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# Whitefly-transmitted viruses threatening cassava production in Africa

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## Abstract

Emerging plant viruses are one of the greatest problems facing crop production worldwide, and have severe consequences in the developing world where subsistence farming is a major source of food production, and knowledge and resources for management are limited. In Africa, evolution of two viral disease complexes, cassava mosaic begomoviruses (CMBs) (*Geminiviridae*) and cassava brown streak viruses (CBSVs) (*Potyviridae*), have resulted in severe pandemics that continue to spread and threaten cassava production. Identification of genetically diverse and rapidly evolving CMBs and CBSVs, extensive genetic variation in the vector, *Bemisia tabaci* (Hemiptera: Aleyrodidae), and numerous secondary endosymbiont profiles that influence vector phenotypes suggest that complex local and regional vector-virus-plant-environment interactions may be driving the evolution and epidemiology of these viruses.

## Highlights

- Cassava mosaic disease is caused by frequently recombining ssDNA virus species.
- Cassava brown streak disease is an emergent concern, caused by two ssRNA viruses.
- Complex genetic structure and endosymbionts may impact vector status of *B. tabaci.*

## Introduction

Two whitefly (Hemiptera: Aleyrodidae) transmitted viral disease complexes, cassava mosaic disease (CMD) and cassava brown streak disease (CBSD), are the primary threats to cassava production across Africa [1]. Cassava, *Manihot esculenta* (Crantz), also referred to as yucca, tapioca and manioc, originated in the New World [2], and is now grown across Central and South America, Asia and Africa as an industrial source of starch and for human and animal consumption [3]. It is an easy crop to grow with exceptional drought resistance [4], which has made it a staple food for close to 1 billion people in the tropics [5]. This is especially true in Africa, where cassava is currently the highest production crop and the most resistant crop to climate change [6]. While cassava production is sometimes affected by viral diseases worldwide [5], in sub-Saharan Africa, these viruses are a persistent and emergent threat to food security, causing losses over US$1billion annually [5,7].

These viruses are believed to have originated in Africa, and have been spread across the continent by human-mediated movement of vegetatively propagated cassava cuttings [8], and whitefly vectors [9–12]. Although cassava viruses have been reported in Africa for more than 70 years, severe epidemics of both CMD and CBSD causing viral complexes have emerged in sub-Saharan Africa during the past 30 years that have caused famine, reduced yields, and in some areas severely restricted cassava production. Research findings during the first 1-2 decades after the emergence of the severe CMD and CBSD addressing disease incidence, mechanisms of spread, virus identification, vectors, management strategies, and proposed theories for the widespread occurrence of the causative virus and abundance of the vectors have been reviewed in [5,13–20,21*]. Molecular biology tools and approaches developed over the past decade such as Next Generation Sequencing (NGS), NextRAD sequencing, and bioinformatics tools have enabled identification and characterization of the genetic diversity of vector [22–24,25*,26*27] and viral [28,29,30*,31] populations which have long been recognized as important factors underlying reported variation in disease severity, vector competence [32] and coevolution of vectors and viruses [33]. The objective of this review is to provide a current synthesis of literature on the diversity of whiteflies, cassava viruses, and their interactions across the African continent, and including Madagascar, Réunion Island, and Seychelles.

## Whitefly-Transmitted Viral Disease Complexes of Cassava

Single-stranded DNA viruses that cause CMD, typified by chlorotic yellow mosaics, deformed leaves and stunted growth [34] have been recognized as a threat to cassava production for a longer period of time than viruses causing CBSD – since the 1894 [35]. Molecular typing and sequencing have revealed CMD is caused by seven related species of cassava mosaic begomoviruses (CMVs) (family *Geminiviridae*) occurring in single or mixed infections: *African cassava mosaic virus* (ACMV), *Cassava mosaic Madagascar virus* (CMMGV)*, East African cassava mosaic virus* (EACMV); *East African cassava mosaic Kenya virus* (EACMKV), *East African cassava mosaic Malawi virus* (EACMMV), *East African cassava mosaic Zanzibar virus* (EACMZV), and *South African cassava mosaic virus* (SACMV) [36] (Figure 1). The CMBs can co-infect a cassava plant, enhancing infection severity [37] and leading to recombinants with altered virulence [38]. While CMD had been a problem for farmers for decades, the emergence of *East African cassava mosaic virus, Uganda variant* (EACMV-UG2), a recombinant of EACMV in which approximately 400 nucleotides of the Coat Protein (CP) gene of ACMV replaced a similar region of EACMV [39–42], in 1997 led to a resurgence of severe CMD that devastated cassava crops causing rampant famine in Uganda [43]. Shortly thereafter, roughly half of all cassava harvested in East Africa had been affected by CMD [44], and by 2005 the CMD pandemic was estimated to cover roughly 3,000,000 square km over nine countries.

The more recently emerged CBSD is not yet as widespread as CMD, but has become the more pressing problem in African cassava production. CBSD exhibits fewer symptoms above ground (fainter yellowing, the titular streaks on the stems [45]), and mainly rots the tubers, leading to damage that fetches much lower prices (90% loss [46]). While it was first described in 1935 [47], it was an isolated disease restricted to the low altitude areas of East Africa [48]. Only in the last twenty years has it spread to higher altitudes and become a problem for a much larger area of cassava production [49,50] (Figure 1). CBSD is caused by two related RNA viruses (*Potyvirus: Ipomovirus*): *Cassava brown streak virus* (CBSV) and *Ugandan cassava brown streak virus* (UCBSV). The two viruses that cause CBSD can be referred to as CBSVs (cassava brown streak viruses).

Both the ssDNA CMBs and RNA CBSVs show high diversity in Africa, as expected for viruses with these genomes. Surveys of CMBs routinely reveal that variants are produced by both recombination and mutation [51*]. While intraspecific and interspecific recombination frequently occur, and major changes in virulence have been associated with recombination events (e.g., the pandemic associated EACMV-UG2), the majority of the diversity in sequenced ACMV and EACMV is due to mutation [52]. Like other ssDNA viruses, EACMV evolves as quickly as RNA viruses, meaning that CMBs can swiftly evolve to cope with environmental changes, novel plant hosts and potentially to overcome host resistance [51*,53]. The RNA CBSVs have been less intensively studied, but already show strong evidence of recombination [28] and high diversity due to mutations [54]. The overall divergence among sequenced genomes of CBSVs has led to high estimates of within species nucleotide diversity [54], and has prompted a reexamination of the number of species capable of causing CBSD [55]. CBSV evolves as fast as other potyviruses [29] strongly suggesting that CBSVs can also evolve quickly to overcome novel challenges like RNAi-mediated host resistance [56]. The evolvability of coat proteins of both CMBs [57–61] and CBSVs [30] may play a role in their use of vectors, and in efficient transmission, but data on co-adaptation of viruses to their vectors is limited [33,62].

## Whitefly Vectors of Cassava Viruses

Although the incidence of cassava viruses in fields is more commonly attributed to the propagation of virus-infected cuttings, vector transmission can cause significant infection in crop fields [11,63] and spreads viruses across their population range and to non-crop reservoir hosts. CMBs are transmitted by *Bemisia tabaci* (Gennadius) [9,32,47,64,65*] in a circulative and non-propagative manner whereas CBSVs are semipersistently transmitted by three whitefly species: *B. tabaci* [10,66], *Trialeuroides vaporariorum* (Westwood), and A*leurodicus dispersus* (Russell) [10,12,66]. Differences in the number of vector species, modes of transmission, and vector competence of these viruses differentially affect incidence, spread, and distribution both locally and across the African continent. Faster acquisition and transmission (<1h) but lower persistence of CBSV in the vector (24-48h) reduces the incidence and distance of virus spread from infected hosts [10,11,66,67]. CMDs require up to 8 hours to circulate in the vector before they can be transmitted, but whiteflies remain viruliferous for at least 9 days which may increase incidence and distance of virus spread [9,47,64,66,68]. This review will focus on the primary vector and most abundant cassava-associated whitefly species in Africa, *B. tabaci*, due to the paucity of information on *T. vaporariorum* [69,70] and *A. dispersus* [70–72].

A growing body of literature is documenting extensive genetic diversity of *B. tabaci* and its symbiome in Africa. *Bemisia tabaci* is a morphologically indistinguishable species complex hypothesized to comprise over 40 genetic groups that are currently distinguished using partial mtCOI gene sequences [73]. Nomenclature describing these groups is inconsistent in the literature because the species delimitations within this group are undergoing constant revision based on new knowledge [17,23]. In this review, this species complex will be referred to as *B. tabaci*, using nomenclature based on mtCOI phylogenies [73]. Working names on whiteflybase.org [24,74] are used because they were most easy to assimilate due to the high number of reports using this, or similar nomenclature, although the status of these groups as reproductively isolated species will change based on new information about evolutionary relationships, species ranges, gene flow, reproductive compatibility (see below), and limitations of mtCOI markers [75–77]. Published sequences of putative *B. tabaci*, not included on whiteflybase.org because they did not meet the exact criteria, are included here along with newly proposed genetic groups not yet present on whiteflybase.org [26*] in order to present a comprehensive representation of the diversity and distribution of African *B. tabaci* reported in the literature. The greatest genetic diversity among *B. tabaci* worldwide has been observed within and among the sub-Saharan Africa clades, and evidence for African origin of *B. tabaci* is supported by phylogenies from multiple studies [22,26*,78–83]. Nineteen putative endemic and introduced species have been reported in Africa [21*,25*,26*,27,63,65*,77–80,84–101] (Figure 2), and include Uganda (Uganda clade) [26*,73], SubSahAf1-6, 8 (sub-Saharan Africa clade) [26*,73], SubSahAf7 (Australia-Asia clade) [26*], SubSahAf10-11, NewWorld1, (New World clade) [26*], SubSahAf12-13, Mediterranean, MidEastAm1, IndianOcean (Africa-Middle East-Asia Minor clade) [26*,73], and Italy1 (Italy clade) [26*,73]. Genetically distinct sub-groups/clades have also been consistently identified within the SubSahAf1 clade, and new genetic diversity continues to be discovered as more robust genetic approaches are developed [24,25*,26*,75,77,102,103].

Research on genetic diversity, genomics, population genetic structure, and gene-flow are providing new information about variation in epidemiologically important biological and ecological characteristics such as host utilization that may play a role in population growth, gene-flow, and evolutionary dynamics of cassava viruses. Only nine *B. tabaci*, including SubSahAf1, SubSahAf2, SubSahAf3, SubSahAf4, SubSahAf9, SubSahAf10, SubSahAf11, Mediterranean, and IndianOcean, have been collected from cassava, but host preference and diet breadth of cassava associated whiteflies is variable, with some collected only from cassava, while others can colonize multiple crop hosts successfully [104–109]. Reciprocal backcross experiments and population genetic experiments have provided evidence for the occurrence of gene-flow and introgression between some cassava associated *B. tabaci* and their sub-groups at local, regional, and continental scales [17,21*,25*,90,94–96,110]. The magnitude and direction of gene flow among putative species and their sub-groups, however, is variable. Long-distance gene flow and admixture is possible through human-mediated dispersal, trade [25*,95] and whitefly dispersal, however, geographic structuring among cassava-associated *B. tabaci* species and their subgroups is generally observed within countries and across Africa [21*,96–98]. Results of studies using genome-wide markers suggest that metapopulation structure of *B. tabaci* is a complex network through which introgression may occur directly between reproductively compatible groups, or indirectly through intermediates in the network [25*,95]. Genomic and transcriptomic approaches are also identifying economically important genes and gene families that may be involved with vector-virus interactions [95,111*], and new methods to investigate vector-endosymbiome-virus interactions [27]. Due to the genetic complexity of species- and population-level boundaries, molecular ecology and genomics approaches will continue to play a major role in advancing our understanding about the geographic scales and temporal stability of genetic structuring, the occurrence of gene-flow, and the implications of genetic structure on economically important traits related to epidemiology and management of whitefly-transmitted viruses [25*,95].

Endosymbionts are an important characteristic of *B. tabaci* that are likely influencing epidemiologically important life history and transmission phenotypes, and should be included in *B. tabaci* characterizations to determine their importance. Several studies have documented genetic diversity of whitefly endosymbionts, their distributions among *B. tabaci* species and populations, and the impact of symbiosis on whitefly fitness, host plant, and vector phenotypes [27,65*,84–90]. Specialized cellular compartments in *B. tabaci* harbor the primary/obligate endosymbiont *Candidatus Portiera aleyrodidarum* that is required to synthesize essential amino acids required for growth and development [112–114]. Secondary/facultative endosymbionts are not required for survival, but may affect fitness. Endosymbionts are primarily maternally transmitted [85], and although absent from some populations, secondary endosymbionts *Arsenophonus, Cardinium, Hamiltonella, Rickettsia,* and *Wolbachia* have been found in 30 combinations of single, double, triple and quadruple infections in African *B. tabaci* [27,65*,84–90] (Table 1). The underlying causes for the large number of endosymbiont profiles for *B. tabaci* is not understood, but introduction of new *B. tabaci* species with overlapping hosts and/or gene-flow may result in the acquisition of new endosymbionts. Studies have shown associations between specific combinations of endosymbiotic bacteria, or strains of a bacteria [84,87], and *B. tabaci* species, sub-groups, and populations [84,85,87,88], but none are clearly associated with host plant utilization. The few laboratory studies examining endosymbiont effects on *B. tabaci* showed that endosymbionts may negatively impact vector competence and fitness of cassava associated *B. tabaci.* Decreased acquisition and retention of EACMV-UG2 by SubSahAf1-subgroup3 was generally observed in a laboratory colony infected with *Arsenophonus* and *Rickettsia* compared to a colony without secondary endosymbionts, and secondary endosymbiont infections were absent from a high number, but not all, field collected SubSahAf1-subgroup1 *B. tabaci*, which is the primary haplotype implicated in spread of CMBs in East Africa [65*,89]. Reductions in adult emergence, and increasing development time from first instar to adult were also observed in SubSahAf1-subgroup3 infected with *Arsenophonus* and *Rickettsia* [65*].

Future research is needed to better understand the incidences, spread and influence of endosymbionts in African *B. tabaci*.

## Conclusions

Accurate identification of distinct species and populations of cassava viruses and their vectors is an essential first step towards understanding vector-virus-plant-environment interactions underlying the epidemiology of cassava viruses in Africa, but knowledge of the similarities and differences of life history traits among CMBs, CBSVs, and *B. tabaci* is still lacking. Many field and laboratory studies were conducted before molecular identification of study populations was available, limiting conclusions that can be drawn about incidence, spread, and severity of viruses and the role of specific vectors, especially when genetic variation in local populations influence vector-virus-crop interactions among research locations. Studies that provide genetic characterizations of vectors and viruses are revealing genetic variation that has the potential to explain regional and phenotypic variation in epidemiological important phenotypes such as host range, vector competence of whiteflies, transmission efficiency of cassava viruses, disease severity, and the timing and magnitude of whitefly spread due to host utilization patterns, population size, and dispersal. Fundamental studies are also needed to examine vector-virus-plant interactions described for other related viruses affecting different cropping systems not examined in this review, including virus mediated changes in vector-plant interactions, localization and circulation in the vector, the role of endosymbionts in virus circulation, variation in transmission efficiency, and mechanisms underlying these interactions reviewed in [20,115-121,122*,123-125]. Ultimately, understanding the emergence, spread and epidemiological potential of whitefly-transmitted cassava viruses will require a whole-systems approach that examines cassava agroecosystems with the recognition that interbreeding whitefly and recombining viral metapopulations extend across landscapes and beyond a single crop.

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## References

1. Patil BL, Legg JP, Kanju E, Fauquet CM: **Cassava brown streak disease: a threat to**

**food security in Africa**. *J Gen Virol* 2015, **96**:956–968.

2. Olsen KM: **SNPs, SSRs and inferences on cassava's origin**. *Plant Mol Biol* 2004, **56**:517–526.

3. Ukwuru MU, Egbonu SE: **Recent development in cassava-based products research**. *Acad J Food Res* 2013, **1**:001-013.

4. Okogbenin E, Egesi CN, Olasanmi B, Ogundapo O, Kahya S, Hurtado P, Marin J, Akinbo O, Mba C, Gomez H: **Molecular Marker Analysis and Validation of Resistance to Cassava Mosaic Disease in Elite Cassava Genotypes in Nigeria**. *Crop Sci* 2012, **52**:2576.

5. Legg JP, Kumar LP, Makeshkumar T, Tripathi L, Ferguson M, Kanju E, Ntawuruhunga P, Cuellar W: *Cassava virus diseases: Biology, epidemiology, and management*. Elsevier Inc.; 2015.

6. Jarvis A, Ramirez-Villegas J, Herrera Campo BV, Navarro-Racines C: **Is Cassava the Answer to African Climate Change Adaptation?** *Trop Plant Biol* 2012, **5**:9–29.

7. Manyong VM, Maeda C, Kanju E, Legg JP: **Economic damages of cassava brown streak disease in sub-Saharan Africa: a framework | CCAFS: CGIAR research program on Climate Change, Agriculture and Food Security**. In *Proceedings of the 11th triennial Symposium of the ISTRC-AB held at the Memling Hotel: Tropical roots and tuber crops and the challenges of globalization and climate changes*. 2010:78–82.

8. Thresh JM, Fishpool LDC, Otim-Nape GW, Fargettey D: **African cassava mosaic virus disease: an under-estimated and unsolved problem**. *Trop Sci* 1994, **34**:3–14.

9. Dubern J: **Transmission of African cassava mosaic gemnivirus by the whitefly (*Bemisia tabaci*)**. *Trop Sci* 1994, **34**:82–91.

10. Maruthi MN, Hillocks RJ, Mtunda K, Raya MD, Muhanna M, Kiozia H, Rekha AR, Colvin J, Thresh JM: **Transmission of Cassava brown streak virus by *Bemisia tabaci* (Gennadius)**. *J Phytopathol* 2005, **153**:307–312.

11. Maruthi MN, Jeremiah SC, Mohammed IU, Legg JP: **The role of the whitefly, *Bemisia***

***tabaci* (Gennadius), and farmer practices in the spread of cassava brown streak ipomoviruses**. *J Phytopathol* 2017, **165**:707–717.

12. Mware B, Narla R, Amata R, Olubayo F, Songa J, Kyamanyua S, Ateka EM: **Efficiency of cassava brown streak virus transmission by two whitefly species in coastal Kenya**. *J Gen Mol Virol* 2009, **1**:040–045.

13. Legg JP, Shirima R, Tajebe LS, Guastella D, Boniface S, Jeremiah S, Nsami E, Chikoti P, Rapisarda C: **Biology and management of Bemisia whitefly vectors of cassava virus pandemics in Africa**. *Pest Manag Sci* 2014, **70**:1446–1453.

14. Macfadyen S, Paull C, Boykin LM, De Barro P, Maruthi MN, Otim M, Kalyebi A, Vassão DG, Sseruwagi P, Tay WT: **Cassava whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) in East African farming landscapes: a review of the factors determining abundance**. 2018, doi:10.1017/S0007485318000032.

15. Legg JP, Jeremiah SC, Obiero HM, Maruthi MN, Ndyetabula I, Okao-Okuja G, Bouwmeester H, Bigirimana S, Tata-Hangy W, Gashaka G: **Comparing the regional epidemiology of the cassava mosaic and cassava brown streak virus pandemics in Africa**. *Virus Res* 2011, **159**:161–170.

16. Legg JP: **Epidemiology of a Whitefly-Transmitted Cassava Mosaic Geminivirus Pandemic in Africa**. In *Bemisia: Bionomics and Management of a Global Pest*. . Springer Netherlands; 2009:233–257.

17. Brown JK: **Phylogenetic Biology of the *Bemisia tabaci* Sibling Species Group**. In *Bemisia: Bionomics and Management of a Global Pest*. Edited by Stansly PA, Naranjo SE. Springer Netherlands; 2010:31–67.

18. Thompson WMO: **Association of *Bemisia tabaci* with the Severe Cassava Mosaic Disease in Uganda**. In *The Whitefly, Bemisia tabaci (Homoptera: Aleyrodidae) Interaction with Geminivirus-Infected Host Plants*. . Springer Netherlands; 2011:89–105.

19. Thompson WMO: **Interaction of *Bemisia tabaci* with East African cassava mosaic virus-Infected Plants**. In *The Whitefly, Bemisia tabaci (Homoptera: Aleyrodidae) Interaction with Geminivirus-Infected Host Plants*. . Springer Netherlands; 2011:107–119.

20. Colvin J, Omongo CA, Govindappa MR, Stevenson PC, Maruthi MN, Gibson G, Seal SE, Muniyappa V: **Host-Plant Viral Infection Effects on Arthropod-Vector Population Growth, Development and Behaviour: Management and Epidemiological Implications**. *Adv Virus Res* 2006, **67**:419–452.

21. Legg JP, Sseruwagi P, Boniface S, Okao-Okuja G, Shirima R, Bigirimana S, Gashaka G, Herrmann HW, Jeremiah S, Obiero H: **Spatio-temporal patterns of genetic change amongst populations of cassava *Bemisia tabaci* whiteflies driving virus pandemics in East and Central Africa**. *Virus Res* 2014, **186**:61–75.

*Documented spatio-temporal changes in *B. tabaci* haplotypes over 14 years during the pandemic, and provided evidence that the emerging mtCOI haplotype associated with the pandemic may be a hybrid between two distinct/divergent haplotypes.

22. Boykin LM, Shatters RG, Rosell RC, McKenzie CL, Bagnall RA, De Barro P, Frohlich DR: **Global relationships of *Bemisia tabaci* (Hemiptera: Aleyrodidae) revealed using Bayesian analysis of mitochondrial COI DNA sequences**. *Mol Phylogenet Evol* 2007, **44**:1306–1319.

23. Boykin LM: ***Bemisia tabaci* nomenclature: lessons learned**. *Pest Manag Sci* 2014, **70**:1454–1459.

24. Boykin LM, Kinene T, Wainaina JM, Savill A, Seal S, Mugerwa H, Macfadyen S, Tay WT, De Barro P, Kubatko L: **Review and guide to a future naming system of African *Bemisia tabaci* species**. *Syst Entomol* 2018, **43**:427–433.

25. Wosula EN, Chen W, Fei Z, Legg JP: **Unravelling the Genetic Diversity among Cassava *Bemisia tabaci* Whiteflies Using NextRAD Sequencing**. *Genome Biol Evol* 2017, **9**:2958–2973.

**Examination of population structuring and gene-flow among cassava associated *B. tabaci* collected across Africa using SNPs markers.

26. Mugerwa H, Seal S, Wang H-L, Patel M V, Kabaalu R, Omongo CA, Alicai T, Tairo F, Ndunguru J, Sseruwagi P: **African ancestry of New World, *Bemisia tabaci*-whitefly species**. *Sci Rep* 2018, **8**:1–11.

*Most recent phylogenetic reconstruction of *Bemisia tabaci* that includes new genetic groups collected from Uganda, and supports African ancestry for this species complex.

27. Sseruwagi P, Wainaina J, Ndunguru J, Tumuhimbise R, Tairo F, Guo J-Y, Vrielink A, Blythe A, Kinene T, De Marchi B: **The first transcriptomes from field-collected individual whiteflies (*Bemisia tabaci*, Hemiptera: Aleyrodidae)**. *Gates Open Res* 2017, **1**:16.

28. Ndunguru J, Sseruwagi P, Tairo F, Stomeo F, Maina S, Djinkeng A, Kehoe M, Boykin LM, Melcher U: **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* 2015, **10**.

29. Alicai T, Ndunguru J, Sseruwagi P, Tairo F, Okao-Okuja G, Nanvubya R, Kiiza L, Kubatko L, Kehoe MA, Boykin LM: **Cassava brown streak virus has a rapidly evolving genome: implications for virus speciation, variability, diagnosis and host resistance**. *Sci Rep* 2016, **6: 36164**.

30. Ateka E, Alicai T, Ndunguru J, Tairo F, Sseruwagi P, Kiarie S, Makori T, Kehoe MA, Boykin LM: **Unusual occurrence of a DAG motif in the *Ipomovirus* Cassava brown streak virus and implications for its vector transmission**. *PLoS One* 2017, **12**:e0187883.

*Identification of a motif associated with aphid transmission of Ipomoviruses in the coat protein of cassava brown strak virus.

31. Brown JK, Zerbini FM, Navas-Castillo J, Moriones E, Ramos-Sobrinho R, Silva JCF, Fiallo-Olivé E, Briddon RW, Hernández-Zepeda C, Idris A: **Revision of *Begomovirus* taxonomy based on pairwise sequence comparisons**. *Arch Virol* 2015, **160**:1593–1619.

32. Bedford ID, Markham PG, Brown JK, Rosell RC: **Geminivirus transmission and biological characterisation of whitefly (*Bemisia tabaci*) types from different geographic regions**. *Ann Appl Biol* 1994, **125**:311–325.

33. Maruthi MN, Colvin J, Seal S, Gibson G, Cooper J: **Co-adaptation between cassava mosaic geminiviruses and their local vector populations**. *Virus Res* 2002, **86**:71–85.

34. Legg JP, Fauquet CM: **Cassava mosaic geminiviruses in Africa**. *Plant Mol Biol* 2004, **56**:585–599.

35. Warburg O: *Die kulturpflanzen usambaras*. Mitt. Deutsch. Schutz; 1894.

36. Rey MEC, Ndunguru J, Berrie LC, Paximadis M, Berry S, Cossa N, Nuaila VN, Mabasa KG, Abraham N, Rybicki EP: **Diversity of dicotyledenous-infecting geminiviruses and their associated DNA molecules in Southern Africa, including the South-west Indian Ocean Islands**. *Viruses* 2012, **4**:1753–1791.

37. Fondong VN, Pita JS, Rey MEC, Kochko A, Beachy RN and, Fauquet CM: **Evidence of synergism between African cassava mosaic virus and new double-recombination geminivirus infecting cassava in Cameroon**. *J Gen Virol* 2000, **81**:287–297.

38. Bull SE, Briddon RW, Sserubombwe WS, Ngugi K, Markham PG, Stanley J: **Infectivity, pseudorecombination and mutagenesis of Kenyan cassava mosaic begomoviruses**. *J Gen Virol* 2007, **88**:1624–1633.

39. Harrison BD, Zhou X, Otim-Nape GW, Liu Y, Robinson DJ: **Role of a novel type of double infection in the geminivirus-induced epidemic of severe cassava mosaic in Uganda**. *Ann Appl Biol* 1997, **131**:437–448.

40. Zhou X, Liu Y, Calvert L, Munoz C, Otim-Nape GW, Robinson DJ, Harrison BD: **Evidence that DNA-A of a geminivirus associated with severe cassava mosaic disease in Uganda has arisen by interspecific recombination.** *J Gen Virol* 1997, **78**:2101–2111.

41. Pita JS, Fondong VN, Sangare A, Otim-Nape GW, Ogwal S, Fauquet CM: **Recombination, pseudorecombination and synergism of geminiviruses are determinant keys to the epidemic of severe cassava mosaic disease in Uganda**. *J Gen Virol* 2001, **82**:655–665.

42. Deng D, Otim-Nape WG, Sangare A, Ogwal S, Beachy RN, Fauquet CM: **Presence of a new virus closely related to East African cassava mosaic gemnivirus, associated with cassava mosaic outbreak in Uganda**. *African J Root Tuber Crop* 1995, **2**:23–28.

43. Otim-Nape GW, Alicai T, Thresh JM: **Changes in the incidence and severity of Cassava mosaic virus disease, varietal diversity and cassava production in Uganda**.

*Ann Appl Biol* 2001, **138**:313–327.

44. Legg JP, Thresh JM: **Cassava virus diseases in Africa**. In *Proceedings of the First International Conference on Plant Virology in Sub-Shaharan Africa*. . 2003:517–552.

45. Mohammed IU, Abarshi MM, Muli B, Hillocks RJ, Maruthi MN: **The Symptom and Genetic Diversity of Cassava Brown Streak Viruses Infecting Cassava in East Africa**. *Adv Virol* 2012, **2012**:1–10.

46. McSween S, Walker T, Salegua V, Pitoro R: *Economic Impact on Food Security of Varietal Tolerance to Cassava Brown Streak Disease in Coastal Mozambique*. 2006.

47. Storey HH, Nichols RFW: **Studies of the mosaic disease of cassava**. *Ann Appl Biol* 1938, **25**:790–806.

48. Nichols RFW: **The Brown Streak Disease of Cassava**. *East African Agric J* 1950, **15**:154–160.

49. Alicai T, Omongo CA, Maruthi MN, Hillocks RJ, Baguma Y, Kawuki R, Bua A, Otim-Nape GW, Colvin J: **Re-emergence of Cassava Brown Streak Disease in Uganda**. *Plant Dis* 2007, **91**:24–29.

50. Mbewe W, Kumar PL, Changadeya W, Ntawuruhunga P, Legg J: **Diversity, Distribution and Effects on Cassava Cultivars of Cassava Brown Streak Viruses in Malawi**. *J Phytopathol* 2015, **163**:433–443.

51. De Bruyn A, Harimalala M, Zinga I, Mabvakure BM, Hoareau M, Ravigné V, Walters M, Reynaud B, Varsani A, Harkins GW: **Divergent evolutionary and epidemiological dynamics of cassava mosaic geminiviruses in Madagascar**. *BMC Evol Biol* 2016, **16**:182.

*Focused on one, isolated African country, and reported the full sequencing of nearly 400 CMB genomic segments, and a thorough analysis of the evolutionary relationships of CMBs in Madagascar and throughout Africa and nearby islands.

52. Lima ATM, Silva JCF, Silva N, Castillo-Urquiza GP, Silva FF, Seah YM, Mizubuti ESG, Duffy S, Murilo Zerbini F: **The diversification of begomovirus populations is**

**predominantly driven by mutational dynamics**. *Virus Evol* 2017, **3: vex005**:1–5.

53. Duffy S, Holmes EC: **Validation of high rates of nucleotide substitution in geminiviruses: Phylogenetic evidence from East African cassava mosaic viruses**. *J Gen Virol* 2009, **90**:1539–1547.

54. Mbewe W, Tairo F, Sseruwagi P, Ndunguru J, Duffy S, Mukasa S, Benesi I, Sheat S, Koerbler M, Winter S: **Variability in P1 gene redefines phylogenetic relationships among cassava brown streak viruses**. *Virol J* 2017, **14**:1–7.

55. Ndunguru J, Sseruwagi P, Tairo F, Stomeo F, Maina S, Djinkeng A, Kehoe M, Boykin LM, Melcher U: **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* 2015, **10**:e0141939.

56. Lafforgue G, Martínez F, Sardanyés J, de la Iglesia F, Niu Q-W, Lin S-S, Solé R V, Chua N-H, Daròs J-A, Elena SF: **Tempo and mode of plant RNA virus escape from RNA interference-mediated resistance.** *J Virol* 2011, **85**:9686–95.

57. Briddon RW, Pinner MS, Stanley J, Markham PG: **Geminivirus coat protein gene replacement alters insect specificity**. *Virology* 1990, **177**:85–94.

58. Höhnle M, Höfer P, Bedford ID, Briddon RW, Markham PG, Frischmuth T: **Exchange of three amino acids in the coat protein results in efficient whitefly transmission of a nontransmissible Abutilon mosaic virus isolate.** *Virology* 2001, **290**:164–171.

59. Noris E, Vaira AM, Caciagli P, Masenga V, Gronenborn B, Accotto GP: **Amino acids in the capsid protein of tomato yellow leaf curl virus that are crucial for systemic infection, particle formation, and insect transmission.** *J Virol* 1998, **72**:10050–7.

60. Wartig L, Kheyr-Pour A, Noris E, De Kouchkovsky F, Jouanneau F, Gronenborn B, Jupin I: **Genetic Analysis of the Monopartite Tomato Yellow Leaf Curl Geminivirus: Roles of V1, V2, and C2 ORFs in Viral Pathogenesis**. *Virology* 1997, **228**:132–140.

61. Wu Z: **Complete Nucleotide Sequence of a Nonvector-Transmissible Strain of Abutilon Mosaic Geminivirus in Hawaii**. *Phytopathology* 1996, **86**:608.

62. Liu S, Bedford ID, Briddon RW, Markham PG: **Efficient whitefly transmission of African cassava mosaic geminivirus requires sequences from both genomic components**. *J Gen Virol* 1997, **78**:1791–1794.

63. Szyniszewska AM, Busungu C, Boni SB, Shirima R, Bouwmeester H, Legg JP: **Spatial Analysis of Temporal Changes in the Pandemic of Severe Cassava Mosaic Disease in Northwestern Tanzania**. *Phytopathology* 2017, **107**:1229–1242.

64. Chant SR: **Studies on the Transmission of Cassava Mosaic Virus By *Bemisia* Spp. (Aleyrodidae)**. *Ann Appl Biol* 1958, **46**:210–215.

65. Ghosh S, Bouvaine S, Richardson SCW, Ghanim M, Maruthi MN: **Fitness costs associated with infections of secondary endosymbionts in the cassava whitefly species *Bemisia tabaci***. *J Pest Sci (2004)* 2018, **91**:17–28.

*First report of the effects of endosymbiont infection of SubSahAf *Bemisia tabaci* on transmission of EACMV-UG and whitefly fitness.

66. Njoroge MK, Mutisya D, Milano D, Kilalo D: **Whitefly species efficiency in transmitting cassava mosaic and brown streak diseases**. *Cogent Biol* 2017, **3: 1311499**:1–8.

67. Jeremiah SC: **The role of whitefly (*Bemisia tabaci*) in the spread and transmission of cassava brown streak disease**. *PhD Thesis, Univ Dar es Salaam* 2014,

68. Bedford J, Innes C, Thomas H: **Geminivirus-transmission and biological characterisation of *Bemisia tabaci* (Gennadius) biotypes from different geographic regions**. *Ann Appl Biol* 1994, **125**:311–325.

69. Njoroge MK, Kilalo DC, Miano DW, Mutisya Kalro-Katumani DL, Correspondence K, Kilalo D, Miano D, Mutisya D: **Whiteflies species distribution and abundance on cassava crop in different agro-ecological zones of Kenya**. *J Entomol Zool Stud JEZS* 2016, **43**:258–262.

70. Guastella D, Lulah H, Tajebe LS, Cavalieri V, Evans GA, Pedata PA, Rapisarda C, Legg JP: **Survey on whiteflies and their parasitoids in cassava mosaic pandemic areas of Tanzania using morphological and molecular techniques**. *Pest Manag Sci* 2015,

**71**:383–394.

71. Neuenschwander P: **The spiralling whitefly, *Aleurodicus dispersus*, a recent invader and new cassava pest**. *African Crop Sci J* 1994, **2**:419–421.

72. Mware B, Olubayo F, Narla R, Songa J, Amata R, Kyamanywa S, Ateka EM: **First Record of Spiraling Whitefly in Coastal Kenya: Emergence, Host Range, Distribution and Association with Cassava Brown Streak Virus Disease**. *Int J Agric Biol* 2010, **12**:411–415.

73. Dinsdale A, Cook L, Riginos C, Buckley YM, De Barro AP: **Refined Global Analysis of *Bemisia tabaci* (Hemiptera: Sternorrhyncha: Aleyrodoidea: Aleyrodidae) Mitochondrial Cytochrome Oxidase 1 to Identify Species Level Genetic Boundaries**. *Ann Entomol Soc Am* 2010, **103**:196–208.

74. Boykin LM, Savill A, De Barro P: **Updated mtCOI reference dataset for the *Bemisia tabaci* species complex.** *F1000Research* 2017, **6**:1835.

75. Elfekih S, Tay WT, Gordon K, Court LN, De Barro PJ: **Standardized molecular diagnostic tool for the identification of cryptic species within the *Bemisia tabaci* complex**. *Pest Manag Sci* 2018, **74**:170–173.

76. Tay WT, Elfekih S, Court LN, Gordon KHJ, Delatte H, De Barro PJ: **The Trouble with MEAM2: Implications of Pseudogenes on Species Delimitation in the Globally Invasive *Bemisia tabaci* (Hemiptera: Aleyrodidae) Cryptic Species Complex**. *Genome Biol Evol* 2017, **9**:2732–2738.

77. Hadjistylli M, Roderick GK, Brown JK: **Global Population Structure of a Worldwide Pest and Virus Vector : Genetic Diversity and Population History of the *Bemisia tabaci* Sibling Species Group**. *PLoS One* 2016, **11(11): e0**:1–32.

78. Mugerwa H, Rey MEC, Alicai T, Ateka E, Atuncha H, Ndunguru J, Sseruwagi P: **Genetic diversity and geographic distribution of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) genotypes associated with cassava in East Africa.** *Ecol Evol* 2012, **2**:2749–62.

79. Sseruwagi P, Legg JP, Maruthi MN, Colvin J, Rey MEC, Brown JK: **Genetic diversity of**

***Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) populations and presence of the B biotype and a non-B biotype that can induce silver-leaf symptoms in squash, in Uganda**. *Ann Appl Biol* 2005, **147**:253–265.

80. Berry SD, Fondong VN, Rey C, Rogan D, Fauquet CM, Brown JK, Berry SD, Fondong VN, Rey C, Rogan D: **Molecular Evidence for Five Distinct *Bemisia tabaci* (Homoptera:Aleyrodidae) Geographic Haplotypes Associated with Cassava Plants in Sub-Saharan Africa**. *Ann Entomol Soc Am* 2004, **97**:852–859.

81. De Barro PJ, Liu S-S, Boykin LM, Dinsdale AB: ***Bemisia tabaci* : A Statement of Species Status**. *Annu Rev Entomol* 2011, **56**:1–19.

82. Brown JK: **Molecular markers for the identification and global tracking of whitefly vector–Begomovirus complexes**. *Virus Res* 2000, **71**:233–260.

83. Brown JK, Idris AM: **Genetic Differentiation of Whitefly *Bemisia tabaci* Mitochondrial Cytochrome Oxidase I, and Phylogeographic Concordance with the Coat Protein of the Plant Virus Genus Begomovirus**. *Ann Entomol Soc Am* 2005, **98**:827–837.

84. Ghosh S, Bouvaine S, Maruthi MN: **Prevalence and genetic diversity of endosymbiotic bacteria infecting cassava whiteflies in Africa.** *BMC Microbiol* 2015, **15**:93.

85. Thierry M, Becker N, Hajri A, Reynaud B, Lett J-M, Delatte H: **Symbiont diversity and non-random hybridization among indigenous (Ms) and invasive (B) biotypes of *Bemisia tabaci***. *Mol Ecol* 2011, **20**:2172–2187.

86. Hélène D, Rémy B, Nathalie B, Anne-Laure G, Traoré RS, Jean-Michel L, Bernard R: **Species and endosymbiont diversity of *Bemisia tabaci* (Homoptera: Aleyrodidae) on vegetable crops in Senegal**. *Insect Sci* 2015, **22**:386–398.

87. Gueguen G, Vavre F, Gnankine O, Peterschmitt M, Charif D, Chiel E, Gottlieb Y, Ghanim M, Zchori-Fein E, Fleury F: **Endosymbiont metacommunities, mtDNA diversity and the evolution of the *Bemisia tabaci* (Hemiptera: Aleyrodidae) species complex**. *Mol Ecol* 2010, **19**:4365–4378.

88. Gnankine O, Mouton L, Henri H, Terraz G, Houndete T, Martin T, Vavre F, Fleury F:

**Distribution of *Bemisia tabaci* (Homoptera: Aleyrodidae) biotypes and their associated symbiotic bacteria on host plants in West Africa**. *Insect Conserv Divers* 2013, **6**:411–421.

89. Tajebe LS, Guastella D, Cavalieri V, Kelly SE, Hunter MS, Lund OS, Legg JP, Rapisarda C: **Diversity of symbiotic bacteria associated with *Bemisia tabaci* (Homoptera: Aleyrodidae) in cassava mosaic disease pandemic areas of Tanzania**. *Ann Appl Biol* 2015, **166**:297–310.

90. Tahiri A, Halkett F, Granier M, Gueguen G, Peterschmitt M: **Evidence of gene flow between sympatric populations of the Middle East-Asia Minor 1 and Mediterranean putative species of *Bemisia tabaci***. *Ecol Evol* 2013, **3**:2619–2633.

91. Manani DM, Ateka EM, Nyanjom SRG, Boykin LM: **Phylogenetic relationships among whiteflies in the *Bemisia tabaci* (Gennadius) species complex from major cassava growing areas in Kenya**. *Insects* 2017, **8**:1–14.

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

93. Tocko-Marabena BK, Silla S, Simiand C, Zinga I, Legg J, Reynaud B, Delatte H: **Genetic diversity of *Bemisia tabaci* species colonizing cassava in Central African Republic characterized by analysis of cytochrome c oxidase subunit I**. *PLoS One* 2017, **12**:1–17.

94. Maruthi MN, Colvin J, Gibson G, Thwaites RM, Banks GK, Seal S: **Reproductive incompatibility and cytochrome oxidase I gene sequence variability amongst host-adapted and geographically separate *Bemisia tabaci* populations (Hemiptera: Aleyrodidae).** *Syst Entomol* 2004, **29**:560–568.

95. Elfekih S, Etter P, Tay WT, Fumagalli M, Gordon K, Johnson E, De Barro P: **Genome-wide analyses of the *Bemisia tabaci* species complex reveal contrasting patterns of admixture and complex demographic histories**. *PLoS One* 2018, **13**:1–18.

96. Delatte H, David P, Lett JM, Goldbach R, Peterschmitt M, Reynaud B: **Microsatellites**

**reveal extensive geographical, ecological and genetic contacts between invasive and indigenous whitefly biotypes in an insular environment**. *Genet Res Camb* 2006, **87**:109–124.

97. Esterhuizen LL, Mabasa KG, Van Heerden SW, Czosnek H, Brown JK, Van Heerden H, Rey MEC: **Genetic identification of members of the *Bemisia tabaci* cryptic species complex from South Africa reveals native and introduced haplotypes**. *J Appl Entomol* 2013, **137**:122–135.

98. Tajebe LS, Boni SB, Guastella D, Cavalieri V, Lund OS, Rugumamu CP, Rapisarda C, Legg JP: **Abundance, diversity and geographic distribution of cassava mosaic disease pandemic-associated *Bemisia tabaci* in Tanzania**. *J Appl Entomol* 2015, **139**:627–637.

99. Delatte H, Reynaud B, Granier M, Thornary L, Lett JM, Goldbach R, Peterschmitt M: **A new silverleaf-inducing biotype Ms of *Bemisia tabaci* (Hemiptera: Aleyrodidae) indigenous to the islands of the south-west Indian Ocean**. *Bull Entomol Res* 2005, **95**:29–35.

100. Laarif A, Saleh D, Clouet C, Gauthier N: **Regional co-occurrence between distinct *Bemisia tabaci* species in Tunisia with new insights into the role of host plants**. *Phytoparasitica* 2015, **43**:135–150.

101. Sseruwagi P, Maruthi MN, Colvin J, Rey MEC, Brown JK, Legg JP: **Colonization of non-cassava plant species by cassava whiteflies (*Bemisia tabaci*) in Uganda**. *Entomol Exp Appl* 2006, **119**:145–153.

102. Hadjistylli M, Brown JK, Roderick GK: **Tools and Recent Progress in Studying Gene Flow and Population Genetics of the *Bemisia tabaci* Sibling Species Group**. In *Bemisia: Bionomics and Management of a Global Pest.* . Springer Netherlands; 2009:69–103.

103. Tay WT, Elfekih S, Court L, Gordon KH, De Barro PJ: **Complete mitochondrial DNA genome of *Bemisia tabaci* cryptic pest species complex Asia I (Hemiptera: Aleyrodidae)**. *Mitochondrial DNA* 2016, **27**:972–973.

104. Abdullahi I, Winter S, Atiri GI, Thottappilly G: **Molecular characterization of whitefly,**

***Bemisia tabaci* (Hemiptera: Aleyrodidae) populations infesting cassava**. *Bull Entomol Res* 2003, **93**:97–106.

105. Legg JP: **Host-associated strains within Ugandan populations of the whitefly *Bemisia tabaci* (Genn.), (Hom., Aleyrodidae)**. *J Appl Entomol* 1996, **120**:523–527.

106. Omondi AB, Obeng-Ofori D, Kyerematen RA, Danquah EY: **Host preference and suitability of some selected crops for two biotypes of *Bemisia tabaci* in Ghana**. *Entomol Exp Appl* 2005, **115**:393–400.

107. Thompson WMO: **A new host plant species for the cassava biotype of *Bemisia tabaci* (Gennadius) (Hom., Aleyrodidae)**. *J Appl Entomol* 2003, **127**:374–376.

108. Burban C, Fishpool LDC, fauquet C, Fargette D, Thouvenel JC: **Host associated biotypes within west-african populations of the whitefly *Bemisia tabaci* (Genn.), Hom., Aleyrodidae)**. *J Appl Ent* 1992, **113**:416–423.

109. Legg, J. P.; Gibson, R. W.; Otim-Nape GW: **Genetic polymorphism amongst Ugandan populations of *Bemisia tabaci* (Gennadius)(Homoptera: Aleyrodidae), vector of African cassava mosaic geminivirus**. *Trop Sci* 1994, **34**:73–81.

110. Romba R, Gnankiné O: **Comparative biology parameters of Q1 and Q3 genotypes of *Bemisia tabaci* MED (Hemiptera: Aleyrodidae) on two host plants in Burkina Faso, West Africa**. *African Entomol* 2018, **26**:1–8.

111. Chen W, Hasegawa DK, Kaur N, Kliot A, Pinheiro PV, Luan J, Stensmyr MC, Zheng Y, Liu W, Sun H: **The draft genome of whitefly *Bemisia tabaci* MEAM1, a global crop pest, provides novel insights into virus transmission, host adaptation, and insecticide resistance**. *BMC Biol* 2016, **14**:1–15.

*First draft genome of a member of the *Bemisia tabaci* species complex.

112. Clark MA, Baumann L, Munson MA, Baumann P, Campbell BC, Duffus JE, Osborne LS, Moran NA: **The eubacterial endosymbionts of whiteflies (Homoptera: Aleyrodoidea) constitute a lineage distinct from the endosymbionts of aphids and mealybugs**. *Curr Microbiol* 1992, **25**:119–123.

113. Baumann L, Thao ML, Funk CJ, Ng JCK, Baumann P, Falk BW: **Sequence Analysis of DNA Fragments from the Genome of the Primary Endosymbiont of the Whitefly *Bemisia tabaci***. *Curr Microbiol* 2004, **48**:77–81.

114. Thao ML, Baumann P: **Evolutionary relationships of primary prokaryotic endosymbionts of whiteflies and their hosts.** *Appl Environ Microbiol* 2004, **70**:3401–6.

115. Wang X-W, Li P, Liu S-S: **Whitefly interactions with plants**. *Curr Opin Insect Sci* 2017, **19**:70–75.

116. Luan J-B, Wang X-W, Colvin J, Liu S-S: **Plant-mediated whitefly–begomovirus interactions: research progress and future prospects**. *Bull Entomol Res* 2014, **104**:267–276.

117. Czosnek H, Hariton-Shalev A, Sobol I, Gorovits R, Ghanim M: **The Incredible Journey of Begomoviruses in Their Whitefly Vector**. *Vruses* 2017, **9**:1–19.

118. Brown JK, Czosnek H: **Whitefly transmission of plant viruses**. *Adv Bot Res* 2002, **36**:65–100.

119. Ghanim M: **A review of the mechanisms and components that determine the transmission efficiency of Tomato yellow leaf curl virus (Geminiviridae; Begomovirus) by its whitefly vector**. *Virus Res* 2014, **186**:47–54.

120. Rosen R, Kanakala S, Kliot A, Cathrin Pakkianathan B, Farich BA, Santana-Magal N, Elimelech M, Kontsedalov S, Lebedev G, Cilia M: **Persistent, circulative transmission of begomoviruses by whitefly vectors**. *Curr Opin Virol* 2015, **15**:1–8.

121. Polston JE, De Barro P, Boykin LM: **Transmission specificities of plant viruses with the newly identified species of the *Bemisia tabaci* species complex**. *Pest Manag Sci* 2014, **70**:1547–1552.

122. Wei J, He Y-Z, Guo Q, Guo T, Liu Y-Q, Zhou X-P, Liu S-S, Wang X-W, Raikhel AS: **Vector development and vitellogenin determine the transovarial transmission of begomoviruses**. *Proc Natl Acad Sci U S A* 2017, **114**:6746–6751.

**Describes the localization of *Tomato yellow leaf curl virus* in the whitefly reporoductive tract and persistence of transovarially transmitted virus for two generations.

123. Navas-Castillo J, López-Moya JJ, Aranda MA: **Whitefly-transmitted RNA viruses that affect intensive vegetable production**. *Ann Appl Biol* 2014, **165**:155–171.

124. Eigenbrode SD, Bosque-p NA, Davis TS: **Insect-Borne Plant Pathogens and Their Vectors : Ecology , Evolution , and Complex Interactions**. *Annu Rev Entomol* 2017, **63**:169–191.

125. Mauck KE: **Variation in virus effects on host plant phenotypes and insect vector behavior: what can it teach us about virus evolution?** *Curr Opin Virol* 2016, **21**:114–123.