boerhavia erecta* | | | | | 1 | NA | NA | |
| | F17 | 2/23/2016 | Fire plant | Malpighiales | Euphorbiaceae | *Euphorbiaceae sp* | | | | | 10 | NA | NA | |
| | F17 | 2/23/2016 | Cabbage | Brassicales | Brassicaceae | *Brassica oleracea* | | | | | 10 | NA | NA | |
| | F18 | 2/24/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Kiroba | 11 | S06°35.558' | E39°04.878' | 100 | 3 | 2 | |
| | F18 | 2/24/2016 | Pumpkin | Cucurbitales | Cucurbitaceae | *Cucurbita* | | | | | 1 | NA | NA | YES |
| | F18 | 2/24/2016 | Okra | Malvales | Malvaceae | *Abelmoschus esculentus* | | | | | 1 | NA | NA | |
| | F18 | 2/24/2016 | Bush weed | | | | | | | | 1 | NA | NA | |
| | F18 | 2/24/2016 | Cassias | Fabales | Fabaceae | *Cassia sp* | | | | | 1 | NA | NA | |
| | F19 | 2/24/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Mfawima | 4 | S06°27.821' | E38°53.364' | 1 | 2 | 1 | |
| | F19 | 2/24/2016 | Cowpea | Fabales | Fabaceae | *Vigna unguiculata* | | | | | 1 | NA | NA | |
| Pwani | F19 | 2/24/2016 | Fish poison | Fabales | Fabaceae | *Tephrosia vogelii* | | | | | 10 | NA | NA | |
| | F19 | 2/24/2016 | Pumpkin | Cucurbitales | Cucurbitaceae | *Cucurbita* | | | | | 1 | NA | NA | NO |
| | F19 | 2/24/2016 | Watermelon | Solanales | Convolvulaceae | *Citrullus lanatus* | | | | | 10 | NA | NA | |
| | F20 | 2/24/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Mfaransa | 3 | S06°22.744' | E38°35.741' | 10 | 3 | 1 | |
| | F20 | 2/24/2016 | Pignut | Lamiales | Lamiaceae | *Carya glabra* | | | | | 100 | NA | NA | |
| | F21 | 2/24/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Mzuri kuonja | | | | 500 | 4 | 4 | – —— |
| | F21 | 2/24/2016 | Bush weed | | | | | | | | 100 | NA | NA | |
| | F21 | 2/24/2016 | Greengram | Fabales | Fabaceae | *Vigna radiata* | | | | | 10 | NA | NA | |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F21 | 2/24/2016 | Morning glorry | Solanales | Convolvulaceae | *Ipomea sp* | | | | | 100 | NA | NA |
| | F22 | 2/25/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Mwali | 5 | S6°9.955' | E39°12.158' | 10 | 2 | 1 |
| | F23 | 2/25/2016 | Fish poison | Fabales | Fabaceae | *Tephrosia vogelii* | | | | | 1 | NA | NA |
| | F23 | 2/25/2016 | Okra | Malvales | Malvaceae | *Abelmoschus esculentus* | | | | | 1 | NA | NA |
| | F23 | 2/25/2016 | Sweetpotato | Solanales | Convolvulaceae | *Ipomea batata* | | | | | 1 | NA | NA |
| | F23 | 2/25/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Muafaka | 3 | | | 100 | 3 | 3 |
| | F23 | 2/25/2016 | Watermelon | Solanales | Convolvulaceae | *Citrullus lanatus* | | | | | 1 | NA | NA |
| | F23 | 2/25/2016 | Zucchin | Cucurbitales | Cucurbitaceae | *Cucurbita pepo* | | | | | 1 | NA | NA |
| | F24 | 2/25/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Mwali | 4 | S06°16.117 | E039°15'.633 | 10 | NA | NA |
| | F24 | 2/25/2016 | Wireweed | Malvales | Malvaceae | *Sida acuta* | | | | | 1 | NA | NA |
| | F24 | 2/25/2016 | Okra | Malvales | Malvaceae | *Abelmoschus esculentus* | | 3 | | | 1 | 2 | 1 |
| Zanzibar | F24 | 2/25/2016 | Sweet peper | Solanales | Solanaceae | *Capsicum annuum Group* | | 0.5 | | | 1 | NA | NA |
| | F24 | 2/25/2016 | Tomato | Solanales | Solanaceae | *Solanum lycopersicum* | | 3 | | | 1 | NA | NA |
| | F24 | 2/25/2016 | Eggplant | Solanales | Solanaceae | *Solanum melongena* | | 2.5 | | | 10 | NA | NA |
| | F25 | 2/26/2016 | Fire plant | Malpighiales | Euphorbiaceae | *Euphorbiaceae sp* | | | S06°14.339' | E039°19.743' | 1 | NA | NA |
| | F25 | 2/26/2016 | Watermelon | Solanales | Cucurbitaceae | *Citrullus lanatus* | | | | | 1 | NA | NA |
| | F25 | 2/26/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Unknown | 6 | | | 0 | 1 | 1 |
| | F25 | 2/26/2016 | Tomato | Solanales | Solanaceae | *Solanum lycopersicum* | | | | | 1 | NA | NA |
| | F26 | 2/26/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Kizimbani | 7 | S06°6.186' | E039°13.474' | 10 | 1 | 1 |
| | F26 | 2/26/2016 | Annual pointesia | Malpighiales | Euphorbiaceae | *Euphorbia heterophylla* | | | | | 10 | NA | NA |
| | F26 | 2/26/2016 | Cucumber | Cucurbitales | Cucurbitaceae | *Cucumis sativus* | | | | | 1 | NA | NA |
| | F27 | 2/27/2016 | Cassava | Malpighiales | Euphorbiaceae | *Manihot esculenta* | Mwali/Joya | 4 | | | 100 | 1 | 2 |
| | F27 | 2/27/2016 | Caesarweed | Malvales | Malvaceae | *Urena lobate* | | | | | 100 | NA | NA |

B

| District | F/N | CD | HP | | FN | | CV | MAP | Latitude | Longtude | WC | CMD | CBSD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mityana | F1 | 2/8/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | Gomboka | 7 | N00.43564 | E032.04041 | 100 | 3 | 1 |
| | | | Sweet potato | Solanales | Convolvulaceae | Ipomea batata | | | N00.43564 | E032.04041 | 1 | NA | NA |
| | | | Tickberry | Lamiales | Verbenaceae | Lanrana camara | | | N00.43564 | E032.04041 | 1 | NA | NA |
| Mpiji | F2 | 2/8/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | Akena | 6 | N00.00979 | E032.00677 | 100 | 1 | 3 |
| | | | Pumpkin | Cucurbitales | Curcubitaceae | Cucurbita | | | N00.00979 | E032.00677 | 1 | NA | NA |
| | | | Eggplant | Solanales | Solanaceae | Solanum melongena | | | N00.00979 | E032.00677 | 1 | NA | NA |
| | | | Sweet potato | Solanales | Convolvulaceae | Ipomea batata | | | N00.00979 | E032.00677 | 1 | NA | NA |
| Wakiso | F3 | 2/9/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | NASE 3 | 2.5 | N00.51831 | E032.63553 | 1 | 1 | 1 |
| Wakiso | F4 | 2/9/2017 | Lion's ear | Lamiales | Lamiaceae | Leonotis leonurus | | | N00.52020 | E032.63834 | 1 | NA | NA |
| Kalungu | F5 | 2/10/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | TME 14 | 4 | S00.16989 | E031.83412 | 1 | 4 | 3 |
| | | | Sweet potato | Solanales | Convolvulaceae | Ipomea batata | | | S00.16989 | E031.83412 | 1 | NA | NA |
| Masaka | F6 | 2/10/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | Uknown | 6 | S00.33294 | E031.70984 | 10 | 3 | 3 |
| | | | Pumpkin | Cucurbitales | Curcubitaceae | Cucurbita | | | S00.33294 | E031.70984 | 1 | NA | NA |
| | | | Sweet potato | Solanales | Convolvulaceae | Ipomea batata | | | S00.33294 | E031.70984 | 1 | NA | NA |
| Rakai | F7 | 2/10/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | Uknown | 6 | S00.52627 | E031.64813 | 100 | 2 | 2 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Sweet potato | Solanales | Convolvulaceae | Ipomea batata | | | S00.52627 | E031.64813 | 1 | NA | NA |
| | | | Beans | Fabales | Fabaceae | Phasiola vulgalis | | | S00.52627 | E031.64813 | 1 | NA | NA |
| Rakai | F8 | 2/10/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | TME 204 | 3 | S00.66515 | E031.53927 | 10 | 2 | 2 |
| | | | Black-jack | Asterales | Asteraceae | Bidens pilosa | | | S00.66515 | E031.53927 | 1 | NA | NA |
| Rakai | F9 | 2/11/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | TME 14 | 4 | S00.69034 | E031.43948 | 10 | 1 | 1 |
| | | | Sweet potato | Solanales | Convolvulaceae | Ipomea batata | | | S00.69034 | E031.43948 | 1 | NA | NA |
| Rakai | F10 | 2/11/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | Kalandila | 7 | S00.89538 | E031.44637 | 100 | 3 | 1 |
| | | | Wandering jew | Commelinales | Commelinaceae | *Commelina benghalensis* | | | S00.89538 | E031.44637 | 1 | NA | NA |
| Rakai | F11 | 2/12/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | TME 14 | 6 | S00.98063 | E031.41873 | 500 | 4 | 2 |
| | | | Black-jack | Asterales | Asteraceae | Bidens pilosa | | | S00.98063 | E031.41873 | 1 | NA | NA |
| Kalungu | F12 | 2/12/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | TME 14 | 3 | S00.12179 | E031.75773 | 500 | 1 | 1 |
| | | | Pokeweeds | Caryophyllaless | Phytolacaceae | Phytolacca decandra | | | S00.12179 | E031.75773 | 1 | NA | NA |
| Gomba | F13 | 2/12/2017 | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | NASE 3 | 5 | N00.17379 | E031.92822 | 100 | 1 | 1 |
| Wakiso | F14 | 2/13/2017 | Sweet potato | Solanales | Convolvulaceae | Ipomea batata | | | N00.52556 | E032.62680 | 1 | NA | NA |
| | | | Cassava | Malpighiales | Euphorbiaceae | Manihot esculenta | NAROCAS 2 | 8 | N00.52556 | E032.62680 | 100 | 3 | 1 |
| | | | Indian Mustard | Brassicales | Brassicaceae | Brassica juncea | | | N00.52556 | E032.62680 | 1 | NA | NA |

Location where sampling conducted, FN = field number, FM = host plant family name, HP = host plant name, CV = cassava variety name, MAP = age of cassava (month after planting), WC (whitefly count) > 100 wc regarded as superabundant, CMD, CBSD symptoms observed from field grown cassava and SL = silver leafing was observed on field grown pumpkin.

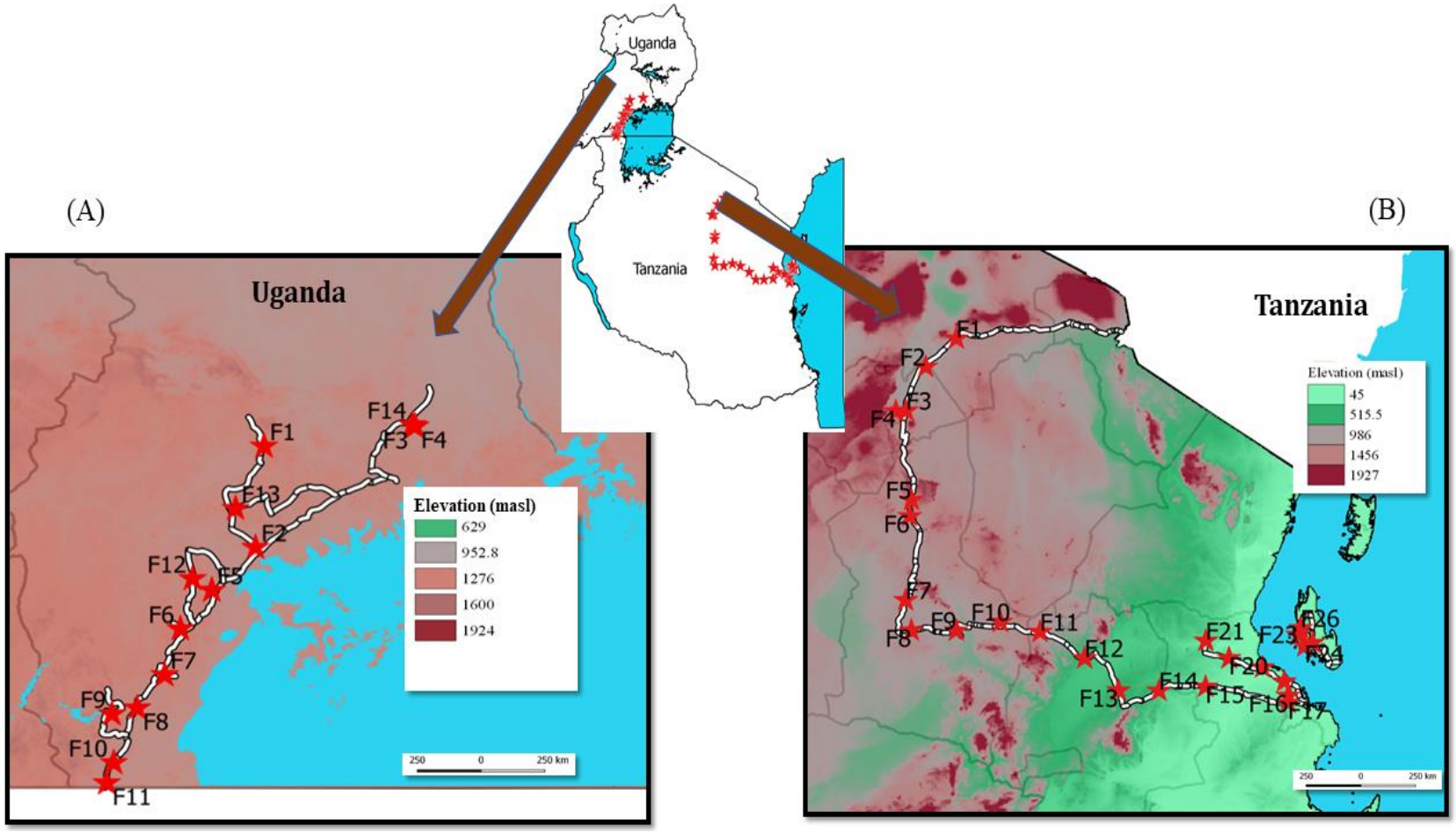



Figure 3. 1: Sampling sites where adult whitefly were collected from (A) Uganda and (B) Tanzania

**DNA extraction**

Twenty adult females of whitefly from each sample were selected whenever possible (some samples had <20 twenty females) using a Leica MZ8 stereomicroscope 100X (Leica Microsystems, Nanterre, France). Only females were used as they are diploid compared to haploid males. A total of 2915 female samples were selected that included 2161 from Tanzania and 754 from Uganda. Each sample was incubated in 25 µl extraction buffer for the DNA extraction (Tocko-Marabena et al. 2017). The extracts were kept at −20 ºC until further use.

**Mitochondrial cytochrome oxidase I gene (mtCOI) PCR amplification and sequencing**

The PCR for partial mtCOI fragment amplification was conducted using a primer pair described by Mugerwa *et al.* (2018). The PCR reaction mixture was conducted in a final volume of 20 µl, containing 10 µl of type-it (2x) QIAGEN© (France), 7 µl of pure HPLC water (CHROMASOLV ®, Sigma-Aldrich), 1 µl of each primer (forward and reverse) and 1 µl of DNA template. Initial denaturation of template DNA was performed at 95°C for 15 min followed by 40 cycles of: denaturation at 95°C for 30 s, primer annealing at 52°C for 45 s, and extension at 72°C for 1 min. A final extension was run at 72°C for 10 min. Amplified products were visualized by QIAxcel (QIAGEN©) prior to sending to Macrogen © Europe laboratory for sequencing.

**Sequences analysis**

All sequences received from Macrogen © were manually edited and aligned using Geneious R10 v.10.2.3 software (Kearse et al. 2012). The number and distribution of haplotypes within surveyed fields were analysed with DnaSP6 software (Rozas et al. 2003). All unique haplotypes were selected and aligned together with reference sequences from the GenBank using ClustalW (Thompson et al. 1994) by means of Geneious R10 v.10.2.3 software, prior to being subjected to Jmodeltest v.2.1.10 (Posada 2008) for optimum model choice. The nucleotide alignment was used to construct a phylogenetic tree in MrBayes (Ronquist and Huelsenbeck 2003) with a GTR +I+ G substitution model (the optimal model identified by Jmodeltest). The analysis was run with 1,100,000 iterations of MCMC (of the first 110,000 iterations were discarded as burning) and sampled trees were made every 200 iterations, using four heated chains.

**Microsatellite genotyping**

A set of 13 microsatellite loci developed for different *B. tabaci* species with different repeat motifs (Dalmon et al. 2008, Delatte et al. 2011, Hadjistylli et al. 2014) were used (Supplementary Table 3.1). Three multiplex fluorescent labelled primer mixes were prepared: the first mix contained Ms145, P59, P7 and WF2HO6; the second mix contained P62, WF1GO3, WF1DO4 and P5; and the third mix contained CIRSSA2, CIRSSA6, CIRSSA7, CIRSSA13 and CIRSSA41. The preparation of PCR mixes and their reactions followed the methodology used in chapter one. The peaks were visualized using Gene mapper v 4.0.

**Nuclear analysis**

The population genetic diversity indices were calculated within species considering a minimum number of individuals of n > 5 per field. Also, since SSA1–SG1 and SSA1–SG2 are similar (Wosula et al. 2017), the two subgroups were merged together in the nuclear analysis. The population genetic parameters were explored using GENETIX v.4.05.2: expected heterozygosity (He), heterozygosity calculated without biased (Hn.b), observed heterozygosity (Ho) and mean number of allele per population following the method of (Nei 1978). Hardy Weinberg equilibrium (probability test) was determined by ALREQUIN v.3.5.2.2. (Excoffier et al. 2005) using a method utilized by Guo and Thompson (Guo and Thompson 1992), and the percentage of null allele was estimated by Brookfield's method (Brookfield 1996) and isolation by distance between *B. tabaci* population were explored using Isolde online software GENEPOP (Rousset 2008). Our data were also checked with micro–checker for scoring error (Van Oosterhout et al. 2004). Genetic diversity among population (Fis) was studied by Weir and Cockerham method (Weir and Cockerham 1984), whereas allelic richness was analysed by FSTAT v.2.9.3.2 (Goudet 2002) using rarefaction method. Analysis of molecular variance (AMOVA) and matrix of genetic distances (Fst) were established by ALREQUIN v.3.5.2.2 (Excoffier et al. 2005).

The genetic structuring between populations was further studied by using STRUCTURE v.2.3.4 software (Pritchard et al. 2000), this method assigned an individual into different genetic clusters of unknown K (unknown population) (Pritchard et al. 2000). The structure output is presented by a bar plot of posterior probability of each individual according to its genetic cluster assignation.

Structure was run with an initial $10^5$ burning iterations, followed by $10^6$ MCMC iterations with potential K ranged from 1–20, this procedure was repeated 10 times. The optimum K (s) were analysed by the Δk method (Evanno et al. 2005) and structure output was visualized by STRUCTURE HARVESTER (Earl 2012). The software CLUMPP (Jakobsson and Rosenberg 2007) was used for averaging the best K assignations of Bayesian probability, then, the software DISTRUCT was used for reconstruction of the averaged bar plots obtained by CLUMPP (Rosenberg 2004) through an online program CLUMPAK (Kopelman et al. 2015). Discriminant analysis of principle component was used to further explore genetic differentiation between populations using R v 3.4.2 software (Lê et al. 2008) with the Adegenet package (Jombart 2008).

Our data were split into separate subsets for all the analyses according to species identified by mtCOI and location (Tanzania and Uganda). All analyses performed on those datasets were done as described above. Three main datasets were arranged: (1) All SSA1 individuals sampled from both countries (including all subgroups of SSA1 identified by mtCOI barcoding analysis), (2) SSA1 individuals collected from Tanzania alone (3) all other species identified (excluding SSA1), these species were IO, Med Q1, Med ASL, Uganda sweetpotato, SSA12 and SSA13. Subsequent runs were conducted to understand substructures in (i) SSA1–SG3 and IO from Tanzania, (ii) SSA12 and SS13 from Uganda and (iii) Med Q1 and Med ASL from both countries.

## Results

### Whitefly species identification in the sampled sites

The mtCOI was amplified (300 nt to 595 nt) from a total of 2734 individuals from the initial 2915 female whiteflies were to produce species barcode nucleotide sequences (nt) The sequences obtained were varied; 595 nt (*n* = 1070), 500 nt (*n* = 600), 400 nt (*n* = 700), 350 nt (*n* = 200) and 300 nt (*n* = 163). Barcoding allowed us to assign 15 mitochondrial genetic groups of *B. tabaci* throughout Tanzania and Uganda: SSA1 (including three genetic subgroups: SG1 (*n* = 302), SG2 (*n* = 287) and SG3 (*n* = 234), SSA11 (*n* = 3), SSA12 (*n* = 15), SSA13 (*n* = 14), IO (*n* = 1536), Med Q1 (*n* =17), Med ASL (*n* = 153), UgSp (*n* = 60), Uganda 1 (n = 6), EA1 (*n* = 2), Sudan II (SII) (*n* =1) and four as yet unidentified groups (*n* =14). We also found *B. afer* (*n* = 90) but was excluded from further analysis.

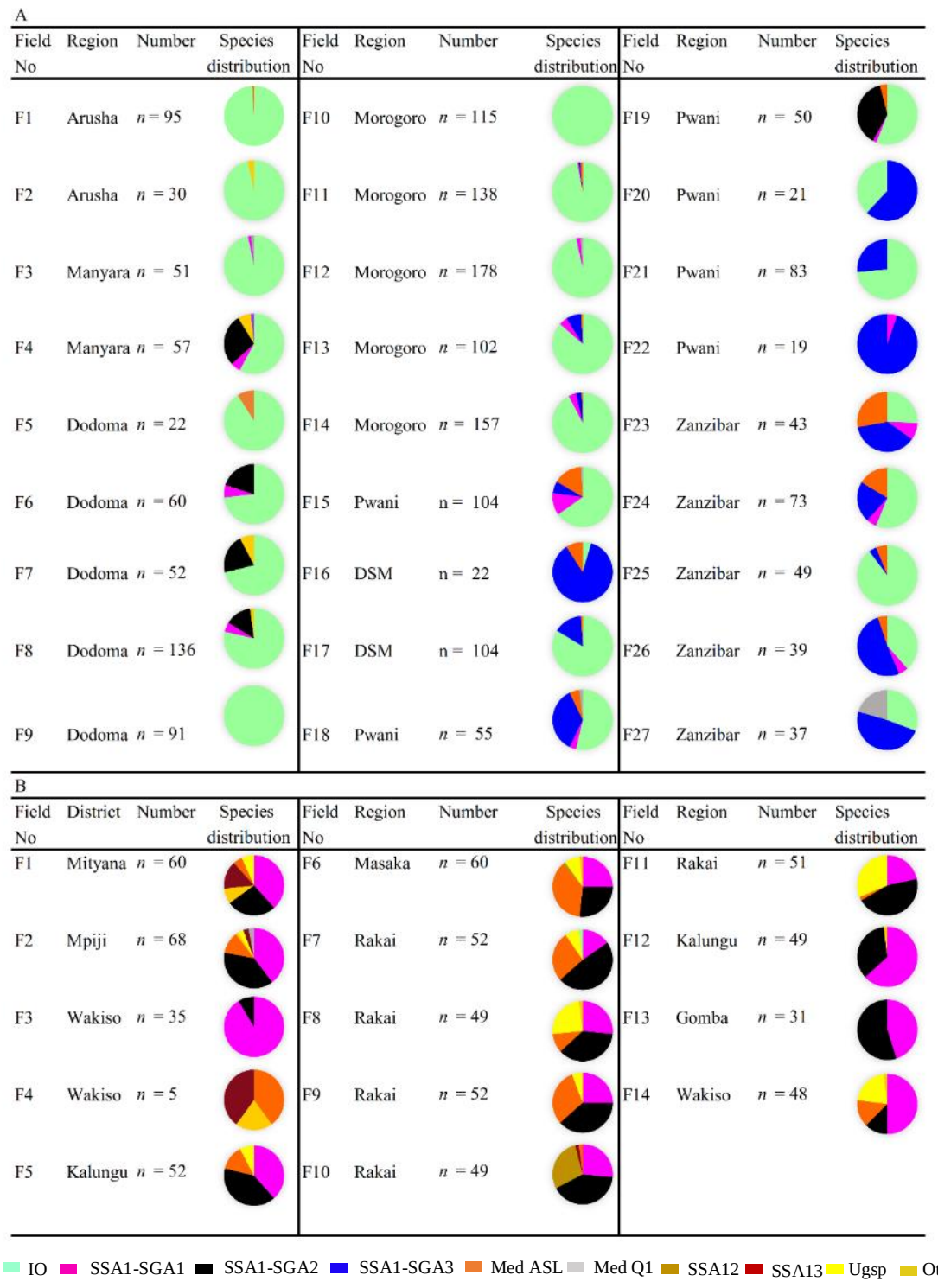



Figure 3. 2: *B. tabaci* species distribution per field A) Tanzania n = 1983 and B) Uganda n = 661.

These mtCOI sequences were further used as species identification tags in the nuclear analysis as well as for host plants species distribution.

SSA1, SSA1–SG1 and–SG2 (*n* = 473, 17.3%) were dominating species in Uganda (Fig. 3.2b). These considered as a single species was widely distributed found in each field visited except one field. SSA1–SG3 was found only in Tanzania. All three subgroups (SG1 to SG3) were observed in Tanzania (n = 116, 4.24%), nevertheless significant variation in occurrence was seen. The SSA1–SG2 (*n* = 58, 2.12%) dominated in the Northern part. The SSA1–SG1 (*n* = 58, 2.12%) were widely distributed and SSA1–SG3 (*n* = 234, 8.56%) was restricted to the regions of Morogoro, Pwani and Zanzibar. Meanwhile, the IO (*n* = 1535, 56.14%) was dominating in Tanzania had found in 26 out of 27 fields (Fig. 3.2a). Only one IO female (0.04%) was found in Uganda.

The higher number of Med was found in Uganda with Med ASL (*n* = 86, 3.15%) than Med Q1 (*n* = 2, 0.07%). The Med ASL was found in 11 of the 14 fields and Med Q1 in only one field surveyed. In Tanzania similar number of Med was found, but not in proportion, with Med ASL found in 2.45% (*n* = 67) and Med Q in 0.55% (*n* = 15), despite the high number of samples analysed. The Med ASL was found more in Pwani and Zanzibar while Med Q1 was only observed in Zanzibar.

Both SSA12 (*n* = 15, 0.55%), SSA13 (*n* = 14, 0.51%) and Ugsp (*n* = 60, 2.19%) were found only in Uganda. The SSA12 was found in two fields, while, SSA13 in four and Ugsp in 10 fields.

Our study also revealed seven more species in different agroecological zones both in Tanzania (*n* = 14) and Uganda (*n* = 4). They include: SSA11 (*n* = 3, 0.11%) and Uganda I (*n* = 6, 0.22%) only in Uganda, Sudan II (*n* = 1, 0.04%) and four yet unidentified species (*n* = 14, 0.51%) only in Tanzania, EA1 (*n* = 2, 0.07%) in both countries.

**Species distribution according to agroecological zones**

Samples were collected in different agroecological zones based on elevation from the low to high land. In Tanzania elevation was ranged from 45 to 1927 masl (Fig 3.2c). In Uganda all sampling fields were made on 952.8 to 1276 masl (Fig 3.2d). Significant variation of species distribution between agroecological zones has been observed

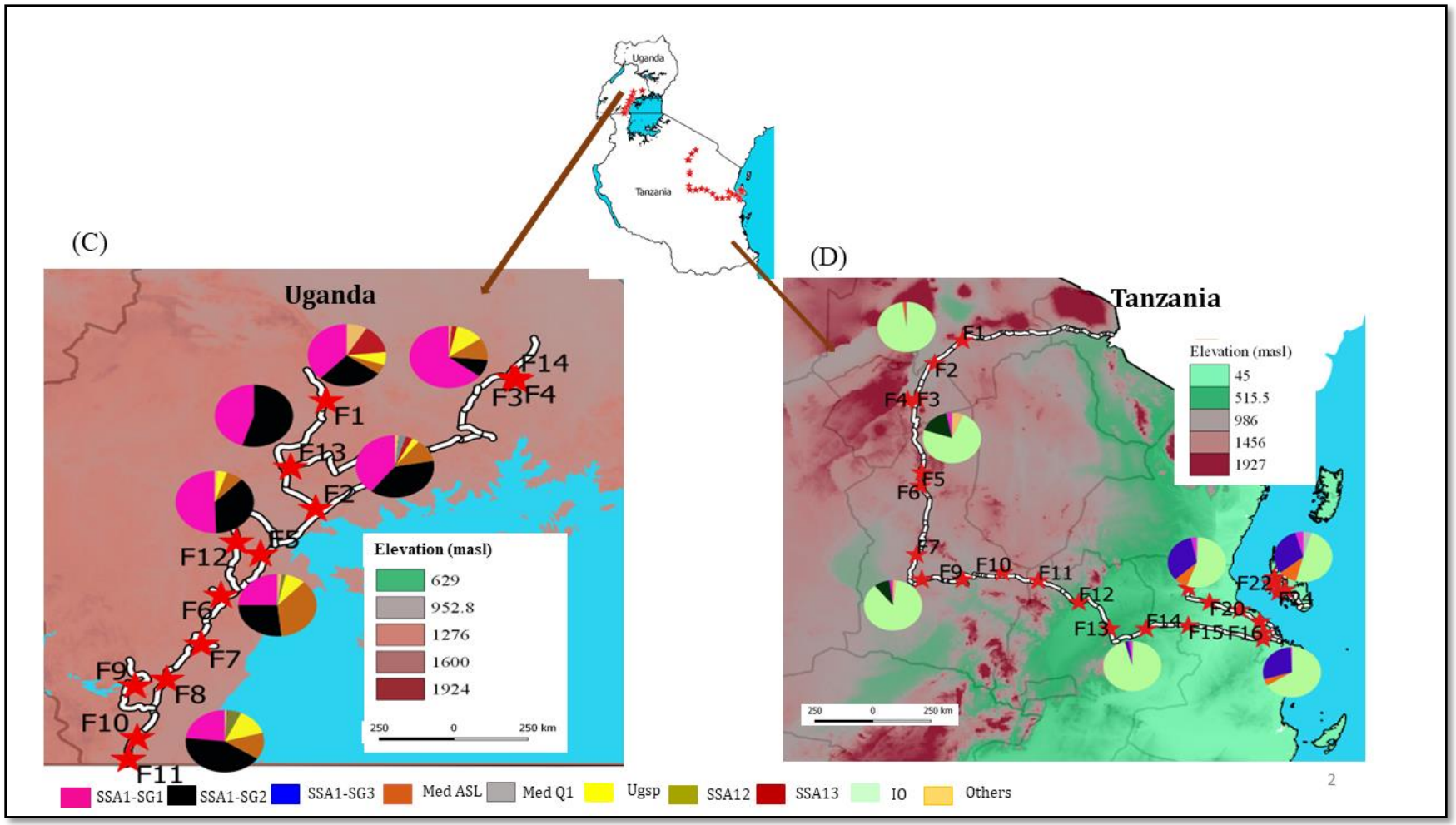



Fig. 3.2: Maps of (C) Uganda and (D) Tanzania showing *B. tabaci* species distribution collected from different agroecological zones/elevation of Uganda.and Tanzania

In Tanzania, SSA1–SG2 was found in high land zones while SSA1–SG1 saw widely distributed SSA1–SG3 (n = 234, 11.79%) was restricted to the low land area (coastal zone).

IO species: IO was observed in all different agroecological zones in Tanzania but in Uganda IO species was found above 900 masl.

Med species: The Med ASL was widely distributed, however both Med Q1 and Med ASL was found in an area above 900 masl in Uganda. Both Med ASL and Med Q1 were restricted to the coastal zone/ low land area in Tanzania.

SSA12, SSA13 and Ugsp: The three species were widely distributed observed in an altitude above 900 masl. Uganda.They were absent in Tanzania.

Low frequency species: Both SSA11, EA1 and Uganda 1 were observed in an altitude above 900 masl.in Uganda. In Tanzania both SII and four unidentified species were found in high land area.

**Host plant utilization**

Sampling was taken from 43 host plants belonging to 16 plant families: Asteraceae, Brassicaceae, Cleomaceae, Convolulaceae, Cucurbitaceae, Euphorbiaceae, Fabaceae, Lamiceae, Malvaceae, Nystaginaceae, Pedaliaceae, Polygonaceae, Solanaceae, Verbernaceae, Phytolacaceae and Commelinaceae over the two countries. Among these, seven families and six plant species were shared by both countries. Three families and six plant species were found only in Uganda, and six families and 33 plant species were only found in Tanzania (Supplementry data Table 3.2).

The ability of plants to host *B. tabaci* species varied, ranging from 1 to 8. Sweetpotato found to harbor the highest (*n* = 8), while several plants hosted only IO species.

The SSA1 species including subgroups: was hosted in 11 families (Supplemental data Table 3.2). Among them cassava which belong to Euphorbiaceae family had the highest number of SSA1 than any other sampled host.

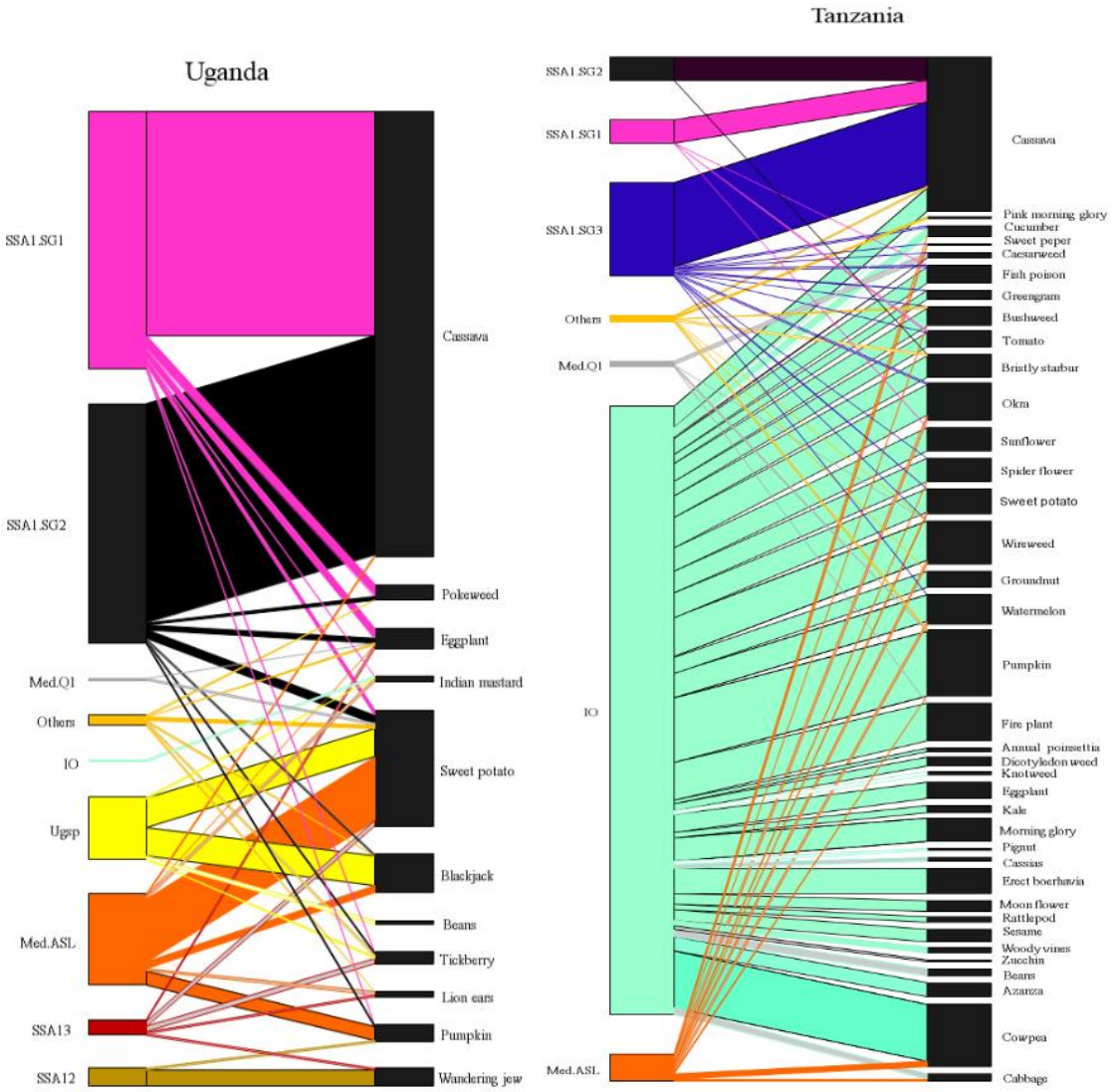



Figure 3. 3: Host plants of *B. tabaci* species distribution collected from different agroecological zones in Uganda and Tanzania, others representing low frequency occurred species (Uganda 1, SSA11, Sudan II, EA1 and unidentified species.

Because SSA1–SG1 and SSA1–SG2 are the same (Wosula et al. 2017) (also see chapter one), the species will be discussed as a single group in this chapter. On cassava the higher number of SSA1–SG1/G2 (Tanzania *n* = 112 and Uganda *n*= 422) than SSA1–SG3 (*Tanzania n* = 210). However, the SSA1–SG3 was seen in many hosts (*n* = 13) belonging to seven families and six orders while in SG1/G2 was found on nine families and eight orders. Apart from cassava the SSA1 subgroups were commonly found on sweetpotato. Other host plants harbored the species are presented in the figure (Fig. 3.3).

IO species: The IO was found on all plant species from agriculture crops to weeds in Tanzania (Fig. 3.3) belonging to 16 families (Supplementry data Table 3.2). This study revealed that the family *Cucurbitaceae* (pumpkin, cucumber and zucchini) had the highest numbers of IO. Among the host plants, the pumpkin was the best host with the highest number of *B. tabaci* identified (*n* = 162, 5.92%). The family *Polygonaceae* (dockweed) contained the fewest number of IO samples than any other families (*n* = 8). Interestingly, IO was found alone on some host plants including beans, kale, sesame, zucchini, eggplants, annual poinsettia, azanza, cassias, moon flower, morning glory, pignut, rattle pod, wood vines and two unknown weeds**.**

Med species: The Med ASL had wider (*n* = 16) host range than Med Q1 (*n* = 4)**.** The species observed on 10 plant families and eight orders compared to four families and three orders for Med Q1. Highest number of Med ASL was found on sweetpotato (Tanzania *n* = 61 and Uganda *n* = 3) and the lowest was on bush weed (*n* = 1). The highest number of Med Q1 was found on caesarweed (*Malvaceae*). The Med ASL and Med Q1shared two host plants (eggplant and sweetpotato) (Fig. 3.3).

SSA12, SSA13 and Ugsp: The three species were observed from nine host plants belonging to nine families and seven orders**.** The highest number was found on wandering jew *n* = 14 (SSA12), tickberry *n* = 5 (SSA13) and for Ugsp *n* = 56 on sweetpotato and black–jack (Fig. 3.3).

**Superabundant whitefly sites**

There was variation in adult whitefly abundances among the 41 fields surveyed in both countries. In Tanzania 10 fields (40.7%) were identified as super abundant, the IO and SSA1–SG3 species were found to dominate those fields. The IO species was dominating five while four fields were dominated by SSA1–SG3 and one field with SSA1–SG1.

Nine host plants were found in those fields including cassava, pumpkin, cowpea, wireweed, fish poison, pignut, bush weed, morning glory and caesarweed. Among all host plants, cassava was grown in eight out of ten super abundant fields. Cassava hosted SSA1–SG3 (*n* = 108), SSA1–SG1 (*n* = 25) and IO (*n* = 23). Caesarweed was harboured majority of Med Q1 (n = 11), IO (n = 2) and SSA1–SG3 (n = 1), while the remaining plants were found to host the IO species (n = 121) and SSA1–SG3 (n = 2 only from bush weed.

This study was also found one cassava field dominated by IO. In Tanzania the super abundant fields were distributed in different agroecological zones such as from moderate > 500 masl to low land area > 50 masl

In Uganda, 61.5% (*n* = 8) of the fields surveyed had super abundant whitefly populations (>100 adults per plant) (Table 1b). The high whitefly abundance was observed only on cassava. The crop observed to harbour SSA1–SG1/G2 (*n* = 257), Uganda 1 (n = 1) and Med ASL (n = 1). These abundance fields were distributed in all agroecological zones surveyed with > 900 masl from Central to Southern part of Uganda bordering Tanzania (Fig. 3.2c).

**CMD and CBSD incidences on cassava in Tanzania and Uganda**

Both CMD and CBSD incidences were scored in the surveyed fields (Table 3.1a and b). Among the surveyd fields, 36 had cassava plants (Tanzania *n* = 23 and Uganda *n* = 13). CMD severity was higher than CBSD in both countries, with 25 fields (69.4%) showing CMD symptoms (Tanzania *n* =17 and Uganda *n* = 8) and 13 fields (36.1%) with CBSD (Tanzania*n* = 7 and Uganda *n* = 6). Twelve fields (33.3%) were co-infected with both diseases (six from each country). The CMD was found in different agroecological zones in Tanzania, while CBSD was restricted in the coastal zone. On the contrary both CMD and CBSD were distributed in all agroecological zones surveyed in Uganda.

Most cassava varieties (*n* = 15) grown in Tanzania (*n* = 13) were mainly local ones (not improved) and only two of these did not show any symptoms of CMD and CBSD incidence.

Among the improved varieties, one field with the variety Kiroba in Tanzania and four fields in Uganda (varieties TME 14, TME 204, NAROCAS2 and Akena) showed the diseases. In addition, two local varieties also showed CMD incidences in Uganda. Twelve in 18 fields counted superabundant whitefly from two countries showed disease symptoms of either CMD or CBSD. The disease symptoms were observed on three to 11 months after planting.

**Silver leafing symptoms**

Of all 27 fields surveyed in Tanzania, pumpkin was grown in ten fields, among which six fields harboured silver leafing symptoms (Table 3 1). Those fields were in Dodoma, Morogoro and Dar es Salaam regions. IO was the only species observed in all the samples made on those symptomatic pumpkins.

**Phylogenetic analysis of whitefly genetic groups**

The phylogenetic analysis was carried out only using the long mtCOI sequences (595 nt) from adult whitefly (*n* = 1070, 39.2%) sampled from Tanzania *n* = 730 and Uganda *n* = 340. All the different haplotypes found in this study are presented in (Table 3.2).

A total of 96 haplotypes was observed from our dataset. All haplotypes from each species were selected, together with reference sequences from GenBank were used to generate a phylogenetic tree (Fig.3 2). The highest number of haplotypes (*n* = 47) was found within IO species (among 571 individuals). All individuals were from Tanzania except one that was from Uganda and shared 100% identity from the P6B9_TZ haplotype from Tanzania. Two dominant haplotypes were seen within IO species (Table 3.2), the first group contained 330 individuals (57.9%) and shared 100% similarity with EU760748 identified from Reunion Island (Gueguen et al. 2010), followed by the second haplotype 27.2% (*n* = 155) that shared 100% identity with AY903523 reported in Uganda (Sseruwagi et al. 2006).

A total of 13 haplotypes were found for the SSA1 species, isolated from 405 individuals among which only two were shared by both countries, eight found only in Tanzania and three in Uganda.

Table 3. 2: Different *B. tabaci* haplotypes and their distribution found during the 2016 and 2017 surveys in Tanzania and Uganda.

| Species | Haplotype name | Host plant | Field observed Tanzania | Field observed Uganda | Number of haplotypes per country | | Accession number |
|---|---|---|---|---|---|---|---|
| | | | | | Tanzania | Uganda | |
| | P5F10_TZ | **Cassava**, Indian mustard, eggplant, tickberry, sweetpotato, pokeweed, | F3, F4, F8 | F1, F2, F3, F5, F6, F7, F8, F9, F10, F11, F12, F13, F14 | 7 | 146 | |
| SSA1-SG1 | P5B11_TZ | **Cassava**, tomato, | F4, F8 | | 4 | | |
| | P5D9_TZ | **Cassava** | F8 | | 1 | | |
| | P4A3_TZ | **Cassava**, eggplant, sweetpotato, pumpkin, tickberry, pokeweed bristly starbur, | F6, F7, F8, | F1, F2, F3, F5, F6, F7, F8, F9, F10, F11, F12, F13, F14 | 31 | 130 | |
| | P6F2_TZ | **Cassava** | F4, F6, F8 | | 19 | | |
| | P9B1_UG | **Cassava** | | F1, F2, F5 | | 4 | |
| SSA1-SG2 | P4H3_TZ | **Cassava** | F6 | | 1 | | |
| | P5A1_UG | **Sweetpotato** | | F5 | | 1 | |
| | P4H11_UG | **Sweetpotato** | | F5 | | 1 | |
| | P6H2_TZ | **Cassava** | F8 | | 1 | | |
| | P22G3_TZ | **Cassava**, okra, spider flower, | F16, F17, F18, F19, | | 55 | | |
| SSA1-SG3 | P17C8_TZ | **Cassava** | F20, F21, F26, F27 | | 3 | | |
| | P26B10_TZ | **Cassava** | F16, F17, F18, F27 | | 1 | | |
| | P5H7_UG | **Sweetpotato,** | | F6, F7, F9, F1, F14 | | 11 | |
| | P22E1_TZ | **Watermelon**, cowpea, wireweed, | F25, F15, F19 | | 8 | | |
| | P22B1_TZ | **Watermelon**, cabbage, pumpkin | F16, F17, F25 | | 5 | | |
| | P3E11_UG | **Eggplant**, pumkin, lion's ear | | F2, F4 | | 3 | |
| Med ASL | P6F1_UG | **Sweetpotato** | | F7 | | 2 | |
| | P17F10_TZ | **Pumpkin** | F18 | | 1 | | |
| | P16B6_TZ | **Watermelon** | F16 | | 1 | | |
| | P17H10_TZ | **Pumpkin** | F18 | | 1 | | |
| | P3C12_UG | **Eggplant** | | | | 1 | |
| | P22C12_TZ | **Caesarweed** | F27 | | 1 | | |
| | P17E9_TZ | **Pumpkin** | F18 | | 1 | | |
| Med Q1 | P22H12_TZ | **Caesarweed** | F27 | | 1 | | |
| | P22D11_TZ | **Caesarweed** | F27 | | 4 | | |
| | P17F12_TZ | **Okra** | F18 | | 1 | | |
| SSA11 | P4B7_UG | **Tickbery** | | F1, F4 | | 3 | |
| SSA12 | P7C5_UG | **Wandering jew** | | F10 | | 1 | |
| | P3G5_UG | **Sweetpotato**, tickbery | | F1, F2 | | 3 | |

| | | | | | | |
|---|---|---|---|---|---|---|
| | P4F7_UG | **Tickberry** | | F4 | | 1 |
| | P3B7_UG | **Tickberry** | | F1 | | 1 |
| SSA13 | P4H6_UG | **Lion's ear** | | F4 | | 1 |
| | P3E3_UG | **Sweetpotato** | | F1 | | 1 |
| | P3F7_UG | **Tickberry** | | F1 | | 1 |
| | P3E5-_UG | **Sweetpotato**, black-jack, | | F1, F2, F5, F6, F7, F8, F9, F11, F14 | | 17 |
| Ugsp | P8C9_UG | **Sweetpotato** | | F14 | | 3 |
| | P3A4_UG | **Sweetpotato** | | F1 | | 1 |
| | P15D11_TZ | **Bushweed**, sunflower, erect boerhavia, cowpea, wireweed, Fish poison, okra, Wireweed Bristly starbur, okra, pumpkin, spider flower, fireplant cabbage, watermelon, tomato, eggplant, sweetpotato beans, kale, cucumber, cassava, moon flower, Groundnut, dicoty weed, seseme, azanza, morning glory greengram, | F1, F2, F3, F4, F5, F6, F7, F8 F14, F17, F18, F24 | | 330 | |
| | P2B3_TZ | **Wireweed**, cucumber, tomato, sunflower, wireweed, groundnut, sunflower, cowpea, morning glory, cabbage fireplant, Erect boerhavia, tomato, zuchini, pumpkin, cowpea, sweetpotato, fish poison, moon flower, cassava, Bristly starbur, spider flower, eggplant, beans, dicoty weed sesame, azanza, watermelon, pink morning glory, okra, greengram, | F1, F2, F3, F4, F5, F6, F7, F8, F9, F10, F14, F17, F20, F24, F26, F24, F25 | | 155 | |
| | P21A8_TZ | **Eggplant**, pumpkin, wireweed, sweetpotato, dicoty weed bristly starbur, groundnut, watermelon, cucmber, sesame, azanza, moon flower, erect boerhavia, morning glory, wireweed, cassava | F1, F2, F4, F5 F7,F8, F9, F14, F17, F18, | | 31 | |
| | P1H4_TZ | **Eggplant**, wiredeed, sesame, spider flower, groundnut | F1, F2, F7, F9, F17 | | 5 | |
| | P1H7_TZ | **Sweetpotato**, pumpkin, cowpea | F1, F3, F8 | | 3 | |
| | P6D12_TZ | **Groundnut**, fish poison, eggplant | F1, F9, F14 | | 3 | |
| | P7A2_TZ | Groundnut, wireweed | F9, F14 | | 2 | |
| | P6B9_TZ | **Morning glory**, mustard green | F8 | F12 | 1 | 1 |
| | P5F1_TZ | **Sesame**, watermelon | F5, F6 | | 2 | |
| | P3B2_TZ | **Poinsettia** | F3 | | 1 | |
| | P17A4_TZ | **Poinsettia** | F17 | | 1 | |
| | P5H11_TZ | **Bristly starbur** | F9 | | 1 | |
| | P4C7_TZ | **Dycotyweed1** | F6 | | 1 | |
| | P1D8_TZ | **Sweetpotato** | F1 | | 1 | |
| | P7D5_TZ | **Sunflower** | F9 | | 1 | |
| | P6F5_TZ | **Cowpea** | F8 | | 1 | |
| | P17A2_TZ | **Poinsettia** | F17 | | 1 | |

| | | | | | | |
|---|---|---|---|---|---|---|
| | P5C12_TZ | **Bristly starbur** | F8 | | 1 | |
| | P3G10_TZ | **Cowpea** | F5 | | 1 | |
| | P6E12_TZ | **Groundnut** | F9 | | 1 | |
| | P3A2_TZ | **Poinsettia** | F3 | | 1 | |
| | P6E6_TZ | **Cowpea** | F8 | | 1 | |
| | P7E11_TZ | **Wireweed** | F9 | | 1 | |
| | P7D6_TZ | **Sunflower** | F9 | | 1 | |
| | P2D12_TZ | **Poinsettia** | F3 | | 1 | |
| | P1D5_TZ | **Eggplant** | F1 | | 1 | |
| | P3E9_TZ | **Bristly starbur** | F4 | | 1 | |
| IO | P13H11_TZ | **Wireweed** | F14 | | 1 | |
| | P7F4_TZ | **Cowpea** | F17 | | 1 | |
| | P1D2_TZ | **Tomato** | F1 | | 1 | |
| | P3C1_TZ | **Poinsettia** | F3 | | 1 | |
| | P17F6_TZ | **Cabbage** | F17 | | 1 | |
| | P21D11_TZ | **Watermelon** | F25 | | 1 | |
| | P7C1_TZ | **Groundnut** | F9 | | 1 | |
| | P7F10_TZ | **Wireweed** | F9 | | 1 | |
| | P7A6_TZ | **Sunflower** | F9 | | 1 | |
| | P14H11_TZ | **Pumpkin** | F14 | | 1 | |
| | P14G11_TZ | **Pumpkin** | F14 | | 1 | |
| | P6C12_TZ | **Groundnut** | F9 | | 1 | |
| | P3F8_TZ | **Bristly starbur** | F4 | | 1 | |
| | P6C8_TZ | **Tomato** | F8 | | 1 | |
| | P2D10_TZ | **Pumpkin** | F3 | | 1 | |
| | P5A1_TZ | **Sesame** | F7 | | 1 | |
| | P6D6_TZ | **Cowpea** | F8 | | 1 | |
| | P7D1_TZ | **Groundnut** | F9 | | 1 | |
| | P17E11_TZ | **Pumpkin** | F8 | | 1 | |
| | P13A10_TZ | **Cowpea** | F14 | | 1 | |
| EA1 | P6G7_UG | Black-jack | F4 | F8 | 1 | 1 |
| Sudan II | P2E8_TZ | **Pumpkin** | F3 | | 1 | |
| Uganda 1 | P3F12_UG | **Eggplant,** sweetpotato, tickberry, pokeweed | | F1, F2, F6, F12 | | 6 |
| *Uknown IV | P2H2_TZ | **Wireweed** | F2 | | 1 | |
| *Uknown III | P4G11_TZ | **Cassava** | F7 | | 1 | |
| *Uknown III | P5F5_TZ | **Pink morning grory** | F7 | | 1 | |
| *Uknown III | P6C3_TZ | **Cassava** | F7 | | 1 | |
| *Uknown III | P5G5_TZ | **Pink morning grory** | F7 | | 1 | |
| *Uknown III | P4F11_TZ | **Cassava** | F7 | | 1 | |
| *Unknown I | P5C11_TZ | **Cassava** | F7 | | 2 | |
| *Unknown II | P3E4_TZ | **Cassava,** bristly starbur, groundnut | F4 | | 4 | |

A total of 1070 adult *B. tabaci* analysed from Tanzania and Uganda in different host plants, the bold ones are used in the construction of phylogenetic tree. Some of the species belong to unidentified species (*), with the closest species found at 85.1% identity from *B. afer* and 94.3% with SSA10. Note plant family for each host plant presented on Table 3.1

The majority of SSA1 belonged to SSA1–SG2 (*n* = 161, 39.8%) and shared 100% with KM377899 reported in Malawi and Uganda (Ghosh et al. 2015). Followed by SSA1–SG1 containing 153 individuals (37.8%) which shared 100% identity with KX570796 originated from Uganda (Mugerwa et al. 2018).

The last subgroup identified was SSA1–SG3 (*n* = 55, 13.6%), which was observed to share 100% nucleotide identity with KM377902 described in Malawi (Ghosh et al. 2015) (Fig. 3.4). Within Med species, 14 haplotypes (*n* = 41) were found, four from Uganda and ten from Tanzania, and they clustered into two subgroups. One group contained individuals *n* = 33 sharing 99.3–100% nucleotide identity with MH205754 known as Med Africa silver leafing (Med ASL) (Vyskočilová et al. 2018), whereas, the second group consisted of *n* = 8 individuals sharing 99 – 100% nucleotide identity identified as Med Q1 from MH205752 (Vyskočilová et al. 2018).

The Ugsp species contained three haplotypes (*n* = 21), which shared 99.5 – 100% nucleotide identity with KX397331 reported in Uganda (Hadjistylli et al. 2016).

Twelve individuals belonging to different unidentified species clustered into six haplotypes. A first haplotype represented as P2H2_TZ (*n* = 1) shared 94.3% nucleotide identity with KX570843 described as SSA10 from Uganda (Mugerwa et al. 2018), whereas the other three haplotypes *n* = 11 shared 79.1 – 85.1% nucleotide identity with *B. afer*.

Additionally, 11 haplotypes belonging to low frequency occurring species such as EA1 (*n* = 2) were observed to share 99.5% nucleotide identity with KF425620 reported by Legg et. al. (Legg et al. 2014b) in Tanzania, SSA11 (*n* = 3) shared 100% identity with KX570855 from Uganda (Mugerwa et al. 2018), SSA12 (*n* =1) shared 100% identity with KX570819 (Mugerwa et al. 2018) found in Uganda, SS13 (*n* = 8) shared 99.0 to 100% identity with KX570833 identified in Uganda (Mugerwa et al. 2018), Uganda I (*n* = 6) shared 100% identity with AY903480 and Sudan II (*n* =1).

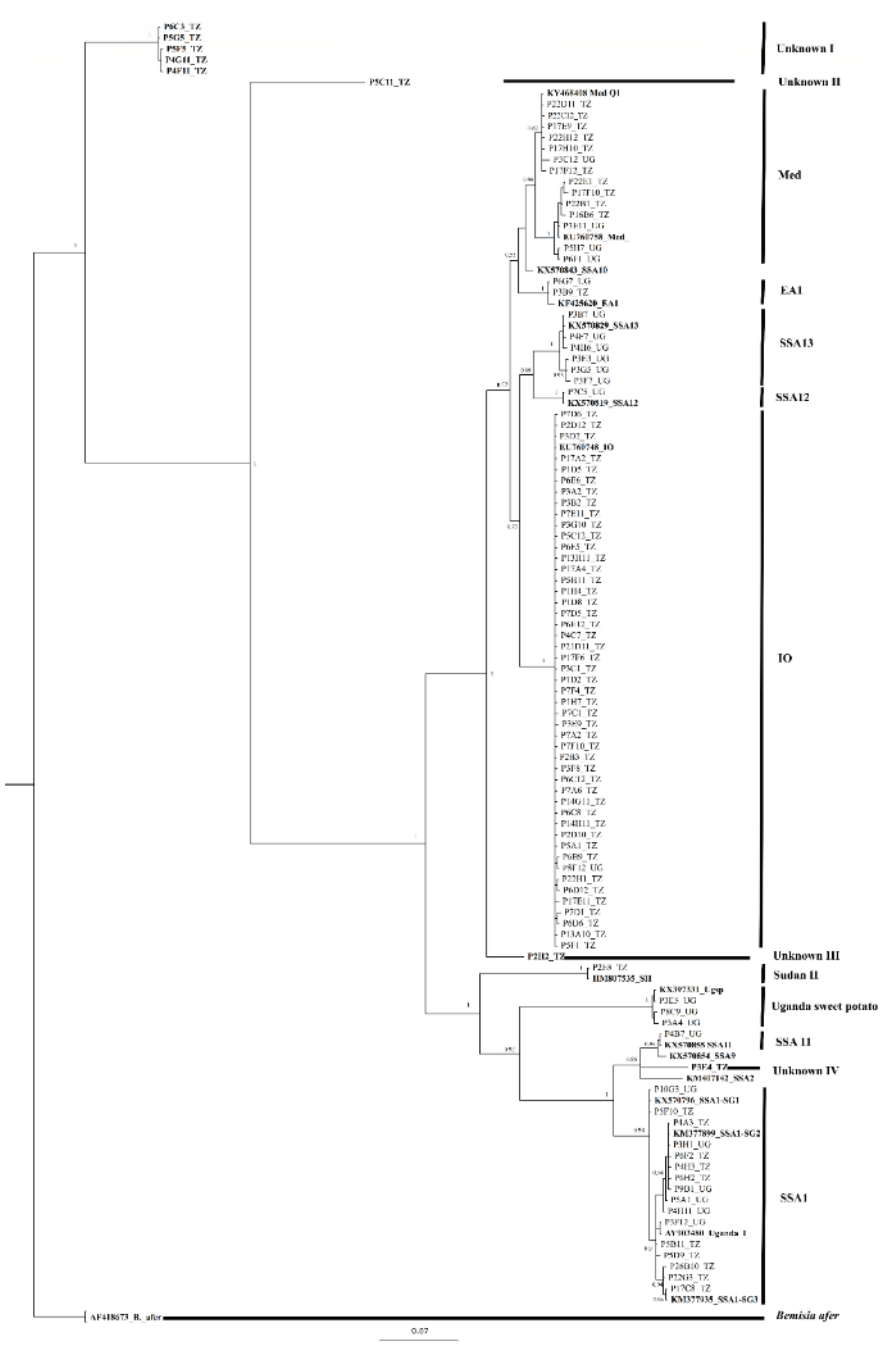



Figure 3. 4:. Mr. Bayes phylogenetic tree generated using 102 mtCOI sequences selected from a total 1071 long sequences with 595 bp obtained from adult *B. tabaci* (cassava and non-cassava) and 14 reference sequences from GenBank. All bold sequences represent references from GenBank and the four new identified groups (>4% of nucleotide identity from the closest Bemisia tabaci sequence).

**Nuclear genetic diversity**

A total of 2728 samples were successfully genotyped at 13 microsatellites loci (Tanzania *n* = 1956 and Uganda *n* = 639). Prior to further analysis the average percentage of missing data and the frequency of null allele were checked per species and locus. A threshold of >15.0 and 40.0% missing data per loci and per individuals was applied and an average of >30.0% for null allele per locus (above these thresholds the individual were discarded). The frequency of null allele was found to vary between loci within species ranging from low, moderate to high (Supplementry Table 3.2).

The IO and SSA1 species showed low (0.0%) to moderate (26.0%) frequency of null allele, while the highest observed on Med ASL (99.0%). The highest percentage of loci missing data (20.0%) were recorded from CIRSSA41 and the lowest were from CIRSSA2, CIRSSA6 and CIRSSA7 (0.2%) (Supplementary Table 3 1). 133 (4.9%) individuals had higher than 30.0% missing data, thus were discarded. This analysis was excluded 117 individuals from *B. afer* and low frequency occurred species. Also, Ms145, HO6, SSA6, SSA7, SSA2 and CIRASSA41 were excluded on analysis of non–SSA1 individuals, while for SSA1 analysis the CIRSSA41 was excluded.

This study revealed lower observed heterozygosity (Ho) across all species than the expected heterozygosity (He) (Table 3.3). $F_{IS}$ ranged from 0.11 to 0.44 overall populations and species. All populations were at the Hardy–Weinberg equilibrium (HWE), similarly to linkage disequilibrium (Table 3.3). The average allelic richness between species was moderate to high with a range of 1.61 – 4.75, the lowest was observed within SSA1–SG1/SG3 from Tanzania and the highest was within Tanzania Med Q1 species.

**Distinct genetic clusters revealed within SSA1 species from Tanzania and Uganda**

This analysis involved the dataset containing SSA1 species including its three sampled subgroups (SG1, SG2 and SG3) from Tanzania and Uganda. A total of 729 individuals and 12 loci were used (Tanzania *n* = 288, Uganda *n* = 441). Bayesian clustering analysis separated our dataset countrywide. The best K considered were K = 2 and 4, using Evanno's method (Evanno et al. 2005).

Table 3. 3: Population genetic diversity indices among the *B. tabaci* found in Tanzania and Uganda.

| **Tanzania** | N | Mean | Ar | Fis | Ho | Hnb | He |
|---|---|---|---|---|---|---|---|
| **IO species** | | | | | | | |
| TZ F1 | 104 | 11.17 | 3.3 | 0.26 | 0.42(0.22) | 0.56(0.24) | 0.56(0.24) |
| TZ F2 | 37 | 7.92 | 3.28 | 0.28 | 0.4(0.21) | 0.56(0.25) | 0.55(0.24) |
| TZ F3 | 48 | 7.75 | 3.24 | 0.18 | 0.46(0.25) | 0.56(0.24) | 0.55(0.24) |
| TZ F4 | 34 | 7.17 | 3.21 | 0.19 | 0.46(0.25) | 0.56(0.24) | 0.55(0.23) |
| TZ F5 | 16 | 5.5 | 3.27 | 0.17 | 0.48(0.26) | 0.58(0.21) | 0.56(0.2) |
| TZ F6 | 44 | 7.42 | 3.25 | 0.22 | 0.44(0.26) | 0.56(0.26) | 0.55(0.26) |
| TZ F7 | 37 | 6.92 | 3.07 | 0.29 | 0.37(0.26) | 0.52(0.26) | 0.52(0.25) |
| TZ F8 | 105 | 10.58 | 3.25 | 0.32 | 0.39(0.22) | 0.57(0.23) | 0.56(0.23) |
| TZ F9 | 98 | 9.83 | 3.15 | 0.17 | 0.45(0.25) | 0.54(0.23) | 0.53(0.23) |
| TZ F10 | 120 | 11.08 | 3.33 | 0.28 | 0.42(0.25) | 0.58(0.25) | 0.58(0.25) |
| TZ F11 | 139 | 11.17 | 3.32 | 0.26 | 0.42(0.24) | 0.57(0.24) | 0.57(0.23) |
| TZ F12 | 83 | 10.17 | 3.32 | 0.23 | 0.44(0.22) | 0.57(0.25) | 0.57(0.25) |
| TZ F13 | 91 | 10 | 3.21 | 0.35 | 0.37(0.19) | 0.56(0.22) | 0.56(0.22) |
| TZ F14 | 156 | 12.08 | 3.29 | 0.28 | 0.41(0.24) | 0.56(0.26) | 0.56(0.26) |
| TZ F15 | 71 | 8.67 | 3.27 | 0.35 | 0.36(0.23) | 0.56(0.28) | 0.55(0.28) |
| TZ F16 | 4 | 3.33 | 3.33 | NA | NA | NA | NA |
| TZ F17 | 71 | 10.42 | 3.57 | 0.31 | 0.44(0.21) | 0.63(0.2) | 0.62(0.2) |
| TZ F18 | 30 | 8.75 | 3.63 | 0.34 | 0.42(0.24) | 0.62(0.23) | 0.61(0.22) |
| TZ F19 | 30 | 7.08 | 3.28 | 0.38 | 0.36(0.19) | 0.58(0.23) | 0.57(0.23) |
| TZ F20 | 10 | 4.17 | 2.95 | 0.32 | 0.36(0.24) | 0.52(0.26) | 0.5(0.25) |
| TZ F21 | 48 | 8.25 | 3.24 | 0.35 | 0.36(0.21) | 0.55(0.25) | 0.55(0.25) |
| TZ F23 | 11 | 4.58 | 3.21 | 0.29 | 0.41(0.26) | 0.57(0.27) | 0.54(0.26) |
| TZ F24 | 43 | 8.5 | 3.24 | 0.28 | 0.39(0.22) | 0.54(0.27) | 0.54(0.27) |
| TZ F25 | 40 | 7.17 | 3.11 | 0.3 | 0.38(0.2) | 0.53(0.24) | 0.53(0.24) |
| TZ F26 | 15 | 5.25 | 3.27 | 0.26 | 0.42(0.16) | 0.56(0.23) | 0.54(0.22) |
| TZ F27 | 5 | 3.25 | 3.06 | 0.4 | 0.31(0.24) | 0.49(0.38) | 0.43(0.34) |
| Grand mean | 57.31 | 8.01 | 3.26 | 0.28 | | | |
| **SSA1 (-SG1&SG2)** | | | | | | | |
| TZ F2 | 3 | 2.33 | | | | | |
| TZ F4 | 19 | 4.67 | 3.45 | 0.1 | 0.54(0.33) | 0.59(0.19) | 0.58(0.18) |
| TZ F6 | 15 | 5.42 | 3.94 | 0.16 | 0.52(0.23) | 0.62(0.17) | 0.6(0.17) |
| TZ F7 | 11 | 4.58 | 3.67 | 0.17 | 0.48(0.25) | 0.57(0.18) | 0.55(0.18) |
| TZ F8 | 26 | 5.92 | 3.62 | 0.22 | 0.44(0.13) | 0.56(0.17) | 0.55(0.16) |
| TZ F11 | 2 | 2.5 | NA | NA | NA | NA | NA |
| TZ F12 | 2 | 2.08 | NA | NA | NA | NA | NA |
| TZ F13 | 2 | 2.5 | NA | NA | NA | NA | NA |
| TZ F14 | 3 | 2.17 | NA | NA | NA | NA | NA |
| TZ F15 | 3 | 2.67 | NA | NA | NA | NA | NA |
| TZ F16 | 1 | 1.42 | NA | NA | NA | NA | NA |
| TZ F17 | 1 | 1.75 | NA | NA | NA | NA | NA |
| TZ F18 | 4 | 2.92 | NA | NA | NA | NA | NA |
| TZ F19 | 2 | 2.42 | NA | NA | NA | NA | NA |
| TZ 21 | 1 | 1.3 | NA | NA | NA | NA | NA |
| TZ 23 | 1 | 1.5 | NA | NA | NA | NA | NA |
| Grand mean | 6.00 | 2.88 | 3.67 | 0.16 | | | |
| **SSA1 (-SG3)** | | | | | | | |
| TZ F13 | 13 | 4.58 | 1.6 | 0.26 | 0.45(0.22) | 0.6(0.18) | 0.57(0.18) |
| TZ F14 | 12 | 4.33 | 1.59 | 0.08 | 0.54(0.24) | 0.59(0.19) | 0.56(0.18) |
| TZ F15 | 18 | 4.92 | 1.63 | 0.15 | 0.54(0.25) | 0.63(0.13) | 0.61(0.13) |
| TZ F16 | 19 | 6.08 | 1.65 | 0.16 | 0.55(0.17) | 0.65(0.14) | 0.63(0.13) |
| TZ F17 | 15 | 5.42 | 1.63 | 0.13 | 0.55(0.15) | 0.63(0.13) | 0.6(0.13) |
| TZ F18 | 16 | 5.5 | 1.63 | 0.36 | 0.41(0.21) | 0.63(0.13) | 0.61(0.12) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| TZ F19 | 14 | 4.67 | 1.58 | 0.3 | 0.41(0.2) | 0.58(0.16) | 0.56(0.15) |
| TZ F20 | 14 | 5 | 1.63 | 0.4 | 0.39(0.24) | 0.63(0.15) | 0.61(0.14) |
| TZ F21 | 12 | 4.58 | 1.61 | 0.32 | 0.43(0.21) | 0.61(0.14) | 0.58(0.13) |
| TZ F22 | 4 | 2.83 | NA | NA | NA | NA | AN |
| TZ F23 | 20 | 6.5 | 1.65 | 0.32 | 0.44(0.16) | 0.65(0.12) | 0.63(0.12) |
| TZ F24 | 5 | 3.17 | 1.59 | 0.29 | 0.44(0.28) | 0.59(0.29) | 0.49(0.23) |
| TZ F25 | 2 | 2.17 | NA | NA | NA | | |
| TZ T26 | 14 | 4.75 | 1.61 | 0.21 | 0.49(0.21) | 0.61(0.13) | 0.59(0.12) |
| TZ 27 | 14 | 5.08 | 1.58 | 0.14 | 0.51(0.23) | 0.58(0.13) | 0.56(0.13) |
| Grand mean | 12.8 | 4.64 | 1.61 | 0.24 | | | |
| **Med Q1** | | | | | | | |
| TZ F15 | 1 | 1.5 | NA | NA | NA | NA | NA |
| TZ F18 | 2 | 2 | NA | NA | NA | NA | NA |
| TZ F27 | 12 | 4.75 | 4.75 | 0.32 | 0.39(0.3) | 0.56(0.22) | 0.54(0.21) |
| Grand mean | 5 | 2.75 | | | | | |
| **Med ASL** | | | | | | | |
| TZ F11 | 2 | 1.5 | NA | NA | NA | NA | AN |
| TZ F12 | 2 | 1.25 | NA | NA | NA | NA | NA |
| TZ F13 | 3 | 1.83 | NA | NA | NA | NA | NA |
| TZ F14 | 1 | 1.17 | NA | NA | NA | NA | NA |
| TZ F15 | 18 | 4 | 3.88 | 0.38 | 0.26(0.19) | 0.42(0.3) | 0.41(0.29) |
| TZ F16 | 2 | 1.83 | NA | NA | NA | NA | NA |
| TZ F17 | 3 | 2.75 | NA | NA | NA | NA | NA |
| TZ F18 | 1 | 1.5 | NA | NA | NA | NA | NA |
| TZ F19 | 2 | 1.83 | NA | NA | NA | NA | NA |
| TZ F23 | 4 | 2.75 | NA | NA | NA | NA | NA |
| TZ F24 | 19 | 4.42 | 4.11 | 0.18 | 0.36(0.26) | 0.44(0.29) | 0.42(0.29) |
| TZ F25 | 4 | 2.5 | NA | NA | NA | NA | NA |
| TZ F26 | 3 | 2.25 | NA | NA | NA | NA | NA |
| Grand mean | 4.92 | 2.28 | 4 | 0.49 | | | |
| **Uganda** | | | | | | | |
| **SSA1 (-SG1&SG2)** | | | | | | | |
| UG F1 | 15 | 6 | 5.65 | 0.17 | 0.44(0.24) | 0.51(0.32) | 0.5(0.31) |
| UG F2 | 23 | 6.08 | 5.00 | 0.24 | 0.38(0.26) | 0.5(0.31) | 0.49(0.3) |
| UG F3 | 36 | 8 | 5.32 | 0.22 | 0.38(0.28) | 0.49(0.3) | 0.48(0.29) |
| UG F4 | 3 | 2.42 | NA | NA | NA | NA | NA |
| UG F5 | 41 | 8.58 | 5.77 | 0.21 | 0.41(0.28) | 0.52(0.33) | 0.52(0.32) |
| UG F6 | 30 | 8.17 | 5.98 | 0.38 | 0.35(0.2) | 0.57(0.29) | 0.56(0.28) |
| UG F7 | 36 | 9 | 6.38 | 0.3 | 0.42(0.23) | 0.59(0.28) | 0.58(0.27) |
| UG F8 | 34 | 9.67 | 6.26 | 0.29 | 0.4(0.24) | 0.55(0.28) | 0.54(0.27) |
| UG F9 | 32 | 8.5 | 5.92 | 0.32 | 0.38(0.25) | 0.56(0.24) | 0.56(0.23) |
| UG F10 | 35 | 9.5 | 6.61 | 0.32 | 0.39(0.22) | 0.57(0.29) | 0.56(0.28) |
| UG F11 | 35 | 9 | 6.43 | 0.37 | 0.37(0.23) | 0.59(0.28) | 0.58(0.28) |
| UG F12 | 50 | 10.5 | 6.16 | 0.31 | 0.39(0.21) | 0.56(0.28) | 0.56(0.27) |
| UG F13 | 35 | 8 | 5.54 | 0.27 | 0.37(0.24) | 0.51(0.32) | 0.5(0.31) |
| UG F14 | 35 | 7.83 | 5.54 | 0.25 | 0.38(0.25) | 0.51(0.3) | 0.5(0.29) |
| Grand mean | | | 5.89 | 0.28 | NA | NA | NA |
| **Med ASL** | | | | | | | |
| UG F1 | 4 | 2.92 | NA | NA | NA | NA | NA |
| UG F2 | 15 | 5.08 | 3.53 | 0.36 | 0.35(0.22) | 0.54(0.29) | 0.52(0.28) |
| UG F4 | 1 | 1.18 | NA | NA | NA | NA | NA |
| UG F5 | 11 | 4.17 | 3.31 | 0.23 | 0.41(0.3) | 0.52(0.29) | 0.49(0.27) |
| UG F6 | 29 | 7 | 3.56 | 0.44 | 0.31(0.24) | 0.54(0.29) | 0.53(0.29) |
| UG F7 | 17 | 5.25 | 3.44 | 0.33 | 0.39(0.29) | 0.58(0.22) | 0.56(0.21) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| UG F9 | 17 | 5.5 | 3.52 | 0.19 | 0.46(0.33) | 0.56(0.29) | 0.54(0.28) |
| UG F11 | 2 | 2.17 | NA | NA | NA | NA | NA |
| UG F14 | 8 | 3.33 | 2.87 | 0.14 | 0.38(0.36) | 0.43(0.33) | 0.4(0.31) |
| Grand mean | 11.56 | 4.07 | 3.37 | 0.28 | | | |
| **Ugsp** | | | | | | | |
| UG F1 | 3 | 2.25 | NA | NA | NA | NA | NA |
| UG F2 | 2 | 1.64 | NA | NA | NA | NA | NA |
| UG F5 | 3 | 2.42 | NA | NA | NA | NA | NA |
| UG F6 | 5 | 3.58 | 2.77 | 0.38 | 0.33(0.3) | 0.51(0.33) | 0.45(0.3) |
| UG F7 | 3 | 2.5 | NA | NA | NA | NA | NA |
| UG F8 | 14 | 4.75 | 2.69 | 0.29 | 0.39(0.29) | 0.54(0.28) | 0.52(0.27) |
| UG F9 | 3 | 2.5 | NA | NA | NA | NA | NA |
| UG F11 | 15 | 6.33 | 2.92 | 0.44 | 0.3(0.28) | 0.53(0.36) | 0.52(0.35) |
| UG F14 | 10 | 5.17 | 2.84 | 0.28 | 0.4(0.28) | 0.56(0.21) | 0.53(0.2) |
| Grand mean | 6.44 | 3.46 | 2.81 | 0.34 | | | |
| **SSA12** | | | | | | | |
| UG F10 | 13 | 4.08 | 4.22 | 0.31 | 0.31(0.31) | 0.44(0.25) | 0.43(0.24) |
| **SSA13** | | | | | | | |
| UG F1 | 8 | 4.58 | 3.97 | 0.26 | 0.48(0.28) | 0.64(0.27) | 0.59(0.25) |
| UG F2 | 1 | 1.27 | NA | NA | NA | NA | NA |
| UG F10 | 1 | 1.5 | NA | NA | NA | NA | NA |
| UG F4 | 3 | 2.08 | NA | NA | NA | NA | NA |
| Grand mean | 3.25 | 2.36 | 3.97 | 0.26 | | | |

*B. tabaci* species analysed according to different sites sampled (see Fig. 2b and supplementary Table 3 for further site description). N = individuals number within a population, Mean = average number of allele per population), Ar = allelic richness, $F_{IS}$ = correlation within population presented together with P value from Hardy–Weinberg equilibrium test (* significant at $P < 0.05$), Ho = observed heterozygosity, He = expected heterozygosity and Hn.b = heterozygosity calculated without biases. The population genetic diversity indices were calculated considering a minimum number of individuals of $n > 5$ per field. NA = inadequate sample.

A first level of differentiation was observed at K = 2 where two genetic clusters are linked to their geographic origin, one is for individuals from Tanzania and the other is for those from Uganda (Fig. 3.5a). At K = 4, two genetic clusters were found in each country. Only SG3 collected in Tanzania were clearly differing from SG1 and SG2 (Fig. 3.5a). Similar results were found using a DAPC analysis at K = 4 (Supplementary Fig. 3.1).

The matrix of pairwise $F_{ST}$ genetic distances between SSA1 populations between and within countries was performed on a total of 694 individuals (Tanzania *n* = 257 and 17 populations; Uganda *n*= 437 and 13 populations). Significant genetic distance variations between populations within a country as well as between countries were seen (Supplementary Table 3.3).

The average lowest $F_{ST}$ genetic distance observed was 0.02 within SG1/SG2 Uganda populations, meanwhile, the highest values within those subgroups was 0.05, found within populations of Tanzania SG2. While, SG3 showed intermediate average $F_{ST}$ distance of 0.03 and the value of 0.09 was recorded between the SG2 and SG3 from Tanzania. Variation between countries revealed, the highest significant average $F_{ST}$ value of 0.16 which was recorded between Uganda SG1/G2 and Tanzania SG2. Meanwhile the genetic distance of 0.14 was recorded between Uganda SG1/G2 and Tanzania SG3.

To understand the genetic clusters within Tanzania SSA1 populations, only SSA1 from Tanzania was analysed separately. This analysis involved a total of 288 individuals of SSA1 with three subgroups (SG1, SG2 and SG3). Following ΔK evaluated by Evanno (Evanno et al. 2005), the best K was observed at K = 2 Two distinct genetic clusters were observed at K = 2, one dominated by SSA1 (SG1 and SG2) (Fig. 3.5b) and the other one was containing individuals of SG3. Indeed, when increasing the number of assumed genetic cluster, at K = 3, no further differentiation observed between subgroup (Fig. 3.5b). Also, no genetic difference observed between SG1 and SG2 (Fig. 3.5b).

Additionally, to understand the substructure within SSA1–SG3, the individuals were analysed alone. At K = 3 three genetic clusters seen (supplemental Fig. 3.3c), indicated there was sub population structuring.

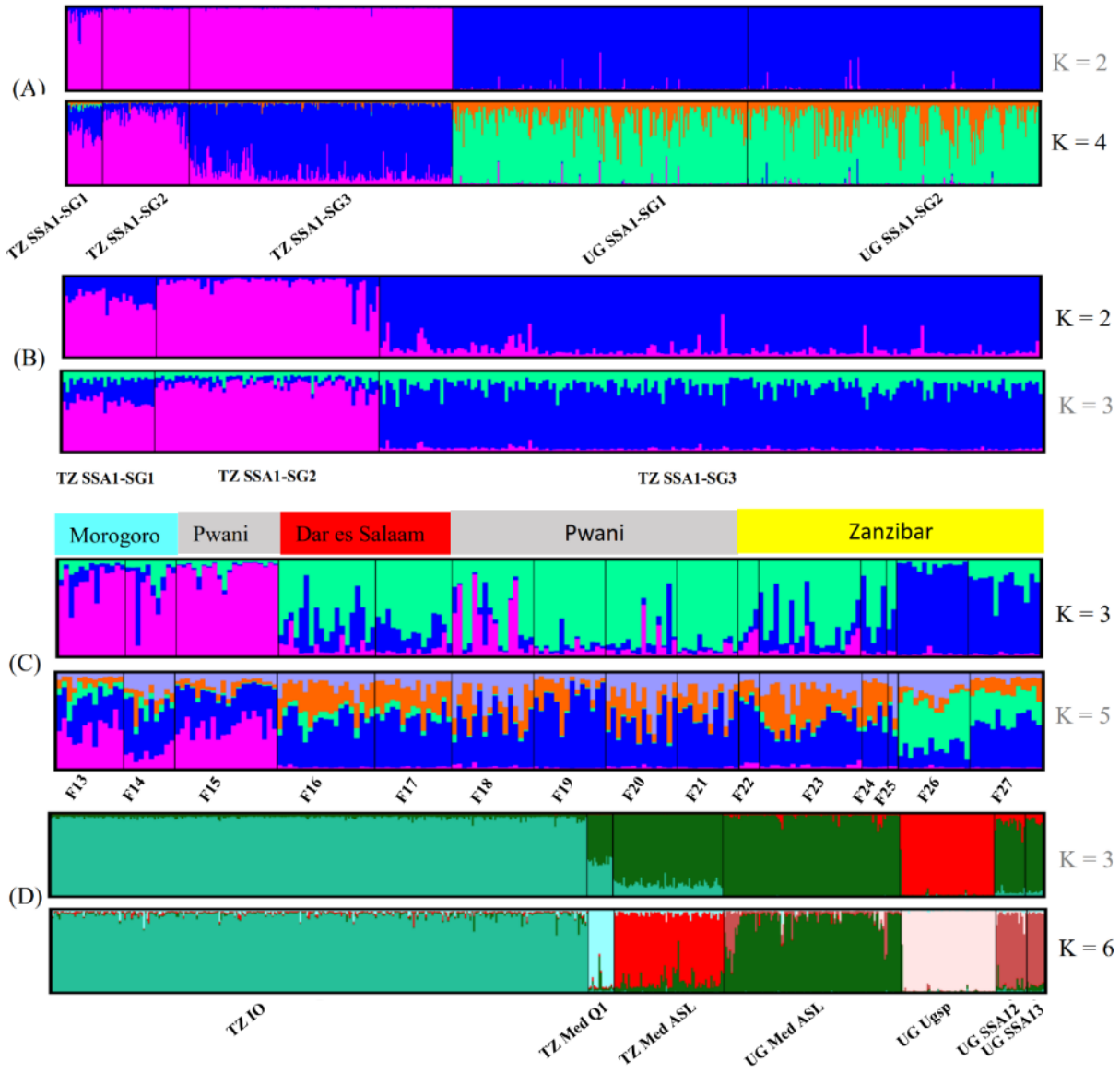



Figure 3. 5: Different K populations of *B. tabaci* (A) SSA1 from Tanzania (TZ) and Uganda (UG), (B) SSA1 from Tanzania (C) SSA1–SG3 from Tanzania and (D) Non–cassava species. Structure bar plots are based on 12 microsatellite loci. Individuals were arranged according to mtCOI species assignation and separated by black line. For each dataset the optimal K selected by STRUCTURE HARVESTER is presented in black.

The first genetic cluster dominated by individuals collected in the eastern part (Morogoro and Pwani), the next clusters were dominated by individuals sampled from different sites where SG3 sampled, where the remained cluster contained individuals from Zanzibar (Supplemental Fig. 3.3c). Despite of distinct clusters observed the structure pattern showed the sharing of genetic information to some few individuals (Supplementary Fig. 3.3c).

**Nuclear genetic diversity of non–cassava species from Tanzania and Uganda**

A subset of 582 individuals (Tanzania *n* = 392 and Uganda n = 190) and 7 loci were used to understand the nuclear genetic diversity and potential gene flows of those different genetic groups. Based on mtCOI marker these individuals belong to IO (*n* = 313), Med Q1 (*n* = 17), Med ASL (*n* = 169) Uganda sweetpotato (*n* = 60), SSA12 (*n* = 12), and SSA13 (*n* = 10). Only a few individuals of IO (*n* = 313, 21%) were randomly selected from the different sites and host plants from the total IO individuals to avoid bias due to occurrence of high number.

The best K population was considered at K = 6 (Evanno et al. 2005). Genetic structure differentiation began to appear at K = 3, three genetic clusters were seen separating IO, Uganda sweetpotato and other species (Fig.3.5d). Furthermore, at K = 6, the genetic clusters were observed, well separating all species except SSA12 and SSA13 (Fig. 3.5d). Med ASL from Tanzania (Fig. 3.5d) appeared to differ from Med ASL from Uganda, though some individuals from the two countries seemed to share similar genetic background

To understand population sub–structuring within Med Q1 and Med ASL species from the two countries, the species were run alone. The best K identified was K = 4. Initially, at K = 2 the genetic clusters were observed to separate populations according to country (Supplementary Fig.3.3b). At K = 4, the genetic clusters observed were differentiating the two species (Med Q1, Med ASL) into four genetic clusters (Supplementary Fig. 3.2a). Two of these clusters were dominated by Med Q1 and Med ASL from Tanzania, and within Uganda Med ASL was further sub–structured. Despite the well-defined structures in this dataset, some admixture was detected between Tanzania and Uganda Med ASL populations, showing sharing of genetic background between few individuals (Supplementary Fig.3 2a).

Finally, to understand further population structure, two different subsets were analysed, one involved SSA12 and SSA13 populations using eight loci. The best K was 2 with each genetic cluster well separating both species, however, some traces of gene flow could be observed (–Supplementary Fig. 3.2c). Lastly, all IO individuals were run alone, and the best K identified by evanno was K = 3, however initial differentiation began at K = 2 (Supplementary Fig. 3.3b). At K = 3 three sub–populations were observed. No linked of the observed structured with sampling fields and hostplants (Supplementary Fig. 3.3b). No isolation by distance revealed for IO (one tailed P value) = 0.152.

## Discussion

The current study assessed the *B. tabaci* species diversity, distribution and population genetic diversity along a geographical transect from central Uganda through Northern, Eastern to coastal part of Tanzania, including Zanzibar island. Fifteen of the *B. tabaci* cryptic species were identified on a wide range of hosts. Among these, IO was the dominant species found in Tanzania. It was recorded in all agroecological zones. In Uganda, the SSA1 (SG1 and SG2) dominated in all agroecological zones surveyed. The nuclear analysis conducted within all those species revealed distinct genetic clusters between SSA1 populations between countries.

### IO distribution, abundance, genetic diversity and host plant utilization

IO was found widely distributed in all regions surveyed in Tanzania. It was also the most abundant species in five out of the 10 super abundant fields observed. IO also had been observed in other countries of East Africa including Uganda, Kenya and Central Africa Republic, but in lower numbers (Sseruwagi et al. 2005, Mugerwa et al. 2012, Legg et al. 2014b, Tocko-Marabena et al. 2017) and being the dominant and indigenous of the SWIO including islands of Réunion, Mauritius, Madagascar, Comoros and Seychelles (Delatte et al. 2006). In Tanzania, IO was previously reported in the Northwest, Central and Eastern part (Tajebe et al. 2015a). Similar climatic conditions are found in the coastal part of Tanzania such as in its wide range of distribution including the tropical islands of the SWIO, which might favour the species.

The nuclear analysis performed on IO provided an evidence of population structuring into three genetic clusters, which showed no link to host plants as well as location. No significant evidence of genetic isolation by distance was observed. The IO seemed to be distributed all over sampling fields with population exchanges between fields, regions and even between mainland and Zanzibar Island. The wide distribution of IO might be facilitated by the movements of horticultural crops, from production sites to the market. Arusha, Moshi, Mbeya, Iringa and Tanga are among the major vegetables growing regions in Tanzania (De Putter et al. 2007). The grown crops are supplied to different markets mainly in the big cities and towns including Zanzibar.

The wide distribution of the IO in all agroecological zones of Tanzania might suggest the capacity of this species to adapt to many different areas, on the contrary to other species observed in this study (ie, Ugsp species only observed in Uganda). IO belong to the phylogenetic clade of the most invasive species of whiteflies known in the world: MEAM1 and Med (De Barro et al. 2011a, Delatte et al. 2011). Although IO is currently found with high numbers only in Tanzania, it is possible that this could become an invasive species in all Eastern African countries. IO therefore should be monitored closely.

*B. tabaci* is polyphagous found on >1000 host plants (Oliveira et al. 2001). From 37 host plants belonging to 16 different plant families sampled with whiteflies in our study in Tanzania, IO was found in all of them. IO species was previously reported to not colonize cassava successfully (Delatte et al. 2006, Delatte et al. 2011), nevertheless, it was found on cassava in 14 of the 23 fields in Tanzania. Among five superabundant fied IO was dominating all plants within the fields including cassava in one field. All those records might suggest that even if this species does not well develop on cassava, at the adult stage it can stand on the plant and might feed on cassava.

IO can also feed on different host plants including annual poinsettia, sweetpotato, tomato and jatropha (Delatte et al. 2005). In Tanzania, cassava and lion's ear (*Leonotis nepetifolia L.*) found to host IO (Tajebe et al. 2015a). It was found on tomato (Tocko-Marabena et al. 2017) in Central Africa Republic, on wandering jew, beans, cotton and eggplant in Uganda (Sseruwagi et al. 2005). The presence of IO on almost all host plants sampled reflects the ability of *B. tabaci* to easily adapt to a new host (Oliveira et al. 2001).

Being found in large populations and colonising a wide host range, the species might in some areas of Tanzania be one of the key species responsible for begomovirus transmission in other crop species than cassava, knowing that this species is able to transmit begomoviruses on tomato (Delatte et al. 2005).

A total of 96 different mitochondrial haplotypes were obtained in the current study, and majority of which ($n$ = 47) were from IO. This is not surprising as 56.14% (1535 out of 2734) of the analysed sequences were from IO. Delatte *et al.* (Delatte et al. 2011) already with a few individuals from Africa, compared the diversity in the islands versus mainland and reported a higher diversity of IO in mainland Africa. Despite this haplotype diversity found in our study, most IO belong to two major haplotypes, which shared 100% nucleotide identity with KX397323 (Hadjistylli et al. 2016) and AY903523 (Sseruwagi et al. 2006) identified from Reunion island and Uganda, respectively. No link was found between those haplotypes, sites, agroecological zones, the nuclear genetic clusters or host plants colonized. Our IO were found widely distributed from mainland to Zanzibar. Interestingly, 60% of fields grown with pumpkins showed silver leafing symptoms in Tanzania, those symptoms were attributed to the presence IO species on those plants. MEAM1 and IO are the species of the *B. tabaci* complex that were reported to induce this physiological damage on Cucurbita species (Yokomi et al. 1990, Costa and Brown 1991, Hoelmer et al. 1991, Jiménez et al. 1995, Delatte et al. 2005).

**SSA1 species distribution, abundance, genetic diversity and host plant utilization**

The other most dominant species collected in our surveys was from SSA1 (30.1%) and its three subgroups (SG1, SG2 and SG3). SSA–SG3 seemed to be a different species from SSA1–SG1/SG2, however, gene flow exists between those individuals (see Fig. 4c). The SSA1 (SG1 and SG2) was the most abundant species in Uganda, comprising 70.7% of all sampled individuals from Uganda. SSA1 (SG1 and SG2) was found across all sampled sites across a wide range of agroecological zones (even larger than for IO), and eight fields showed super abundant populations that were attributed to this species.

Several studies reported the presence of SSA1 (SG1 and SG2) in Uganda (Legg et al. 2002, Sseruwagi et al. 2005, Mugerwa et al. 2012, Legg et al. 2014b, Mugerwa et al. 2019), Tanzania, Rwanda, Burundi, Kenya, and the Democratic Republic of Congo (DRC) (Legg et al. 2014b, Manani et al. 2017, Wosula et al. 2017), Malawi (Gnankine et al. 2013b), Central Africa Republic, Cameroon (Tocko-Marabena et al. 2017, Wosula et al. 2017), Benin, and Togo (Gnankine et al. 2013b). Being reported in so many different countries within different agroecological zones of Central and East Africa this species seems well adapted to this area.

This study further observed that SSA1–SG1/SG2 were dominated on cassava. Previously, several studies reported an outbreak of the species linked to the CMD and CBSD pandemic (Legg et al. 2002, Colvin et al. 2004, Legg et al. 2014b, Tajebe et al. 2015a, Tocko-Marabena et al. 2017). Despite the wide distribution of the species we saw no neighbouring host plant other than cassava harboured high numbers of SSA1-SG1/SG2, instead we saw the two subgroups SG1 and SG2 occurred in sympatry and the nuclear analysis revealed that both subgroups fully hybridize (Fig. 5a). Previous studies reported similar findings (Wosula et al. 2017). Despite of the lack of genetic differentiation between both subgroups, the genetic structure of the two subgroups between countries differed.

This result suggested that the SSA1–SG1/SG2 in Uganda are different from Tanzania SSA1–SG1/SG2 and the positive correlation between genetic distance and geography exist. By distance the sampling made are far apart, about 1137 km separated the closest fields sampled, one field in Arusha in northern parts of Tanzania and another located closer to Tanzania–Uganda border in Rakai district. To confirm this clear differentiation between countries, it could be interesting to analyse more samples closer to each other from the Ugandan border to closer sites in Tanzania.

Furthermore, high allelic richness was found within the Uganda SSA1–SG1/SG2 species compared to TanzaniaSSA1–SG2 species. The presence of high allelic richness indicates high genetic diversity within populations (Hadjistylli et al. 2016). The high genetic diversity within SSA1 subgroups from Uganda is supported by high genetic diversity ($F_{is}$) observed within Uganda populations. This diversity could be linked to high altitude where individuals were sampled, with different crops grown.

However, we can not conclude as we got few individuals of SSA1–SG1/SG2 from Tanzania compared to Uganda. Better understanding the occurance of high diversity in Uganda is crucial as Uganda also known to host high number of *B. tabaci* species (Mugerwa et al. 2018, Sseruwagi et al. 2005) Cassava in known as major host to SSA1 species (Sseruwagi et al. 2005, Mugerwa et al. 2012, Legg et al. 2014b, Tajebe et al. 2015a, Tocko-Marabena et al. 2017). However, in our study the adult SSA1–SG1/SG2 were sampled from diverse host plants including food crops and weeds. Previous studies reported the occurrence of SSA1 on non–cassava species (Sseruwagi et al. 2006, Tocko-Marabena et al. 2017, Malka et al. 2018, Mugerwa et al. 2018). The ability of other plants to host the SSA1–SG1/SG2 could serve as alternative host hence ensuring its survival throughout the year.

The last subgroup of SSA1 found in the current survey with quite high numbers in Tanzania coastal area was SSA1–SG3 (Fig. 3.2a). This subgroup was found as the dominant population in three sampled fields on cassava and few on other sympatric host plant species, creating high outbreaking populations (>100 whiteflies per plant) similar to SSA1 (-SG1 and -SG2) and IO. Despite restricted to the coastal zones, SSA1-SG3 was found on seven plant families belonging to six orders, showing its polyphagous behaviour. The occurrence of SSA–SG3 in similar agroecological zones was also reported (Tajebe et al. 2015a, Mugerwa et al. 2019) in Tanzania.

Additionally, previous studies revealed its occurrence in Central Africa Republic, Malawi and DRC (Legg et al. 2014b, Ghosh et al. 2015, Tocko-Marabena et al. 2017, Wosula et al. 2017). The presence of SG3 in the coastal part of Tanzania in highest number than the other SSA1 subgroups on cassava, together with the higher occurrence of CBSD in this area, might suggest that this subgroup is most implicated in the spread of the disease.

Three mtCOI haplotypes were found within SSA1–SG3. The major haplotype (n = 55) contained individuals sampled from different sites and host plants, however, majority of them were sampled from cassava. Additionally, three distinct genetic clusters were observed analysing the nuclear diversity within SSA1–SG3. At least one of the genetic clusters consisted of individuals (*n* = 121, 63%) spread all over sampled site and different host plants (Fig. 5c).

The other two clusters were site restricted, one in Morogoro and Pwani and the other in Zanzibar. Similar to IO, despite one genetic cluster mostly linked to Zanzibar, the other genetic cluster (light green Fig. 4c) spread in most sites, was also found in Zanzibar showing the strong interactions between mainland Tanzania and Zanzibar. The different agroecological zones might favour those population in semiarid conditions of Morogoro while Zanzibar belong to coastal zone.

**Med species distribution, abundance, genetic diversity and host plant utilization**

Two distinct populations of Med: Med ASL and Med Q1 - were found, which have been recently proven to be two separate species (Vyskočilová et al. 2018). They were found in both sampled countries, however, only two adults of Med Q1 were found in Uganda. The Med ASL species was widely distributed in both countries, nevertheless, Med Q1 from Tanzania was restricted in the coastal zone. Previous studies reported the occurrence of Med Q1 in East Africa (Sseruwagi et al. 2005, Legg et al. 2014b, Tocko-Marabena et al. 2017). Similarly, both Med ASL and Med Q1 were observed in West Africa, with a different range of distribution according to the sampled countries. Med ASL was reported as dominating in Benin and Togo whereas, Med Q1 dominated in Burkina Faso (Gnankine et al. 2013b). Med ASL, is a species that has not been found out of Africa, it is mostly reported from Sub-Saharan Africa. In our survey it has been found in several agroecological zones in both sampled countries showing its ability to adapt to different environments in both Tanzania and Uganda.

The Med Q was reported as a recent invader in South Africa (Esterhuizen et al. 2013). The species, considered as originating from the Mediterranean basin, was observed in many different agroecological zones from both sampled countries of our study, this species had also been extensively reported in the literature from many countries and is being considered as one of the top invaders among the whitefly species (together with the MEAM1) (Esterhuizen et al. 2013, Tocko-Marabena et al. 2017). Med Q could also be an invader in both sampled countries as the blasted sequence shared 100% nuclear identity with sequences from China and Italy (Parrella et al. 2012, Li et al. 2017).

Additionally, our study revealed that Med ASL was more often found on agricultural crops including vegetables (cabbage, cowpea, cucumber, okra, pumpkin, sweet pepper, eggplant and sweetpotato), however, weed crops harboured the species too, albeit in lower number. The occurrence of Med ASL on both vegetable and weed crops was reported previously (Gnankine et al. 2013b, Malka et al. 2018, Vyskočilová et al. 2018).

The nuclear analysis was also able to separate clearly both Med Q1 and Med ASL species into distinct genetic clusters. It was also observed that the genetic composition of Med ASL from the two countries differ. Thus, the structure difference we saw could probably be associated with geographical isolation between populations, showing few migrations of this species between countries, but to confirm that hypothesis, more samples will be needed.

**Other *B. tabaci* species their distribution, genetic diversity and host plant utilization**

In the current study we found SSA11, SSA12, SSA13, Uganda 1 and Ugsp only in Uganda, which might reveal that some species could be country specific. The occurrence of these species was also reported in previous studies only in Uganda (Sseruwagi et al. 2004b, Mugerwa et al. 2018). In addition, four undescribed genetic groups of *B. tabaci* were found in Tanzania based on mitochondrial sequencing. Three of them shared 79.1 to 85.1% with *B. afer*, while for the last one shared 94.4% nuclear identity with SSA10 (Mugerwa et al. 2018). Those species were sampled from cassava, groundnuts, bristly starbur, pink morning glory and wireweed. The species were found in northern highland, arid and semiarid agroecological zones of Tanzania. These findings indicate that the SSA has a higher diversity than expected, and thus more research is needed for further understanding of potential new species. Further nuclear analysis for SSA12 and SSA13 revealed that they are different species although they showed some similar genetic background.

**CMD and CBSD severity**

The current study revealed a higher number of fields with CMD-symptomatic plants than those with CBSD, and they were widely distributed in almost all regions surveyed from both countries. Both CMD and CBSD are indigenous from these regions (Legg and Raya 1998, Legg 1999, Pita et al. 2001, Ntawuruhunga and Legg 2007, Legg et al. 2014b).

Since the 1980's the CMD incidence and CBSD since the mid 2000s (Otim-Nape et al. 1994, Legg and Ogwal 1998, Alicai et al. 2007).

The increase in whitefly vector densities were incriminated in the rising disease incidence to facilitate the spread of those disease (Legg et al. 2002, Colvin et al. 2004, Tajebe et al. 2015a). In our study no, clear correlation with high whitefly abundances and high CBSD or CMD incidences were observed on cassava. Nonetheless, our sampling was not large enough to conclude on that as cassava are growing for over 8 months, the virus transmission can occur at any moments and our survey was made only once.

The use of local varieties could be one of the reasons of high number of infected fields with CMD and CBSD. Higher number of susceptible local varieties was observed in the sampled field of Tanzania compared to Uganda. Correspondingly, some improved varieties showed both CBSD and CMD disease symptoms including the variety Kiroba from Tanzania and TME 14, TME 204, NAROCAS2 and Akena from Uganda. The susceptibility to CMD and CBSD of improved variety TME 204 was reported previously (Legg et al. 2006). Similarly, Bigirimana et al. reported an incidence of 19.6% of CBSD on improved varieties than local varieties (1.1%) in Burundi (Bigirimana et al. 2011). *B. tabaci* abundance is a result of different combination of factors including ecological niche, climatic conditions, virus and cassava genotypes all of these need more research attention to better understand this process driving those outbreaks. Therefore, research should concentrate on developing varieties with multiple resistance including virus and *B. tabaci* species.

## Conclusion

This study provides insights of a more complex picture than expected, with the capacity of not only SSA1 (SG1/SG2) species to induce superabundant populations in East Africa, but other species, including IO and SSA1-SG3. The species community and its genetic diversity differ between both sampled countries, which implies also different situation and the causes of those outbreaking populations seem multifactorial.

This made us to reject our hypothesis saying that the outbreaking populations observed toward the eastern part of Tanzania were linked to an invasion of populations from Uganda. As a conclusion, this study allowed us to think that under favorable environmental conditions local populations have the potential to outbreak even without invasion of populations from other areas.

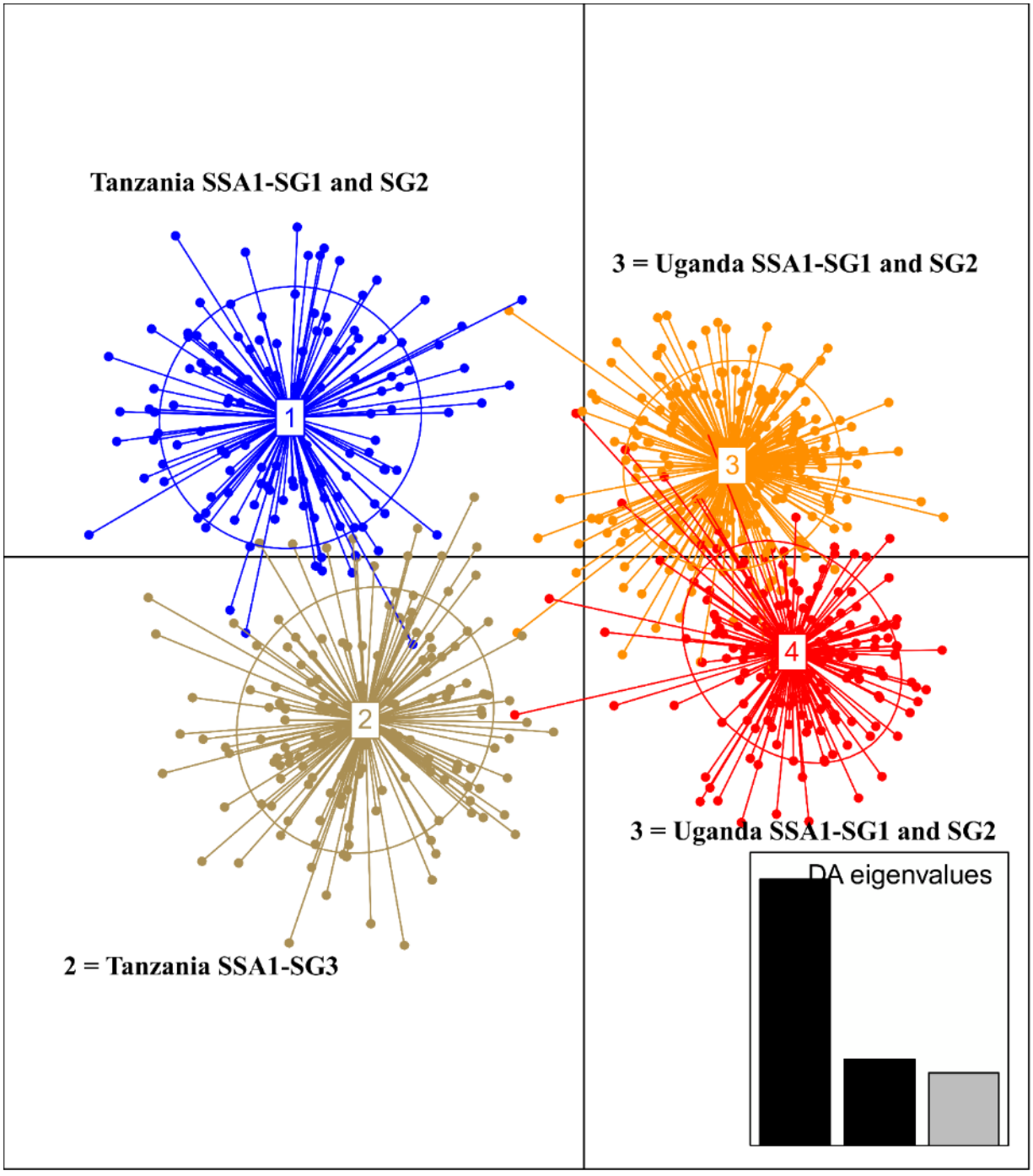
## Acknowledgements

We would like to thank all farmers from Tanzania that allowed us to sample whiteflies in their cassava fields and for their warm welcome during the survey. This work was supported by the Natural Resources Institute, University of Greenwich, from a grant provided by the Bill & Melinda Gates foundation (Grant Agreement OPP1058938), and by CIRAD and the European Agricultural Fund for Rural Development (EAFRD). The authors acknowledge the Plant protection Plate form (3P, IBISA).

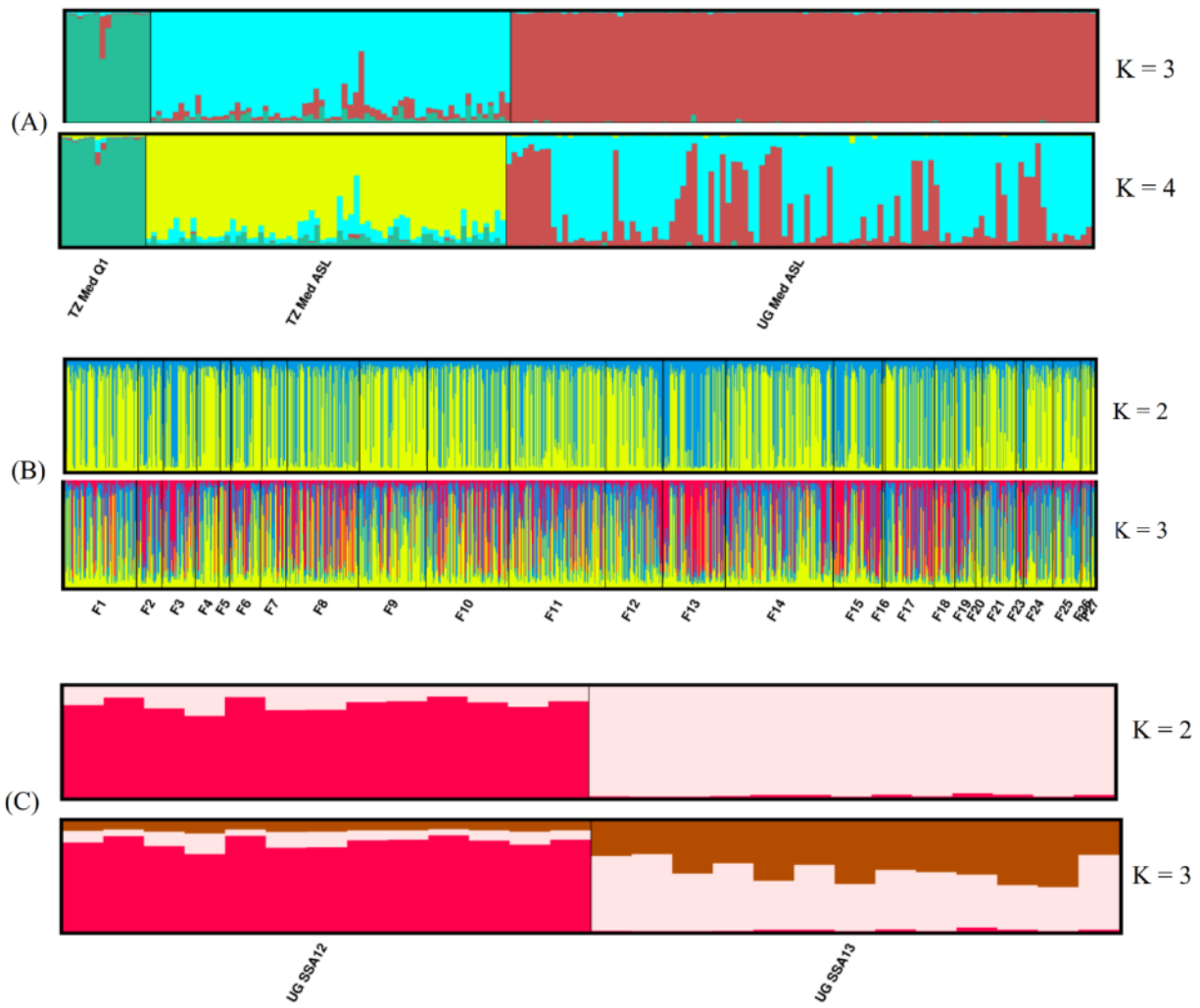
### Authors' contributions

H.D., J.C. and M.N.M. designed the experiment, H.M.A, H.D, M.N.M., conducted field sampling and data collection. H.M.A, H.E.H, H.D. and C.S. performed laboratory analysis. H.M.A, H.D. and C.S. carried out data analysis. H.M.A and H.D. drafted manuscript. M.N.M. and J.C. edited the manuscript.

**Supplementary information**




Supp Fig. 3.1: DAPC analysis performed at K = 4 on 729 individuals of SSA1 species ($n_{Tanzania}$ = 288, $n_{Uganda}$=and 441). Each cluster represents the dominant individuals within SSA1 species.




Supp Fig. 3.2: Different population structures bar plot of *B. tabaci* (A) Med from Tanzania and Uganda analysed with 7 microsatellite markers (B) IO (Tanzania) analysed with 12 microsatellite markers (C) SSA12 and SSA13 from Uganda analysed with nine markers. Individuals were arranged according to mtCOI per site but due to few individuals observed per site for Med and SSA12 and SSA13 they were merged but for IO was presented per site. Black line separated population. For each data set optimal K selected by STRUCTURE HARVESTER.

Supp Table 3.1: Characteristics of microsatellite loci used in the nuclear analysis.

| LN | Reference | Primer sequence | Motif | FL | %MS | Range |
|---|---|---|---|---|---|---|
| MS145 | Dalmon et al., 2008 | F: CCTACCCATGAGAGCGGTAA | (AC)9 | PET | 4.2 | 124-234 |
| | | R: TCAACAAACGCGTTCTTCAC | | | | |
| P59 | Delatte et al., 2006 | F: CGGCGTTTCTCGTTTTCTT | (T)44(G)18 | 6-FAM | 2.3 | 148-220 |
| | | R: TTTGCCAACTGAAGCACATCAATCA | | | | |
| P7 | Delatte et al., 2006 | F: AGGGTGTCAGGTCAGGTAGC | 8(GT) | VIC | 2 | 117-287 |
| | | R: TTTGCGTAATAGAAAA | | | | |
| WF2H06 | Hadjistylli et al., 2014 | F: TATTCGCCAATCGATTCCTT | (TTTG)11 | NED | 4.4 | 102-214 |
| | | R: CGGCGGAAATTTCGATAAA | | | | |
| P62 | Delatte et al., 2006 | F: CTTCCTTAGCACGGCAGAAT | (GT)8 | 6-FAM | 2.2 | 126-288 |
| | | R: TTTGGCGCAATTTTTAGCGTCTGT | | | | |
| WF1G03 | Hadjistylli et al., 2014 | F: CTCCAAAATGGGACTTGAAC | (GTTT)8 | PET | 1.2 | 102-292 |
| | | R: GTAGAAGCCACACATACTAGCAC | | | | |
| WF1D04 | Hadjistylli et al., 2014 | F: GTTGTTAGGTTACAGGGTTTGTC | (CAAA)16 | VIC | 1.8 | 100-172 |
| | | R: GTCTTTACTTCTTTTCCTCCG | | | | |
| P5 | Delatte et al., 2006 | F: ATTAGCCTTGCTTGGGTCCT | (GT)8 | NED | 4.8 | 100-288 |
| | | R: TTTGCAAAAACAAAAGCATGTGTCAAA | | | | |
| CIRSSA2 | Ally et al., submitted | F: ACAATGCATGTTGATTGTGAA | (AG)6 | VIC | 0.2 | 100-126 |
| | | R: TGAAAATGTCTACGGCCAGA | | | | |
| CIRSSA6 | Ally et al., submitted | F: CATATCGGTCATTATCCGCA | (TC)6 | VIC | 0.2 | 117-173 |
| | | R: CATCAGGCTGGAAAGACGAG | | | | |
| CIRSSA7 | Ally et al., submitted | F: TGGCGATCCTCTTCTTGTTT | (TC)5 | PET | 0.2 | 122-152 |
| | | R: AAGAAGCAGCAGTTCATCCG | | | | |
| CIRSSA13 | Ally et al., submitted | F: AGTGCTGAAGGTCCACCGTA | (CT)6 | NED | 12.8 | 145-291 |
| | | R: GGGATTTCCAGGGGTTAAGA | | | | |
| CIRSSA41 | Ally et al., submitted | F: TGGGTGCATGGTTCTTACAG | (CT)6 | 6-FAM | 25 | 112-184 |
| | | R: TATCCGGTCGACAAACACAA | | | | |

Locus name (LN), source reference, primer sequence, microsatellite repeat motif, fluorochromes used for labelling primers (FL), percentage of missing data in the whole dataset (%MS), allele size range (Range, bp).

Supp Table 3.2: Host plant utilization (A) all plants sampled from Tanzania and B) from Uganda

A

| Species | Location | Order name | Familyname | Crop/weed |
|---|---|---|---|---|
| SSA1-SG1/SG2 | Arusha, Dar es Salaam, Dodoma, Morogoro, Pwani, Zanzibar | Fabales | Fabaceae | Fish poison |
| | | Malpighiales | Euphorbiaceae | Cassava |
| | | Solanales | Solanaceae | Tomato |
| | | Asterales | Asteraceae | Sunflower |
| | | Asterales | Asteraceae | Bristly starbur |
| SSA1-SG3 | Dar es salaam, Morogoro, Pwani, Zanzibar | Malpighiales | Euphorbiaceae | Cassava |
| | | | | Bushweed |
| | | Malvales | Malvaceae | Caesarweed |
| | | Cucurbitales | Cucurbitaceae | Cucumber |
| | | Fabales | Fabaceae | Fish poison |
| | | Fabales | Fabaceae | Greengram |
| | | Malvales | Malvaceae | Okra |
| | | Brassicales | Cleomaceae | Spider flowers |
| | | Solanales | Solanaceae | Sweet peper |
| | | Solanales | Convolvulaceae | Sweetpotato |
| | | Solanales | Solanaceae | Tomato |
| | | Solanales | Convolvulaceae | Watermelon |
| | | Malvales | Malvaceae | Wireweed |
| | | | | Bushweed |
| IO | Arusha, Dar es Salaam, Dodoma, Manyara, Morogoro, Pwani, Zanzibar | Fabales | Fabaceae | Fish poison |
| | | Malpighiales | Euphorbiaceae | Annual pointesia |
| | | Malvales | Malvaceae | Azanza |
| | | Fabales | Fabaceae | Beans |
| | | Asterales | Asteraceae | Bristly starbur |
| | | | | Bushweed |
| | | Brassicales | Brassicaceae | Cabbage |
| | | Malvales | Malvaceae | Caesarweed |
| | | Malpighiales | Euphorbiaceae | Cassava |
| | | Fabales | Fabaceae | Cassias |
| | | Fabales | Fabaceae | Cowpea |
| | | Fabales | Fabaceae | Rattlepods |
| | | Cucurbitales | Cucurbitaceae | Cucumber |
| | | Caryophyllales | Polygonaceae | Dockweed |
| | | | | Dycotyweed1 |
| | | Solanales | Solanaceae | Eggplant |
| | | Caryophyllales | Nyctaginaceae | Erect boerhavia |
| | | Malpighiales | Euphorbiaceae | Fire plant |
| | | Fabales | Fabaceae | Fish poison |
| | | Fabales | Fabaceae | Greengram |
| | | Fabales | Fabaceae | Groundnuts |
| | | Brassicales | Brassicaceae | Kale |
| | | Solanales | Solanaceae | Moon flower |
| | | Solanales | Convolvulaceae | Morning glory |
| | | Malvales | Malvaceae | Okra |
| | | Lamiales | Lamiaceae | Pignut |
| | | Solanales | Convolvulaceae | Pink morning glory |
| | | Cucurbitales | Cucurbitaceae | Pumpkin |
| | | Lamiales | Pedaliaceae | Sesame |
| | | Brassicales | Cleomaceae | Spider flowers |
| | | Asterales | Asteraceae | Sunflower |
| | | Solanales | Solanaceae | Sweet peper |
| | | Solanales | Convolvulaceae | Sweetpotato |
| | | Solanales | Solanaceae | Tomato |
| | | Solanales | Convolvulaceae | Watermelon |
| | | Malvales | Malvaceae | Wireweed |
| | | Fabales | Fabaceae | Woody vines |
| | | Cucurbitales | Cucurbitaceae | Zucchin |
| Med Q1 | Morogoro, Pwani, Zanzibar | Malpighiales | Euphorbiaceae | Fire plant |
| | | | Malvaceae | Caesarweed |

| | | | | |
|---|---|---|---|---|
| Med ASL | Arusha, Dar es Salaam, Dodoma | Brassicales | Brassicaceae | Cabbage |
| | Morogoro, Pwani, Zanzibar | Fabales | Fabaceae | Cowpea |
| | | Cucurbitales | Cucurbitaceae | Cucumber |
| | | | | Dicotyledon weed |
| | | Malvales | Malvaceae | Okra |
| | | Cucurbitales | Cucurbitaceae | Pumpkin |
| | | Brassicales | Cleomaceae | Spider flowers |
| | | Solanales | Solanaceae | Sweet pepper |
| | | Solanales | Convolvulaceae | Sweetpotato |
| | | Solanales | Convolvulaceae | Watermelon |
| | | Malvales | Malvaceae | Wireweed |
| EA1 | Manyara | Cucurbitales | Cucurbitaceae | Pumpkin |
| Sudan II | Manyara | Malvales | Malvaceae | Wireweed |
| Unknown Species | Arusha, Manyara, Dodoma | Asterales | Asteraceae | Bristly starbur |
| | | Fabales | Fabaceae | Groundnuts |
| | | Malpighiales | Euphorbiaceae | Cassava |
| | | Solanales | Convolvulaceae | Pink morning glory |

B

| **Spicies** | **Location** | | **Familyname** | **Crop/weed** |
|---|---|---|---|---|
| | | Malpighiales | Euphorbiaceae | Cassava |
| SSA1-SG1 | Mityana, Mpiji, Wakiso masaka, Rakai, Kalungu Gomba | Solanales | Solanaceae | Eggplant |
| | | Lamiales | Verbenaceae | Tickberry |
| | | Caryophyllaless | Phytolacaceae | Pokeweeds |
| | | Solanales | Cucurbitaceae | Pumpkin |
| | | Solanales | Convolvulaceae | Sweet potao |
| | | Brassicales | Brassicaceae | Indian mustard |
| | | Asteraceles | Asteraceae | Black-jack |
| Med ASL | Mityana, Mpiji, Wakiso masaka, Rakai, Kalungu | Solanales | Solanaceae | Eggplant |
| | | Cucurbitales | Cucurbitaceae | Pumpkin |
| | | Solanales | Convolvulaceae | Sweetpotato |
| | | Lamiales | Lamiaceae | Lion's ear |
| | | Lamiales | Verbenaceae | Tickberry |
| Med Q1 | Mityana, Mpiji | Solanales | Solanaceae | Eggplant |
| | | Solanales | Convolvulaceae | Sweetpotato |
| Ugsp | Mityana, Mpiji, Masaka Rakai, Kalungu | Lamiales | Verbenaceae | Tickberry |
| | | Fabales | Fabaceae | Beans |
| | | Asteraceles | Asteraceae | Black-jack |
| | | Solanales | Convolvulaceae | Sweetpotato |
| | | Brassicales | Brassicaceae | Indian mustard |
| SSA11 | Mityana, Wakiso | Solanales | Convolvulaceae | Sweetpotato |
| | | Lamiales | Verbenaceae | Tickberry |
| | | Lamiales | Lamiaceae | Lion's ear |
| SSA12 | Masaka, Rakai | Cucurbitales | Cucurbitaceae | Pumpkin |
| | | Commelinales | Commelinaceae | Wandering jew |
| SSA13 | Mityana, Mpiji, Wakiso Rakai | Commelinales | Commelinaceae | Wandering jew |
| | | Solanales | Solanaceae | Eggplant |
| | | Lamiales | Verbenaceae | Tickberry |
| | | Solanales | Convolvulaceae | Sweetpotato |
| | | Lamiales | Lamiaceae | Lion's ear |
| Uganda 1 | Mityana, Mpiji, Wakiso Masaka, Kalungu | Solanales | Convolvulaceae | Sweetpotato |
| | | Solanales | Solanaceae | Eggplant |
| | | Lamiales | Verbenaceae | Tickberry |
| | | Caryophyllales | Phytolacaceae | Pokeweeds |
| EA1 | Rakai | Asterales | Asteraceae | Black-jack |
| IO | Rakai, Wakiso | Fabales | Fabaceae | Beans |
| | | Brassicales | Brassicaceae | Indian mustard |

Ugsp = Uganda sweetpotato, EA1 = East Africa1, IO = Indian Ocean, SSA = sub–Sahara Africa

Supplementry Table 3.3: Frequency of null allele observed in each locus per *B. tabaci* species.

| **TZ SSA1SG1/G2** | | **TZ IO** | | **TZ SSA1-SG3** | | **TZ MedQ1** | | **TZ MedASL** | |
|---|---|---|---|---|---|---|---|---|---|
| Ms145 | 0.04 | Ms145 | 0.16 | Ms145 | 0.12 | Ms145 | 0.79 | Ms145 | 0.12 |
| P59 | 0.17 | P59 | 0.13 | P59 | 0.11 | P59 | 0.15 | P59 | 0.18 |
| P7 | 0.19 | P7 | 0.26 | P7 | 0.25 | P7 | 0.30 | P7 | 0.26 |
| WF2H06 | 0.13 | WF2H06 | 0.00 | WF2H06 | 0.11 | WF2H06 | 0.56 | WF2H06 | 0.00 |
| P62 | 0.08 | P62 | 0.00 | P62 | 0.18 | P62 | 0.00 | P62 | 0.00 |
| WF1G03 | 0.00 | WF1G03 | 0.03 | WF1G03 | 0.05 | WF1G03 | 0.00 | WF1G03 | 0.24 |
| WF1D04 | 0.00 | WF1D04 | 0.10 | WF1D04 | 0.10 | WF1D04 | 0.17 | WF1D04 | 0.17 |
| P5 | 0.03 | P5 | 0.09 | P5 | 0.09 | P5 | 0.05 | P5 | 0.05 |
| CIRSSA2 | 0.15 | CIRSSA2 | 0.01 | CIRSSA2 | 0.00 | CIRSSA2 | 0.00 | CIRSSA2 | No info |
| CIRSSA6 | 0.04 | CIRSSA6 | 0.21 | CIRSSA6 | 0.05 | CIRSSA6 | 0.86 | CIRSSA6 | 0.14 |
| CIRSSA7 | 0.00 | CIRSSA7 | 0.01 | CIRSSA7 | 0.00 | CIRSSA7 | 0.86 | CIRSSA7 | 0.00 |
| CIRSSA13 | 0.07 | CIRSSA13 | 0.22 | CIRSSA13 | 0.11 | CIRSSA13 | 0.16 | CIRSSA13 | 0.09 |
| CIRSSA41 | 0.40 | CIRSSA41 | 0.52 | CIRSSA41 | 0.49 | CIRSSA41 | 0.65 | CIRSSA41 | 0.62 |
| **UG SSA1SG1/G2** | | **UG MedASL** | | **UG Ugsp** | | **SSA12** | | | **UG SSA13** |
| Ms145 | 0.22 | Ms145 | 0.99 | Ms145 | 0.29 | Ms145 | No info | Ms145 | 0.92 |
| P59 | 0.14 | P59 | 0.16 | P59 | 0.07 | P59 | 0.09 | P59 | 0.20 |
| P7 | 0.09 | P7 | 0.26 | P7 | 0.15 | P7 | 0.19 | P7 | 0.22 |
| WF2H06 | 0.13 | WF2H06 | 0.00 | WF2H06 | 0.12 | WF2H06 | 0.17 | WF2H06 | 0.16 |
| P62 | 0.10 | P62 | 0.00 | P62 | 0.14 | P62 | 0.00 | P62 | 0.08 |
| WF1G03 | 0.07 | WF1G03 | 0.19 | WF1G03 | 0.01 | WF1G03 | 0.10 | WF1G03 | 0.00 |
| WF1D04 | 0.08 | WF1D04 | 0.13 | WF1D04 | 0.00 | WF1D04 | 0.00 | WF1D04 | 0.15 |
| P5 | 0.16 | P5 | 0.13 | P5 | 0.00 | P5 | 0.00 | P5 | 0.04 |
| CIRSSA2 | 0.03 | CIRSSA2 | 0.12 | CIRSSA2 | 0.96 | CIRSSA2 | 0.77 | CIRSSA2 | 0.00 |
| CIRSSA6 | 0.09 | CIRSSA6 | 0.11 | CIRSSA6 | 0.14 | CIRSSA6 | 0.28 | CIRSSA6 | 0.00 |
| CIRSSA7 | 0.07 | CIRSSA7 | 0.00 | CIRSSA7 | 0.19 | CIRSSA7 | 0.88 | CIRSSA7 | 0.92 |
| CIRSSA13 | 0.07 | CIRSSA13 | 0.45 | CIRSSA13 | 0.23 | CIRSSA13 | 0.33 | CIRSSA13 | 0.53 |
| CIRSSA41 | 0.48 | CIRSSA41 | 0.51 | CIRSSA41 | 0.41 | CIRSSA41 | 0.52 | CIRSSA41 | 0.58 |

Supplemental Table 3.4: Pairwise FST values among SSA1 populations sampled from Tanzania and Uganda based on 12 microsatellites, individuals n > 5 from one site considered as a population. Non-significant FST values are indicated in bold with P < 0.05

| | | | F13 | F14 | F15 | F16 | F17 | F18 | F19 | F20 | F21 | F23 | F24 | F26 | F27 | F7 | F8 | F4 | F9 | F1 | F2 | F3 | F5 | F6 | F7 | F8 | F9 | F10 | F11 | F12 | F13 | F14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Tanzania** | **SSA1-SG3** | F13 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | F14 | 2 | 0.06 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | F15 | 3 | 0.04 | 0.05 | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | F16 | 4 | 0.05 | **0.01** | 0.05 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | F17 | 5 | 0.05 | 0.03 | 0.05 | **0** | | | | | | | | | | | | | | | | | | | | | | | | | |
| | | F18 | 6 | 0.05 | **0.01** | 0.04 | **0.01** | **0** | | | | | | | | | | | | | | | | | | | | | | | | |
| | | F19 | 7 | 0.07 | 0.03 | 0.06 | **0.01** | 0.03 | 0.02 | | | | | | | | | | | | | | | | | | | | | | | |
| | | F20 | 8 | 0.05 | 0.03 | 0.05 | **0.01** | **0** | **0** | 0.03 | | | | | | | | | | | | | | | | | | | | | | |
| | | F21 | 9 | 0.05 | 0.03 | 0.06 | **0** | **0** | **0** | 0.02 | **0.01** | | | | | | | | | | | | | | | | | | | | | |
| | | F23 | 10 | 0.05 | 0.02 | 0.05 | **0.01** | **0.01** | **0.01** | 0.02 | **0.01** | 0.02 | | | | | | | | | | | | | | | | | | | | |
| | | F24 | 11 | **0.03** | **0.02** | **0.04** | **0.01** | **0.01** | **0.01** | **0.01** | **0.01** | **0.03** | **0.05** | | | | | | | | | | | | | | | | | | | |
| | | F26 | 12 | 0.08 | 0.05 | 0.08 | 0.03 | 0.03 | **0.02** | 0.08 | 0.03 | 0.04 | 0.03 | **0.02** | | | | | | | | | | | | | | | | | | |
| | | F27 | 13 | 0.07 | 0.06 | 0.08 | 0.03 | 0.02 | 0.03 | 0.02 | 0.04 | 0.04 | 0.03 | **0.02** | 0.04 | | | | | | | | | | | | | | | | | |
| | **SSA1-SG2** | F7 | 14 | 0.06 | 0.08 | 0.04 | 0.08 | 0.09 | 0.09 | 0.11 | 0.08 | 0.09 | 0.08 | 0.06 | 0.1 | 0.12 | | | | | | | | | | | | | | | | |
| | | F8 | 15 | 0.1 | 0.14 | 0.11 | 0.13 | 0.13 | 0.14 | 0.16 | 0.13 | 0.14 | 0.13 | 0.09 | 0.15 | 0.14 | **0.02** | | | | | | | | | | | | | | | |
| | | F4 | 16 | 0.1 | **0.02** | 0.07 | 0.05 | 0.06 | 0.05 | 0.07 | 0.05 | 0.06 | 0.05 | 0.04 | 0.08 | 0.1 | 0.06 | 0.1 | | | | | | | | | | | | | | |
| | | F9 | 17 | 0.08 | 0.07 | 0.07 | 0.08 | 0.08 | 0.09 | 0.11 | 0.08 | 0.08 | 0.08 | 0.06 | 0.12 | 0.11 | 0.02 | 0.06 | 0.04 | | | | | | | | | | | | | |
| **Uganda** | **SSA1-SG1 and SSA1-SG2** | F1 | 18 | 0.16 | 0.1 | 0.17 | 0.12 | 0.11 | 0.12 | 0.17 | 0.13 | 0.12 | 0.13 | 0.08 | 0.14 | 0.18 | 0.16 | 0.23 | 0.13 | 0.16 | | | | | | | | | | | | |
| | | F2 | 19 | 0.14 | 0.09 | 0.15 | 0.11 | 0.09 | 0.1 | 0.16 | 0.11 | 0.1 | 0.11 | 0.08 | 0.12 | 0.17 | 0.12 | 0.2 | 0.11 | 0.11 | 0.02 | | | | | | | | | | | |
| | | F3 | 20 | 0.15 | 0.11 | 0.17 | 0.13 | 0.11 | 0.12 | 0.18 | 0.14 | 0.12 | 0.12 | 0.1 | 0.15 | 0.18 | 0.16 | 0.24 | 0.13 | 0.14 | 0.02 | **0** | | | | | | | | | | |
| | | F5 | 21 | 0.17 | 0.1 | 0.17 | 0.12 | 0.11 | 0.12 | 0.18 | 0.13 | 0.1 | 0.12 | 0.09 | 0.13 | 0.19 | 0.14 | 0.22 | 0.11 | 0.13 | 0.02 | **0** | 0.02 | | | | | | | | | |
| | | F6 | 22 | 0.16 | 0.1 | 0.16 | 0.12 | 0.11 | 0.1 | 0.17 | 0.12 | 0.1 | 0.12 | 0.09 | 0.13 | 0.18 | 0.15 | 0.22 | 0.11 | 0.14 | 0.02 | 0.02 | 0.02 | 0.01 | | | | | | | | |
| | | F7 | 23 | 0.17 | 0.1 | 0.16 | 0.12 | 0.11 | 0.11 | 0.17 | 0.13 | 0.11 | 0.12 | 0.1 | 0.14 | 0.18 | 0.14 | 0.22 | 0.1 | 0.14 | 0.03 | 0.03 | 0.04 | 0.02 | **0** | | | | | | | |
| | | F8 | 24 | 0.16 | 0.1 | 0.16 | 0.12 | 0.1 | 0.1 | 0.17 | 0.12 | 0.1 | 0.12 | 0.09 | 0.13 | 0.18 | 0.15 | 0.23 | 0.12 | 0.14 | 0.03 | 0.01 | 0.02 | 0.01 | **0** | 0.01 | | | | | | |
| | | F9 | 25 | 0.18 | 0.12 | 0.17 | 0.13 | 0.12 | 0.12 | 0.19 | 0.14 | 0.12 | 0.13 | 0.12 | 0.15 | 0.19 | 0.16 | 0.24 | 0.12 | 0.15 | 0.05 | 0.04 | 0.05 | 0.02 | 0.02 | 0.02 | **0** | | | | | |
| | | F10 | 26 | 0.16 | 0.1 | 0.16 | 0.12 | 0.11 | 0.11 | 0.17 | 0.12 | 0.09 | 0.12 | 0.07 | 0.13 | 0.17 | 0.15 | 0.23 | 0.11 | 0.14 | 0.05 | 0.04 | 0.04 | 0.02 | 0.01 | **0.01** | 0.01 | 0.02 | | | | |
| | | F11 | 27 | 0.15 | 0.09 | 0.16 | 0.11 | 0.1 | 0.1 | 0.16 | 0.12 | 0.09 | 0.1 | 0.09 | 0.13 | 0.17 | 0.14 | 0.22 | 0.1 | 0.14 | 0.04 | 0.02 | 0.03 | 0.02 | **0.01** | 0.01 | **0** | 0.01 | 0.01 | | | |
| | | F12 | 28 | 0.17 | 0.11 | 0.16 | 0.13 | 0.12 | 0.11 | 0.18 | 0.14 | 0.11 | 0.13 | 0.11 | 0.15 | 0.2 | 0.15 | 0.24 | 0.11 | 0.15 | 0.04 | 0.03 | 0.03 | 0.02 | 0.01 | 0.01 | 0.01 | 0.02 | 0.01 | 0.01 | | |
| | | F13 | 29 | 0.21 | 0.14 | 0.2 | 0.16 | 0.15 | 0.14 | 0.22 | 0.17 | 0.15 | 0.17 | 0.17 | 0.18 | 0.23 | 0.19 | 0.28 | 0.15 | 0.18 | 0.04 | 0.03 | 0.03 | 0.01 | 0.01 | 0.01 | **0.01** | 0.02 | 0.01 | 0.02 | **0** | |
| | | F14 | 30 | 0.18 | 0.11 | 0.18 | 0.14 | 0.13 | 0.13 | 0.19 | 0.15 | 0.12 | 0.14 | 0.12 | 0.17 | 0.21 | 0.15 | 0.24 | 0.12 | 0.14 | 0.03 | 0.01 | 0.02 | **0.01** | 0.02 | 0.02 | **0** | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 |

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# Chapter 4

## Chapter 4: The whitefly, *Bemisia tabaci*, species distribution and genetic diversity in Malawi

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**Abstract**

Understanding the distribution of insect vectors is important for developing control strategies for diseases they spread. One of the destructive vectors threatening cassava production in sub–Sahara Africa is *B. tabaci,* which transmits >300 plant viruses. Among the important ones are cassava mosaic begomoviruses and cassava brown streak ipomoviruses, which together can cause up to 70% yield reduction in infected cassava fields. This study was conducted to understand the distribution of *B. tabaci* species in different agroecological zones and host plants in Malawi for understanding genetic diversity and structure. A total of 698 *B. tabaci* were analysed. Based on mtCOI barcoding sequencing, four major *B. tabaci* species were identified including SSA1 and its three subgroups (SG1, SG2 and SG3), Med ASL, Med Q1 and SSA12. The SSA1–SG3 was the dominant species found in all agroecological zones surveyed. Nuclear analysis using nuclear markers was performed on the dominant groups (SSA1 and Med). Four subpopulations within SSA1–SG3 with two being restricted to different agroecological zone were found, one each in the northern and southern parts of the country. However, other SSA1–SG3 populations were widely distributed. These results suggested that whitefly movement is restricted to Northern and Southern region.

Key words: *B. tabaci*, mtCOI, microsatellites, subpopulations

## Introduction

*Bemisia tabaci* (Gennadius) is considered as one among the top 100 invasive alien species in the world according to the International Union for the Conservation of Nature and Natural Resources (Lowe et al. 2000). *B. tabaci* causes great economic losses to agriculture and ornamental crops including cassava (Hillocks et al. 2008, Masinde et al. 2016). Over the past decades, an outbreak of *B. tabaci* had been reported in many regions of sub–Sahara Africa colonizing different crops (Thresh et al. 1994, Thresh et al. 1997, Legg and Fauquet 2004, Legg et al. 2011). Recently, the number of *B. tabaci* had increased to more than 200 folds in many regions of East and Central Africa on cassava fields (Legg et al. 2002, Legg et al. 2014a, Tajebe et al. 2015, Tocko-Marabena et al. 2017).

*B. tabaci* is a vector of several plant viruses. Among the wide range of viruses that it is able to transmit, two are of economic importance in cassava: the cassava mosaic begomo virus (CMBs) and the cassava brown streak ipomo virus (CBSIs). Both of those viruses continue to be threatening cassava in major cassava growing areas in sub–Saharan African regions (Monger et al. 2001, Colvin et al. 2004, Mbanzibwa et al. 2011).

*B. tabaci* is a species complex with more than 40 cryptic species. The species are morphologically similar, however, differ hugely by behaviour and genetics (Dinsdale et al. 2010, Lee et al. 2013, Mugerwa et al. 2018). Currently, several species of *B. tabaci* were identified in various sub–Sahara Africa regions including: the SSA1 to SSA13, MEAM1, Med (ASL, Q1, Q2 and Q3), East Africa 1 (EA1), Indian Ocean (IO) and Uganda sweet potato (Ugsp) (Gnankine et al. 2013b, Legg et al. 2014b, Mugerwa et al. 2018). Although whitefly species are known as polyphagous, some such as SSA1 appears to be monophagous colonizing mainly cassava (Legg et al. 2002, Berry et al. 2004).

Cassava is the third important staple food crop in Malawi after maize and sweet potato. It contributes 7% calories intake per capita consumption and reported to feed 30 to 40% of Malawi population (Minot 2010). Estimated annual production during 2017 was 4,960,556 T, ranking Malawi the number one producer in Southern Africa Zone (FAOstat 2017).

Cassava has gained popularity after severe droughts in the late and mid-1990s, resulted from severe yield reduction of maize (Chipeta and Bokosi 2013). Despite of its importance, cassava production in Malawi is threatned by both CMBs and CBSIs, 70% yield loss due to CBSV was reported (Shaba et al. 2003, Benesi 2005, Mbewe et al. 2015).

Understanding the vectors which are facilitating CMV and CBSV pandemic in Malawi are essential prerequisites for the development of management strategies. Almost no data are available on the vector distribution, movements and range of species affecting different crops, particularly cassava, in Malawi. This study was carried out fill this gap in knowledge to understand whitefly vectors in the different agroecological areas of Malawi.

## Materials and methods

### Study area

Whitefly samples were collected from the 16 – 23 November 2016 in Malawi. A total of 23 fields were surveyed in three regions in 11 districts: Southern (Thyolo, Chiradzu, Zomba and Machinga districts), Central (Nticheu, Dedza, Salima and Nkhotakota districts) and North (Nkhata bay, Rumphi and Chitipa). Adult whiteflies were collected using a mouth operated aspirator and stored in eppendorf tubes containing pure ethanol. Each tube contained individuals collected from the same site, the same host plant at the same time and was labelled with a unique code. The sampling was made from the first five leaves of the shoot tip of cassava and on the leaves of other crops and weeds found around or within cassava fields. These included annual poinsettia (*Euphorbiaceae*), cowpea (*Vigna unguiculata*), tick clover *Desmodium* sp, green beans (*Phaseolus vulgaris),* Lantana (*Lantana camara),* legume weeds, Caesarweed (*Ureno lobata*), mtananere, pumpkin (*Cucurbita*), wireweed (*Sida acuta),* heart leaf sida (*Sida cordifolia*), soya bean (*Glycine max*), sweet potato (*Ipomea batata*), tomato (*Solanum lycopersicum*), *Vernonia sp,* and bitter apple (*Solanum campylacanthum*) (Table 4.1). The geographical information points (GPS) were taken in each field surveyed. The GPS points was used to generate the map (Fig.4.1).

Table 4. 1: Sampling information on adult whitefly collected in different districts of Malawi.

| District | Fno | Plant order name | Family name | Scientific name | Common name | CV | MAP | Location x | Location y | WC | CMD | CBSD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Thyolo | F1 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Sauti | 11 | -16.082750° | 35.128312° | 1 | 1 | 1 |
| | F1 | Malvales | Malvaceae | *Sida acuta* | Wireweed | NA | NA | | | NA | NA | NA |
| Machinga | F2 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Maniocola | 11 | -15.321521 | 34.896778 | 1 | 3 | 1 |
| | F3 | Malpighiales | Euphorbiaceae | *Euphorbia heterophylla* | Annual poinsentia | NA | NA | S14°59.028 | E034°45.019' | NA | NA | NA |
| | F3 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Maniocola | 6 | | | 1 | 3 | 1 |
| Ntcheu | F3 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Maniocola | 6 | | | 1 | 3 | 1 |
| | F3 | Solanales | Solanaceae | *Solanum campylacanthum* | Bitter apple | NA | NA | | | NA | NA | NA |
| | F3 | Malvales | Malvaceae | *Urena lobate* | Caesarweed | NA | NA | | | NA | NA | NA |
| Dedza | F4 | Solanales | Solanaceae | *Solanum lycopersicum* | Tomato | NA | NA | S14°24.065' | E034°23.634' | NA | NA | NA |
| Salima | F6 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Uknown | Unkown | S13°34.079' | E034°17.660' | 1 | 1 | 1 |
| Nkhotakota | F7 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Betalece | 11 | S13°04.287' | E034°18.004' | 1 | 3 | 1 |
| | F7 | Malvales | Malvaceae | *Sida cordifolia* | Heart leaf sida | NA | NA | | | NA | NA | NA |
| Nkhotakota | F8 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Mkawazi | 13 | | | 1 | 2 | 3 |
| | F8 | Solanales | Convolvulaceae | *Ipomea batata* | Sweet potato | NA | NA | | | NA | NA | NA |
| | F8 | Fabales | Fabaceae | *Crotaralia* | Rattlepod | NA | NA | | | NA | NA | NA |
| Nkhotakot | F9 | | | | Tananere | NA | NA | S12°25.136' | E034°05.235' | NA | NA | NA |
| | F10 | Malvales | Malvaceae | *Sida acuta* | Wireweed | NA | NA | S11°55.099' | E034°08.062' | NA | NA | NA |
| Nkhata bay | F10 | Malvales | Malvaceae | *Sida cordifolia* | Heart leaf sida | NA | NA | | | NA | NA | NA |
| | F10 | Malpighiales | Euphorbiaceae | *Euphorbia heterophylla* | Annual poinsentia | NA | NA | | | NA | NA | NA |
| Nkhata bay | F11 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Maniocola | 6 | S11°34.715' | E034°13.892' | 1 | 2 | 2 |
| | F11 | | Asteraceae | *Vernonia sp* | Vernonia | NA | NA | | | NA | NA | NA |
| | F11 | Malvales | Malvaceae | *Sida acuta* | Wireweed | NA | NA | | | NA | NA | NA |
| | F11 | Fabales | Fabaceae | *Vigna unguiculata* | Cowpea | NA | NA | | | NA | NA | NA |
| | F12 | Fabales | Fabaceae | *Desmodium sp* | tick clover, | NA | NA | S11°30.311' | E034.004.337' | NA | NA | NA |
| Mzimba | F13 | Malpighiales | Euphorbiaceae | *Euphorbia heterophylla* | Annual poinsentia | NA | NA | S11°27.656' | E034°81.115' | NA | NA | NA |
| | F14 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Nbundumali | 11 | S:10°51.185' | E:34°04.216' | 1 | 2 | 2 |
| Uknown | F14 | Fabales | Fabaceae | *Vigna unguiculata* | Cowpea | NA | NA | | | NA | NA | NA |
| | F14 | Solanales | Convolvulaceae | *Ipomea batata* | Sweet potato | NA | NA | | | NA | NA | NA |
| | F14 | Malvales | Malvaceae | *Sida acuta* | Wireweed | NA | NA | | | NA | NA | NA |
| | F15 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Thupula | 11 | S10°37.250' | E034°11451' | 1 | 2 | 3 |
| Rumphi | F15 | Solanales | Convolvulaceae | *Ipomea batata* | Sweet potato | NA | NA | | | NA | NA | NA |
| | F15 | Malvales | Malvaceae | *Urena lobate* | Caesarweed | NA | NA | | | NA | NA | NA |
| | F17 | Malvales | Malvaceae | *Sida acuta* | Wireweed | NA | NA | -9.642772° | 33.112383° | NA | NA | NA |
| Chitipa | F17 | Fabales | Fabaceae | *Tephrosia sp* | Tephrosia | NA | NA | | | NA | NA | NA |
| | F18 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Mbundumali | 12 | S:15°31.071 | E:035°13.041 | 1 | 1 | 1 |
| Zomba | F19 | Solanales | Solanaceae | *Solanum lycopersicum* | Tomato | NA | NA | S: 15°31.969 | E: 035°13.501 | NA | NA | NA |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F20 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Mbundumali | 12 | S:15°36.968 | E:035°16.158 | 1 | 1 | 1 |
| | F21 | Solanales | Convolvulaceae | *Ipomea batata* | Sweet potato | NA | NA | S: 15°25.334 | E:035°14.932 | NA | NA | NA |
| Chiradzulu | F22 | Solanales | Convolvulaceae | *Ipomea batata* | Sweet potato | NA | NA | S: 15°25.334 | E:035°14.932 | NA | NA | NA |
| | F23 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Kachamba | 8 | S: 15°55.278 | E: 035°04.264 | 1 | 1 | 1 |
| | F23 | Fabales | Fabaceae | *Glycine max* | Soya Bean | NA | NA | | | NA | NA | NA |
| Thyolo | F23 | Solanales | Convolvulaceae | *Ipomea batata* | Sweet potato | NA | NA | | | NA | NA | NA |
| | F24 | Solanales | Solanaceae | *Solanum lycopersicum* | Tomato | NA | NA | S:15°36.869 | E:035°09.997 | NA | NA | NA |
| | F24 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Sagonja | 24 | | | 1 | 1 | 1 |
| Chiradzulu | F24 | Cucurbitales | Cucurbitaceae | *Cucurbita* | Pumpkin | NA | NA | | | NA | NA | NA |
| | F25 | Malpighiales | Euphorbiacea | *Euphorbia heterophylla* | Cassava | Uknown | | S: 15°31.794 | E:035°14.265 | 1 | 1 | 1 |
| | F25 | Solanales | Convolvulaceae | *Ipomea batata* | Sweet potato | NA | NA | S: 15°54.468 | E: 035°17.639 | NA | NA | NA |
| | F25 | Solanales | Solanaceae | *Solanum lycopersicum* | Tomato | NA | NA | S: 15°31.794 | E:035°14.265 | NA | NA | NA |

Location where sampling conducted, Fno = field number, CV = cassava variety name, MAP = age of cassava (month after planting), WC (whitefly count) > 100 wc regarded as superabundant, CMD, CBSD symptoms observed from field grown cassava.

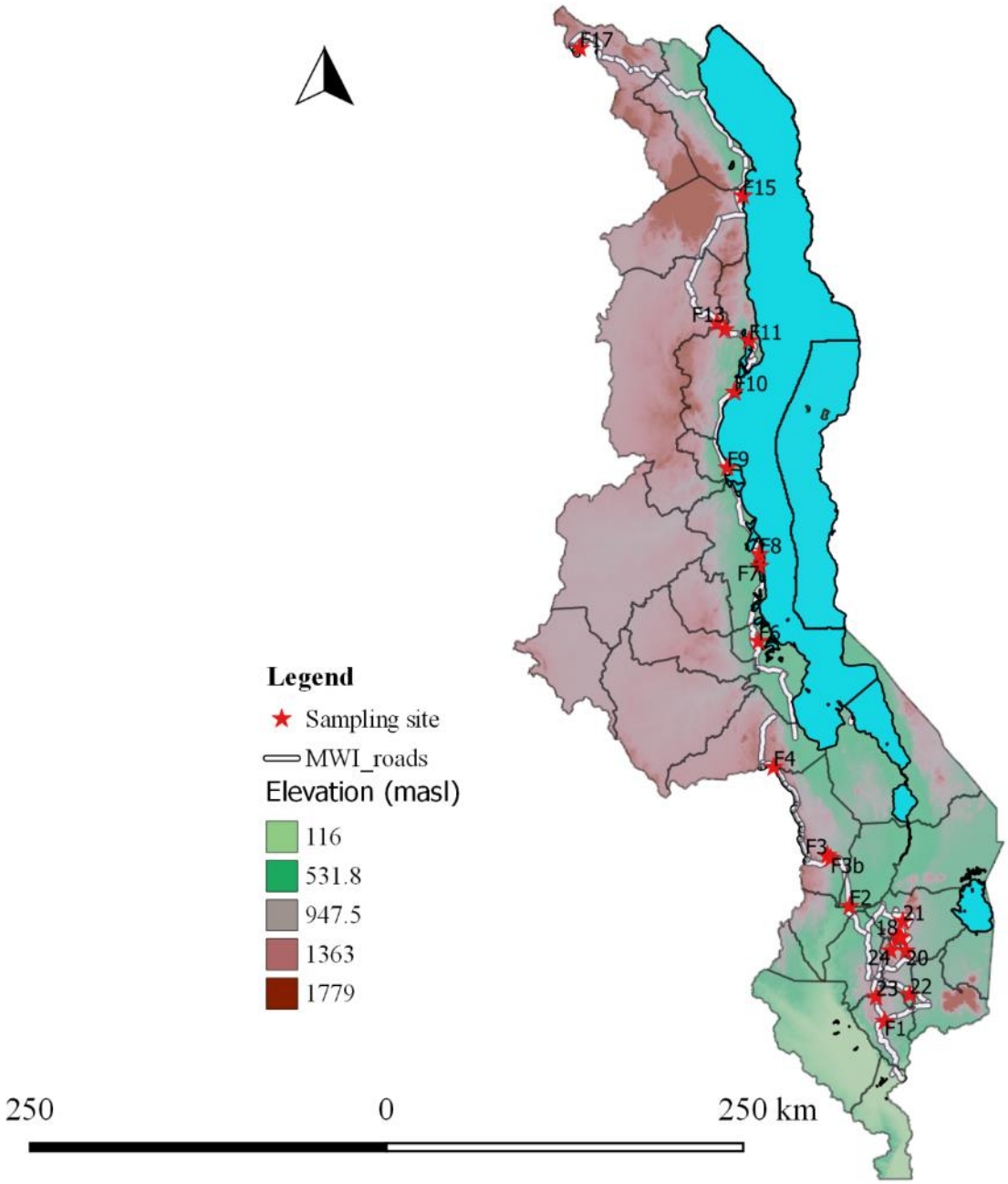



Figure 4. 1:Malawi sampling sites, sampling made from 16 to 23rd of November 2016.

Both cassava mosaic (CMD) and cassava brown streak (CBSD) diseases severity were scored in the range of 1 – 5 by using the methodology applied by Mahungu (Mahungu et al. 1994) where, 1 shows no disease and 5 shows severe disease symptoms. The number of adult whiteflies was counted from five random selected plants in each field (Sseruwagi et al. 2004b) to evaluate the infestation level.

**DNA extraction**

A maximum of 20 adult whitefly females were selected from each tube by using a Leica MZ8 stereomicroscope 100X (Leica Microsystems, Nanterre, France). A total of 763 female individuals were selected. The DNA extraction was conducted following the method utilized by Tocko-Marabena et al. (2017). Prior to utilization the DNA extracts were kept at –20ºC.

**Mitochondrial cytochrome oxidase I (mtCOI) PCR amplification and sequencing**

The mtCOI barcoding gene was amplified by using the primer pair derived by Mugerwa et al., (Mugerwa et al. 2018). The PCR reaction mixture was conducted in a final volume of 20 µl comprising, 10 µl of type-it (2x) QIAGEN© (France), 7 µl of pure HPLC water (CHROMASOLV ®, Sigma-Aldrich), 1 µl of each primer and 1 µl of DNA template. Initial denaturation of template DNA was conducted at 95 ℃ for 15 min followed by 40 cycles of: denaturation at 95 ℃ for 30 s, primer annealing at 52 ℃ for 30 s, and extension at 72 ℃ for 1 min. A final extension was run at 72 ℃ for 10 min. The amplified products were sent to Macrogen © Europe laboratory for sequencing. The DNA sequences produced were manually edited and aligned using Geneious R10 v.10.2.3 software (Kearse et al. 2012). The DNA sequence polymorphism (haplotypes) analysis was investigated using DnaSP 6 software (Rozas et al. 2017). The different haplotypes observed from this study were selected together with reference sequences from GenBank and aligned by Clustal W (Thompson et al. 1994). The aligned sequences were subjected to Jmodel test for determination of the best model prior phylogenetic contraction using MrBayes software (Ronquist and Huelsenbeck 2003). The analysis was run with 1,100,000 iterations of MCMC (of the first 110,000 iterations were discarded as burn in) and sampled trees were made every 200 iterations, using four heated chains. This resulted in effective sample sizes for the posterior probability of 5500 for the analysis.

**Microsatellite genotyping**

A total of 12 microsatellite loci were amplified. The microsatellite loci were chosen from previous studies on whiteflies together with the currently developed (chapter 1) (Dalmon et al. 2008, Delatte et al. 2011, Hadjistylli et al. 2016) contained different repeat motifs (Supplemental data Table 4.1). The selection for those markers was based on the ability to amplify most of the *B. tabaci* expected species in Malawi. Based on discrete allele size ranges, three multiplex loci mixes were prepared: the first mix contained Ms145, P59, P7 and WF2HO6; the second mix contained P62, WF1GO3, WF1DO4 and P5; and the third mix contained CIRSSA2, CIRSSA6, CIRSSA7 and CIRSSA13. The PCR was done as described in chapter two.

**Nuclear marker analysis**

Population genetic indices including observed (Ho) and expected (He) heterozygosity, and mean number of alleles per population were estimated using GENETIX v.4.05.2 following the method of (Nei 1978). An online software GENEPOP (Rousset 2008) was explored for analysing null allele followed the method of Brookfield's (Brookfield 1996). Genetic diversity among population (Fis) was studied by Weir and Cockerham method (Weir and Cockerham 1984) such as the Hardy Weinberg equilibrium (probability test) were determined by Arlequin following the method utilized by Guo and Thompson (1992). Linkage disequilibrium was explored by GENEPOP using Fisher's method (Fisher et al. 1932). The allelic richness was obtained by FSTAT v.2.9.3.2 (Goudet 2002). To assess the level of differentiation between whitefly populations within species, $F_{ST}$ matrix were computed by ARLEQUIN v.3.5.2.2 (Excoffier et al. 2005).

The threshold of >20% null allele frequency, >20% percentage missing data per loci and >30% per individuals were set. This analysis can only be conducted on samples with at least 5 individuals, so it was conducted only on one species SSA1–SG3 due to deficit number to other identified *B. tabaci* species on the different sites surveyed.

The genetic structure among populations was examined using STRUCTURE v.2.3.3 (Pritchard et al. 2000).

A total of $10^6$ simulations with $10^5$ burn in steps and Markov Monte Carlo algorithm (MCMC) steps were run for all samples ($n$ = 562) simultaneously considering a K interval of 1 to 20 with five iteration each.

The optimal number of clusters was analysed by Δk a method of Evanno (Evanno et al. 2005). The graphical output was developed by Structure harvester (Earl 2012), clump (Jakobsson and Rosenberg 2007) and distruct (Rosenberg 2004).

## Results

### Whitefly abundance, CMD and CBSD symptoms severity

A total of 15 fields out of the 23 surveyed had cassava plants in them. No whitefly super abundance (>100 adults per plant) was recorded in any fields visited. The level of CMD and CBSD was low to moderate (Table 4.1). There were higher numbers of fields with CMD ($n$ = 8) than CBSD ($n$ = 4). Four fields showed both CMD and CBSD disease symptoms.

### Whitefly species diversity

The barcoding marker mtCOI gene was amplified successfully from 563 (91.5%) of the extracted *B. tabaci* individuals and they were sequenced. The number of sequences obtained ranged from 300 to 553 nt and split into three different size data sets for further analyses (553 nt $n$ = 213, 400 nt $n$ = 110 and 240 nt $n$ = 238). mtCOI analysis showed the presence of eight *B. tabaci* genetic groups; SSA1 with three subgroups (SG1 $n$ = 17, SG2 $n$ = 20 and SG3 $n$ = 286), Med ASL ($n$ = 173), Med Q1 ($n$ = 23), SSA12 ($n$ = 42), Ugsp (n = 1), and an unidentified group ($n$ = 1).

### *B. tabaci* species distribution

Results on species distribution are presented in (Table 4.2). SSA1–SG3 was the dominating species, found in 22 fields of the 23 fields surveyed. The highest number of SSA1–SG3 (n = 65) was observed at field number 11, which was on the shores of the Lake Malawi in Nkota bay district. The lowest number of single SSA1–SG1 adult was observed in field numbers 2, 9, 13 and 19 (Fig. 2; Table 2).

Table 4. 2: *B. tabaci* species distribution in Malawi during 2016 survey collection.

| District | Field no. | SSA1-SG1 | SSA1-SG2 | SSA1-SG3 | Med ASL | Med Q1 | SSA12 | *Bemisia* Uganda 1 | Unknown |
|---|---|---|---|---|---|---|---|---|---|
| Thyolo | F1 | 4 | 2 | 9 | | | | | |
| Machinga | F2 | | | 1 | | | | | |
| Nticheu | F3 | 7 | 7 | 23 | 1 | 1 | 2 | | |
| Dedza | F4 | | | 7 | | | 3 | | |
| Salima | F6 | | | 26 | | | | | |
| Nkotakota | F7 | | | 24 | | 12 | | | |
| Nkotakota | F8 | 2 | | 13 | 1 | | 1 | | |
| Nkotakota | F9 | | | 1 | | | | | |
| Nkhota bay | F10 | | | | 8 | 9 | | | |
| Nkhota bay | F11 | | 3 | 65 | 31 | | 2 | | 1 |
| Mzimba | F12 | 1 | 1 | 5 | | | | | |
| Mzimba | F13 | | | 1 | 3 | | | | |
| Mzimba | F14 | 2 | 1 | 18 | 63 | 1 | | | |
| Rumphi | F15 | | | 14 | 7 | | | | |
| Chitipa | F17 | | | 16 | 1 | | | | |
| Zomba | F18 | | 4 | 4 | | | | | |
| Zomba | F19 | | | 1 | 2 | | 4 | | |
| Zomba | F20 | | | 3 | 1 | | | | |
| Zomba | F21 | | | | | | 1 | | |
| Chiradzuru | F22 | | | 6 | 16 | | | | |
| Chiradzuru | F23 | 1 | 1 | 34 | 39 | | | 1 | |
| Chiradzuru | F24 | | 1 | 8 | | | 3 | | |
| Chiradzuru | F25 | | | 7 | | | 27 | | |
| Total | | 17 | 20 | 286 | 173 | 23 | 42 | 1 | 1 |

The SSA1–SG1 was found in low numbers compared to SSA1–SG3. The SSA1–SG1 was found in six fields located in five different districts of Malawi. Similarly, SSA1–SG2 was also observed in low numbers in eight fields within six different districts

The second most abundant group was found in this sampling was Med ASL. The Med ASL was observed in 12 fields (Table 2) within eight different districts however, it was the most abundant species in four fields. The highest number of Med ASL observed was 63 in the Mzimba district in the Northern region. Also, the current study observed the sympatric occurrence of Med Q1 and Med ASL. Med Q1 was observed in four fields in four different districts with the highest number found at field number seven in Nkotakota district.

The SSA12 was observed in eight fields distributed in six different districts. The highest number of SSA12 observed was 27 found in field number 25 in Chiradzuru district. Other female individuals of Ugsp and unidentified species were found in fields 21 and 23, respectively.

**Host plant usage**

The SSA1–SG3 was found in a wide range of host plants including cassava, poinsettia, cowpea, soybean, sweetpotato, pumpkin, tomato and *Lantana* (Fig. 4.2). The SSA1–SG3 was found in all sampled host plants except in bitter apple (*Solanum campylacanthum*). Only 63.64% of SSA1–SG3 individuals were collected on cassava. Other host plants where the SSA1–SG3 sampled (with >10 individuals) were sweetpotato (4.1%), soybean (2.7%), wireweed (2.3%) and *Vernonia* (2.3%) (Fig. 4.2).

The highest number of Med ASL was found on sweetpotato ($n$ = 75, 45.7%) (Fig.4.2). Other host plants harboring the species were wireweed (20.0%), cowpea (16.8%), cassava (3.4%) and the remaining 13.7% of the Med ASL were sampled on annual poinsettia, caesarweed, tephrosia, tomato and vernonia. The Med Q1 was observed on three host plants, with 91.1% of the species collected on heart leaf sida. Other, host plant where the Med Q1 found were sweetpotato and bitter apple. (Fig.4.2).

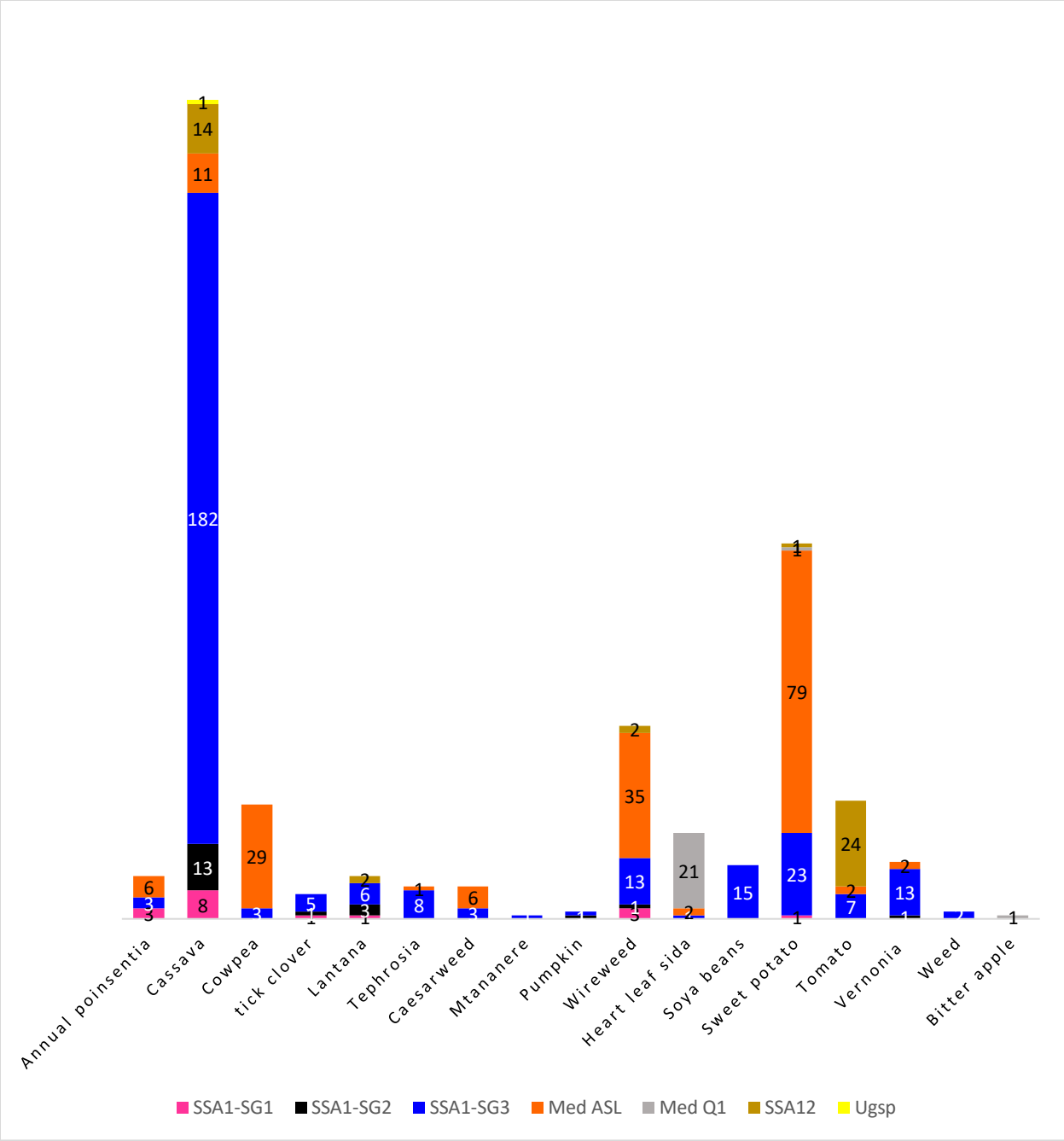



Figure 4. 2: *B. tabaci* species distribution per host plant collected in Malawi.

The SSA12 was observed on five host plants and majority on tomato 55.8% and cassava 32.5%, and on another hosts *Lantana* (4.7%), wireweed (2.7%) and sweetpotato (2.3%). Other low frequency species of Ugsp and an unidentified species was found on cassava and wireweed, respectively.

**Phylogenetic analysis and haplotype diversity**

A total of 26 haplotypes were found from the analysis of longest sequences within our dataset (553 nt, *n* = 213). The SSA1–SG3 exhibited highest haplotype diversity (*n* = 10 in 26) but was the most abundant group found in the dataset (*n* = 89).

The most abundant haplotype of SSA1–SG3 (*n* = 76) was blasted on Genbank and it clustered with Mal Chitala KY523857 from Malawi, (Ghosh et al. 2015), KY523857 from Kenya (Manani et al. 2017) and KX397322 from Mozambique (Hadjistylli et al. 2016), sharing 100% nucleotide identity with each. This haplotype also shared 100% nuclear identity with SSA1–SG3 individuals sampled in Tanzania and Uganda (Chapter 2).

The SSA1–SG1 genetic group (*n* = 8) had four haplotypes, which shared 99.8 to 100% with AY903480 sequences from Uganda (Sseruwagi et al. 2006). Meanwhile one of these haplotypes P5C7_MW was observed shared 99.21% nuclear identity with the sequences identified in Tanzania and Uganda (chapter two). The SSA1–SG2 genetic group showed two haplotypes, the major haplotypes (*n* = 9) shared 100% nuclear identity with sequences different countries including Malawi KX570790 (Ghosh et al. 2015), Uganda MH410711 (Kalyebi et al. 2018, Mugerwa et al. 2018) and Burundi KF425595 (Legg et al. 2014) (Fig. 4.3).

Two distinct groups of Med were found: Med ASL (*n* = 83) and Med Q1 (*n* = 7). Med ASL was the most abundant species and has a higher number of haplotypes (*n* = 5) than Med Q1 (*n* = 2).The dominant group of Med ASL (*n* = 35) was observed to share 99.82% nucleotide identity with MH205754 and EU760758 (Gueguen et al. 2010, Vyskočilová et al. 2018) identified in Uganda and Cameroon, respectively. The same haplotype shared 99.01 and 99.8% with Uganda and Tanzania sequences, respectively (Chapter two). The closest sequences to the Med Q1 haplotype was found out of the African continent.

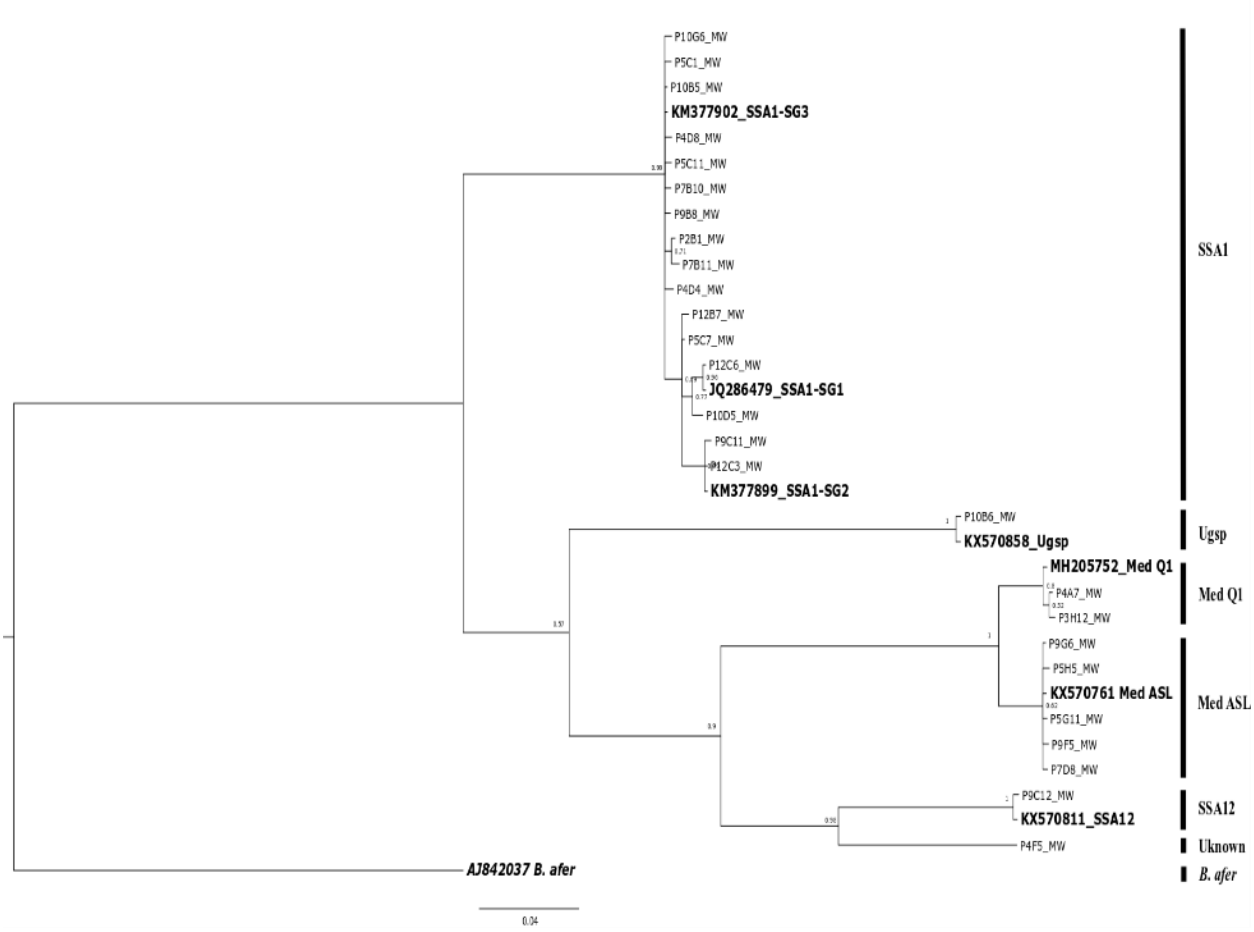



Figure 4. 3: Phylogenetic tree generated by Mr. Bayes involving the 30 different haplotypes collected from different districts in Malawi. Reference sequences obtained from the GenBank are in bold.

The major haplotype (*n* = 5) shared 100% nucleotide identity with KY468415 observed in China (Li et al. 2017). The same haplotype also shared 99.82% with MH205752 and MF447849 from Uganda and Italy, respectively (Bertin et al. 2018, Vyskočilová et al. 2018). Those haplotypes where aligned with Med Q1 retrieved from Tanzania and Uganda sequences of the present study (Chapter two) and shared 100% nuclear identity.

A single haplotype was retrieved for SSA12, which shared 99.8% nucleotide identity with KX570811 from Uganda (Mugerwa et al. 2018). Another group comprised a single haplotype sharing 99.6% with Ugsp from Uganda (Hadjistylli et al. 2016).

This study also found one haplotype close to KX570811 by 89.31% and included in the SSA12 group described by Mugerwa et al. (Mugerwa et al. 2018) (Fig.4.3).

**Nuclear analysis**

A total of 626 (100%) whiteflies were successfully genotyped. Prior to analysis the data set was checked for null alleles and percentage missing data per population (fields) and per loci. Our data set was below the thresholds however 66 individuals were excluded in the analysis, 64 (unamplified mtCOI) individuals and 2 were low frequency occurring species (Uganda sweetpotato and unidentified species).

The frequency of null alleles ranged between 0 to 19%, with the lowest observed on CIRSSA7 and the highest on WF1GO3 and P59 loci. The percentage of missing data ranged between 1.1 to 15.1%. The average allelic richness was ranged between 3.17 to 3.89 with the lowest observed in field six and the highest in field four. The Fis ranged from 0.19 in field 23 to 0.7 in field 12. All populations were in accordance with Hardy–Weinberg equilibrium (Table4.3) and no one deviated from linkage disequilibrium

**Distinct genetic clusters among *B. tabaci* populations of Malawi**

This analysis involved individuals from SSA1 (*n* = 322) including its three sub-groups (–SG1, –SG2 and –SG3), Med ASL (*n* = 173), Med Q1 (*n* = 23) and SSA12 (n = 42).

Table 4. 3: Population genetic diversity indices for SSA1–SG3.

| SSA1-SG3 | N | Mean | Ar | Fis | Ho | He |
|---|---|---|---|---|---|---|
| F1 | 9 | 5.17 | 3.79 | 0.42 | 0.4(0.2) | 0.63(0.23) |
| F3 | 21 | 8.08 | 3.72 | 0.28 | 0.47(0.19) | 0.63(0.21) |
| F4 | 7 | 4.75 | 3.89 | 0.22 | 0.56(0.24) | 0.65(0.18) |
| F6 | 26 | 6.75 | 3.17 | 0.02 | 0.55(0.26) | 0.55(0.24) |
| F7 | 24 | 6.83 | 3.33 | 0.05 | 0.57(0.28) | 0.58(0.24) |
| F8 | 13 | 5.25 | 3.44 | 0.34 | 0.42(0.25) | 0.6(0.21) |
| F11 | 65 | 11.33 | 3.52 | 0.3 | 0.43(0.16) | 0.61(0.2) |
| F12 | 5 | 3.5 | 3.28 | 0.7 | 0.19(0.2) | 0.52(0.28) |
| F14 | 18 | 6.42 | 3.7 | 0.46 | 0.36(0.23) | 0.63(0.21) |
| F15 | 14 | 6.25 | 3.84 | 0.41 | 0.4(0.2) | 0.65(0.2) |
| F17 | 16 | 6.25 | 3.69 | 0.23 | 0.48(0.3) | 0.6(0.26) |
| F22 | 6 | 4 | 3.33 | 0.38 | 0.36(0.26) | 0.51(0.29) |
| F23 | 34 | 9.08 | 3.76 | 0.19 | 0.54(0.2) | 0.65(0.18) |
| F24 | 8 | 4.42 | 3.32 | 0.27 | 0.44(0.22) | 0.56(0.18) |
| F25 | 7 | 4.33 | 3.51 | 0.29 | 0.45(0.28) | 0.56(0.22) |
| Grand mean | 18.20 | 6.16 | 3.55 | | | |

*B. tabaci* species analysed according to different sites sampled N = individuals number within a population, Mean = average number of alleles per population), Ar = allelic richness, $F_{IS}$ = correlation within population presented together with P value from Hardy–Weinberg equilibrium test (* significant at $P < 0.05$), Ho = observed heterozygosity and He = expected heterozygosity.

The best Ks identified were K = 6 and K = 8 (Supplemental Fig. 1a, b). At K = 6, six distinct clusters were observed, well separating the species SSA1, Med ASL, Med Q1 and SSA12 (Fig. 4.4a)**.** At K = 6, we saw faint distinction within SSA1 subgroups, the SG1 and SG2 seemed to share the same genetic clusters but SG3 was slightly different from the others.

To understand the genetic substructure within SSA1 subgroups, SSA1 individuals were run separately from the other species. Structure harvester identified the best K at K = 3 (Fig.4.4b). The first level of differentiation started at K = 3 (Fig.4.4b), we saw distinct genetic clusters however some individuals were observed to share genetic background within subgroups. Going further to K = 4, a clear separation between the subgroups were observed, though few individuals seemed to share genetic information.

A sub–structuring within SSA1–SG3 was also observed. At K = 6 no further differentiation between the subgroups was found (Fig. 4.4b).

Further analysis was conducted for SSA1–SG3, to understand its substructure. The best K analyzed by cluster harvester was at K = 4 (Evanno et al. 2005), however the first level of differentiation began at K = 3, three distinct genetic clusters were observed (Fig. 4.4c). Those genetic clusters were well linked to agroecological zones and oriented the first genetic cluster (Fig.4.4c), which contained individuals collected from Thyolo and Chiradzuru district, both are in the southern part. The second genetic cluster consisted of individuals from the districts of Salima, Nkhotakota, and Nkhata bay, which were sampled along the shore of Lake Malawi. The remaining genetic clusters contained individuals sampled from the northern part in the district of Chitipa. Despite distinct genetic clusters observed according to agroecological zones, a few individuals within each district were also found to belong to the other clusters, showing restricted movements of whitefly populations between districts.

Furthermore, a pairwise $F_{ST}$ distance matrix was run on the SSA1–SG3 populations. Twelve populations were significantly different (Table 4.5). The highest average $F_{ST}$ distance was 0.24 found between individuals of fields 22 and 6.

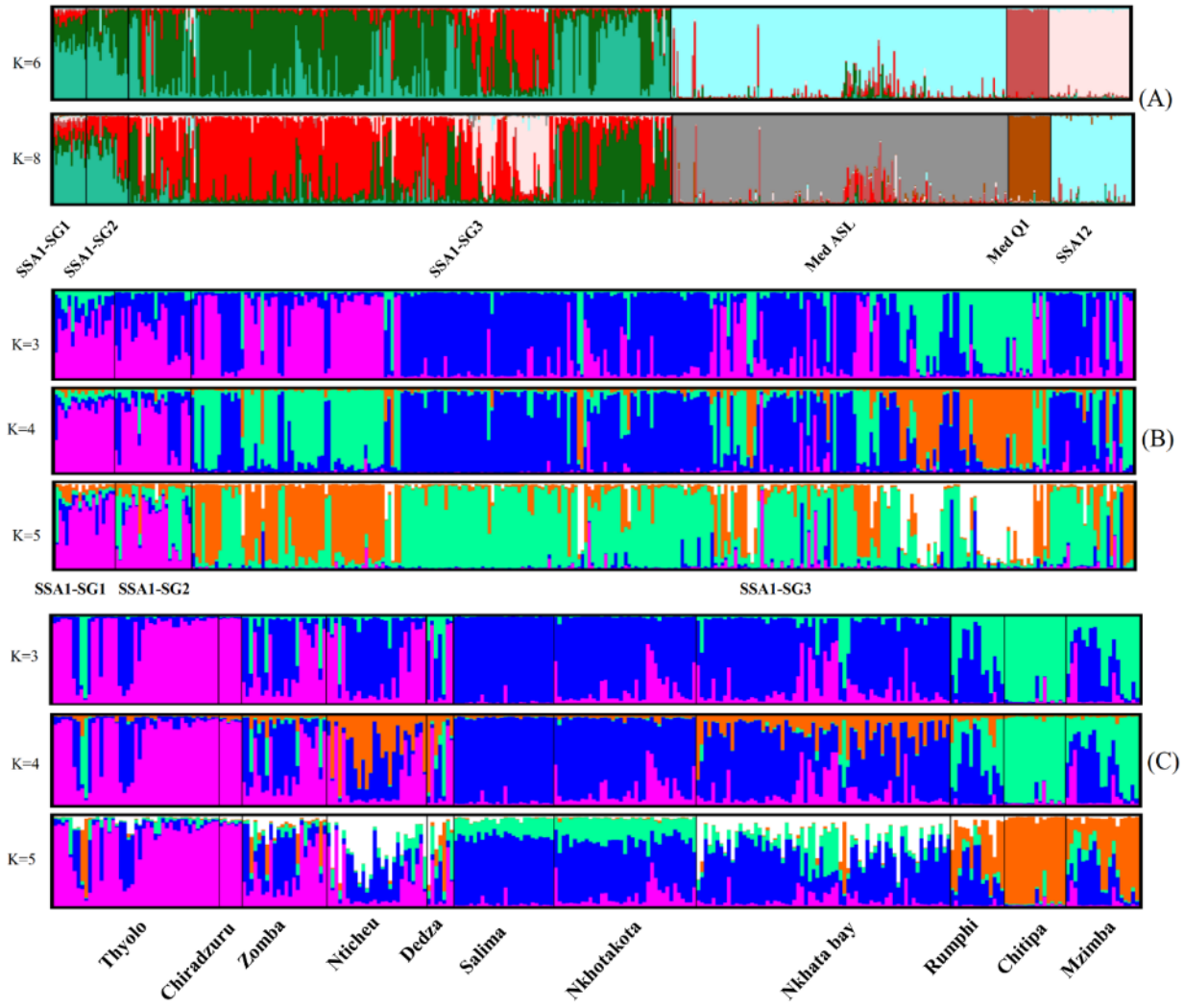



Figure 4. 4: Different population structures of *B. tabaci* (A) the whole dataset (n = 560) with four *B. tabaci* species, (B) The SSA1 with its three subgroups (n = 322) and (C) The SSA1–SG3 (n = 286) collected from Malawi. Structure bar plot based on 12 microsatellite loci. Individuals were arranged according to mtCOI and separated by black line. For each data set optimal K selected by STRUCTURE HARVESTER.

Table 4.5. Matrix of pairwise $F_{ST}$ values among SSA1–SG3 *B. tabaci* populations (n ≥ 5 for each site), based on 12 microsatellite loci.

| | | F1 | F3 | F4 | F6 | F7 | F8 | F11 | F12 | F14 | F15 | F17 | F22 | F23 | F24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Thyolo | F1 | | | | | | | | | | | | | | |
| Nticheu | F3 | **0.04** | | | | | | | | | | | | | |
| Dedza | F4 | 0.01 | 0.05 | | | | | | | | | | | | |
| Salima | F6 | 0.11 | 0.06 | 0.09 | | | | | | | | | | | |
| Nkhotakota | F7 | 0.08 | 0.05 | 0.05 | **0.01** | | | | | | | | | | |
| Nkhotakota | F8 | 0.05 | 0.03 | 0.05 | 0.05 | 0.03 | | | | | | | | | |
| Nkhatabay | F11 | 0.06 | 0.03 | 0.05 | 0.04 | 0.02 | 0.02 | | | | | | | | |
| Mzimba | F12 | 0.09 | 0.11 | 0.06 | 0.21 | 0.16 | 0.1 | 0.13 | | | | | | | |
| Mzimba | F14 | 0.06 | 0.04 | 0.03 | 0.08 | 0.05 | 0.04 | 0.03 | 0.13 | | | | | | |
| Rumphi | F15 | 0.08 | 0.06 | 0.05 | 0.09 | 0.05 | 0.08 | 0.06 | 0.18 | 0.02 | | | | | |
| Chitipa | F17 | 0.14 | 0.15 | 0.1 | 0.22 | 0.18 | 0.16 | 0.15 | 0.19 | 0.05 | 0.08 | | | | |
| Chiradzuru | F22 | 0.08 | 0.12 | 0.11 | 0.24 | 0.19 | 0.13 | 0.16 | 0.06 | 0.15 | 0.19 | 0.22 | | | |
| Zomba | F23 | 0.02 | 0.07 | 0.06 | 0.13 | 0.11 | 0.05 | 0.09 | 0.07 | 0.09 | 0.12 | 0.17 | 0.05 | | |
| Chiradzuru | F24 | 0.07 | 0.03 | 0.07 | 0.04 | 0.06 | 0.03 | 0.03 | 0.16 | 0.07 | 0.08 | 0.2 | 0.15 | 0.07 | |
| Zomba | F25 | 0.03 | 0.09 | 0.07 | 0.17 | 0.13 | 0.06 | 0.11 | 0.05 | 0.12 | 0.16 | 0.18 | **0.02** | **0** | 0.13 |

| |
|---|
| 0 - 0.05 |
| 0.06 - 0.1 |
| 0.11 - 0.15 |
| 0.16 - 0.2 |
| 0.21 - 0.25 |

## Discussion and conclusion

This study assessed the genetic diversity and population structures of *B. tabaci* populations sampled from different districts of Malawi. The use of the barcoding region of mtCOI markers revealed eight distinct genetic groups: SSA1 further sub-grouped into SG1, SG2 and SG3, Med ASL, Med Q1, SSA12, Ugsp and an unknown group. All species identified, except Med Q1, were found on cassava, however, the largest number of individuals was from SSA1–SG3. Further analysis using nuclear markers showed population sub-structuring within SSA1-SG3 which matched with the agroecological zones.

### Genetic diversity of *B. tabaci*

Among the eight genetic *B. tabaci* groups found in Malawi, SSA1–SG3 was dominant. The occurrence of SSA1–SG3 was previously reported in Malawi (Ghosh et al. 2015). The species was also reported in the coastal areas of the Indian ocean in Tanzania and Madagascar, and in Central Africa Republic (Tajebe et al. 2015a, Tocko-Marabena et al. 2017, Wosula et al. 2017, Mugerwa et al. 2019). The SSA1–SG3 recently observed in Tanzania (see chapter two) was sub-structured with a pattern following roughly the different agroecological zones such as Malawi. This finding is showing that populations of this species do not extensively move between regions of Malawi. Kambewa and Nyembe (2008) observed major cassava growing areas include the districts from the Northern and Central parts along the shores of Lake Malawi (Nkhotakhota, Nkhota bay, Karonga and Rumphi) grow cassava as a staple food crop.

The two subpopulations identified in this study one found in the northern part and the other in the southern provided an interpretation that agroecological climate might favor their survival, or that so few movements of populations exists that they have evolved in allopatry. That conclusion is supported by the different planting season as the Southern parts receives earlier rainfall than Northern parts (Kambewa 2010).

Most of the earlier studies made in sub-Saharan Africa identified the SSA1–SG3 only on cassava (Tajebe et al. 2015a, Wosula et al. 2017). The SSA1–SG3 in Malawi was found on many different host plants, showing its polyphagous feeding behavior with a preference for cassava.

Similar findings were discussed in chapter two from Tanzania. The polyphagous behavior of the species might ensure their existence in the absence of cassava, thus it might also facilitate the transmission of plant virus associated diseases in cassava as well as other crops. This needs verification.

On the contrary to other countries, such as in Tanzania, The SSA1–SG3 was not found at high levels in Malawi (i.e., not superabundant population). Incidences of CMD and CBSD and severity were also low (Chapter 2). It was probably because the survey was conducted in November during the dry season after most of cassava was harvested.

Two different genetic groups of Med were observed, the Med ASL and Med Q1. The co-occurrence of these species was also reported in other countries of Africa such as in Burkina Faso, Benin, Cameroon, Ivory Coast, Senegal and Togo (Gueguen et al. 2010, Gnankine et al. 2013a, Gnankine et al. 2013b), Uganda (Malka et al. 2018, Vyskočilová et al. 2018), Tunisia (Saleh et al. 2012, Laarif et al. 2015) and South Africa (Esterhuizen et al. 2013). The two species occurred in sympatry, however in some fields only Med ASL was found. Nonetheless, Med ASL was only reported in Sub-Saharan Africa compare to Med Q1 which originates from the Mediterranean basin, and being reported as invasive species in several countries such as the USA (McKenzie and Osborne 2017), Asia (China) (Parrella et al. 2012, Li et al. 2017) and Europe (Martinez-Carrillo and Brown 2007). The ability of Med Q1 group to adapt to different agroecological areas could have facilitated its rapid spread in some countries such as China reported to replace the former invasive whitefly MEAM1 (Sun et al. 2013). In our study, the few haplotypes retrieved were mostly clustering with samples of invasive Med Q1 populations in the World such as in China (Li et al. 2017) and Italy (Bertin et al. 2018), so we could hypothesize that Malawi had suffered also from a recent invasion of this species.

This study also revealed the occurrence of SSA12 species in Malawi, sampled from food crops and weeds, however the species was first reported from Uganda on *Commelina benghalensis* (Mugerwa et al. 2018). These results showing the large distribution of the species throughout countries in East Africa on different host plants.

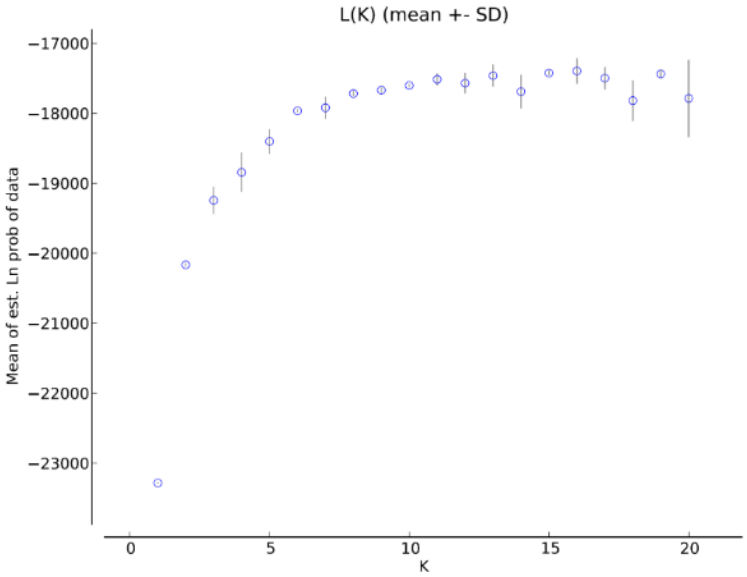
This study provided a new knowledge on *B. tabaci* distribution in Malawi. Further research needed for better understanding the species including SSA1–SG3 distribution for establishment of better control measure.

## Acknowledgements

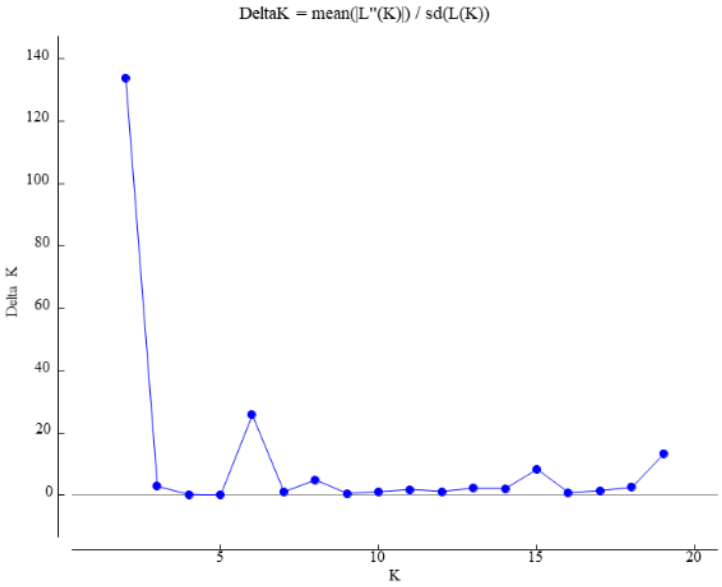
We would like to thank all farmers from Malawi for their warm welcome during the survey and allowed us to sample whiteflies in their cassava fields. This work was supported by the Natural Resources Institute, University of Greenwich, from a grant provided by the Bill & Melinda Gates foundation (Grant Agreement OPP1058938), and by CIRAD and the European Agricultural Fund for Rural Development (EAFRD). The authors acknowledge the Plant protection Plate form (3P, IBISA).

## Supplementary information accompanied this chapter

(A)




(B)




**Supp. Fig. 4.1. (A)** Plot showing the number of likely genetic clusters (K) against the estimated Ln probability of data (B) Number of genetic clusters K assessed with the ΔK estimator derived from STRUCTURE HARVESTER using Evanno method for all dataset (n = 560) sampled from Malawi.

Supplementary Table 4.1; Characteristics of microsatellite marker used in genotyping.

| LN | Reference | Sequence sequence | Motif | FL | %MS | NA | Range |
|---|---|---|---|---|---|---|---|
| MS145 | Dalmon et al., 2008 | F: CCTACCCATGAGAGCGGTAA<br>R: TCAACAAACGCGTTCTTCAC | (AC)9 | PET | 6.6 | 0.16 | 140 - 222 |
| P59 | Delatte et al., 2006 | F: CGGCGTTTCTCGTTTTCTT<br>R: TTTGCCAACTGAAGCACATCAATCA | (T)44(G)18 | 6-FAM | 2.5 | 0.19 | 142 - 238 |
| P7 | Delatte et al., 2006 | F: AGGGTGTCAGGTCAGGTAGC<br>R: TTTGCGTAATAGAAAA | 8(GT) | VIC | 9.7 | 0.11 | 103 - 295 |
| WF2H06 | Hadjistylli et al., 2014 | F: TATTCGCCAATCGATTCCTT<br>R: CGGCGGAAATTTCGATAAA | (TTTG)11 | NED | 10.1 | 0.09 | 102 - 240 |
| P62 | Delatte et al., 2006 | F: CTTCCTTAGCACGGCAGAAT<br>R: TTTGGCGCAATTTTTAGCGTCTGT | (GT)8 | 6-FAM | 6.2 | 0.18 | 120 - 288 |
| WF1G03 | Hadjistylli et al., 2014 | F: CTCCAAAATGGGACTTGAAC<br>R: GTAGAAGCCACACATACTAGCAC | (GTTT)8 | PET | 8.9 | 0.18 | 102 - 292 |
| WF1D04 | Hadjistylli et al., 2014 | F: GTTGTTAGGTTACAGGGTTTGTC<br>R: GTCTTTACTTCTTTTCCTCCG | (CAAA)16 | VIC | 1.1 | 0.19 | 100 - 188 |
| P5 | Delatte et al., 2006 | F: ATTAGCCTTGCTTGGGTCCT<br>R: TTTGCAAAAACAAAAGCATGTGTCAAA | (GT)8 | NED | 15.1 | 0.01 | 100 - 278 |
| CIRSSA2 | Ally et al., submited | F: ACAATGCATGTTGATTGTGAA<br>R: TGAAAATGTCTACGGCCAGA | (AG)6 | VIC | 2.6 | 0.02 | 100 - 126 |
| CIRSSA6 | Ally et al., submited | F: CATATCGGTCATTATCCGCA<br>R: CATCAGGCTGGAAAGACGAG | (TC)6 | VIC | 1.5 | 0.14 | 125 - 155 |
| CIRSSA7 | Ally et al., submited | F: TGGCGATCCTCTTCTTGTTT<br>R: AAGAAGCAGCAGTTCATCCG | (TC)5 | PET | 2.9 | 0 | 108 - 198 |
| CIRSSA13 | Ally et al., submited | F: AGTGCTGAAGGTCCACCGTA<br>R: GGGATTTCCAGGGGTTAAGA | (CT)6 | NED | 11.7 | 0.16 | 179 - 299 |

Locus name (LN), source reference, primer sequence, microsatellite repeat motif, fluorochromes used for labelling primers (FL), percentage of missing data (%MS), allele size range (Range, bp) all analyzed using the whole dataset and Null allele (NA) analyzed from SSA1–SG3 data

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# Chapter 5

# Chapter 5: General discussion

This study aimed to understand *B. tabaci* species dynamic and factors leading to super abundant population in Eastern part of Africa. We wanted also to know if the outbreaking *B. tabaci* populations seen in Tanzania were the result of invasion from the neighbouring country Uganda. Using newly developed microsatellites markers together with previously developed ones and mtCOI barcoding sequences we were able to insight the distribution of *B. tabaci* and the population dynamics in those countries.

**What has changed over two decades on cassava growing fields of Uganda?**

Within two decades we recorded the same *B. tabaci* species that has continued to colonize cassava. Several factors lead to population differentiation and speciation including geographical isolation triggered by occurrence of natural situations that lead individuals from a given population to separate from the other for a long time (Carroll et al. 1997, Losos et al. 1998, Orr and Smith 1998). Speciation can also occur within the same environment such as assortative mating which rely on genotypic marker or ecological characters. When assortative mating involves genotypic marker traits, it may increase homozygosity within population and speciation occurs when genetic drift break the linkage equilibrium between marker and ecological trait (Dieckmann and Doebeli 1999) The *B. tabaci* species analysed in this study were collected in almost similar areas and on cassava twenty years apart. Despite no new species were involved, species dynamic observed suggested mating preference within *B. tabaci* occurred, favouring one of the populations within the SSA1 species.

Both maternal lineages of SSA1: –SG1 and –SG2 were found similar numbers and occurred in sympatry within the surveyed fields. Those mitochondrial haplotypes were previously found in different cassava growing fields (Legg et al. 2014b, Ghosh et al. 2015). Through the nuclear analysis performed in this PhD, we were able to show that both haplotypes SSA1–SG1 and SSA1–SG2, previously considered as different species, share the same genetic clusters, indicating that the two subgroups can hybridize. Wosula et al. (2017) revealed similar findings using other molecular markers scattered on the whole genome.

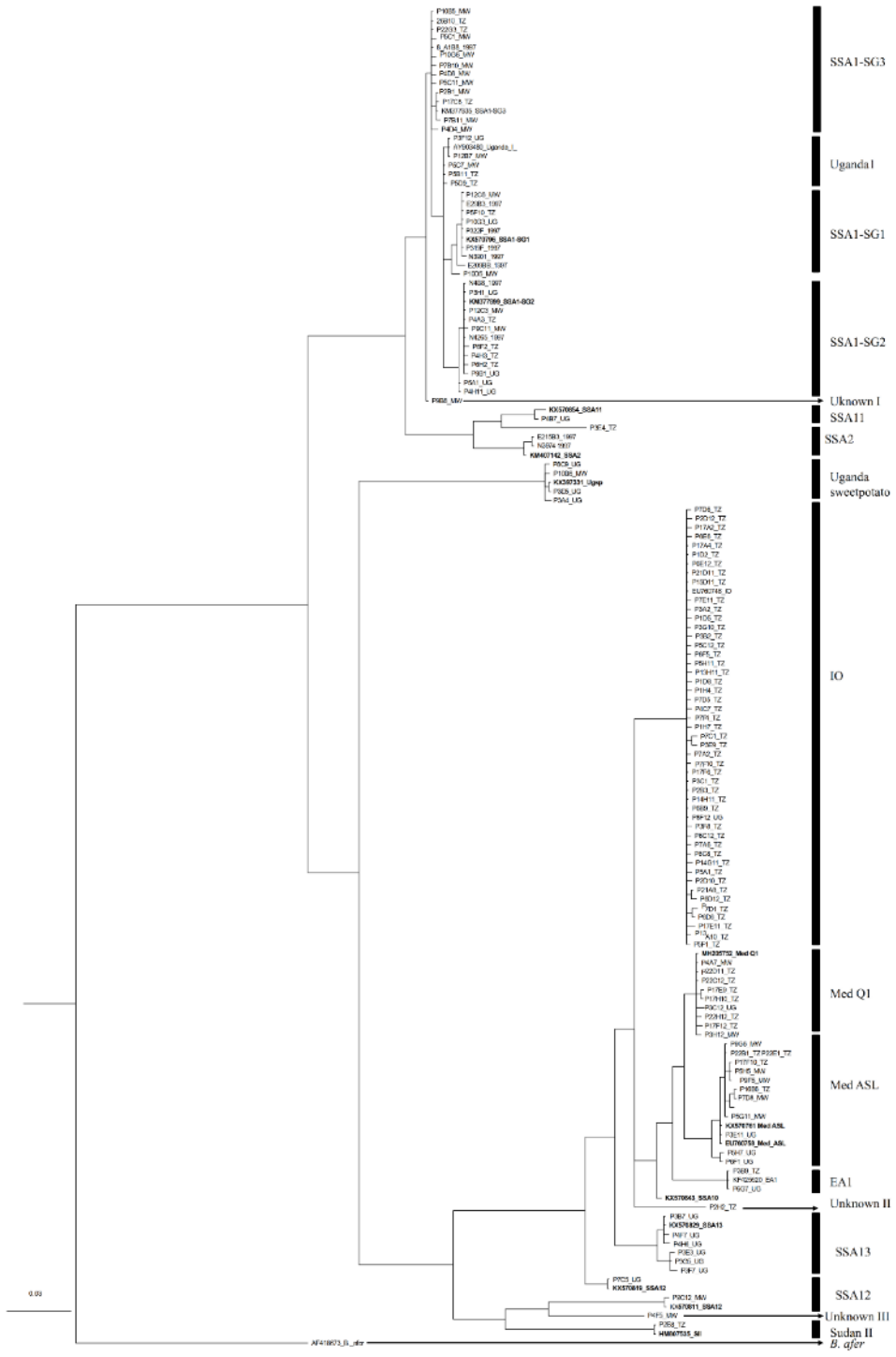


Figure 5. 1: Phylogenetic tree generated by Mr.Bayes with all the different *B. tabaci* mtCOI haplotypes (n = 131) from this PhD sampled from Malawi (MW), Tanzania (TZ) and Uganda (UG) together with 17 reference sequences obtained from Genebank. The tree was rooted by *B. afer*.

The authors showed that SSA1–SG1 and SSA1–SG2 from Burundi, CAR, DRC, Tanzania and Rwanda shared similar genetic background (Wosula et al. 2017).

No SSA2 were observed during the 2017 sampling. Similar observations were also given out in some part of Uganda (Sseruwagi et al. 2006, Mugerwa et al. 2012). However, the species was found in other agroecological areas, in the Northern part of Uganda (Mugerwa et al. 2018). The shift of SSA2 populations could have been triggered by several factors, such as competition between sympatric species, or abiotic conditions such as climatic conditions, which might have evolved in twenty years in those regions. Previously SSA1 and SSA2 were occurred in sympatry and they were linked to the CMD (Legg et al. 2002). Reduction or disappearance of SSA2 in some parts of Uganda made some researchers to assume the two species can interbreed (Maruthi et al. 2004). Unfortunately, we obtained too few samples to possibly draw a clear conclusion, on the few data analysed, we assumed no clear genetic flow between both species.

**Do we have the same *B. tabaci* species distribution between countries?**

Species differentiation within the cryptic *B. tabaci* species complex was performed using barcoding analysis of the core region of the mtCOI gene on the whole sampling made in the three eastern African countries. This analysis allowed us to identify eight major *B. tabaci* species including SSA1 with three subgroups (SG1, SG2 and SG3), SSA2, IO, Med ASL, Med Q1, Ugsp, SSA12, SSA13 (Fig. 5.1). Other low frequency occurring species were also found including SSA11, Uganda 1, Sudan II, EA1 and unidentified species. Those different species had already been reported from eastern Africa, but, are also occurring in other parts of Africa. All the observed species were not distributed similarly in the three sampled countries.

The distribution of those species was found to vary between countries (Fig. 5.2), for instance SSA1–SG1 and SSA1–SG2 were dominating in Uganda and found in each agroecological zones surveyed. In Tanzania IO was dominating and found in all field surveyed, whereas in Malawi the SSA1–SG3 was dominating throughout the country. Three species (SSA1: -SG1 and -SG2, Med ASL and Med Q1) were found in the three sampled countries. The occurrence of mentioned *B. tabaci* in surveyed countries were previous recorded (Ghosh et al. 2015, Tajebe et al. 2015a, Mugerwa et al. 2018).

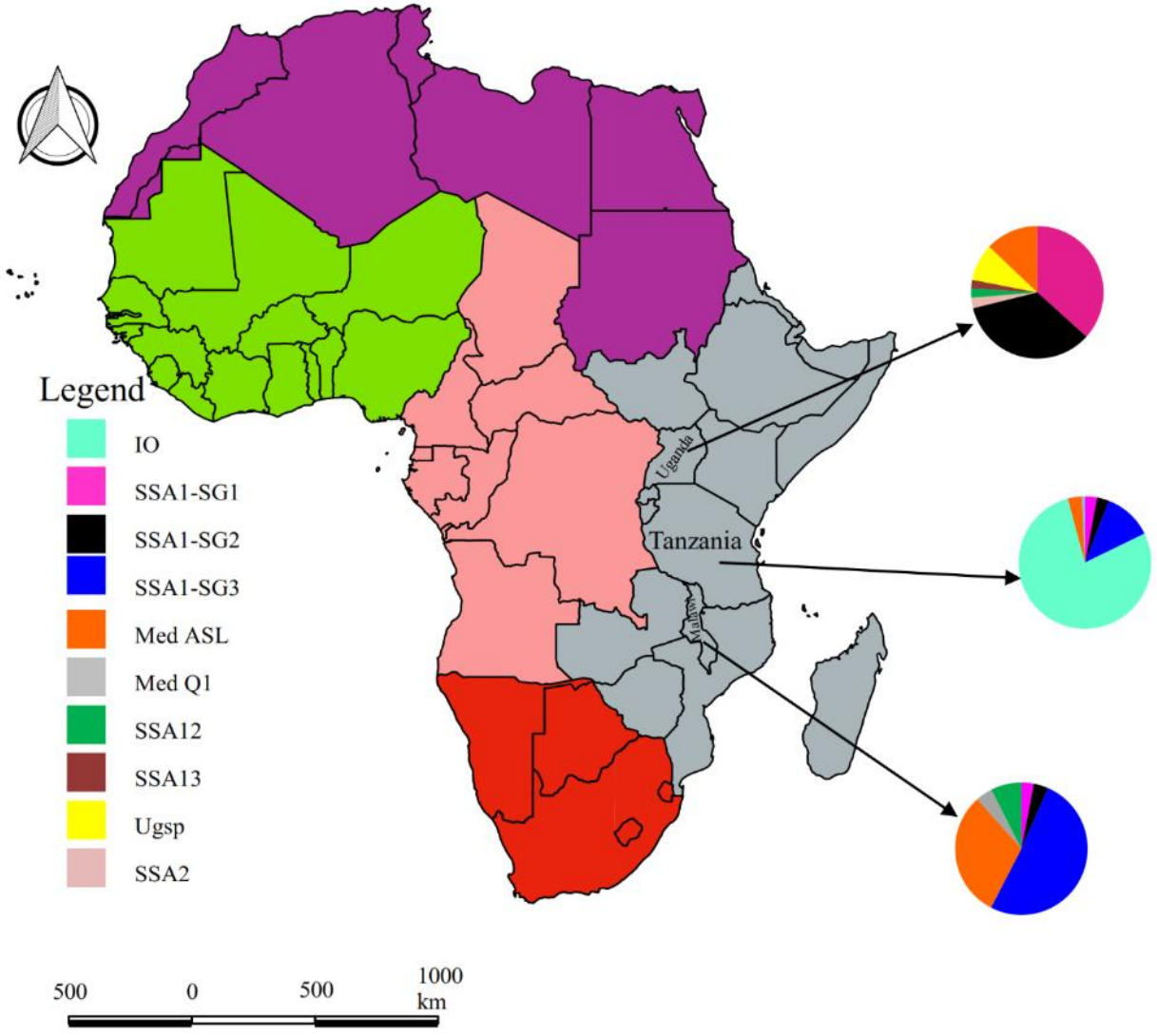


Figure 5. 2: A map showing *B. tabaci* species distribution according to country surveyed: Malawi (n = 562), Tanzania (n = 1967) and Uganda (n = 650)

Among the identified species some species were restricted to certain agroecological zones, for example SSA13, SSA11 and Uganda 1 were only found in Uganda mainly in Lake Victoria crescent zone. The SSA1–SG3 seemed to prefer coastal areas of the Indian Ocean and Lake Malawi areas. Previous studies observed the SSA1–SG3 in similar environment (Ghosh et al. 2015, Wosula et al. 2017). Despite being reported along the coast zone, the underlaying mechanism for SSA1–SG3 ensure its survival yet not known. Further research needs to be conducted. IO showed preference to all Tanzania agroecological zones, but further sampling should be conducted to know if its range of distribution reaches the western part of the country. Understanding species distribution across different sub–Sahara Africa regions will enable better implementation of control measure practices.

Haplotypes analysis revealed largest discrepancies between two haplotypes of a same species within SSA12. In Malawi the P9C12_MW sequence shared 100% nucleotide identity with KX570819 named as SSA12 (Mugerwa et al. 2018), but when blasted this haplotype again the diversity of haplotypes published for the species, we saw that it shared only 86.6% nuclear identity with KX570811 also, named as SSA12 (Mugerwa et al. 2018). Therefore, there is the possibility that the two haplotypes might belong to two different species within SSA12. This finding using only molecular markers, should however be checked by crossing experiments such as (Vyskočilová et al. 2018) did to resolve the "Med" clade.

**What are the range of *B. tabaci* species host plant utilization in three surveyed countries?**

Adults whitefly were sampled on 49 plant hosts belonging to 16 families and 11 orders. The SSA1 species including its subgroups was found on 26 host plant species, belonging to 11 families and 10 orders across the three countries. The plant families where the SSA1 was most often observed in the three countries were from Eurphorbiaceae, Malvaceae, Solanaceae and Fabaceae. The SSA1 is known as a cassava colonizing species (Legg et al. 2002), however, the occurrence of SSA1 observed on non–cassava host plants were previously reported (Sseruwagi et al. 2006, Mugerwa et al. 2018) such as in the current study. Malka et al. (2018) discussed the presence of metabolic pathways in SSA1 that should allow it to feed on different host plants, other than cassava.

Despite the SSA1 being found in diverse host plants, cassava was reported as the most preferred host for the species (Tajebe et al. 2015a, Wosula et al. 2017), such as in the current study. The polyphagous characteristics of SSA1 could let us hypothesize that it gives the species better capacity to spread between fields without its preferred host and increased capacity of survival even in the absence of cassava.

Other species were observed in diverse host plant species including IO. The IO had a huge diversity of host plant species (n = 37, families n = 13 and orders n = 9) interestingly, it was dominating on cassava in one of the superabundant fields. Occurrence of IO on cassava was found elsewhere but with low number (Tajebe et al. 2015a, Mugerwa et al. 2018). The existence of IO in Tanzania ecological niche suggests that the IO is well adapted to the area, and might be a threat to vegetable crops by virus vectoring in some areas, knowing its capacity to transmit TYLCV on tomato (Delatte et al. 2005). Thus, special attention should be given to this species. Med ASL and Med Q1 are known as polyphagous species (Gnankine et al. 2013b). Compare with Med Q1, Med ASL had higher number of host plants than Med Q1 with the highest number found in Malawi. Considering wrong sampled time, Malawi had shown huge host plants utility by *B. tabaci* species. This support previous finding that *B. tabaci* can easily adapt to new host plants (Oliveira et al. 2001). Despite IO, Med ASL and Med are polyphagous, but their preference is on non–cassava plants host.

**Do wee see superabundant fields and what species are involved?**

No superabundant fields were observed in Malawi. The highest number of whiteflies per plant were observed in Tanzania and Uganda. The most abundant fields scoring over 100 whiteflies per plant showed different *B. tabaci* species to be linked to those high populations. In Tanzania two major species occurred in high abundance fields: the SSA1–SG3 and IO. In some fields the IO and SSA1–SG3 occurred in sympatry, however higher number of superabundant fields were observed with IO. This study is the first to report the capacity of IO species to outbreak in a wide range of agroecological zones as well a wide range of host plants. More attention should be given to the species particularly testing the effectiveness of the species in transmission of cassava related viruses.

The SSA1–SG3 was found abundantly in three fields in Tanzania. SSA1–SG3 was more restricted to the coast zone.

In Uganda the SSA1–SG1 and SSA1–SG2 were the only species found in eight superabundant fields observed. This species was also reported in other study to be responsible of such high populations (Tajebe et al. 2015a). Currently the two subgroups are linked to the transmission of CMD as well as CBSD (Legg et al. 2011). The variation in *B. tabaci* species distribution we found provided an interpretation that apart from SSA1–SG1 and SG2, other *B. tabaci* species including SSA1–SG3 and IO can result into outbreaking populations within sub–Sahara Africa.

No Med ASL and Med Q1 were observed in super abundant fields. However, Med Q1 was able to invade in other countries including China and Italy (Chu et al. 2010, Parrella et al. 2012, Li et al. 2017) and in West Africa Med ASL and Med Q1 invaded on cotton (Gnankine et al. 2013a).

**Do we see different populations within *B. tabaci* species between countries?**

Despite some *B. tabaci* individuals such as SSA1–SG1 and SSA1–SG2 shared 100% mtCOI sequences, their genetic clusters differ between countries (Fig. 5.3a). At K = 4, the best K the species was structured according to countries, with significant isolation by distance of the different genetic groups. This result suggests that few movements of SSA1 populations happen between countries. Thus, *B. tabaci* outbreaks seen in eastern or central Tanzania are not as a result of a new invasion from the southern part of Uganda. However, sampling at the Northern part of Tanzania around Lake Victoria basin will confirm this.

Similarly, comparison of populations of SSA1–SG3 between Malawi and Tanzania showed distinct genetic clusters according to countries (Fig. 5.3b). Indeed, the SSA1–SG3 seemed to have a strong structure link to country which is further sub–structured into populations restricted to agroecological zones (ie Malawi). Suggesting also restricted movement of SSA1–SG3 between countries and even within Malawi, which is not the case for Tanzania.

A similar structure was found for Med ASL (Fig. 5.3c), however in this structure Med ASL from three countries, at least, slightly shared genetic background.

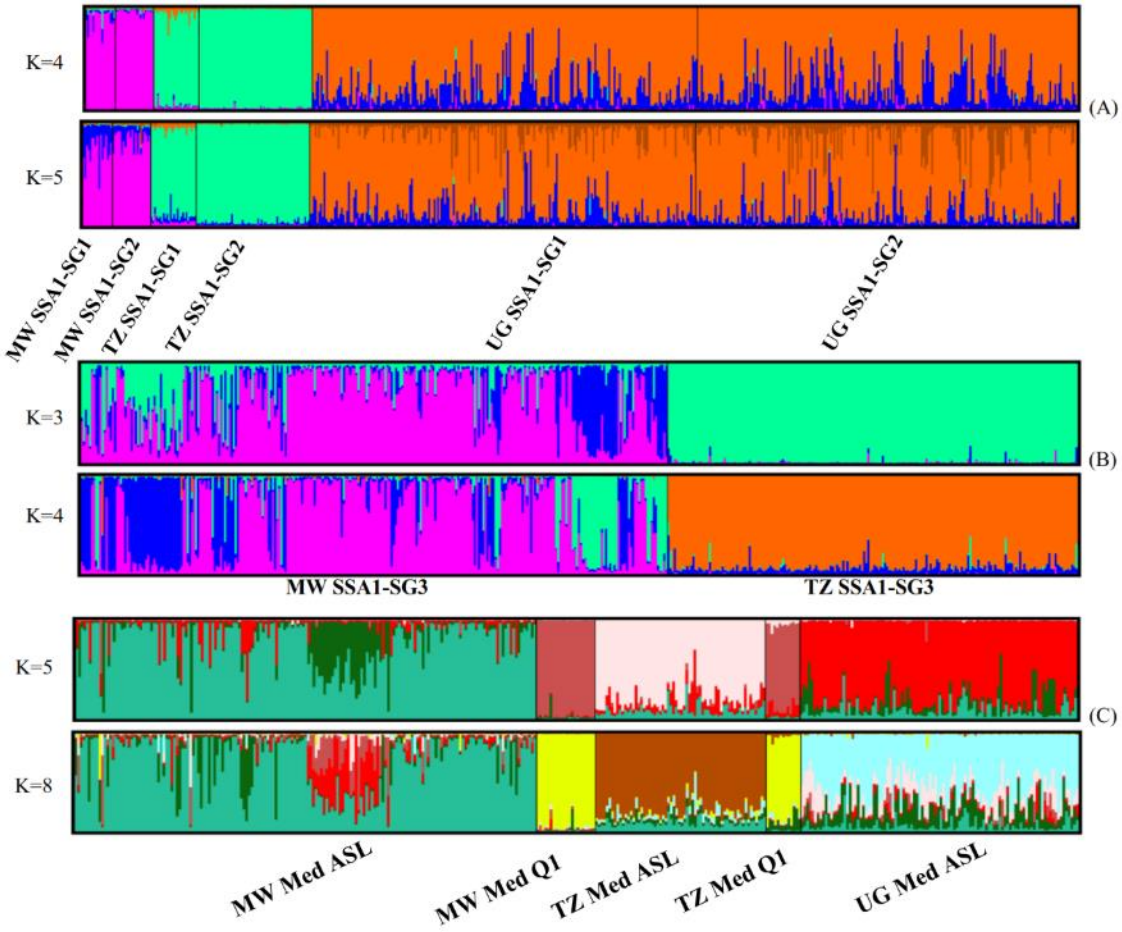


Figure 5. 3: Different K populations of *B. tabaci* (A) SSA1 from Malawi (MW), Tanzania (TZ) and Uganda (UG), (B) SSA1–SG3 from Malawi and Tanzania (C) Med from Malawi, Tanzania and Uganda. Structure bar plots are based on 12 microsatellite loci. Individuals were arranged according to mtCOI species assignation and separated by a black line. For each dataset the two best K are presented and were selected by STRUCTURE HARVESTER.

This is shown in (Fig 5.3) at K = 5, some individuals presenting red Pattern from Uganda Populations and green from Malawi populations were assigned to other genetic clusters. The occurrence of Med ASL into different countries suggesting broad adaptation capacity.

On the contrary of the others, Med Q1 from Malawi seemed to share the same genetic clusters from Tanzania Med Q1 (Fig C). The mtCOI sequences found between countries were also similar and shared nucleotide identity with Med Q1 species from Italy and invasive population reported in China (Parrella et al. 2012, Li et al. 2017). This result suggested that Med Q1 could be an invasive species in both countries.

**Do we have the same levels of incidence of CMD and CBSD between countries?**

The level of CMD and CBSD incidence was low to moderate in Malawi compared to the ones observed in Tanzania and Uganda. In Tanzania, the CBSD symptoms were found on the coast zone together with high numbers of the whitefly species SSA1-SG3. Legg and Raya (1998) observed similar findings for CBSD distribution in the late 90s. This disease is currently considered to be the most devastating disease of cassava in coastal areas of East Africa (Winter et al. 2010), first reported in 1936 from Tanzania (Story 1936) it is now found in all areas, from Kenya to Mozambique (Alicai et al. 2007). Several studies made on the diversity of this disease found that it is caused by at least two virus species and several strains that seems to be country specific (Mbanzibwa et al. 2009, Winter et al. 2010). Regarding to the fact that whitefly species distribution varies between countries, and CBSD incidence and strains, one might hypothesise that transmission of this virus might vary according to vector species and strains.

## Conclusion and perspective

This study was conducted to understand the population dynamic of *B. tabaci* populations by comparing the populations collected during the initial outbreak of 1990s with current outbreaking populations (2017). Also, to understand factors leading to whitefly outbreaks.

i) Our results showed the sympatric occurrence of SSA1–SG1 and SSA1–SG2, and we prove that both subgroups can hybridize (by the use of nuclear markers).

ii) Our results revealed that no new population was involved between 1997 and 2017, instead we saw the disappearance of SSA2 and increase in abundance of the mtCOI haplotype SSA1–SG2, in the sampling locations.

iii) Apart from both subgroups of SSA1 (–SG1 and –SG2), other *B. tabaci* species including SSA1–SG3 and IO have shown their capacity to have similar high outbreaking populations, depending on the location sampled.

iv) Different genetic groups of the same species (SSA1–SG1, SSA1–SG2, SSA1–SG3, Med ASL), well-structured according to countries were observed, resulting in few exchanges of populations between those countries, however Med Q1 from Tanzania and Malawi shared the same genetic clusters, which might imply that both countries have suffered a recent invasion of this species.

v) Different *B. tabaci* species were found dominating in the three countries on cassava. SSA1–SG1 and SSA1–SG2 were found dominating in Uganda, SSA1–SG3 in Tanzania and SSA1–SG3 in Malawi.

vi) On non-cassava hosts, Med ASL were found dominating in both Malawi and Uganda on sweetpotato, IO in Tanzania on wireweed (*Sida acuta*) and Med ASL in Malawi.

vii) All *B. tabaci* we found on several host plants showing their polyphagous capacity, nevertheless, the SSA1 (and three subgroups) were most often found on cassava, while the other sampled species were most often found on non–cassava hosts.

All these findings allowed us to see that the origin of outbreaking populations of whiteflies in those three countries are not linked to the arrival of new species, or to a specific population/species, or movements of those populations between countries through waves of invasions, such as it was thought. Nonetheless, our sampling did not cover the North West part of Tanzania, border to Uganda, where similar populations between countries might occur (due to their proximity), and should be sampled.

We found that population dynamic varies according to agroecological zones, however climate might be a very important factor as it has been shown on other arthropods (Myers 2018), so that ecological and abiotic factors need to be further address in order to better understand this mechanism of sporadic upsurges of populations. Nonetheless, these findings are relying on only one sampling conducted in one season for each country and might need to be repeated.

Our study was focusing on three countries of East Africa, in a North-South transect, despite the fact that strong population movements were not seen between countries, the threat of CBSD is very important toward West Africa. Indeed, to better test our hypothesis of non "invasive" cassava whiteflies between countries should be tested in neighbouring countries going westward such as DRC. If that hypothesis stands, long range movement (between countries) of cassava diseases are most probably Human-mediated and short-range movements linked to the vector populations as hypothesised by (Legg et al. 2011). Taken the fact that most of the whitefly species sampled were also found on cassava (in a lower extend) if cassava infected cuttings are planted, even in low quantities, the whitefly population will be able to spread the inoculum. Nonetheless, acquisition and transmission experiments of the main viral diseases CBSD and CMD (known to be vectored by SSA) (Legg and Fauquet 2004, Maruthi et al. 2005) should be conducted on the other most abundant whitefly species found in those samples countries in cassava fields (IO, Med Q1, Med ASL).

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