Cassava whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), in sub-Saharan African farming landscapes: a review of the factors determining abundance

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Abstract

Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae) is a pest species complex that causes widespread damage to cassava, a staple food crop for millions of smallholder households in Sub-Saharan Africa. Species in the complex cause direct feeding damage to cassava and are the vectors of multiple plant viruses. Whilst significant work has gone into developing virus-resistant cassava cultivars, there has been little research effort aimed at understanding the ecology of these insect vectors. In this review we critically assess the knowledge base relating to factors that may lead to high population densities of Sub-Saharan African (SSA) *Bemisia tabaci* species in cassava production landscapes of East Africa. We focus first on empirical studies that have examined biotic or abiotic factors that may lead to high populations. We then identify knowledge gaps that need to be filled to deliver long-term sustainable solutions to manage both the vectors and the viruses that they transmit. We found that whilst many hypotheses have been put forward to explain the increases in abundance witnessed since the early 1990s, there are little available published data and these tend to have been collected in a piecemeal manner. The most critical knowledge gaps identified were: (i) understanding how cassava cultivars and alternative host plants impact *B. tabaci* population dynamics and its natural enemies; (ii) the impact of natural enemies in terms of reducing the frequency of outbreaks and (iii) the use and management of insecticides to delay or avoid the development of resistance. In addition, there are several fundamental methodologies that need to be developed and deployed in East Africa to address some of the more challenging knowledge gaps.

Introduction

Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae) is a pest species complex that causes widespread damage to cassava, a staple food crop in many millions of smallholder households in Sub-Saharan Africa (Otim-Nape *et al*., 2000; Colvin *et al*., 2004; Legg *et al.,* 2006; Patil *et al.,* 2015). *Bemisia tabaci* cause direct feeding damage to cassava and vector multiple plant viruses that in combination lead to significant yield loss (Holt & Colvin, 2001). Whilst substantial effort has gone into developing virus-resistant cassava cultivars, there has been little research effort aimed at understanding this insect vector, which alone can reduce yields, by 40% (Thresh *et al.,* 1997). Based on partial mtCO1 gene sequence phylogenetic analysis, the *B. tabaci* complex is composed of four major clades (a clade is a group of organisms believed to have all descended from a common ancestor). The Sub-Saharan Africa clade forms the ancestral root (Boykin *et al.,* 2013) of the complex and over the last 20 years, species in this clade have been responsible for an increased frequency of outbreaks in cassava growing areas of East Africa. *B. tabaci* causes direct damage through feeding and the excretion of sugar-rich honeydew, which acts as a substrate for sooty moulds that reduces both respiration and photosynthesis. Furthermore, these species transmit several cassava infecting viruses (Maruthi *et al*., 2002a; Maruthi *et al*., 2002b) and there has been a significant research effort around understanding the plant viruses, but little effort aimed at the vector. This disproportionate approach to managing insect-vectored plant diseases is not unusual, but has led repeatedly to management solutions that are not sustainable. This review of the empirical evidence is timely and necessary as we need to identify clearly the biotic and abiotic factors that may have contributed to high population growth in the past, before we can develop urgently needed and sustainable management recommendations for

the future.

Whilst many hypotheses have been put forward about the factors that may be contributing to high *B. tabaci* populations on cassava in East Africa, there are little data available and these tend to have been collected in a piecemeal manner. The aim of this review is to summarise the published data and assess the evidence base through synthesis and detection of knowledge gaps. We focus on research conducted in the East African countries of Tanzania, Uganda, Rwanda, Burundi, South Sudan and Malawi, but have excluded studies that look solely at virus impacts on the crop. We start by listing factors that, from an *a priori* perspective, are likely to be important determinants of whitefly abundance (Table 1). There have been several important review articles that have summarised information on cassava virus disease epidemics and these speculated on some of the likely causes (Table 3). In addition, there are reviews by Legg *et al.* (1994), Fishpool & Burban (1994) and Colvin *et al.* (2006) that provide a good baseline of ecological and biological information. A complicating factor in reviewing the evidence-base for factors relating to East African *B. tabaci* is that our understanding of *B. tabaci* as a species has changed in the previous decade and so it is at times unclear as to the actual identity (as determined by their partial mtCO1 gene sequence) of the species being referred to, especially in older references. Where possible, we attempt to resolve these issues.

Our objectives for this review are firstly to synthesise the existing literature on the Sub-Saharan African (SSA) *B. tabaci* species' ecology and to review critically this knowledge-base. We focus on empirical studies that have examined biophysical factors that may lead to high

populations or outbreaks of the SSA *B. tabaci.* We then identify the gaps in knowledge and understanding that need to be filled to deliver long-term sustainable solutions to manage both the vector species and the viruses that they transmit.

African *B. tabaci* species complex: naming and identification

Throughout this review we use *B. tabaci* to mean the *B. tabaci* species complex found in East Africa. However, the identification of the species involved in these outbreaks based on genetic differences has only recently been attempted. Due to morphological similarities, *B. tabaci* was originally thought to be one species world-wide, but based on genetic differences (Colvin *et al.,* 2004; Sseruwagi *et al.,* 2005; Boykin *et al.,* 2007; Boykin *et al.,* 2013; Wang *et al.,* 2014); and mating incompatibility (Colvin *et al.,* 2004; Liu *et al.,* 2007; Xu *et al.,* 2010) it is now recognized as a species complex with at least 34 to 36 species (Boykin *et al.,* 2012, Barbosa *et al.,* 2015). This discovery of further species diversity has led to many nomenclatural changes over the last 10 years causing confusion in the literature (Boykin & De Barro, 2014).

The sub-Saharan African *B. tabaci* species (SSA) are no exception to the nomenclatural confusion. Identification of species in the *B. tabaci* pest complex currently relies on the 3' region of 657bp partial mtDNA COI gene identity. However, many names have been used for the same SSA entities with little consistency from study to study. The naming confusion has made it difficult to compare studies of ecological importance across time or from different researchers. For example, Sseruwagi (2005a) used "Ug1", Legg (2014a) used "SSA1 sub-groups 1-3" and Mugerwa (2012) used "SSA1 sub-clades I-III" based on mtCO1 data. Are these the same entity? In short, no. Relevant to this study are the SSA1 and SSA2 species of *B. tabaci*

where Ug1 = SSA1 and further subdivisions of that species include SSA1 subgroup 1 (Legg *et al.,* 2014a) = SSA1 subclade I (Mugerwa *et al.,* 2012). However, Ug2 (Sseruwagi et al., 2005) translates directly to SSA2 (Mugerwa *et al.,* 2012; Legg *et al.,* 2014a) with little confusion. Most of the confusion involves the SSA1 species, because most studies did not compare their SSA1 mtCO1 sequences against the then known available diversity. This meant that their data was not set firmly within our understanding of *B. tabaci* diversity.

Greater clarity around the species identity of individuals involved in future outbreaks will help to uncover the causes of these outbreaks. Conclusions and findings from past work in this region, however, are still useful to understanding the ecology of the species complex. In addition, species-specific management strategies and interventions will play a larger role in the future (see "Knowledge gaps" section towards the end of this review).

History of *B. tabaci* abundance on cassava, outbreaks and responses

There are a range of factors (both top-down and bottom-up) that may influence the abundance of any pest herbivore on a host plant. Understanding how these factors relate to population dynamics and distributions at the scale of a field and region is critical for determining if an outbreak of a pest is likely to occur. We define an outbreak situation as one in which the pest herbivore or plant-virus vector has been released from control, has reached high abundances, and is causing economic injury to the crop. This problem usually manifests at the field or regional-scale. Importantly, crop damage can occur at low pest abundance, especially in the case of virus transmission. Thus, whilst outbreaks are often obvious to farmers and the general community, significant yield loss and damage can occur

in non-outbreak situations. Here we focus on the documented evidence of factors that influence abundance of *B. tabaci* on cassava in East Africa.

There has been a change in the abundance of *B. tabaci* in cassava production landscapes in East Africa in general over time (Fig. 1 and citations), however, quantitative definitions of what is a high or low population abundance has also changed across time. The standard approach has been to count the number of adults found on the top five leaves of multiple cassava plants within a field (Sseruwagi *et al.,* 2004). The threshold of the number of adults considered highly abundant, however, differs between studies. For example, in Legg *et al*., (2011) when >5 adults per top five leaves per plant were recorded on cassava, this was considered highly abundant. In contrast, Omongo *et al.,* (2012) only considered populations >20 adults per top five leaves per plant as high. Some quantitative studies have been summarised in Table 1, however, it is still challenging to compare across studies that have used different sampling methodologies to document overall trends. Sseruwagi *et al.,* (2004) provides a summary of mean number of *B. tabaci* from top five leaves from African studies prior to 2004. Colvin *et al.* (2006) examined the densities of cassava whitefly on virus-symptomatic and non-symptomatic leaves and found that densities were significantly higher on the symptomatic leaves. Few of these studies describe the relationship between the quantitative estimates of abundance per plant and outbreaks that occur at the field or regional-scale (the exception being Colvin *et al.,* 2004).

Early research from Ivory Coast considered cassava a poor host of cassava *B. tabaci*, as numbers rarely exceeded 300 adults per plant and more often there were 150 adults per

plant (Fishpool *et al.*, 1995; Colvin et al., 1998; Fishpool & Burban, 1994 cited Fargette's 1985 thesis). However, other researchers might consider these to be relatively high numbers. More recently, greater abundance of *B. tabaci* has been confirmed on resistant compared to susceptible cassava cultivars (Otim *et al.,* 2006; Adriko *et al.,* 2011; Omongo et al., 2012). Survey data from across five regions in four countries (Uganda, Kenya, Tanzania and Burundi) showed that high numbers of *B. tabaci* coincided with CBSD prevalence and the rapid geographical spread of the disease (Legg *et al.,* 2011). It is not clear if this pattern is the result of increased plantings of newer cultivars resistant to CMD, that are also more attractive to *B. tabaci* (Otim *et al.,* 2006; Adriko *et al.,* 2011; Omongo *et al.,* 2012).

We have summarised the available evidence on the historical outbreaks of *B. tabaci*, CMD, and CBSD across East African countries in figure 1. There are records of high populations of *B. tabaci* causing problems for farmers since the 1990's. As with most pest outbreaks, there is a focus on data collection and analysis during the outbreak phase, until an intervention (e.g. the introduction of new cultivars) or change in the environment stops the outbreak, but a lack of information in the intervening periods. This makes it challenging to assess the causes and frequency of outbreaks, both at the local level and across the East African region. It is notable that the movement of infected cuttings (between regions within countries, and between countries) was implicated in a number of historical outbreaks (Alicai *et al.,* 2007). Importantly, the introduction and dissemination of new CMD-resistant cultivars to combat food shortages because of epidemics was also facilitated through these routes. Less well-documented is that disease sources can be present in endemic host plants such as *Jatropha* sp., and trade routes between India and Africa may have also facilitated disease spread

(Swanson & Harrison, 1994).

Plant virus transmission by *B. tabaci*

CMD outbreaks, that are at least partially whitefly-borne, have been occurring in East Africa since the 1960s (Jameson 1964). Many species in the *B. tabaci* species complex vector a range of damaging plant viruses and their life-history parameters can vary depending on the environmental conditions and the host plant they develop on. The published information suggests that the development period of *B. tabaci* from egg to adult emergence is between 19 to 29 days and the species goes through four nymphal instars before entering a pupal phase (Colvin *et al*., 2006). Depending on the environmental conditions there can be 11 to 12 generations of *B. tabaci* per year (Asiimwe *et al.,* 2007). A description of the different developmental stages of *B. tabaci* on cassava, using a colony established in Uganda, is presented in Thompson (2000). Adult female *B. tabaci* produce 4 to 5 eggs per day and these are oviposited on the underside of the leaves and the leaf petiole. Both the adults and nymphs have sucking mouthparts to pierce the leaf tissue and consume phloem sap. Adults prefer to congregate and alight on the immature upper leaves of the cassava plant (Sseruwagi *et al.,* 2004). The first nymphal stage is mobile until it finds a suitable feeding location. The nymphs exude honeydew, which falls onto the lower leaves of the plant leading to sooty mould development.

A detailed description of both major diseases of cassava, cassava mosaic disease (CMD) and cassava brown streak disease (CBSD) can be found in Mabasa (2007), but we will summarise some of the key points here. There are seven cassava mosaic begomoviruses (CMBs),

(Geminiviridae; genus Begomovirus) that are related to cassava mosaic disease (CMD) (Legg *et al.,* 2015). The first widespread outbreaks of CMD were reported in the 1930s in East Africa (Storey & Nichols, 1938; Fig. 1) and the presence of CMD is now confirmed in cassava across East Africa. CMD can be recognised by the characteristic chlorotic patination in the leaves. The leaf turns yellow and becomes distorted. Severe infection causes stunting of shoots, leaves and stems which reduce tuber growth and subsequently yield (Fauquet & Fargette, 1990; Maruthi *et al.,* 2002; Omongo, 2003). Cassava grown from disease-free cuttings takes two to three weeks to shoot. There is a latent period after the first leaves appear of about one month between time of infection by *B. tabaci* and CMD symptom expression in cassava (Fauquet & Fargette, 1990). Symptoms increase until approximately 60 days after planting. However, infection introduced beyond five months after planting (MAP) via *B. tabaci* has very little impact on the yield. This is because at five MAP the tubers have started to form and the plant is still able to provide significant yield (Fargette *et al.,* 1990).

Cassava brown streak disease (CBSD) is often found together with CMD, but this was not always the case (Alicai *et al.,* 2007). Historically, CBSD was thought to be caused by two distinct viruses*, Cassava brown streak virus* (CBSV) and *Ugandan cassava brown streak virus* (UCBSV) but Ndunguru *et al.,* (2015) have recently found more genetic distinctiveness in both CBSV and UCBSV. Both groups of Both viruses belong to the genus Ipomovirus, and family Potyviridae (Mbewe *et al.,* 2015), however CBSV has a five times faster rate of evolution, and is more virulent compared with UCBSV (Alicai *et al.,* 2016). Unlike CMBs, CBSV's are semi-persistent in *B. tabaci* (Maruthi *et al.,* 2005). Symptoms of CBSD include yellow blotchy patches on the leaves and a change in the colour of the leaf veins, especially

on the lower more mature leaves. The symptoms in the leaves are sometimes less apparent and are not noticed until the roots have been infected. Brown coloured vertical lesions occur on the stems and roots can become contorted and constricted. Cross sections of root from infected plants often show various degrees of brown necrotic tissue, which are usually more obvious towards the edges (Nichols, 1950; Hillocks & Jennings, 2003; Ntawuruhunga & Legg, 2007).

Bemisia tabaci species can carry and potentially transmit hundreds of different plant viruses (Morales & Jones, 2004, Polston *et al.,* 2014). Harrison (1997) makes the argument that selection and subsequent spread of viruses by certain *B. tabaci* species might be possible. "Geminiviruses with different coat proteins were believed to be differentially adapted for transmission by different biotypes of *B. tabaci"* (McGrath & Harrison, 1995; Morales & Jones, 2004; Maruthi *et al.,* 2002). This may be important; however, methods to test for these synergistic virus-vector relationships are rare (Patil & Fauquet, 2010). Both CMD and CBSD are spread through the propagation of infected cassava cuttings and vectored by *B. tabaci* in East Africa (Maruthi *et al.,* 2005; Jeremiah *et al.*, 2014, confirmed *B. tabaci* transmits CBSVs). Transmission of CMBs by *B. tabaci* has been confirmed in Africa (Burban *et al.,* 1992; Fishpool & Burban, 1994; Gibson *et al.,* 1996; Legg *et al.,* 2002; Antony *et al.,* 2006). Survey of cassava across Tanzania during the 1993-1994 growing season showed 9.4% of African cassava mosaic disease (ACMD) infections could be attributed to *B. tabaci* transmission, compared to 55.9% of infections to the use of infected cuttings (Legg & Raya, 1998). More recently it has been shown that a greater proportion of CMD is cutting borne compared to being vectored by *B. tabaci* (Night *et al.,* 2011). Research by Dubern (1994)

indicated that *B. tabaci* was not an efficient vector of CMBs. However, Maruthi *et al.* (2002) used CMB isolates and *B. tabaci* sourced from four different areas (three African locations and one culture from India) to show that African CMBs were transmitted by African *B. tabaci* to 60-79% of the cassava plants. However, inoculation was significantly less when Indian *B. tabaci* transmitted an African CMD isolate and vice versa when *B. tabaci* from Tanzania transmitted CMB isolates from India. These results were used to support the idea that there is virus and or vector co-adaptation and that there is variability in vector competence and biological traits between *B. tabaci* species (Maruthi *et al.,* 2002b). However, there is little quantifiable evidence for this hypothesis, and what evidence there is has been drawn from data that has a small number of samples (Xu *et al.,* 2010).

Factors influencing *B. tabaci* abundance

There are likely to be a number of factors that will, in isolation or in combination, influence the abundance of *B. tabaci* in cassava landscapes. We have classified these into biotic (cassava cultivar, cassava age, cassava virus infection status, non-cassava host plants, natural enemies, competition with other herbivores and endosymbionts), abiotic (altitude, climate and weather) and other factors (pesticides, hybridization) in Table 2. Below we summarise the available evidence that may demonstrate a link with each factor and changes in abundance of *B. tabaci* populations.

Biotic factors

Cassava cultivar effects

The primary way to manage disease in cassava has been to develop cultivars that are disease

resistant. Observations that some cultivars were susceptible to disease have been evident since the first outbreak of CMD in the 1930s (Storey & Nichols, 1938). The key response to the 1990's CMD epidemic was to distribute cassava cuttings from resistant cultivars (Oliveira *et al.,* 2001). In recent times, greater numbers of adult *B. tabaci*, and sometimes nymphs, have been associated with recently developed cultivars, although the dynamics of *B. tabaci* populations in semi-field situations have not been well documented (e.g. Katono *et al.,* 2015). Severity of cassava green mite (*Mononychellus tanajoa*) and CMD were higher on local cultivars of cassava, although *B. tabaci* populations were higher on improved cultivars (Night *et al.,* 2011). To determine which cultivars had resistance to *B. tabaci,* 19 cultivars were exposed to *B. tabaci* for colonization. Numbers of nymphs, eggs, damage and sooty mould were greatest for cultivar I92/0067 and least for Njule Red (a local cultivar) (Omongo *et al.,* 2012). Cassava leaf area did affect the severity of sooty mould (i.e. a cultivar with a lower number of *B. tabaci* could have a higher sooty mould severity score, presumably due to broader leaves). However, there was no obvious correlation between the numbers of *B. tabaci* adults and cultivar plant traits such as leaf width, leaf colour or bitterness (Omongo et al., 2012).

Beyond the obvious differences in plant morphology seen between different cassava cultivars, plant biochemistry may also play a role in determining suitability for growth and development of *B. tabaci* populations. Research on the phytochemistry of cassava has largely concentrated on defensive metabolites such as flavonoids, hydroxycoumarins, terpenoids and cyanogenic glucosides and their distribution within plant tissue. This work was recently reviewed by Blagbrough *et al.*, (2010). Cassava phytochemistry can impact

phloem feeders, with examples including the effect of its flavonoids and cyanogenic glucosides on the cassava mealybug, *Phenacoccus manihoti* (Calatayud *et al.*, 1994a, b; Calatayud *et al.*, 1997) and the cassava hemipteran pest, *Cyrtomenus bergi* (Riis *et al.*, 2003). *Bemisia tabaci* can also be affected, and has been shown to induce cyanide-metabolizing enzymes when feeding on cassava compared to sweet potato (Antony *et al.*, 2006). These results provide evidence that defensive plant metabolites play an important role in cassava colonization by phloem feeders including *B. tabaci*. However, how the phytochemistry of different cassava cultivars and tissues influences *B. tabaci* resistance remains unknown. Future efforts should be directed at confirming these mechanisms and explaining the effect of cassava plant chemistry on phloem feeders and other herbivores within the East African cassava environment.

Cassava age

As cassava matures, the degree to which it is a suitable host plant for *B. tabaci* changes. There are likely to be several factors associated with the aging process such as changes to leaf morphology, plant biochemistry and *B. tabaci* preference and learning that impact this process. The population of *B. tabaci* builds up starting at 3 MAP and peaks between 5 and 7 MAP (Sseruwagi *et al.*, 2003), when the foliage is very well formed and succulent after which it drops drastically as the plants grow taller, become more woody (less succulent) and shade the leaves. However, overall, the dynamics of *B. tabaci* populations in the field in response to factors that change as cassava ages have not been well documented.

All the cultivars surveyed in Uganda in 1990-92 were susceptible to CMD (Otim-Nape *et al.,* 1998), but as cassava plants age the rate at which the CMD spreads is reduced (Fargette *et*

al., 1993). Cuttings taken from the top of the plant are more likely to be virus free for CBSD compared to those taken from the bottom of the plant (Mohammed *et al.,* 2016), which may be related to plant age. During sampling for virus detection, virus titre is always highest in the older leaves for CBSVs, especially in the young (<6 months old) cassava plants. Research to identify the resistance mechanisms in cassava cultivars shows that some cultivars can recover as the plants age (known as reversion, Adriko *et al.,* 2011). CMD symptoms disappeared and cuttings taken from initially infected plants developed without disease symptoms (Gibson and Otim-Nape, 1997a; Adriko *et al.,* 2011).

Cassava virus-infection status

There is some evidence to support the hypothesis that there is a relationship between disease severity in a plant and *B. tabaci* abundance (Gregory, 1948; Leuschner, 1977; Bock, 1987; Robertson, 1987; Fargette *et al.,* 1993; Otim-Nape *et al.,* 1995; Colvin *et al.,* 2004). If this is due to correlation or causation is often hard to untangle. The abundance of *B. tabaci* adults was shown to be significantly higher on healthy cassava plants compared to infected plants, but adults stayed longer on diseased plants and aggregated on the green plant tissue. This resulted in higher density of adults by photosynthetic leaf area (area of living leaf tissue) compared to plants without disease. Omongo (2003) posits that this increased density might trigger the adults to disperse. Results also show that adults are more likely to move from clean to infected plants, and diseased plants increased fecundity (Omongo, 2003).

Cassava plants infected with CMBs have been reported to be more suitable for growth and development of *B. tabaci*. A summary of the studies showing the effect of virus infection of

host plants on *B. tabaci* population growth, development and behaviour can be found in Colvin *et al.,* (2006). Concentrations of amino acids have been shown to be greater in infected cassava, and these may benefit *B. tabaci* fitness (Colvin *et al.,* 1999, 2006). However, other laboratory studies have found that the status of cassava disease and *B. tabaci* (i.e. viruliferous or non-viruliferous for East African cassava mosaic virus, EACMV) had no significant effect on life history factors, sex ratio, and developmental period, or percent adult emergence (Thompson, 2011). Additionally, the longevity of *B. tabaci* was shown to be reduced when they carry viruses such as *Tomato yellow leaf curl virus* (TYLCV) (Berlinger *et al.,* 1996). So whilst infection status plays some role in altering the bottom-up resources for *B. tabaci*, we cannot say when and how this will lead to high abundance in a field situation.

Non-cassava host plants

B. tabaci is a polyphagous herbivore that can potentially use a wide range of different host plants in cassava production landscapes. Evidence from outside of Africa (Belotti, 2005) and from West Africa (Burban *et al.,* 1992) shows that *B. tabaci* can have very different associations with different host plants in different locations indicating the likelihood of host-plant associated genotypes. Research in West Africa showed two genotypes of *B. tabaci*; one polyphagous on a range of plants (excluding cassava) and the second found only on *Euphorbia* species (this group includes cassava) (Burban *et al.,* 1992). Laarif *et al.,* (2015) found that *B. tabaci* MED (formally named biotype Q) preferred host plants in the families Verbenaceae and Malvaceae, and MEAM1 (formally named biotype B) were found on Cucurbitaceae and Solanaceae. SSA2 only occurred on Datura and eggplant (Laarif *et al.,* 2015). Their results support the argument that the genetic differentiation of *B. tabaci*

species does not operate at the plant species level, but more likely in response to broader taxonomic grouping, for example plant families. Table 4 documents host plants that have been recorded in recent publications that included a genetic determination of the species. Most of these rely on adults (which are highly mobile) recorded on host plants, except Sseruwagi *et al*., (2006) who used nymphs to confirm the results obtained with adults for host plant colonization. There is a supposition that the number of eggs laid on a plant is a better indicator of a preferred host compared to counts of adults (Laarif *et al.,* 2015). Further information is required that shows clear species-host plant relationships in field contexts, such as preference tests and tests of nymphal development on host plants (not just presence/absence).

Experiments transferring *B. tabaci* from natal host plants to different local host plants result in failure or variable establishment. These results were used to support the idea that there are different *B. tabaci* genotypes with restricted host ranges (Burban *et al.,* 1992). However, this research did not test the influence of host plant transfer on ability of *B. tabaci* to transmit disease. Research by Antony (2006) showed that natal host plants influence the ability of *B. tabaci* to transmit *Indian cassava mosaic virus* (ICMV). Whereas *B. tabaci* reared from cassava could transmit ICMV to cassava, *B. tabaci* reared on sweet potato were unable to transmit ICMV to cassava. There was a significant difference in the presence of the cyanide detoxifying enzymes in cassava reared *B. tabaci* compared to those reared on sweet potato. Together, the results show the ability of *B. tabaci* to adapt to different host plants.

Intercropping cassava with other crop plants (e.g. coffee, maize, sweet potato, bean,

groundnut) is common practice in many parts of East Africa. However, beyond saying if a crop is likely to be a host plant or not, we cannot yet make recommendations about which intercrop would be most useful for reducing *B. tabaci* abundance on cassava. Intercropping cassava with maize was shown to influence *B. tabaci* in the Ivory Coast (Fargette *et al.,* 1988), although the mechanism here may not be related to host-plant preferences, but rather host plant availability and physical barriers (i.e. maize are not host plants and may create a barrier to accessing host plants). Intercropping cassava with cowpea has been shown to decrease numbers of *B. tabaci* in Colombia (Gold *et al.,* 1989). Results of surveying cassava cultivars for pests and CMD in Uganda in 2007 showed that cassava that was intercropped had significantly less *B. tabaci* than monocrops. Results from this study also showed adjacent cassava had no effect on populations of *B. tabaci*. Local cassava cultivars had more CMD, but improved cultivars had a greater density of *B. tabaci* nymphs (Night *et al.,* 2011). Experiments intercropping cassava with *Vigna unguiculata* and *V. radiata* (cowpea and green gram mung bean) showed reduced *B. tabaci* populations and severity of CMD. Disease-free cuttings of two cultivars (one susceptible local cultivar, and one improved cultivar) were used in field experiments. Compared to monocrop treatments, the cultivars intercropped with mung bean had significantly less *B. tabaci* and disease incidence and severity for both the local and improved cultivar (Uzokwe *et al.*, 2016).

Spatial and temporal arrangement of host plants

As well as the influence of intercropping *per se* on *B. tabaci* populations in cassava fields, the spatial and temporal arrangement of crops and other potential non-crop hosts around cassava fields may also influence population growth and abundance in the crop field,

especially early in the growing season. In theory, if host plants surrounding cassava fields facilitated the early arrival (and high numbers of colonizers) of the first generation of *B. tabaci* into the cassava field in the early stages of the crop, this may lead to an outbreak. Furthermore, if the spatial and temporal arrangement of host plants negatively impacted the dynamics of natural enemies of *B. tabaci* this could also lead to an outbreak.

In a farming landscape where a species of *B. tabaci* (MEAM1) has been shown to be polyphagous with several crops and wild host plants suitable to support population growth (Queensland, Australia, Sequeira *et al.*, 2009; De Barro, 2012), it was possible to develop a landscape model to simulate how the spatial and temporal arrangement of host plants influences *B. tabaci* abundance and 'outbreaks'. The model simulations indicated that peak densities of MEAM1 *B. tabaci* were higher for low or non-suitable crops than for crops with a medium suitability. This counter-intuitive result was explained by the fact that medium suitability winter crops supported high parasitoid (*Eretmocerus hayati*) populations, which can suppress *B. tabaci* populations in summer crops (De Barro, 2012; Kristensen *et al.,* 2013). Therefore, both the surrounding landscape, and crop rotation choices had a significant effect on simulated *B. tabaci* population dynamics.

Understanding how the farming landscapes in East Africa offer resources for both *B. tabaci* and its natural enemies is challenging due to the variegated nature of the land-use patterns characteristic of smallholder farming. Often there are multiple crops planted in each field or garden and rotation practices are flexible and dependent on the family, village, and regional demand for certain food-types. However, studies to quantify the effect (even is small) of the

spatial and temporal arrangement of host plants is needed because this knowledge may lead to easily adoptable changes in management practices.

Natural enemies

Breeding cassava cultivars that are resistant to disease has been the main approach used to manage epidemics of CMD. However, as part of an integrated management plan to control *B. tabaci* identifying ways to enhance naturally occurring predators and parasitic wasps also needs to be considered (Legg *et al.,* 2003). Fishpool & Burban (1994) noted there were 30 parasitoids of *B. tabaci* worldwide, and 40 generalist predators. However, the ecology and impact of parasitoids and predators of *B. tabaci* in East Africa remains relatively unknown.

Regarding predators, Phytoseiidae mites, such as *Euseius scutalis,* have been recorded predating *B. tabaci* populations on cassava in Kenya (Otim-Nape *et al.,* 1995), and a mirids, such as *Nesidiocoris tenuis,* have predated *B. tabaci* on other crops such as tomato (Calvo *et al.,* 2012). Results from petri dish experiments with *B. tabaci* from cotton showed that the predatory mite *Amblyseius aleyrodis* Elbadry, readily consumed *B. tabaci* eggs in a no-choice environment (Elbadry, 1968). Similarly, from work carried out in the USA *Euseius hibisci* were shown to consume and complete their development on *B. tabaci* (Meyerdirk & Coudriet, 1985). Other predators from around the world of *B. tabaci* nymphs include *Stethorus jejunus* Casey, Coccinellidae, *Holoborus pallidicornis* (Cameron) Staphylinidae, *Scolothrips latipennis* Priesner, and Thysanoptera (Fishpool & Burban, 1994). The Neuropteran *Conwentzia africana* Meinander is considered an important predator of *B. tabaci* (Legg *et al.,* 2003). *Serangium* sp. (Coleoptera: Coccinellidae) can complete their development feeding on

juvenile stages of *B. tabaci* on cassava (Asiimwe *et al.,* 2007). No-choice laboratory experiments showed that *Serangium* larvae could consume over 1000 nymphs in total. The maximum number of nymphs consumed per day was mid-way through their development, when *Serangium* larvae consumed over 200 nymphs per day (Asiimwe *et al.,* 2007). We know that cultivars of cassava with different morphologies can influence the activities of predators such as *Typhlodromalus aripo,* the mite that preys on the pest cassava green mite *Mononychellus tanajo*a (Zundel *et al.,* 2009).

Legg (2003) lists the parasitoids attacking *Bemisia* genus in Sub-Saharan Africa. Thirty-four species of *Encarsia* and 14 species of *Eretmocerus,* with *Eretmocerus mundus* Mercet and *Encarsia sophia* Girault and Dodd being the most dominant (Legg *et al.,* 2003). Surveys of *B. tabaci* parasitoids in cassava in Tanzania resulted in 10 species of parasitoid (Guastella *et al.* 2015a). Hoelmer (1995) summarised several papers that suggested that parasitoids may be insufficient to control *B. tabaci* without other control methods. However, parasitism rates of up to 58% have been recorded in Uganda (Table 5). Some work has been completed to quantify the impact of parasitoids on *B. tabaci*. *Eretmocerus mundus* and *Encarsia sophia* were shown to parasitise *B. tabaci* on cassava in Uganda and accounted for 34% parasitism of fourth instar nymphs (Legg, 1995). Significantly higher number of *B. tabaci* and the two species of parasitoids occurred on the CMD resistant cultivar compared to a susceptible cultivar although parasitism rate was similar. Although not tested for specifically the cultivar and presence or absence of CMD did not seem to influence parasitism rates. Percent parasitism was recorded as <20%, and on three occasions <50%. However, results showed a significant negative relationship between parasitism rate and nymph numbers indicating

that these parasitoids did not respond in a density dependent manner (Otim *et al.,* 2006). Life history studies conducted under field conditions showed that dislodgement was the key mortality factor for eggs and that parasitism (mostly by *E. sophia* and *E. mundus)* caused the highest mortality to fourth instar nymphs. There was no difference in results from the treatments exposed to, or sheltered from, the rain (Asiimwe *et al.,* 2007).

There has been little research to understand how different cassava cultivars might influence the activities of natural enemies of *B. tabaci.* We know that cultivars of cassava with different morphologies can influence predators such as *T. aripo* (the mite that preys on *M. tanajo*a, Zundel *et al.,* 2009), and there have been some basic experiments conducted using parasitoids (Otim *et al.,* 2008a). However, a comprehensive understanding of cultivar impacts at higher trophic levels is critically needed.

Competition with other herbivores on cassava

Competition between *B. tabaci* and other herbivores on cassava may impact the abundance of *B. tabaci*. For example, the cassava green mite *M. tanajoa* (CGM) is often found on the top leaves of the cassava plant, making these leaves less suitable for *B. tabaci* adults (Legg *et al.,* 2015). Interspecific interactions between pests on the same crop can significantly influence invertebrate behaviour and host plant defences; for example, the duration and density of the aphid *Myzus persicae* on tomato significantly affected the number of *B. tabaci* (Tan *et al.,* 2014). We could find no studies that examine the interactions between the community of pest and non-pest herbivores on cassava in East Africa.

Endosymbionts

Some evidence exists that endosymbiotic bacteria within *B. tabaci* can have both positive and negative effects on *B. tabaci* fitness (Kontsedalov *et al.,* 2008; Himler *et al.,* 2011; Ghosh *et al.,* 2015). *Portiera aleyrodidarum* is a primary obligate bacterial endosymbiont of *B. tabaci,* and is essential to their development. As well as obligate bacteria, they have an association with many facultative bacteria or secondary endosymbionts. In theory, these bacteria may confer some advantage for transmission of CMBs by *B. tabaci* and help them adapt to new host plants (Gottlieb *et al.,* 2010, Kilot *et al.*, 2014).

The association between facultative secondary endosymbionts and various species of *B. tabaci* was explored using samples collected in Tanzania from cassava and adjacent host plants, mostly crops and one weed (Tajebe *et al.,* 2014a, see graphic depicting relationships between different groups of *B. tabaci* such as SSA1-SG1). Most *B. tabaci* collected from cassava were SSA1 and most were uninfected by any of the secondary symbionts. A later study found contrasting results (Ghosh *et al.,* 2015). Samples of *B. tabaci* were collected from cassava crops across East African countries were found to be infected with a range of endosymbionts, with the predominant species being *Wolbachia*, *Rickettsia* and *Arsenophonus*. The prevalence of these secondary endosymbionts including *Wolbachia* varied characteristically across each *B. tabaci* population (Ghosh *et al.,* 2015). Association of the endosymbionts varied across geographical boundaries and the *B. tabaci* species. SSA1-SG3 in coastal eastern Africa had high levels of *Arsenophonus* and *Rickettsia* in single or mixed infections (84%), while a small proportion (13%) was free of detectable secondary endosymbionts (Ghosh *et al.,* 2015). In contrast, SSA1-SG1 collected in the highland regions

of Uganda and around Lake Victoria had different secondary endosymbiont profiles. About 25% of SSA1-SG1 individuals were infected with *Arsenophonus* and *Rickettsia* in single or mixed infections, while equal proportion of endosymbiont-free (38%) and *Wolbachia*-infected individuals (37%) were found in Uganda. In laboratory studies, all three bacteria (*Wolbachia*, *Arsenophonus* and *Rickettsia*) were shown to negatively impact *B. tabaci* population development by reducing adult emergence and simultaneously increasing nymph development time, thereby reducing number of adults and the number of generations that can be developed per unit time (Ghosh *et al.,* 2015). In addition to several factors discussed above, it has been proposed that high levels of bacteria-free *B. tabaci*, which are fitter and more fecund, may have contributed to high abundances in certain regions. Similar effects have been observed in *Drosophila* and mosquitoes infected with *Wolbachia* (McMeniman & O'Neill, 2010). Thus, it is possible that the negative effects of endosymbionts in *B. tabaci* have been important population control mechanisms in these regions.

Abiotic factors

Altitude

There is some evidence to suggest that cassava virus infection was lower in areas above 800 metres above sea level (Nyirenda *et al.*, 1993 cited in Legg (1994a)). Historically it has been noted that at high altitudes (>1,000 metres above sea-level) there are less plant disease problems and an absence of *B. tabaci* in cassava, presumably due to cold temperatures. In general, there is evidence of a trend of declining CBSD incidence with increasing altitude in the coastal zone of Tanzania, but not in the lake zone (Jeremiah *et al.,* 2014). However, the mechanism underlying any altitudinal variations seen (e.g. temperature) has not been

tested.

Climate and Weather

As with all invertebrate pest species, long-term climate patterns and short term weather events will influence population growth and development of *B. tabaci*. However, drawing conclusions beyond general statements is challenging due to a lack of information. In general *B. tabaci* populations are favoured by high temperatures and moderate rainfall (Sseruwagi *et al.,* 2004). Recent analyses of *B. tabaci* adult abundance and environmental factors have shown that abundance was higher with high minimum temperatures and lower mean annual rainfall in the coastal zone of Tanzania (Jeremiah e*t al.,* 2014). However, in the lake zone of Tanzania mean annual rainfall and the length of the growing season were the most important environmental factors. Some studies note the times of the year when temperatures are low and the environment is unsuitable for *B. tabaci* therefore you are likely to see low numbers (Mbewe *et al.,* 2015). At a finer-scale, we know that micro-climate variability within a field can influence the numbers of *B. tabaci* found on cassava plants. *B. tabaci* adults decrease as planting density decreased and canopy temperatures increased. An increase in plant shoots also resulted in less CMD (Otim-Nape & Ingroot, 1986) at the plant-level.

Other factors and hypotheses

Pesticides

The overuse of pesticides and rapid development of resistance in *B. tabaci* has been shown to cause high abundance and change *B. tabaci* species diversity in other cropping systems

around the world (e.g. Crowder *et al.,* 2008). For example, a shift from *B. tabaci* MED species to MEAM1 species was found in cotton fields in Israel and this change in species composition had an impact on resistance to insecticides, with one population showing less resistance to Insect Growth Regulators (IGR) (Horowitz & Ishaaya, 2014). However, the use of pesticides by East African smallholder farmers has historically been low due to their cost and availability, although their use is increasing each year (de Bon *et al.,* 2014). Insecticide application in cassava production landscapes in East Africa is limited to crops such as tomatoes and other fruit and vegetables (de Bon *et al.,* 2014). Documented statistics on pesticides use (and especially insecticide use) patterns in cassava by smallholder farmers in East Africa is rare. Surveys of honeybee hives throughout Kenya showed low levels of pesticide contamination in the hives (Muli *et al.*, 2014). Documentation of the change in insecticide use patterns over time (products, active ingredients, crops, and application rates) may help predict the onset of resistance development and help in the development of an integrated resistance management strategy.

A new invasive species in East Africa

Given the confusion surrounding the taxonomy of species in the *B. tabaci* complex, we cannot rule out that there have been one or multiple incursions of an entirely new species into this region. As an analogous example from outside of East Africa, the exotic pest *B. tabaci* MEAM1 was first detected in Australia on ornamental plants in 1994, but it was not until 2001 that high numbers on fruit and vegetable required control (Gunning *et al.,* 1995, Sequeria *et al.*, 2009). After this new species entered East Africa it may have been better able to exploit resources in cassava production landscapes, avoid attack by natural enemies,

and outcompete domestic *B. tabaci* species. In addition to natural spread within the African continent, movement of species into new areas is possible via human-assisted transport (Caciagli, 2007). As yet there is no empirical evidence to support this idea in East Africa (Table 2).

Hybridization

The *B. tabaci* abundance associated with the spread of the severe CMD pandemic in Uganda in the late 1990s was believed to be due to the appearance of an invasive SSA2 *B. tabaci* species (Legg *et al.,* 2002; Maruthi *et al.,* 2004). However, subsequent studies by Sseruwagi (2005) and Mugerwa *et al.* (2012) showed SSA2 to be less abundant in Uganda post-invasion. Instead, the areas with high *B. tabaci* populations had a distinct clade of SSA1 (SSA1-SG1), and what was believed to be a hybrid of SSA2 and SSA1. More recently, Tajebe *et al.* (2014) also suggested hybridization as the underlying cause in the change from *B. tabaci* SSA2 to *B. tabaci* SSA1-SG1 in Tanzania, and that the CMD pandemic was now associated with high abundances of *B. tabaci* SSA1-SG1 genotype. However, empirical studies to confirm this hypothesis in East Africa have not yet occurred.

Empirically detecting such changes in field studies on a pest complex can be very challenging (but not impossible, see discussion in Lui *et al.,* 2012). The process of hybridization is unlikely to be reflected by the mtDNA COI gene currently used for identification purposes. Given the mitochondrial DNA genome's overall maternal inheritance property and its general lack of recombination (e.g., Crozier, 1990), hybridization between a population carrying the SSA2 mtDNA COI haplotypes with the SSA1 mtDNA COI haplotypes would result in the hybrid

offspring being either SSA2 or SSA1 mtDNA COI haplotypes, but is unlikely to generate the SSA1-SG1 mtDNA COI haplotype signature. To show evidence of hybridization we need to focus on changes in patterns in the nuclear genome, and then link these patterns with ecologically relevant fitness traits that may increase population growth and abundance on cassava.

Knowledge gaps

Given that many of the factors that potentially influence *B. tabaci* abundance listed in Table 1 have had very little research surrounding them in East Africa, and may interact with each other in antagonistic ways, identifying which are the critical knowledge gaps is challenging. Our focus here is on identifying knowledge gaps, which if filled, may lead to more sustainable and durable solutions to *B. tabaci* associated crop damage in East Africa. Underpinning all the knowledge gaps highlighted below is the species identification issue. Without well-documented species nomenclature, set within a robust framework for identifying new species, the biological and ecological information generated may be lost rapidly. The high priority knowledge gaps are:

<u>Which East African *B. tabaci* species commonly use cassava as a reproductive host plant?</u>

Whilst *B. tabaci* adults are highly mobile and can be found on a number of plants, establishing which species commonly use cassava as a reproductive host plant (i.e. they can oviposit and complete nymphal development) is important. It is these species for which we need to devise targeted management interventions to control. To address this research question requires the identification of large numbers of field-collected nymphs using nuclear

molecular markers, and reciprocal crossing experiments using cultures developed from nymphs reared through to adults. This is also the first step in establishing if these target species also use alternate host plants besides cassava.

To what extent do non-cassava host plants contribute to the population dynamics of *B. tabaci* and the spread of cassava diseases?

Whilst establishing the diversity of potential host plants that can be used by *B. tabaci* in production landscapes is important, we must take this one step further and establish if, when and how, these alternate host plants impact *B. tabaci* abundance and disease spread in cassava crops. For example, can alternate host plants for *B. tabaci* serve as reservoirs of viruses that may be transmitted to cassava (Alabi *et al.,* 2008)? If an alternative host plant is identified, but is relatively rare in the landscape will it impact the population dynamics in cassava? Conversely, if an alternate host plant is common in the landscape, will its removal impact population dynamics in cassava? There are straightforward management recommendations that can be developed from improved understanding about alternate host plants and the role they play in an agricultural landscape.

How does the proportional availability of infected versus un-infected cassava plants in a landscape influence disease risk and spread?

It has been suggested that *B. tabaci* shows preferences for infected cassava plants, and infection can alter the performance of *B. tabaci* at the population-level. However, we do not understand how this manifests in real cassava production landscapes, with a diversity of cassava cultivars, showing different levels of disease. Modelling the spread of CMD via

infected cuttings assuming that *B. tabaci* prefer infected over uninfected plants, in combination with the proportion of infected plants available, indicated this could have major implications for disease spread. Incorporating information at a landscape scale about which species of *B. tabaci* are efficient vectors of each virus would also improve model predictions.

How can we use choice of cassava cultivars in production landscapes to reduce population abundances of *B. tabaci*?

Besides establishing the effect of different cassava cultivars on the fitness and performance of *B. tabaci,* we need to provide recommendations that lead to population reductions or lower risk of outbreaks at the landscape-level. An understanding of the relationship between disease dynamics across a landscape, *B. tabaci* movement between cultivars, and cultivar diversity and abundance is needed. From this understanding we may be able to provide location-specific recommendations about the selection of ideal cultivars, guidance on rouging, and cassava-free periods. Historically, the adoption of new and improved cassava cultivars has been variable within countries, so more effort to understand the best mechanisms for ensuring that the new cultivars that are adopted also lead to *B. tabaci* population reductions would be valuable.

What is the impact of natural enemies in East Africa on *B. tabaci* and can they reduce the risk of outbreaks?

Whilst we know there are a diversity of natural enemies present in cassava fields that can cause mortality of *B. tabaci*, we cannot say what role these species play in reducing the frequency or likelihood of outbreaks. Given that cassava is a crop with a relatively long

growth season (compared to many vegetables), and now receives relatively little pesticide applications, it is important that we explore further the potential impact of natural enemies. Furthermore, the integration of natural enemies with other management options (e.g. host plant resistance and habitat management) is critical.

There is very little information about the natural enemies that prey on different stages of *B. tabaci* in field conditions and the impact they have on *B. tabaci*. Therefore, there is a need to better understand their biology and behaviour (life history of individual species), their relationships and interactions with other predators and parasitoids, and quantify the impact they have on *B. tabaci* populations. For some groups, we lack fundamental information on whether they frequently predate on *B. tabaci*. For others factors, such as the effect of alternative host plants (i.e. do any provide an alternative source of natural enemies to recolonise cassava crops and attack *B. tabaci*), dispersal ability, response to semiochemicals, and methods to increase fitness and population growth need to be determined. It is important to quantify the scale at which natural enemies may have an impact (i.e. within a few tens of metres or within 100 metres of a source field), to enable us to make specific management recommendations to farmers.

<u>How can we sustainably manage the use of insecticides in East Africa to delay or avoid resistance in *B. tabaci*?</u>

If insecticide use increases in the coming years, such as in vegetable crops in near cassava, or in cassava itself, there is the potential for *B. tabaci* species attacking cassava to be exposed to strong resistance selection pressures. Experiences in cotton production landscapes

elsewhere have shown that resistance can develop quickly in *B. tabaci* (Crowder *et al.,* 2008; Gnankine *et al.,* 2013) and studies should consider establishing baseline-levels of resistant alleles in populations now. Furthermore, the testing and development of products based on newer chemistries, which have less non-target impacts, needs to be conducted in East Africa.

What research methodologies do we need to develop now to enable scientists to ask the right questions in the future?

Throughout this review we have highlighted methodological limitations that restrict research and the questions that scientists can address. For example, we need a smarter way of estimating *B. tabaci* adult numbers in fields with high abundances. In cases where nymphal or egg data may provide a more informative picture of a certain ecological process counting adults could be avoided. We can develop new and fast approaches to count, collect, record and identify nymphs if that is what is needed to address a research question. A field-based method that allows us to separate virus infection borne by *B. tabaci*, from that borne by cuttings (or a combination of both agents) would greatly aid in our understanding of *B. tabaci* as a vector (see an example in Tajebe *et al.,* 2014). A rapid diagnostic test for virus infection at the cutting stage would enable researchers to decide which factors they wanted to examine in their study, and be confident of their results. In addition, advent of infield diagnostic strip would allow scientists detect virus at given time period and easily map patterns of disease spread. In another example, the recent development of a transcriptome technique that can provide data from one *B. tabaci* individual by Sseruwagi *et al.* (2017 submitted), will reduce reliance on the use of isolines for transcriptomics studies, and could

therefore help to resolve some of the urgent questions about the biological differences between *B. tabaci* species.

What are the economic trade-offs associated with different management options for smallholder farmers, and what networks need to be available to support adoption?

Fundamental to the deployment of new management interventions, and adoption by farmers, is strong extension networks with smallholder farmers and the wider cassava value-chain actors. Without this network the adoption of durable solutions to *B. tabaci* control will be slow or unlikely to occur. Furthermore, a complete economic assessment of the trade-offs for smallholder farmers associated with adopting different practices is needed to ensure that management options are set in the current-day economic realities of these farmers. Often researchers spend a lot of time understanding the biophysical constraints on a system but neglect the linked socio-economic system in which farmers operate. To bring about change in how this pest is managed in the future we need to assess both systems at the same time.

Conclusions

Given the right combination of factors we have identified above, many species of *B. tabaci* within the complex have the potential to become a pest at any one point in time and exhibit outbreaks in certain locations. Furthermore, these critical factors may vary from country-to-country and even region-to-region across East Africa. Our challenge is greater than just identifying factors, we must go one step further and identify which factors are the most important for smallholder farmers to manage to minimise the risk of outbreaks. This review

represents a comprehensive summary of the knowledge to date, and should be used to guide future research questions by scientists all over the world addressing this challenge.

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Table 1. Studies quantifying the mean number of *B. tabaci* on cassava. General method used was counting the numbers of adults observed on the top five expanded leaves on 30 plants per field and on cassava aged 3-6 months after planting (Sseruwagi *et al.,* 2004). There was some variation in methods between studies.

Mean count of *B. tabaci*	**Country**	**Citation**
Max. weekly 35 per plant (method not confirmed)	Ivory Coast	Fargette *et al.,* 1988
Max. 14 per plant, over 6 months, on 25 plants (one site)	Ivory Coast	Fauquet *et al.,* 1988
Max. 35	Ivory Coast	Fargette *et al.,* 1990
Max. 16 per shoot	Uganda	Otim-Nape, 1993 (thesis)
4.6 ± 0.54 adults 5.0 ± 0.38 adults	Uganda	Gibson & Otim-Nape, 1997b
Max. 21.8 ± 55.9 adults Min. 0.2 ± 0.3 adults	Zambia	Muimba-Kankolongo *et al.,* 1997
Max. ~ 12 adults	Uganda	Legg & Ogwal, 1998
Max. > 3 adults per shoot Min. 1-3 (One shoot = top 5 expanded leaves)	Uganda	Otim-Nape *et al.,* 2001
Average Max. 37 adults Average Min. 0.2 adults	Uganda	Colvin *et al.,* 2004
Mean nymph count = 35.8 for resistant cultivars Mean nymph count = 17.2 susceptible cultivars	Uganda	Otim *et al.,* 2006
0.74 ± 0.03 inter-cropped cassava 0.94 ± 0.07 mono-cropped cassava	Rwanda	Night *et al.,* 2011
Max. average 39.2 ± 4.4 occurred for cultivar I92/0067 Min. average 5.4 ± 1.7 for cultivar Njule Red	Uganda	Omongo et al., 2012
Max. 2.12 Min. 0.02	Zambia	Chikoti *et al.,* 2013
Max. 71.99±22.07 Min. 2.35±0.86	Tanzania	Tajebe *et al.,* 2014a
Max. 50 Min. 0	Tanzania	Jeremiah *et al.,* 2014
0.4 per plant	Malawi	Mbewe *et al.,* 2015
Average range 1.0 - 37.5	Tanzania	Uzokwe *et al.,* 2016

Table 2. Potential factors influencing *B. tabaci* abundance on cassava (does not include interactions between these factors).

Factors	**Potential mechanisms**	**Citations from East Africa for empirical studies**
Cassava cultivar	Leaf architecture (e.g. width of leaves) Growth habit (e.g. long versus short growing season) Plant chemistry	Omongo et al., 2012
Cassava age	Number of new leaves at top of plant Plant chemistry	Sseruwagi *et al.*, 2003
Infection status of cassava	Whitefly fecundity enhanced on infected hosts Promotion of emigration	Otim-Nape *et al.,* 1995, Colvin *et al.,* 2006
Non-cassava host plants	Other crops as host plants Natural vegetation and weeds as host plants	Laarif *et al.,* 2015 (but from Tunisia), Tajebe *et al.*, 2014
Spatial arrangement and amount of host plants surrounding cassava fields	More resources at important times, more resources for natural enemies.	None
Other pests on cassava	Cassava green mite damage to top leaves	Legg *et al.*, 2015 (but not an empirical test)
Altitude	Temperature changes, or other changes.	Thresh *et al.,* 1997; Jeremiah *et al.,* 2014
Climate	Long-term changes in temperature and precipitation	Jeremiah *et al.,* 2014
Weather	Heavy rainfall events Dry conditions (drought)	Robertson, 1987; Jeremiah *et al.,* 2014
Natural enemies	Predators consuming *B. tabaci* Parasitoids using *B. tabaci* as host	Otim *et al.,* 2005, 2006; Asiimwe *et al.,* 2007; Asiimwe *et al.,* 2007; Otim *et al.,* 2008a
Pesticides	Resistance in *B. tabaci* Pesticides killing natural enemies or competitors	None
Endosymbionts	Presence of some endosymbiont species can decrease the number of adults emerging, increase development time, thus reducing overall population development	Ghosh *et al.,* 2015
New invasive species in East Africa	Totally new species has taken over from local species in cassava (species turnover)	None
Hybridization	'invader biotype'	None

Table 3. Review articles with relevant information about *B. tabaci* biology and ecology.

Citation	Topics covered
Legg *et al.,* 2014b	● Historical account of virus outbreaks. ● Emergence of "superabundant" *B. tabaci.* ● Control options for *B. tabaci.*
Legg *et al.,* 2011	● Regional epidemiology of CMV and CBSV pandemics across Africa. ● Comparison of characteristics of CMD and CBSD outbreaks.
Patil & Fauquet, 2010	● Cassava mosaic geminiviruses: actual knowledge and perspectives. ● Very comprehensive review of the viruses.
Legg & Thresh, 2000	● CMV disease dynamics in East Africa. ● Mechanisms behind the spread of the CMD pandemic.
Legg, 1999	● Describes the pandemic of CMD across east and central Africa. ● Strategies to control the pandemic.
Otim-Nape *et al.,* 1995	● *B. tabaci* and cassava mosaic virus disease in Africa ch 28 (34 pages) in Bemisia: 1995. Taxonomy, biology, damage, control and management. ● Very comprehensive treatment of all aspects of the disease and vector story.
Fishpool & Burban, 1994	● Biology of *B. tabaci* including morphology, taxonomy, bionomics. ● Ecology on cassava in Africa. ● Some discussion about natural enemies and control.
Legg, 1994	● Ecology of whitefly and CMV pathosystem ● Factors affecting population development of *B. tabaci*; temperature, climate, rainfall, host plant chemistry, architecture and age, natural enemies. ● Interactions between *B. tabaci* and other cassava pests.

Table 4 Host plants of *B. tabaci* in East Africa from the published literature

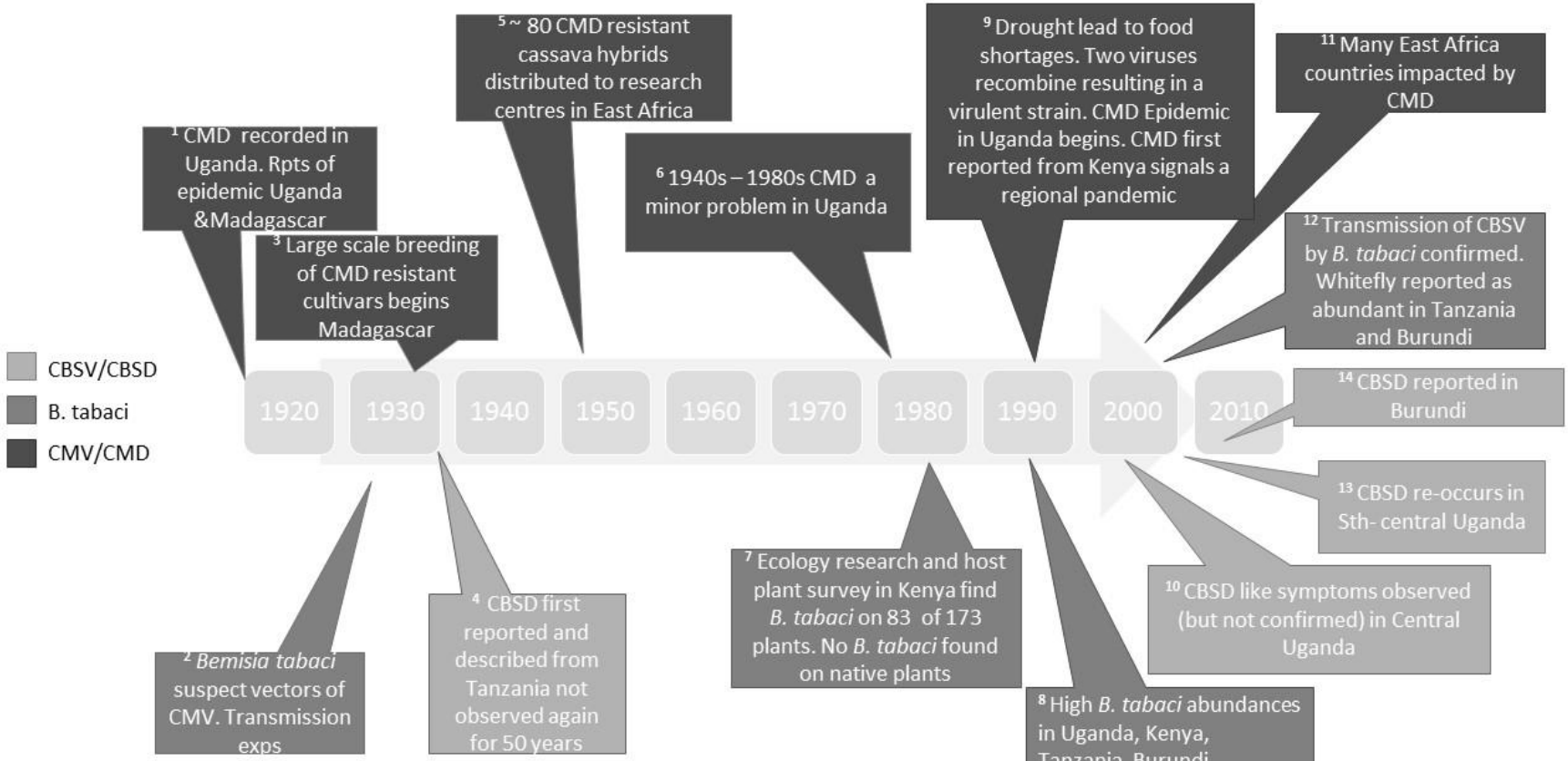
Host Plant	Common name	*B. tabaci* genotype *	References
Manihot esculenta	cassava	Ug1, Ug2, SSA1,IO	Sseruwagi et al., 2005; Tajebe *et al.,* 2014
Ocimum gratissimum	wild basil	Ug3	Sseruwagi et al., 2005
Cucurbita pepo	squash	Ug4, MED,EA1	Sseruwagi et al., 2005;Tajebe *et al.,* 2014b
Cucurbita sativus	cucumber	Ug4	Sseruwagi et al., 2005
Leonotis nepetifolia	weed	Ug4 EA1, MED, IO	Sseruwagi et al., 2005; Tajebe *et al.,* 2014
Pavonia urens	Malvaceae, hibiscus-like flower	Ug4	Sseruwagi et al., 2005
Commelina benghalensis	wandering dew	Ug7	Sseruwagi et al., 2005
Phaseolus vulgaris	bean	Ug7	Sseruwagi et al., 2005
Abelmoschus esculentus	okra	Ug1, Ug 6, EA1	Sseruwagi et al., 2005; Tajebe *et al.,* 2014
Lycopersicon esculentum	tomato	Ug1, Ug8, SSA1, IO	Sseruwagi et al., 2005; Tajebe *et al.,* 2014; Delatte *et al.,* 2011
Gossypium hirsutum	cotton	Ug8, EA1	Sseruwagi et al., 2005; Tajebe *et al.,* 2014
Ipomoea batatas	Sweet potato	Ug1, EA1, MED, SSA1	Tajebe *et al.,* 2014
Solanum melongena and *Datura* sp.	Eggplant	SSA1 (very few specimens), Tunisia	Laarif *et al.,* 2015
Euphorbia heterophylla, Aspilia africana	Non-crop weeds	Ug1	Sseruwagi et al., 2005
Manihot glaziovii Jatropha gossypifolia	Tree cassava	Ug1	Sseruwagi *et al.,* 2006
Lantana spp.	Lantana and Hibiscus	MED, in Tunisia	Laarif *et al.,* 2015

*The names used here is the same as authors used in their paper, however see section on species identification.

Table 5. Records of parasitism of *B. tabaci* from field studies in East Africa

citation	location/study type	Host plant	Parasitoid species recorded	Percentage parasitism
Otim *et al.,* 2005	Namulonge, Uganda. Survey data.	Cassava with *B. tabaci*	*Eretmocerus mundus* *Encarsia mineoi* *Encarsia sophia* *Encarsia* "blackhead"(undescribed)	40-58%
Otim *et al.,* 2006	Namulonge, Uganda. Field study on cassava cultivars.	Cassava with *B. tabaci*	*Eretmocerus mundus* *Encarsia sophia*	20-58%
Otim *et al.,* 2008b	Namulonge, Uganda. Potted plant study.	Cassava potted plants with *B. tabaci*	*Eretmocerus mundus* *Encarsia sophia*	11-67% hirsute cultivar 0-42% glabrous (trial 1) 0-46% hirsute cultivar 0-67% glabrous (trial 2)
Guastella *et al.,* 2015b	Mwanza, Shinyanga and Tabora. Survey data	Cassava	*Encarsia sophia* *En. guadeloupae* *En. dispersa* *En. lutea* *En.mineoi* *En. sp. pr. circumsculpturata* *Eretmocerus mundus* *Er. sp. pr. hayati or Queenslandensis* *Er. sp. 1* *Er. sp. 2*	Parasitism levels not determined

Figure 1. Timeline of events of *B. tabaci* and associated disease 'outbreaks' in East Africa



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