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

S. Macfadyen1*, C. Paull2, L.M. Boykin3, P. De Barro2, M.N. Maruthi4, M. Otim5, A. Kalyebi5,6, D.G. Vassão7, P. Sseruwagi6, W.T. Tay2, H. Delatte8, Z. Seguni6, J. Colvin4 and C.A. Omongo5

1CSIRO, Clunies Ross St. Acton, ACT, 2601, Australia: 2CSIRO, Boggo Rd. Dutton Park, QLD, 4001, Australia: 3University of Western Australia, School of Molecular Sciences, 35 Stirling Highway, Crawley, WA 6009, Australia: 4Natural Resources Institute, University of Greenwich, Chatham Maritime, Kent, ME4 4TB, UK: 5National Crops Resources Research Institute, Kampala, Uganda: 6Mikocheni Agricultural Research Institute, P.O. Box 6226 Dar es Salaam, Tanzania: 7Max Planck Institute for Chemical Ecology, Hans-Knoell Str. 8 D-07745 Jena, Germany: 8CIRAD, UMR PVBMT, Saint Pierre, La Réunion 97410-F, France

Abstract

*Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) is a pest species complex that causes widespread damage to cassava, a staple food crop for millions of households in East 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. Here we assess critically the knowledge base relating to factors that may lead to high population densities of sub-Saharan African (SSA) *B. 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 sustainable management solutions. We found that whilst many hypotheses have been put forward to explain the increases in abundance witnessed since the early 1990s, there are little 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 population dynamics and 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 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.

Keywords: cassava, ecology, natural enemies, climate change, cultivars

(Accepted 28 December 2017; First published online 13 February 2018)
Introduction

*Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) is a pest species complex that causes widespread damage to cassava, a staple food crop in many millions of smallholder households in Africa (Otim-Nape *et al.*, 2000; Colvin *et al.*, 2004; Legg *et al.*, 2006; Patil *et al.*, 2015). *Bemisia tabaci* causes direct feeding damage to cassava, excretes a sugar-rich honeydew, which acts as a substrate for sooty moulds that reduces both respiration and photosynthesis (Nelson, 2008). In addition, *B. tabaci* vector multiples plant viruses that cause two damaging diseases: cassava mosaic disease (CMD) and cassava brown streak disease (CBSD), that in combination lead to significant yield loss in cassava (Holt & Colvin, 2001; Maruthi *et al.*, 2002a, b). 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). This disproportionate approach to managing insect-vectored plant diseases is not unusual, but has led repeatedly to management solutions that are not sustainable. 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 (SSA) clade forms the ancestral root (Boykin *et al.*, 2013) of the complex, and in recent history, species in this clade have been associated with an increased frequency of cassava viral disease outbreaks in East Africa. 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 of *B. tabaci* 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.

Our objectives for this review are firstly, to synthesize the existing literature on the SSA *B. tabaci* species’ ecology in East Africa and to review critically this knowledge base. We focused on empirical studies that have examined factors that may lead to high populations or outbreaks of the SSA *B. tabaci*. We then identified 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. We started by listing factors that, from an a priori perspective, are likely to be important ecological determinants of *B. tabaci* abundance (table 1) in any farming context. Factors that may support or limit population growth were equally considered (as these both may facilitate outbreaks). We then searched for studies based in East African production landscapes, preferring those focused on cassava. We included the countries of Tanzania, Uganda, Rwanda, Burundi, South Sudan and Malawi as part of the geographical region of Eastern Africa. In cases where we could not find published studies based in East Africa, we cited geographically related work if relevant. We excluded studies that look solely at virus impacts on the crop, and there have been several important review articles that have summarized information on cassava virus disease epidemics and speculated on some of the likely causes (table 2). In addition, there are reviews by Fishpool & Burban (1994); Legg (1994) and Colvin *et al.* (2006) that provide a good baseline of ecological and biological information on what was known about *B. tabaci* complex and cassava viruses up until the late 1990s. 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 attempted to resolve these issues.

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 (see example from Kenya in Manani *et al.*, 2017). Due to morphological similarities, *B. tabaci* was originally thought to be one species worldwide, but based on genetic differences (Colvin *et al.*, 2004; Sseruwagi *et al.*, 2005; Boykin *et al.*, 2007; 2013; Wang *et al.*, 2014); and mating incompatibility (Colvin *et al.*, 2004; Xu *et al.*, 2010; Liu *et al.*, 2012), it is now recognized as a species complex with at least 34–36 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; Boykin *et al.*, 2018).

The SSA *B. tabaci* species are no exception to the nomenclatural confusion. Identification of species in the *B. tabaci* pest complex currently relies on the 3’ region of 657 bp 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 (2005) used ‘Ug1’, Legg *et al.* (2014a) used ‘SSA1 subgroups 1–3’ and Mugerwa *et al.* (2012) used ‘SSA1 subclades 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 were not set firmly within a complete understanding of *B. tabaci* diversity at the time (Boykin *et al.*, 2018).

Greater clarity around the species identity of individuals involved in future outbreaks may help to uncover the causes of these outbreaks. Even closely related species may differ in their host-plant use, ability to transmit viruses, fecundity and response to management actions. 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 could play a larger role in the future (see ‘Knowledge gaps’ section towards the end of this review).

Overview of the life cycle of *B. tabaci*

The life-history parameters of many species in the *B. tabaci* complex vary depending on the environmental conditions and

https://doi.org/10.1017/S0007485318000032 Published online by Cambridge University Press
Table 1. Potential factors influencing *Bemisia tabaci* abundance on cassava included in this review (does not include interactions between these factors). We have suggested the likely direction of the effect in terms of an increase (↑) or decrease (↓) in *B. tabaci* abundance, but note there are many possible outcomes for some of these factors.

| Factors                                | Potential mechanisms that may lead to a change in abundance                                                                 | Likely direction of effect                                                                 |
|----------------------------------------|-------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------|
| Cassava cultivar                       | Leaf architecture (e.g. width of leaves)                                                                                      | Wider leaves = ↑ nymph density                                                             |
|                                        | Growth habit (e.g. long vs. short growing season)                                                                             | ↑ Up to ~6 months after planting, then steady ↓. Exact cause unknown                       |
|                                        | Plant chemistry differences between cultivars                                                                                | Unknown – depends on compounds involved                                                    |
| Cassava age                            | Number of new leaves at the top of the plant                                                                               | More new leaves = ↑ adult density                                                         |
|                                        | Change in plant chemistry as cassava ages                                                                                  | Unknown – depends on compounds involved                                                    |
| Infection status of cassava            | Fecundity and survivorship enhanced on infected hosts                                                                         | ↑ Adult and nymph density on cassava plants                                               |
|                                        | Promotion of emigration of *B. tabaci* adults                                                                               | Unknown – may increase populations, but also spread densities                              |
| Non-cassava host plants                | Other crops, natural vegetation and weeds act as host plants for *B. tabaci*                                                 | ↑ Population density in cassava if more resources present in landscape year-round          |
| Spatial arrangement and amount of host plants surrounding cassava fields | More resources for *B. tabaci* at important times                                                                           | ↑ Population density in cassava if more resources present in landscape year-round          |
|                                        | More resources for natural enemies                                                                                        | ↓ Population density in cassava if more resources present in landscape year-round          |
|                                        | Predators consuming *B. tabaci*                                                                                             | ↓ Nymph density from increased mortality due to natural enemies                            |
| Natural enemies                        | Parasitoids using *B. tabaci* as host                                                                                         | Unknown – intra-guild predation effects                                                    |
| Other pests on cassava                 | Cassava green mite damage to top leaves. Reduces suitable space on plant for *B. tabaci* adults                            | ↓ Adult density on top leaves may lead to reduced oviposition                              |
| Endosymbionts                          | Presence of some endosymbiont species in *B. tabaci* can decrease the number of adults emerging, increase development time, thus reducing overall population development | Unknown – synergistic effects of multiple pests overcoming host-plant defences             |
| Altitude                               | Unclear, combination of temperature, rainfall and host-plant availability. Less suitable conditions at higher altitudes      | Unknown                                                                                  |
| Climate                                | Long-term changes in temperature and rainfall                                                                               | Unknown                                                                                  |
| Weather                                | Heavy rainfall events                                                                                                        | ↓ Nymph density, through increasing mortality due to heat stress and dislodgement          |
|                                        | Very high temperatures                                                                                                       | ↓ Population density perhaps through disrupting adult behaviour                           |
| Pesticides                             | Resistance in *B. tabaci*                                                                                                     | ↑ Population density in landscape                                                         |
| New invasive species in East Africa    | Pesticides killing natural enemies or competitors                                                                             |                                                                                           |
|                                        | Totally new species has taken over from local species in cassava (species turnover)                                       | Unknown. It is unclear how this would lead to a change in abundance in isolation from other factors |
| Hybridization                          | ‘Invader biotype’ out-competes domestic species and is better able to use resources                                          |                                                                                           |
especially in the case of virus transmission. Thus, whilst crop damage can occur at low pest abundance, high abundances, and is causing economic injury to the crop. This problem usually manifests at the field or regional scale.

The plant-virus vector has been released from control, has reached break situation as one in which the pest herbivore or enemies, etc.) that may influence the abundance of any pest herbivore on a host plant. Understanding how these factors relate to population dynamics and distributions measured at the field level and scale-up to the regional level is critical for determining if a pest outbreak 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 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 1.

| 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 cassava virus pandemics across Africa                |
|                         | Comparison of characteristics of CMD and CBSD outbreaks                       |
| Patil & Fauquet (2010)  | CMBs, knowledge and perspectives                                              |
|                         | Very comprehensive review of the cassava viruses                              |
| Legg & Thresh (2000)    | CMD 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 CMD in Africa                                                   |
| Fishpool & Burban (1994)| Very comprehensive treatment of all aspects of the disease and vector story  |
|                         | Biology of B. tabaci including morphology, taxonomy, biometrics               |
|                         | Ecology on cassava in Africa                                                  |
|                         | Some discussion about natural enemies and control                              |
| Legg (1994)             | Ecology of whitefly and CMBs 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                        |

CMBs, cassava mosaic begomoviruses; CMD, cassava mosaic disease; CBSD, cassava brown streak disease.

There has been a change in the abundance of B. tabaci in cassava production landscapes in East Africa in general over time (fig. 1). However, quantitative definitions of what is a high or low population abundance have also changed across time; therefore, empirical evidence documenting this change is weak. The threshold of the number of adults considered highly abundant, however, differs between studies, and we cannot translate abundance data into likely yield loss. Early research from Ivory Coast considered cassava a poor host for B. tabaci, as numbers rarely exceeded 300 adults per plant and more often there were 150 adults per plant (Fishpool & Burban, 1994; Fishpool et al., 1995; Colvin et al., 1998). However, other researchers might consider these to be relatively high numbers. In Legg et al. (2011) when >5 adults per top five leaves per plant were recorded, 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 summarized in table 3; 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.
We have summarized the available evidence on the historical outbreaks of *B. tabaci*, and the two major diseases of cassava, CMD and CBSD, across East African countries in fig. 1. There are records of high populations of *B. tabaci* causing problems for farmers since the 1990s. 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 cassava 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***

Outbreaks of CMD, which are at least partially whitefly-borne, have been occurring in East Africa since the 1960s (Jameson, 1964). A detailed description of both CMD and CBSD can be found in Mabasa (2007), but we will summarize some of the key points here. There are seven cassava mosaic begomoviruses (CMBs) (Geminiviridae; genus Begomovirus) that are related to 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. CMBs appear to be persistent in *B. tabaci*; however, there may be some co-adaptation between the viruses and different vector species that alter their ability to transmit virus to cassava (see Maruthi et al., 2002b). Severe infection causes stunting of shoots, leaves and stems which reduce tuber growth and subsequently yield (Fauquet & Fargette, 1990). Symptoms increase until approximately 60 days after planting. However, infection introduced beyond 5 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).

The second major cassava plant disease associated with *B. tabaci* is CBSD. 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 diversity in both CBSV and UCBSV, suggesting that there may be more than two viruses involved. Both virus groups 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, CBSVs 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

![Fig. 1. Timeline of events of *Bemisia tabaci* and associated disease outbreaks in East Africa. CMV, cassava mosaic virus; CMD, cassava mosaic disease; CBSV, cassava brown streak virus, CBSD, cassava brown streak disease.](https://doi.org/10.1017/S0007485318000032 Published online by Cambridge University Press)
Table 3. Studies quantifying the mean number of adults (unless otherwise mentioned) Bemisia 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. ~30 (method not confirmed) | Ivory Coast | Fargette et al. (1985) |
| Max. ~25 | Ivory Coast | Fargette et al. (1988) |
| Min. ~3 | | |
| Max. ~35 intercropped low maize density | Ivory Coast | Fauquet et al. (1988) |
| Min. ~2.5 intercropped low maize density (method not confirmed) | Uganda | Fargette et al. (1990) |
| Max. ~18 intercropped high maize density | Uganda | Gibson et al. (1996) |
| Min. ~ 2 intercropped high maize density | Zambia | Muimba-Kankolongo et al. (1997) |
| Max. 14 Min. 2.4 | | |
| Max. ~35 | | |
| 4.6 ± 0.54 adults and 43 ± 6.0 nymphs (cassava no mosaic disease symptoms) | Uganda | Otim-Nape et al. (2001) |
| 5.0 ± 3.8 adults and 46 ± 6.4 nymphs (cassava with mosaic disease symptoms) | | |
| Max. 21.8 | | |
| Min. 0.2 | | |
| Max. 3.7 | | |
| Min. 0.3 | | |
| >3 per shoot (three districts) | Uganda | Legg & Ogwal (1998) |
| >1 (14 districts) | | |
| between 1–3 (ten districts) | | |
| (One shoot = top four expanded leaves) | | |
| Max. ~37 | | |
| Min. ~1 | | |
| 3–4 instar nymphs = 35.8 (early season) 59.1 (late season) resistant cultivars | Uganda | Otim et al. (2006) |
| 3–4 instar nymphs = 17.2 (early season) 31.2 (late season) susceptible cultivars | Rwanda | Night et al. (2011) |
| Nymphs 11.81 ± 0.84 improved cultivars | | |
| Nymphs 4.30 ± 0.12 local cultivars | | |
| 2.12 ± 0.17 improved cultivars | | |
| 0.60 ± 0.03 local cultivars | | |
| 0.74 ± 0.03 inter-cropped cassava | | |
| 0.94 ± 0.07 mono-cropped cassava | | |
| Max. 39.2 ± 4.4 cultivar TMS I92/0067 | Uganda | Omongo et al. (2012) |
| Min. 5.4 ± 1.7 cultivar Njule Red | Zambia | Chikoti et al. (2013) |
| Max. 2.12 | Tanzania | Tajebe et al. (2015) |
| Min. 0.02 | Tanzania | Jeremiah et al. (2015) |
| Max. 76 | Malawi | Mbewe et al. (2015) |
| Min. <1 | | |
| Max. 1.35 | | |
| Min. 0.1 | | |
| Max. 50 | | |
| Min. 0 | | |
| Max. 41.5 | Tanzania | Uzokwe et al. (2016) |
| Min. 1.0 | | |

Table 4. Quantification of whitefly vectors and their role in the spread of Cagoglossa virus (CBSV) in five different countries. CBSVs. Transmission of CMFs by B. tabaci has been confirmed in Africa (Burbank et al., 1993; Fishpool & Burbank, 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 that on average 27% of plants had CMD symptoms, of which 3% could be attributed to B. tabaci transmission, compared with 24% 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 with being vectored by B. tabaci (Night et al., 2011). A modelling study exploring CBSD spread showed that in a scenario with whitefly dispersal alone, large-scale epidemics were less likely than when trade of infected cuttings is also included in the model (McQuaid et al., 2017). Research by Dubern (1994) indicated that B. tabaci was not an efficient vector of CMFs. However, Maruthi et al. (2002a, b) used CMF isolates and B. tabaci sourced from four different areas (three African locations and one culture from India) to show that African CMFs were transmitted by African B. tabaci to

colour of the leaf veins, especially on the lower more mature leaves. Brown coloured vertical lesions occur on the stems and roots can become contorted and constricted. Cross-sections of roots from infected cassava plants show brown necrotic tissue (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 et al. (1997) makes the argument that selection and subsequent spread of viruses by certain B. tabaci species might be possible. Different species of B. tabaci are believed to be able to transmit Geminiviruses with different coat proteins (McGrath & Harrison, 1995; Maruthi et al., 2002a; Morales & Jones, 2004, b). 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).
60–79% of the cassava plants. However, inoculation was significantly less when Indian \textit{B. tabaci} transmitted an African CMD isolate and vice versa when \textit{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 \textit{B. tabaci} species (Maruthi \textit{et al.}, 2002b). However, there is little quantifiable evidence for this hypothesis, and what evidence there is has been drawn from data that have a small number of samples (Xu \textit{et al.}, 2010).

**Factors influencing \textit{B. tabaci} abundance**

Below we summarized the available evidence that may demonstrate a link with each factor and change in abundance of \textit{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 or tolerant (these are often referred to as ‘improved cultivars’). 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 1990s CMD epidemic was to distribute cassava cuttings from improved cultivars (Oliveira \textit{et al.}, 2001). In recent times, greater numbers of adult \textit{B. tabaci}, and sometimes nymphs, have been associated with recently developed cultivars, although the dynamics of \textit{B. tabaci} populations in semi-field situations have not been well documented (e.g. Katono \textit{et al.}, 2015). Severity of cassava green mite (CGM; \textit{Mononychellus tanajoa}) and CMD were higher on local cultivars of cassava, although \textit{B. tabaci} populations were higher on improved cultivars (Night \textit{et al.}, 2011). To determine which cultivars showed some level of phenotypic resistance or tolerance to \textit{B. tabaci}, 19 cultivars were exposed to \textit{B. tabaci} for colonization. Numbers of nymphs, eggs, damage and sooty mould were greatest for cultivar 192/0067 and least for Njule Red (a local cultivar) (Omono \textit{et al.}, 2012). Cassava leaf area did affect the severity of sooty mould (i.e. a cultivar with a lower number of \textit{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 \textit{B. tabaci} adults and cultivar plant traits such as leaf width or colour (Omono \textit{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 \textit{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 \textit{et al.} (2010). Cassava phytochemistry can impact phloem feeders, with examples including the effect of its flavonoids and cyanogenic glucosides on the cassava mealybug, \textit{Phenacoccus manihoti} (Calatayud \textit{et al.}, 1994a, b, 1997) and the cassava hemipteran pest, \textit{Cyrtomenus bergi} (Riis \textit{et al.}, 2003). \textit{Bemisia tabaci} can also be affected, and has been shown to induce cyanide-metabolizing enzymes when feeding on cassava compared with sweet potato (Antony \textit{et al.}, 2006). These results provide evidence that defensive plant metabolites play an important role in cassava colonization by phloem feeders including \textit{B. tabaci}. However, how the phytochemistry of different cassava cultivars and tissues influences \textit{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 virus infection status**

There are some empirical studies that have tested the hypothesis that there is a relationship between disease severity in a plant and \textit{B. tabaci} abundance (Gregory, 1948; Leuschner, 1977; Robertson, 1987; Fargette \textit{et al.}, 1993; Otim-Nape \textit{et al.}, 1995; Colvin \textit{et al.}, 2004). If this is due to correlation or causation it is often hard to untangle. The abundance of \textit{B. tabaci} adults was shown to be significantly higher on healthy cassava plants compared with 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 with plants without disease. Omono (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 (Omono, 2003).

Cassava plants infected with CMBs have been reported to be more suitable for growth and development of \textit{B. tabaci}. A summary of the studies showing the effect of virus infection of host plants on \textit{B. tabaci} population growth, development and behaviour can be found in Colvin \textit{et al.} (2006). Concentrations of amino acids have been shown to be greater in infected cassava, and these may benefit \textit{B. tabaci} fitness (Colvin \textit{et al.}, 1999, 2006). However, other laboratory studies have found that the status of cassava disease and \textit{B. tabaci} (i.e. viruliferous or non-
viruliferous) had no significant effect on life-history factors, sex ratio and developmental period, or per cent 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* (Berlinger et al., 1996). Therefore, 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**

*Benmsia 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 (Bellotti et al., 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). Larif et al. (2015) found that *B. tabaci* Mediterrenean (MED, formally named biotype Q) preferred host plants in the families Verbenaceae and Malvaceae and Middle East-Asia Minor 1 (MEAM1, formally named biotype B) were found on Cucurbitaceae and Solanaceae. SSA2 only occurred on *Datura* and eggplant (Larif 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 plant families. Table 4 documents host plants that have been recorded in recent publications that included a genetic determination of the species. Most of the studies 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 suppression that the number of eggs laid on a plant is a better indicator of a preferred host compared with counts of adults (Larif et al., 2015). Further information is required that shows clear species host-plant relationships in field contexts, such as preference tests, rate of nymphal development and mortality on host plants (not just presence or 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 et al. (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 with 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 reduce *B. tabaci* population abundances 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 surveys in Uganda in 2007 showed that intercropped cassava had significantly less *B. tabaci* than monocrops (Night et al., 2011). Experiments intercropping cassava with *Vigna unguiculata* and *Vigna 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 with 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-suited 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 hayatii*) 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 if small) of the spatial and temporal arrangement of host plants are 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 that 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 preying on B. tabaci populations on cassava in Kenya (Otim-Nape et al., 1995), and 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 the work carried out in the USA, Euseius hibisci were shown to consume and complete their development on B. tabaci (Meyerdick & Coudriet, 1985). Other predators of B. tabaci nymphs from around the world include Sthenorus jejunus Casey, Coccinellidae, Holoborus pallidicornis (Cameron) Staphylinidae and Scathophaga atripennis Priesner, Thysanoptera (Fishpool & Burban, 1994). The Neotropical Conventzania 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 (Asimwe et al., 2007a, b). 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 (Asimwe et al., 2007a, b). 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 CGM M. tanajoa (Zundel et al., 2009).

Legg & Hillocks (2003) lists the parasitoids attacking Bemisia genus in SSA. 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 identified using a molecular approach, ten species of parasitoids (Guastella et al., 2015). Hoelmer et al. (1995) summarized 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 E. sophia were shown to parasitize B. tabaci on cassava in Uganda and accounted for 34% parasitism of fourth instar nymphs (Legg, 1995). Significantly higher number of B. tabaci and parasitoids occurred on the CMD-resistant cultivar compared with 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. Per cent 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 (Asimwe et al., 2007a, b).

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. tanajoa, Zundel et al., 2009), and there have been some basic experiments conducted using parasitoids (Otim et al., 2008). However, a comprehensive understanding of cultivar impacts at higher trophic levels is critically needed.

Table 4. Host plants of Bemisia 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. (2015) |
| Ocimum gratissimum          | Wild basil                   | Ug3                 | Sseruwagi et al. (2005)         |
| Cucurbita pepo              | Squash                       | Ug4, MED, EA1       | Sseruwagi et al. (2005); Tajebe et al. (2015) |
| Cucurbita sativas           | Cucumber                     | Ug4                 | Sseruwagi et al. (2005); Tajebe et al. (2015) |
| Leonotis nepetifolia        | Klip dagga, Christmas candlestick or lion’s ear | EA1, MED, IO | Sseruwagi et al. (2005) |
| Psorospermum esculentus     | Okra                         | Ug1, Ug6, EA1       | Sseruwagi et al. (2005); Tajebe et al. (2015) |
| Lycopersicon esculentum     | Tomato                       | Ug1, Ug8, SSA1, IO  | Sseruwagi et al. (2005); Tajebe et al. (2015) |
| Gossypium hirsutum          | Cotton                       | Ug8, EA1            | Sseruwagi et al. (2005); Tajebe et al. (2015) |
| Ipomoea batatas             | Sweet potato                 | Ug1, EA1, MED, SSA1 | Tajebe et al. (2015) |
| Solanum melongena and Datura sp. | Eggplant                  | SSA1 (very few specimens), Tunisia | Laari et al. (2015) |
| Euphorbia heterophylla, Aspilia africana | Non-crop weeds | Ug1 | Sseruwagi et al. (2005) |
| Manihot glaziovii, Jatropha gossypioidea | Tree cassava | Ug1 | Sseruwagi et al. (2006) |
| Lantana ssp.                | Lantana and hibiscus         | MED, in Tunisia     | Laari et al. (2015) |

*The names used here are the same as authors used in their papers, however see section on species identification.
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 CGM *M. tanajoa* 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 CMVs by *B. tabaci* and help them adapt to new host plants (Gottlieb et al., 2010; Kliot 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 (Tajbe et al., 2015, 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 evidence in the literature that altitude relates to population abundance of *B. tabaci*. However, the mechanism underlying any altitudinal variations seen in the few studies available (e.g. temperature, rainfall gradients, change in farming systems and crops grown) have not been tested (or in some cases even described). There is some evidence to suggest that cassava virus infection was lower in areas above 800 m above...
sea level (Legg (1994)). Legg & Raya (1998) found a significant negative correlation between CMD incidence and altitude in Tanzania. Historically, it has been noted that at high altitudes (>1000 m 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., 2015).

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 for the species associated with cassava in East Africa. In general, B. tabaci populations are favoured by high temperatures and moderate rainfall (Sseruwagi et al., 2004). Robertson (1987) described increases in the abundance of B. tabaci along coastal Kenya related to an increase in annual rainfall, and increased activity of flying adults after the end of rainy periods. 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 et al., 2015). 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 generally when numbers of B. tabaci are likely to be low in cassava fields based on the time of the year when temperatures are low and the environment is unsuitable for B. tabaci (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. Bemisia tabaci adults decrease as planting density decreased and canopy temperatures increased (Otim-Nape & Ingroot, 1986).

If we examine studies that include B. tabaci species more broadly (i.e. not just East African studies), humidity extremes (low humidity <20% and high humidity >80%) can increase mortality of immature stages, and development rate of multiple life stages decreases dramatically with temperatures above 30-33°C (Gerling et al., 1986). Drost et al. (1998) used an upper lethal temperature of 36°C to fit a development rate model for immature B. tabaci on cotton. Laboratory studies have shown that B. tabaci survival ranges from ~90% survival at 25°C and 100% RH, to <2% survival at 41°C and 20% RH (during a 2 h exposure) (Berlinger et al., 1996).

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 the identity of the common B. tabaci species in other cropping systems around the world (e.g. Crowder et al., 2008). For example, a shift from B. tabaci MEAM1 species to MED 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 (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, application rates and baseline levels of resistance) 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 over the recent historical period. 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; Sequeira 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). Yet there is no empirical evidence to support this idea in East Africa (table 1).

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). 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, Tajbe et al. (2015) 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 Liu 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 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 or synergistic ways; therefore, 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 outlined below.

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

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. Laboratory studies looking at basic life-history parameters of the different species under different temperatures and humidities could then be conducted. 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 vs. uninfected 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. Extending this to a detailed quantification of yield loss due to cassava diseases in the presence and absence of *B. tabaci* at the field and landscape level is also necessary to inform future management options.

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 roguing 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 *B. tabaci* outbreaks (and if this will impact disease outbreaks). Given that cassava is a crop with a relatively long growth season (compared with 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 other factors, such as the effect of alternative host plants (i.e. do any provide an alternative source of natural enemies to recolonize 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 m of a source field), to enable us to make specific management recommendations to farmers.
Conclusions

Given the right combination of environmental factors, 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 minimize 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.

Acknowledgements

The authorship list is made up of members of the African Cassava Whitefly Project (ACWP) team (http://cassavawhitefly.org/people) who made a significant contribution to the writing of this manuscript; however, all members of the team contributed thoughts, discussion and ideas. The authors thank them for their contribution. Hazel Parry and Paul Mwebaze helpfully reviewed an early version of this manuscript. 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). Mark Parnell (NRI) was very helpful in facilitating this work and the broader project goals.

References

Adriko, J., Sserubombwe, W.S., Adipala, E., Bua, A., Thresh, J. M. & Edema, R. (2011) Response of improved cassava varieties in Uganda to cassava mosaic disease (CMD) and their inherent resistance mechanisms. African Journal of Agricultural Research 6, 521–531.

Alabi, O.J., Ogbe, F.O., Bandyopadhyay, R., Kumar, P.L., Dixon, A.G.O., Hughes, J. & Naidu, R.A. (2008) Alternate hosts of African cassava mosaic virus and East African cassava mosaic Cameroon virus in Nigeria. Archives of Virology 153, 1743–1747. doi: 10.1007/s00705-008-0169-8.

Alicai, T., Omongo, C.A., Maruthi, M.N., Hillocks, R.J., Baguma, Y., Kwakki, R., Bua, A., Otim-Nape, G.W. & Colvin, J. (2007) Re-emergence of cassava brown streak disease in Uganda. Plant Disease 91, 24–29. doi: 10.1094/pd-91-0024.

Alicai, T., Ndunguru, J., Sseruwagi, P., Taibo, F., Okao-Okuja, G., Nanvubya, R., Kiiza, L., Kubiakko, L., Kehoe, M.A. & Boykin, L.M. (2016) Cassava brown streak virus has a rapidly evolving genome: implications for virus speciation, variability, diagnosis and host resistance. Scientific Reports 6, 36164. doi: 10.1038/srep36164.

Antony, B., Lisha, V.S., Palaniswami, M.S., Sugunan, V.S., Makesh Kumar, T. & Henneberry, T.J. (2006) Bemisia tabaci (Homoptera : Aleyrodidae) and Indian cassava mosaic virus transmission. International Journal of Tropical Insect Science 26, 176–182. doi: 10.1079/ijt2006110.

Asiimwe, P., Ecaut, J.S., Guershon, M., Kyamunya, S., Gerling, D. & Legg, J.P. (2007a) Evaluation of Sermingium n. sp. (Col., Coccinellidae), a predator of Bemisia tabaci (Hom., Aleyrodidae) on cassava. Journal of Applied Entomology 131, 76–80. doi: 10.1111/j.1439-0418.2006.01122.x.

Asiimwe, P., Ecaut, J.S., Otin, M., Gerling, D., Kyamunya, S. & Legg, J.P. (2007b) Life-table analysis of mortality factors...
affecting populations of *Bemisia tabaci* on cassava in Uganda. *Entomologia Experimentalis Et Applicata* 122, 37–44. doi: 10.1111/j.1570-7458.2006.00487.x.

Barbosa, L., Yuki, V.A., Maruyabashi, J.M., De Marchi, B.R., Perini, F.L., Pavan, M.A., de Barros, D.R., Ghanim, M., Moriones, E., Navas-Castillo, J. & Kraske-Sakate, R. (2015) First report of *Bemisia tabaci* Mediterranean (Q Biototype) species in Brazil. *Pest Management Science* 71(4), 501–504. doi: 10.1002/ps.3909.

Bellotti, A., Peña, J., Arias, B., Guerrero, J.M., Trujillo, H., Holguin, C. & Ortega, A. (2005) Biological control of whiteflies by indigenous natural enemies for major food crops in the Neotropics. pp. 313–323 in Anderson, P.K. & Morales F.J. (Eds) Whitefly and Whitefly-Borne Viruses in the Tropics: Building A Knowledge Base for Global Action. Colombia, International Centre for Tropical Agriculture.

Berlinger, M.J., Lehmann-Sigura, N. & Taylor, R.A.J. (1996) Survival of *Bemisia tabaci* adults under different climatic conditions. *Entomologia Experimentalis Et Applicata* 80, 511–519.

Bigirimana, S., Barurambane, P., Ndayihanmaso, P., Shirima, R., & Legg, J.P. (2011) First report of cassava brown streak disease and associated Ugandan cassava brown streak virus in Burundi. *New Disease Reports* 24, 2044–2088.

Blagbrough, I.S., Bayoumi, S.A.L., Rowan, M.G. & Beeching, J.R. (2010) Cassava: an appraisal of its phytochemistry and its biotechnological prospects. *Phytochemistry* 71, 1940–1951. doi: 10.1016/j.phytochem.2010.09.001.

Bouwmeester, H., Heuvelink, G.B.M., Legg, J.P. & Stoovogel, J. (2012) Comparison of disease patterns assessed by three independent surveys of cassava mosaic virus disease in Rwanda and Burundi: comparison of crop virus disease patterns in Rwanda and Burundi. *Plant Pathology* 61, 399–412. doi: 10.1111/j.1365-3059.2011.02500.x.

Boykin, L.M. & De Barro, P. (2014) A practical guide to identifying members of the *Bemisia tabaci* species complex: and other morphologically identical species. *Frontiers in Ecology and Evolution* 2, doi: 10.3389/fevo.2014.00045.

Boykin, L.M., Shatters, R.G., Jr., Rosell, R.C., McKenzie, C.L., Bagnall, R.A., De Barro, P.J. & Frohlich, D.R. (2007) Global relationships of *Bemisia tabaci* (Hemiptera: Aleyrodidae) revealed using Bayesian analysis of mitochondrial COI DNA sequence. *Molecular Phylogenetics and Evolution* 44, 1306–1319.

Boykin, L.M., Armstrong, K.F., Kubatko, L. & De Barro, P.J. (2012) Species delimitation and global biosecurity. *Evolutionary Bioinformatics* 8, 1–37.

Boykin, L.M., Bell, C.D., Evans, G., Small, I. & De Barro, P.J. (2013) Is agriculture driving the diversification of the *Bemisia tabaci* species complex (Hemiptera: Sternorrhyncha: Aleyrodidae)? Dating, diversification and biogeographic evidence revealed. *BMC Evolutionary Biology* 13, 228. doi: 10.1186/1471-2148-13-228.

Boykin, L.M., Kinene, T., Wainaina, J., Seal, S., Mugera, H., Macfadyen, S., De Barro, P., Tay, W.T., Kubatko, L., Alicai, T., Omongo, C.A., Taiko, F., Ndunguru, J. & Sseruwagi, P. (2018) Review and future guide to the naming system of African *Bemisia tabaci* species. *Systematic Entomology*. Accepted January 2018.

Burban, C., Fishpool, L.D.C., Fauteau, C., Fargette, D. & Thouvenel, J.C. (1992) Host-associated biotypes within West African populations of the whitefly *Bemisia tabaci* (Genn.), (Hom., Aleyrodidae). *Journal of Applied Entomology* 113, 416–423.

Caciagli, P. (2007) Survival of whiteflies during long-distance transportation of agricultural products. in Czosnek, H. (ed.) *Tomato Yellow Leaf Curl Virus Disease Management, Molecular Biology, Breeding for Resistance*. Dordrecht, Springer.

Calatayud, P.A., Rahbé, Y., Delobel, B., Khuong-Huu, F., Tertuliano, M. & Le Rü, B. (1994a) Influence of secondary compounds in the phloem sap of cassava on expression of antibiotic towards the mealybug *Pseudococcus mansi.* *Entomologia Experimentalis et Applicata* 72, 47–57. doi: 10.1111/j.1570-7458.1994.tb0801.x.

Calatayud, P.A., Rahbé, Y., Tjallingii, W.F., Tertuliano, M. & Le Rü, B. (1994b) Electrically recorded feeding behaviour of cassava mealybug on host and non-host plants. *Entomologia Experimentalis et Applicata* 72, 219–232. doi: 10.1111/j.1570-7458.1994.tb08121.x.

Calatayud, P.A., Rouland, C. & Le Rü, B. (1997) Influence de la linamarin dans la relation manioc-cochenille. *Acta Botanica Gallica* 144, 427–432. doi: 10.1080/12538087.1997.10515782.

Calvo, F., Boickmann, K. & Belda, J. (2012) Release rate for a pre-plant application of *Nesidiocoris tenuis* for *Bemisia tabaci* control in tomato. *Biocontrol* 57, 809–817.

Chikoti, P.C., Ndunguru, J., Melis, R., Taiko, F., Shanahan, P. & Sseruwagi, P. (2013) Cassava mosaic disease and associated viruses in Zambia: occurrence and distribution. *International Journal of Pest Management* 59, 63–72. doi: 10.1080/09670874.2012.752887.

Colvin, J., Fishpool, L.D.C., Fargette, D., Sherington, J. & Faquet, C. (1998) *Bemisia tabaci* (Hemiptera: Aleyrodidae) trap catches in a cassava field in cote d’Ivoire in relation to environmental factors and the distribution of African cassava mosaic disease. *Bulletin of Entomological Research* 88, 369–378.

Colvin, J., Otim-Nape, G.W., Holt, J., Omongo, C., Seal, S., Stevenson, P.C., Cooter, R.J. & Threat, J.M. (1999) Factors driving the current epidemic of severe cassava mosaic disease in East Africa. pp. 76–77 in VIIIth International Plant Virus Epidemiology Symposium—Plant Virus Epidemiology: Current Status and Future Prospects, Aguadulce. Almeria, Spain, International Society of Plant Pathology.

Colvin, J., Omongo, C.A., Maruthi, M.N., Otim-Nape, G.W. & Threat, J.M. (2004) Dual begomovirus infections and high *Bemisia tabaci* populations: two factors driving the spread of a cassava mosaic disease pandemic. *Plant Pathology* 53, 577–584. doi: 10.1111/j.1365-3059.2004.01062.x.

Colvin, J., Omongo, C.A., Govindappa, M.R., Stevenson, P.C., Maruthi, M.N., Gibson, G., Seal, S.E., Muniyappa, V. (2006) Host-plant viral infection effects on arthropod-vector population growth, development and behaviour: management and epidemiological implications. *Advances in Virus Research* 67, 419–452. doi: 10.1016/s0065-3527(06)67011-5.

Cours, G., Fargette, D., Otim-Nape, G.W. & Threat, J.M. (1997) The epidemic of cassava mosaic virus disease in Madagascar in the 1930s-1940s: lessons for the current situation in Uganda. *Tropical Science* 37, 238–248.

Crowder, D.W., Ellers-Kirk, C., Yafuso, C.M., Dennehy, T.J., Degain, B.A., Harpol, V.S., Tabashnik, B.E. & Carrière, Y. (2008) Inheritance of resistance to Pyriproxyfen in *Bemisia tabaci* (Hemiptera: Aleyrodidae) males and females (B biotype). *Journal of Economic Entomology* 101, 927–932. doi: 10.1603/022-0493(2008)101[927:IORTPI.2.CO;2.

De Barro, P. (2012) Getting the Most out of *Eretmocerus Hayati*, an Effective Natural Enemy of Silverleaf Whitefly. Horticulture Australia Ltd, Final Report VG08051, Elizabeth Street Sydney NSW, Australia.

de Bon, H., Huat, J., Parrot, L., Sinzogan, A., Martin, T., Malézieux, E. & Vassylières, J.F. (2014) Pesticide risks from fruit and vegetable pest management by small farmers in sub-Saharan Africa. A review. *Agronomy for Sustainable Development* 34, 723–736. doi: 10.1007/s13593-014-0216-7.
Delatte, H., Holota, H., Warren, B.H., Becker, N., Thierry, M. & Reynaud, B. (2011) Genetic diversity, geographical range and origin of Bemisia tabaci biotype Ms. Bulletin of Entomological Research 101, 487–497.

Drost, Y.C., van Lenteren, J.C. & van Roermund, H.J.W. (1988) Life-history parameters of different biotypes of Bemisia tabaci (Hemiptera: Aleyrodidae) in relation to temperature and host plant: a selective review. Bulletin of Entomological Research 88(3), 219–229.

Dubern, J. (1994) Transmission of African cassava mosaic geminivirus by the whitefly Bemisia tabaci. Tropical Science 34, 82–91.

Elbadry, E.A. (1986) Biological studies on Amblyseius alegrodis a predator of the cotton whitefly (Acarina, Phytoseiidae). Entomopathaga 13, 323–329. doi: 10.1007/BF02371914.

Fargette, D., Fauquet, C. & Thouvenel, J. (1985) Field studies on the spread of African Cassava Mosaic. Annals of Applied Biology 106(2), 285–294. doi: 10.1111/j.1744-7348.1985.tb03118.x.

Fargette, D., Fauquet, C. & Thouvenel, J. (1988) Yield losses induced by African cassava mosaic virus in relation to the mode and the date of infection. Tropical Pest Management 34, 89–91. doi: 10.1080/096788089371216.

Fargette, D., Fauquet, C., Grenier, E. & Thresh, J.M. (1990) The spread of African cassava mosaic virus into and within cassava fields. Journal of Phytopathology-Phytopathologische Zeitsschrift 130, 289–302. doi: 10.1111/j.1439-0434.1990.tb1179.x.

Fargette, D., Jeger, M., Fauquet, C. & Fishpool, L.D.C. (1993) Analysis of temporal disease progress of African cassava mosaic virus. Phytopathology 84, 91–98. doi: 10.1094/Phyto-84–91.

Fauquet, C. & Fargette, D. (1990) African cassava mosaic virus, etiology, epidemiology, and control. Plant Disease 74, 404–411. doi: 10.1094/pd-74-0404.

Fauquet, C., Fargette, D. & Thouvenel, J.C. (1988) Some aspects of the epidemiology of African cassava mosaic virus in Ivory Coast. Tropical Pest Management 34, 92–96. doi: 10.1080/096788089371217.

Fishpool, L.D.C. & Burban, C. (1994) Bemisia tabaci: the whitefly vector of African cassava mosaic geminivirus. Tropical Science 34, 55–72.

Fishpool, L.D.C., Fauquet, C., Fargette, D., Thouvenel, J.C., Burban, C. & Colvin, J. (1995) The phenology of Bemisia tabaci (Homoptera: Aleyrodidae) populations on cassava in southern Côte d’Ivoire. Bulletin of Entomological Research 85, 197–207. doi: 10.1017/S0007485300004271.

Gerling, D., Horowitz, A.R. & Baumgaertner, J. (1986) Autoecology of Bemisia tabaci. Agriculture Ecosystems & Environment 17, 5–19. doi: 10.1016/0167-8809(86)90022-8.

Ghosh, S., Bouvaine, S. & Maruthi, M. (2015) Prevalence and genetic diversity of endosymbiotic bacteria infecting cassava whiteflies in Africa. BMC Microbiology 15 doi: 10.1186/s12866-015-0425-5.

Gibson, R.W. & Otim-Nape, G.W. (1997) Factors determining recovery and reversion in mosaic-aFFECTed African cassava mosaic virus resistant cassava. Annals of Applied Biology 131, 259–271. doi: 10.1111/j.1744-7348.1997.tb05155.x.

Gibson, R.W., Legg, J.P. & Otim-Nape, G.W. (1996) Unusually severe symptoms are a characteristic of the current epidemic of mosaic virus disease of cassava in Uganda. Annals of Applied Biology 128, 479–490. doi: 10.1111/j.1744–7348.1996.tb07108.x.

Gnankine, O., Ketoh, G. & Martin, T. (2013) Dynamics of the invasive Bemisia tabaci (Homoptera: Aleyrodidae) Mediterranean (MED) species in two West African countries.

Harrison, B.D., Zhou, X., Otim-Nape, G.W., Liu, Y. & Robinson, D.J. (1997) Role of a novel type of double infection in the geminivirus-induced epidemic of severe cassava mosaic in Uganda. Annals of Applied Biology 131, 437–448. doi: 10.1111/j.1744–7348.1997.tb05171.x.

Hillocks, R.J. & Jennings, D.L. (2003) Cassava brown streak disease: a review of present knowledge and research needs. International Journal of Pest Management 49, 225–234. doi: 10.1080/0967087031000101061.

Holt, J. & Colvin, J. (2001) Observation and theory of whitefly-borne virus disease epidemics. pp. 331–343 in Edited for the British Society for Plant Pathology by Jeger, M.J. & Spence, N.J. (Eds) Biotic Interactions in Plant-Pathogen Associations. Wallingford, Oxon, UK, CABI publishing. ISBN no s 0 85199 512 8.

Horowitz, A.R. & Ishaya, I. (2014) Dynamics of biotypes B and Q of the whitefly Bemisia tabaci and its impact on insecticide resistance. Pest Management Science 70, 1568–1572. doi: 10.1002/ps.3752.

Ijumba, J.N. & Legg, J.P. (1997) Factors determining the date of infection. Reduced by African cassava mosaic virus in relation to the mode and the date of infection. Tropical Pest Management 34, 92–96. doi: 10.1080/096788089371217.

Jameson, J.D. (1964) Cassava mosaic disease in Uganda. East African Agricultural and Forestry Journal 29, 208–213. doi: 10.1080/00128325.1964.11661927.

Jeremiah, S.C., Ndyetabula, I.I., Mkamilo, G.S., Haji, S., Mulawana, M.M., Chuwa, C., Kasele, S., Bouwmeester, H., Ijumba, J.N. & Legg, J.P. (2015) The dynamics and environmental influence on interactions between cassava brown streak disease and the whitefly, Bemisia tabaci. Phytopathology 105, 646–655. doi: 10.1094/PHYTO-05-14-0146-R.

Katonu, K., Alicai, T., Baguma, Y., Edema, R., Bua, A. & Omono, C. (2015) Influence of host plant resistance and...
Kliot, A., Cilia, M., Czosnek, H. & Ghanim, M. (2014) Implication of the bacterial endosymbiont Rickettsia spp. in interactions of the whitefly Bemisia tabaci with tomato yellow leaf curl virus. *Journal of Virology* 88, 5652–5660. doi: 10.1128/JVI.00071–14.

Kontsedalov, S., Zchori-Fein, E., Chiel, E., Gottlieb, Y., Inbar, M. & Ghanim, M. (2008) The presence of rickettsia is associated with increased susceptibility of Bemisia tabaci (Homoptera: Aleyrodidae) to insecticides. *Pest Management Science* 64, 789–782. doi: 10.1002/ps.1595.

Kristensen, N.P., Schellhorn, N.A., Hulthen, A.D., Howie, L.J. & Brown, J.K. (2013) Wind-borne dispersal of a parasitoid: the process, the model, and its validation. *Environmental Entomology* 42, 1137–1148. doi: 10.1603/EN12243.

Laarif, A., Saleh, D., Clouet, C. & Gauthier, N. (2015) Regional co-occurrence between distinct Bemisia tabaci species in Tunisia with new insights into the role of host plants. *Plant Pathology* 34, 135–150. doi: 10.1007/s12112-014-0437-y.

Legg, J.P. (1994) Bemisia tabaci: the whitefly vector of cassava mosaic geminiviruses in Africa: an ecological perspective. *African Crop Science Journal* 2, 437–448.

Legg, J.P. (1995) The ecology of Bemisia tabaci (Gennadius) (Homoptera), vector of African cassava mosaic geminivirus in Uganda. PhD, University of Reading, UK.

Legg, J.P. (1999) Emergence, spread and strategies for controlling the pandemic of cassava mosaic virus disease in east and Central Africa. *Crop Protection* 18, 627–637. doi: 10.1016/S0261-2194(00)00626-9.

Legg, J.P. & Hillocks, R.J. (2003) Cassava brown streak virus disease; past present and future. pp. 89 in Legg, J.P. & Hillocks, R.J. (Eds) *Proceedings of an International Workshop, Mombasa, Kenya, 27–30 October 2002*. Aylesford, UK, Natural Resources International Limited.

Legg, J.P. & Ogwal, S. (1998) Changes in the incidence of African cassava mosaic virus disease and the abundance of its whitefly vector along south-north transects in Uganda. *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie* 122, 169–178.

Legg, J.P. & Raya, M.D. (1998) Survey of cassava virus diseases in Tanzania. *International Journal of Pest Management* 44, 17–23.

Legg, J.P. & Thresh, J.M. (2000) Cassava mosaic virus disease in East Africa: a dynamic disease in a changing environment. *Virus Research* 71, 135–149. doi: 10.1016/S0168-1702(00)00194-5.

Legg, J.P., French, R., Rogan, D., Okao-Okuja, G. & Brown, J.K. (2002) A distinct Bemisia tabaci (Gennadius) (Hemiptera: Sternorrhyncha: Aleyrodidae) genotype cluster is associated with the epidemic of severe cassava mosaic virus disease in Uganda. *Molecular Ecology* 11, 1219–1229.

Legg, J., Gerling, D. & Neueneschwander, P. (2003) Biological control of whiteflies in sub-Saharan Africa. pp. 87–100 in Neueneschwander, P. & Langevald, J. (Eds) *Biological Control in IPM Systems in Africa*. Wallingford, UK, CAB International.

Legg, J., Owor, B., Sseruwagi, P. & Ndunguru, J. (2006) Cassava mosaic virus disease in East and Central Africa: epidemiology and management of a regional pandemic. *Advances in Virus Research* 67, 355–418.

Legg, J.P., Jeremiah, S.C., Obiero, H.M., Maruthi, M.N., Ndyetabula, I., Okao-Okuja, G., Bouwmeester, H., Bigirimana, S., Tata-Hangy, W., Gashaka, G., Mkamilu, G., Alicai, T. & Kumar, P.L. (2011) Comparing the regional epidemiology of the cassava mosaic and cassava brown streak virus pandemics in Africa. *Virus Research* 159, 161–170. doi: 10.1016/j.virusres.2011.04.018.

Legg, J.P., Sseruwagi, P., Boniface, S., Okao-Okuja, G., Shirima, R., Bigirimana, S., Gashaka, G., Herrmann, H.W., Jeremiah, S., Obiero, H., Ndyetabula, I., Tata-Hangy, W., Masembe, C. & Brown, J.K. (2014) Spatio-temporal patterns of genetic change amongst populations of cassava Bemisia tabaci whiteflies driving virus pandemics in East and Central Africa. *Virus Research* 186, 61–75. doi: 10.1016/j.virusres.2013.11.018.

Legg, J.P., Shirima, R., Tajebe, L.S., Guastella, D., Boniface, S., Jeremiah, S., Nsami, E., Chikoti, P. & Rapisarda, C. (2014b) Biology and management of Bemisia whitefly vectors of cassava virus pandemics in Africa. *Pest Management Science* 70, 1446–1453. doi: 10.1002/ps.3793.

Legg, J.P., Lava Kumar, P., Makeshkumar, T., Tripathi, L., Ferguson, M., Kanju, E., Ntwuwuruhunga, P. & Cuellar, W. (2015) Cassava virus diseases. *Advances in Virus Research* 91, 85–42.

Leuschner, K. (1977) Whiteflies: biology and transmission of African mosaic disease. pp. 51–58 in Brekelbaum, T., Bellotti, A. & Lozano, C.J. (Eds) *Proceedings of the Cassava Protection Workshop, CIAT, 7–12 November, 1977 Cali, Colombia*. The International Center for Tropical Agriculture.

Liu, S.S., Colvin, J. & De Barro, P. (2012) Species concepts as applied to Bemisia tabaci systematics: how many species are there? *Journal of Integrative Agriculture* 11, 176–186.

Mabasa, K.G. (2007) Epidemiology of Cassava Mosaic Disease and Molecular Characterization of Cassava Mosaic Viruses and Their Associated Whitefly (Bemisia tabaci) Vector in South Africa. Johannesburg, University of the Witwatersrand.

Manani, D.M., Ateka, E.M., Nyanjom, S.R.G. & Boykin, L.M. (2017) Phylogenetic relationships among whiteflies in the Bemisia tabaci (Gennadius) species complex from major cassava growing areas in Kenya. *Insects* 8, 1–14. doi: 10.3390/insects8010025.

Maruthi, M.N., Colvin, J., Seal, S. & Thresh, J.M. (2002a) First report of a distinct begomovirus infecting cassava from Zanzibar. *Plant Disease* 86, 187.

Maruthi, M.N., Colvin, J., Seal, S., Gibson, G. & Cooper, J. (2002b) Co-adaptation between cassava mosaic geminiviruses and their local vector populations. *Virus Research* 86, 71–85. doi: 10.1016/s0168-1702(02)00051-5.

Maruthi, M.N., Hillocks, R.J., Mtunda, K., Raya, M.D., Muhanna, M., Kiozia, H., Rekha, A.R., Colvin, J. & Thresh, J.M. (2005) Transmission of cassava brown streak virus by Bemisia tabaci (Gennadius). *Journal of Phytopathology* 153, 307–312. doi: 10.1111/j.1439-0434.2005.00974.x.

Mbewe, W., Kumar, P.L., Changadeya, W., Ntwuwuruhunga, P. & Legg, J. (2015) Diversity, distribution and effects on cassava cultivars of cassava brown streak viruses in Malawi. *Journal of Phytopathology* 163, 433–443. doi: 10.1111/jph.12339.

McGrath, P.F. & Harrison, B.D. (1995) Transmission of tomato leaf curl geminiviruses by Bemisia tabaci: effects of virus isolate and vector biotype. *Annals of Applied Biology* 126, 307–316. doi: 10.1111/j.1744-7348.1995.tb05368.x.

McMeniman, C.J. & O’Neill, S.L. (2010) A virulent Wolbachia infection decreases the viability of the dengue vector *Aedes aegypti* during periods of embryonic quiescence (C-C Chen, Ed.). *PLoS Neglected Tropical Diseases* 4, e478. doi: 10.1371/journal.pntd.0000748.

McQuaid, C.F., van den Bosch, F., Szyminskewska, A., Alicai, T., Pariyo, A., Chikoti, P.C. & Gilligan, C.A. (2017) Spatial dynamics and control of a crop pathogen with mixed-mode transmission. *PLoS Computational Biology* 13, e1005654.
Meyerdirk, D.E. & Coudriet, D.L. (1985) Predation and developmental studies of Euseius hibisci (Chant) (Acarina, Phytoseiidae) feeding on Bemisia tabaci (Gennadius) (Homoptera, Aleyrodidae). *Environmental Entomology* 14, 24–27.

Mohammed, I.U., Ghosh, S. & Maruthi, M.N. (2016) Host and virus effects on reversion in cassava affected by cassava brown streak disease. *Plant Pathology* 65, 593–600. doi: 10.1111/ppa.12458.

Morales, F.J. & Jones, P.G. (2004) The ecology and epidemiology of whitefly-transmitted viruses in Latin America. *Virus Research* 100, 57–65. doi: 10.1016/j.virusres.2003.12.014.

Mugerwa, H., Rey, M.E., Alicai, T., Ateka, E., Atuncha, H., Ndunguru, J. & Sseruwagi, P. (2001) Genetic diversity and geographic distribution of Bemisia tabaci (Gennadius) (Homoptera: Aleyrodidae) genotypes associated with cassava in East Africa. *Ecol Evol* 2, 2749–2762. doi: 10.1002/ee3.379.

Muimba-Kankolongo, A., Chalwe, A., Sisupo, P. & Kang, M. (1997) Distribution, prevalence and outlook for control of cassava mosaic disease in Zambia. *Roots* 4, 2–7.

Muli, E., Patch, H., Frazier, M., Frazier, J., Torto, B., Baumgarten, T., Kilonzo, J., Kimani, J.N., Mumoki, F., Masiga, D., Tumlinson, J. & Grozinger, C. (2014) Evaluation of the distribution and impacts of parasites, pathogens, and pesticides on honey bee (Apis mellifera) populations in East Africa. *PLoS ONE* 9, e94459. doi: 10.1371/journal.pone.0094459.

Ndunguru, J., Sseruwagi, P., Tafo, F., Stomeo, F., Maina, S., Djikeng, A., Kehoe, M. & Boykin, L.M. (2015) Analyses of twelve new whole genome sequences of cassava brown streak viruses and Ugandan cassava brown streak viruses from east Africa: diversity, supercomputing and evidence for further speciation. *PLoS ONE* 10, e0139321.

Nelson, S. (2008) Sooty Mold. *Plant Disease* PD-52. Mānoa, Honolulu, Hawai‘i Cooperative extension Service, College of Tropical Agriculture and Human Resources, University of Hawaii.

Nichols, R.F. (1950) The brown streak disease of cassava distribution climatic effects and diagnostic symptoms. *The East African Agricultural Journal* 15, 154–160.

Night, G., Asiimwe, P., Gashaka, G., Nkezabahizi, D., Legg, J.P., Okao-Okuja, G., Obonyo, R., Nyiaruharana, C., Mukakanya, C., Mukase, F., Munyabarenzi, I. & Mutumwinka, M. (2011) Occurrence and distribution of cassava pests and diseases in Rwanda. *Agriculture Ecosystems & Environment* 140, 492–497. doi: 10.1016/j.agee.2011.01.014.

Ntawuruhunga, P. & Legg, J. (2007) New Spread of Cassava Brown Streak Virus Disease and its Implications for the Movement of Cassava Germplasm in the East and Central African Region. International Institute of Tropical Agriculture-Uganda & Eastern Africa Root Crops Research Network, Kampala, Uganda. *Network Report*.

Oliveira, M.R.V., Henneberry, T.J. & Anderson, P. (2001) History, current status, and collaborative research projects for Bemisia tabaci. *Crop Protection* 20, 709–723.

Omongo, C.A. (2003) Cassava whitefly, Bemisia tabaci, behaviour and ecology in relation to the spread of the cassava mosaic epidemic in Uganda. PhD, University of Greenwich, UK.

Omongo, C.A., Kawuki, R., Bellotti, A.C., Alicai, T., Baguma, Y., Maruthi, M.N., Bua, A. & Colvin, J. (2012) African cassava whitefly, Bemisia tabaci, resistance in African and South American cassava genotypes. *Journal of Integrative Agriculture* 11, 327–336. doi: 10.1016/s2095-3119(12)60017-3.

Otím, M., Legg, J., Kyamanywa, S., Polaszek, A. & Gerling, D. (2005) Occurrence and activity of Bemisia tabaci parasites on cassava in different agro-ecologies in Uganda. *Biocontrol* 50, 87–95. doi: 10.1007/s10526-004-0822-4.

Otím, M., Legg, D.J., Kyamanywa, S., Polaszek, A. & Gerling, D. (2006) Population dynamics of Bemisia tabaci (Homoptera: Aleyrodidae) parasites on cassava mosaic disease–resistant and susceptible varieties. *Biocontrol Science and Technology* 16, 205–214. doi: 10.1080/0951578990355558.

Otím, M., Kyalo, G., Kyamanywa, S., Asiimwe, P., Legg, J.P., Guershon, M. & Gerling, D. (2008) Parasitism of Bemisia tabaci (Homoptera: Aleyrodidae) by Eretmocerus mundus (Hymenoptera: Aphelinidae) on cassava. *International Journal of Tropical Insect Science* 28, 158. doi: 10.1017/s1742758408093181.

Otím-Nape, G.W. & Ingroot, D. (1986) Effect of cultural practices on the African cassava mosaic disease and its vector. pp. 105–108 in Terry, E.R., Akoroda, M.O. & Arene, O.B. (Eds) *Proceedings of the Third Triennial Symposium of the International Society for Tropical Root Crops*, Owerri, Nigeria 17–23 August 1986. IDRC 258E. Owerri, Nigeria, Ottawa International Development Research Centre.

Otím-Nape, G.W., Thresh, J.M. & Fargette, D. (1995) Bemisia tabaci and cassava mosaic virus disease in Africa. pp. 319–350 in Gerling, D. & Mayer, R.T. *Bemisia 1995: Taxonomy, Biology, Damage, Control and Management*. Andover, England, Intercept Ltd.

Otím-Nape, G.W., Thresh, J.M. & Shaw, M.W. (1998) The incidence and severity of cassava mosaic virus disease in Uganda: 1990–92. *Tropical Science* 38, 25–37.

Otím-Nape, G.W., Bua, A., Thresh, J.M., Baguma, Y., Ogwal, S., Ssemakula, G.N., Acola, G., Byabakama, B., Colvin, J., Cooter, R.J. & Martin, A. (2000) *The Current Pandemic of Cassava Mosaic Virus Disease in East Africa and its Control*. Chatham, UK, Natural Resources Institute Catalogue Services No. PSTC28, University of Greenwich.

Otím-Nape, G.W., Alicai, T. & Thresh, J.M. (2001) Changes in the incidence and severity of cassava mosaic virus disease, varietal diversity and cassava production in Uganda. *Annals of Applied Biology* 138, 313–327.

Patil, B.L. & Fauquet, C.M. (2010) Differential interaction between cassava mosaic geminiviruses and geminivirus satellites. *Journal of General Virology* 91, 1871–1882. doi: 10.1099/vir.0.019513-0.

Patil, B., Legg, J., Kanju, E. & Fauquet, C. (2015) Cassava brown streak disease: a threat to food security in Africa. *Journal of General Virology* 96, 956–968.

Polston, J.E., De Barro, P. & Boykin, L.M. (2014) Transmission specificities of plant viruses with the newly identified species of the Bemisia tabaci species complex. *Pest Management Science* 70, 1547–1552. doi: 10.1002/ps.3738.

Riis, L., Bellotti, A.C., Bonierbale, M. & O’Brien, G.M. (2003) Cyanogenic potential in cassava and its influence on a generalist insect herbivore *Cyrtomenus lenta* (Hemiptera: Cydnidae). *Journal of Economic Entomology* 96, 1905–1914. doi: 10.1603/0022-0493-6.6.1905.

Robertson, I.A.D. (1987) The whitefly, Bemisia tabaci (Gennadius) as a vector of African cassava mosaic virus at the Kenya coast and ways in which the yield losses in cassava, *Manihot esculenta* Crantz caused by the virus can be reduced. *Insect Science and its Application* 8, 797–801.

Sequeira, R.V., Shields, A., Moore, A. & De Barro, P. (2009) Inter-seasonal population dynamics and pest status of Bemisia tabaci (Gennadius) biotype B in an Australian cropping system. *Bulletin of Entomological Research* 99, 325. doi: 10.1017/s000748530800638X.

Sseruwagi, P. (2005) Molecular variability of cassava Bemisia tabaci and its effect on the epidemiology of cassava mosaic
geminiviruses in Uganda. PhD Thesis, The University of Witwatersrand, Johannesburg, South Africa.

Sseruwagi, P., Otim-Nape, G.W., Osiru, D.S.O. & Thresh, J.M. (2003) Influence of NPK fertiliser on populations of the whitefly vector and incidence of cassava mosaic virus disease. African Crop Science Journal 11, 171–179.

Sseruwagi, P., Sserumbombwe, W.S., Legg, J.P., Ndunguru, J. & Thresh, J.M. (2004) Methods of surveying the incidence and severity of cassava mosaic disease and whitefly vector populations on cassava in Africa: a review. Virus Research 100, 129–142. doi: 10.1016/j.virusres.2003.12.021.

Sseruwagi, P., Sserubombwe, W.S., Legg, J.P., Ndunguru, J. & Thresh, J.M. (2004) Methods of surveying the incidence and severity of cassava mosaic disease and whitefly vector populations on cassava in Africa: a review. African Crop Science Journal 11, 171–179.

Sseruwagi, P., Sserubombwe, W.S., Legg, J.P., Ndunguru, J. & Thresh, J.M. (2004) Methods of surveying the incidence and severity of cassava mosaic disease and whitefly vector populations on cassava in Africa: a review. Virus Research 100, 129–142. doi: 10.1016/j.virusres.2003.12.021.

Sseruwagi, P., Legg, J.P., Maruthi, M.N., Colvin, J., Rey, M.E.C. & Brown, J.K. (2005) Genetic diversity of Bemisia tabaci (Gennadius) (Homoptera: Aleyrodidae) populations and presence of the B biotype and a non-B biotype that can induce silverleaf symptoms in squash, in Uganda. Annals of Applied Biology 147, 253–265. doi: 10.1111/j.1744–7348.2005.00026.x.

Sseruwagi, P., Maruthi, M.N., Colvin, J., Rey, M.E.C., Brown, J.K. & Legg, J.P. (2006) Colonization of non-cassava plant species by cassava whiteflies (Bemisia tabaci) in Uganda. Entomologia Experimentalis et Applicata 119, 145–153.

Sseruwagi, P., Otim-Nape, G.W., Legg, J.P., Fargette, D. (1997) African cassava mosaic virus disease: the magnitude of the problem. African Journal of Root and Tuber Crops 2, 13.

Tan, X-L., Wang, S., Ridsdill-Smith, J. & Liu, T-X. (2014) Direct and indirect impacts of infestation of tomato plant by Myzus persicae (Homoptera: Aphididae) on Bemisia tabaci (Homoptera: Aleyrodidae). PLoS ONE 9, e94310. doi: 10.1371/journal.pone.0094310.

Thompson, W.M.O. (2000) Development, morphometrics and other biological characteristics of the whitefly Bemisia tabaci (Gennadius) on cassava. Insect Science and its Application 20, 251–258.

Thompson, W.M.O. (2011) Interaction of Bemisia tabaci with East African cassava mosaic virus-infected plants. pp. 107–119 in Thompson, W.M.O. (Ed.) The Whitefly, Bemisia tabaci (Homoptera: Aleyrodidae) Interaction with Geminivirus-Infected Host Plants. Netherlands, Springer. doi:10.1007/978-94-007-1524-0_6.

Thresh, J.M., Otim-Nape, G.W., Legg, J.P. & Fargette, D. (1997) African cassava mosaic virus disease: the magnitude of the problem. African Journal of Root and Tuber Crops 2, 13.

Uzokwe, V.N.E., Mlay, D.P., Masunga, H.R., Kanju, E., Odeh, I. O.A. & Onyeka, J. (2016) Combating viral mosaic disease of cassava in the Lake Zone of Tanzania by intercropping with legumes. Crop Protection 84, 69–80. doi: 10.1016/j.cropro.2016.02.013.

Wang, H-L., Yang, J., Boykin, L.M., Zhao, Q-Y., Wang, Y-J., Liu, S-S. & Wang, X-W. (2014) Developing conversed microsatellite markers and their implications in evolutionary analysis of the Bemisia tabaci complex. Scientific Reports 4, 6351. doi: 10.1038/srep06351.

Xu, J., De Barro, P.J. & Liu, S.S. (2010) Reproductive incompatibility among genetic groups of Bemisia tabaci supports the proposition that the whitefly is a cryptic species complex. Bulletin of Entomological Research 100, 359–366. doi: 10.1017/S0007485310000015.

Zundel, C., Nagel, P., Hanna, R., Korner, F. & Scheidegger, U. (2009) Environment and host-plant genotype effects on the seasonal dynamics of a predatory mite on cassava in sub-humid tropical Africa. Agricultural and Forest Entomology 11, 321–331. doi: 10.1111/j.1461-9563.2009.00429.x.