

Virus-vector relationship and epidemiology

Session III

***Bemisia tabaci*-transmitted viruses, a threat to vegetable crops: learning from virus-vector interactions to control epidemics**

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Recent unprecedented upsurges in the populations of the whitefly *Bemisia tabaci* Gen. (Hemiptera: Aleyrodidae) have resulted in the emergence of virus diseases that are vectored by this insect. Epidemics caused by begomoviruses (genus *Begomovirus*, family *Geminiviridae*), criniviruses (genus *Crinivirus*, family *Closteroviridae*) or ipomoviruses (genus *Ipomovirus*, family *Potyviridae*) are causing severe damage to vegetable crops worldwide and frequently are the limiting factor to production. Efforts are then being conducted to characterize the viruses involved in the epidemics and to understand their biology and mechanisms of plant infection. Simultaneously, much has been learned about the vector *B. tabaci*, its biology and population differences. Thus, variants of *B. tabaci* that exhibit biotic and genetic differences have been reported. Biological differences might influence the equilibrium between populations in nature and/or the ability to interact with the viruses that are transmitted. In addition, differences in the efficiency or selectivity of virus transmission can affect the pattern of virus dissemination during epidemics either in crop or in weed species. Specific interactions should occur between the virus and the vector for efficient transmission. In this interactions are involved both *B. tabaci* and virus determinants that are poorly understood at present. However, knowledge on this aspect will have a special importance to search for mechanisms that interfere in the transmission process. Therefore, learning from virus-vector relationships might probably help to design more efficient strategies to control virus epidemics.

Cassava mosaic geminiviruses, *Bemisia* whiteflies, and the African pandemic of cassava mosaic disease

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A pandemic of unusually severe Cassava mosaic virus disease (CMD) has spread during the last 15 years to cover a large swathe of East and Central Africa. Passage of the 'front' of the pandemic has been shown to give rise to a complex set of changes in the dynamics of cassava host, virus and virus vector interactions. New, more virulent virus strains and mixtures have resulted in changes in patterns of transmission by *Bemisia tabaci*, influencing in turn both the local and regional epidemiology. Yield losses have increased as mixed virus infections have become more frequent, although this has been offset in earliest affected areas by the increasing prevalence of apparently cross-protecting mild strains. *Bemisia tabaci* super-abundance in pandemic zones, particularly at the 'front', appears to result from either synergistic interactions between severely diseased cassava host plants and *B. tabaci* or the occurrence of a distinct *B. tabaci* genotype or a combination of the two. The sum of this complex web of interactions is a devastating and growing disease phenomenon that has cut the production of cassava substantially, has had a disastrous effect on the livelihoods of the millions of small-holder farmers in the affected areas and has had a measurable impact on the prosperity of countries affected. Effective control measures based around the deployment of host plant resistance have been developed and are being widely implemented. However, the rate of pandemic spread continues to exceed the pace of the implementation of control measures. As a result, it is essential that yet greater scientific and financial resources are directed towards solving the problem posed by this continental-scale *Bemisia* driven disease pandemic.

The effect of begomoviruses on their whitefly vector

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It has been proposed that begomoviruses have deleterious effects on their insect vector, the whitefly *Bemisia tabaci*. It has also been proposed that these effects result from begomovirus replication in the whitefly. More recently it has been proposed that the more severe the symptoms caused by a begomovirus the less suitable is the host for virus acquisition, presumably because the infected plant is a less suitable feeding host. Studies were conducted with two begomoviruses, Tomato mottle virus and Tomato yellow leaf curl virus, to determine how begomoviruses may affect the reproduction of their insect vector. It was found that whiteflies reared on virus-free hosts laid fewer eggs on begomovirus-infected plants than on healthy plants. Also fewer instars emerged from eggs laid on begomovirus-infected plants, and the number of adults which emerged in a given time period were reduced on begomovirus-infected plants. In contrast, whiteflies reared on begomovirus-infected plants laid the same number of eggs on non-virus host plants as whiteflies reared on virus-free plants. These data suggest that begomoviruses may have an impact on whiteflies by reducing the reproductive suitability of their plant host.

The effect of host plant resistance to Tomato yellow leaf curl virus (TYLCV) on virus acquisition and transmission by its whitefly vector

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The effect that Tomato yellow leaf curl virus (TYLCV)-infected resistant tomato plants may have on virus epidemiology was studied. Four different tomato genotypes that exhibit different levels of viral resistance, ranging from fully susceptible to highly resistant, served as TYLCV-infected source plants. Viral acquisition and transmission rates by whiteflies following feeding on the different source plants were evaluated. TYLCV transmission rate by whiteflies that had fed on infected source plants 21 days post-inoculation (DPI), shortly after appearance of TYLCV symptoms, was negatively correlated with the level of resistance displayed by the source plant. Therefore, the higher the resistance, the lower the transmission rate. In addition, TYLCV DNA accumulation was shown to be lower in the resistant source plants compared with the susceptible plants. Whitefly survival rate, following feeding on source plants 21 DPI, was similar for all the varieties tested. Significant differences in whitefly survival were found however, following feeding on the infected source plants at 35 DPI; here, whitefly survival rate increased with higher levels of resistance displayed by the source plant. At 35 DPI the susceptible plants had developed severe TYLCV disease symptoms, and transmission rates from these were the lowest, presumably due to the poor condition of these plants. Transmission rates from source plants displaying medium level of resistance level were highest, with rates declining following feeding on source plants displaying higher levels of TYLCV resistance. TYLCV DNA accumulation in whiteflies following feeding on infected source plants at both 21 and 35 DPI was directly correlated with viral DNA accumulation in source plants. Results show that in essence, the higher the resistance expressed, the less suitable the plant was as a viral source. Consequently, following acquisition from a highly resistant plant, TYLCV transmission by whiteflies will be less efficient.

Transmission of Cucumber vein yellowing ipomovirus (CVYV) by two *Bemisia tabaci* biotypes

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Cucumber vein yellowing virus (CVYV), a virus that causes an economically important disease on cucurbit crops, is a member of the genus *Ipomovirus* (family *Potyviridae*). Originally found in the eastern Mediterranean area, it was detected in Spain in the year 2000. The virus is semipersistently transmitted by *Bemisia tabaci* whiteflies. To identify putative means of interference with the spread of CVYV, we have initiated studies on the transmission process by whitefly vectors. Experimental transmissions between cucumber host plants have been performed, using an Spanish isolate of the virus and two biotypes of whiteflies, Q and B. Preliminary results suggested that both biotypes were able to transmit the virus with comparable effectiveness. In our conditions, 20 insects and periods of acquisition and inoculation of 24 hours were needed to achieve transmission rates above 50% of assayed plants. Reductions in the number of vectors, or in the periods of time for acquisition and inoculation of the virus, resulted in decreased transmission rates. We are specially interested to know if the transmission requires, in addition to the virus particles, an accessory factor acting in a manner similar to the helper component of aphid transmitted potyviruses. To test the dependency of such a helper factor for transmission, purified virus preparations are needed. Previous literature reports about difficulties to purify CVYV particles were confirmed, and attempts to obtain purified preparations of our isolate using standard purification methods for potyviruses have failed. Different alternatives to overcome this problem are being followed.

Analysis of Squash leaf curl virus coat protein mutants for ingestion, acquisition, and transmission by the whitefly vector *Bemisia tabaci* B biotype

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Single and multiple amino acid substitutions were introduced into the coat protein gene (AV1) of Squash leaf curl virus to identify the specific amino acids that are required for whitefly-mediated transmission. Loss or gain of function mutations were based on the corresponding amino acid(s) found in the naturally occurring non-whitefly transmissible mutant begomovirus, Abutilon mosaic virus-Rothamsted isolate. Pumpkin seedlings (2-leaf stage) were biolistically inoculated with infectious SLCV clones containing a chimeric protein gene, and/or CP gene into which point mutations were introduced to alter one or more amino acids in either the AbMV or SLCV CP sequence to achieve all possible combinations of the amino acids that differ between the transmissible and non-transmissible viruses, respectively. Plants were assessed for systemic symptom development (5-10 days, PI) and symptom phenotype was recorded. DNA extracts were subjected to polymerase chain reaction (PCR) and Southern analysis, and to western blot analysis using polyclonal antibody raised against purified virions of Tomato golden mosaic virus to determine if viral DNA and CP were present in leaves that developed 12 d post-inoculation. Adult whiteflies were allowed a 24-h acquisition access period (AAP) on virus source plants, followed by a 48-h inoculation access period on pumpkin test plants to which they were transferred. Whiteflies were collected from plants and subjected to PCR and Southern analyses to demonstrate virus ingestion by the vector. Whitefly hemolymph was collected from individuals of the same vector cohort that was also examined for virus ingestion and vector transmissibility. Detection of SLCV DNA by PCR and Southern analysis in whitefly hemolymph indicated virions were capable of crossing the gut membrane barrier(s). Vector-mediated transmission of CP mutants between virus sources and test plants was considered evidence for the successful interaction of virions both with GROEL (heat shock protein) present in whitefly hemolymph and the putative salivary gland receptor to facilitate transmission to pumpkin plants. Both transmissible and non-transmissible CP mutants were identified, and two apparently failed to assemble. Among the non-transmissible mutants, one was defective for passage of the gut barrier, while the other was incapable of successfully interacting with the (putative) whitefly salivary gland receptor.

Closely related DNA satellites are essential for Cotton leaf curl Gezira virus disease symptom induction in malvaceous species

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The same (>99% identity) monopartite begomoviral species, Cotton leaf curl Gezira virus (CLCuGV), has recently been cloned from symptomatic cotton, okra and *Sida alba* plants collected in central Sudan. Field-infected plants exhibited vein thickening and leaf curl symptoms typical of those previously attributed to cotton leaf curl disease (CLCuD). However, wild type leaf curl disease symptoms were not reproducible when several putative susceptible test species were inoculated with an apparent full-length clone for CLCuGV. Subsequently, the plant species from which the CLCuGV genome was cloned were examined for the possible presence of satellite DNA molecules (sat DNAs) that might be required for pathogenicity when co-inoculated with the helper CLCuGV. Satellite ssDNAs were obtained from cotton (sat41-C) at 1348 nt, okra (sat43-O) at 1349 nt, and *S. alba* (sat32-S) at 1350 nt. All sat DNAs contained one predicted ORF (~13.7 kDa) in the complementary orientation. The only sequence found to be shared by both the CLCuGV genome and the satDNAs was the nonanucleotide sequence, TAATATTAC, which contains the nicking site for initiation of replication of begomoviruses. Sequence comparisons for the apparent full-length satellite DNAs (~1350 nt) revealed 96.7-98.7% shared nt identity, indicating they probably the same satDNA, which hereafter is referred to as Cotton leaf curl Gezira virus associated satellite DNA (CLCuGV-satDNA). Amongst other begomoviral associated satDNAs described thus far, the closest relative to CLCuGV-sat is the Okra leaf curl virus-associated satDNA from Egypt, at 81.2- 85.4%. Phylogenetic analysis of CLCuGV-sat DNA placed it with several satDNAs from okra plants from Egypt. Co-inoculation of cotton and *Nicotiana benthamiana* seedlings with cloned, linearized CLCuGV-satDNAs and the *S. alba* isolate of CLCuGV resulted in development of typical CLCuD symptoms, thereby, demonstrating proof of pathogenicity. The CLCuV-satDNAs were also found to be infectious and produced leaf curl symptoms in cotton when co-inoculated with the distinct begomoviral species, Cotton leaf curl Multan virus. It is hypothesized that different, single or even possibly suites of satDNAs, when present, together with the same helper begomovirus, may modulate viral functions relevant to the infection cycle, including symptom phenotype, and/or host range, thereby influencing fitness for satDNA-helper complexes.

Begomovirus replication in *Bemisia tabaci*

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Geminiviruses affect a large number of crops worldwide and can cause dramatic yield losses. Begomoviruses are one of the three genera described in the Geminiviridae family and are transmitted by the whitefly, *Bemisia tabaci*, in a persistent manner. Herein we report on the virus-vector interactions of two begomoviruses, the bipartite Tomato mottle virus (ToMoV) and the monopartite Tomato yellow leaf curl virus (TYLCV). Studies were performed on whiteflies maintained on virus infected tomato plants and transferred to cotton (a virus nonhost). Transcripts of three virus genes representing genomic and complementary strand products were detected and quantified via real-time RT PCR in the whitefly vector after 4 and 7 days of continuous feeding on cotton. Results indicate virus transcriptional differences in the interactions between ToMoV and TYLCV within their vector.

Effects of the use of TYLCV-resistant cultivars on the proportion of TYLCV-Is/TYLCV-Sar in tomato crops of southeast Spain

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Tomato yellow leaf curl virus is the cause of important losses in the tomato crops of the southeast of Spain. The control of its vector, *Bemisia tabaci*, by chemical, biological or integrated means has been insufficient to reduce the incidence of the virus during the demographic highs of the insect in the summer months. The widespread use of TYLCV-resistant cultivars can induce changes in the virus populations which should be studied for a better management of the problem. A survey of the TYLCV incidence in tomato crops of resistant and susceptible cultivars was made in Murcia through the 2001/02 campaign. The presence of TYLCV-Is and TYLCV-Sar was detected in both plants and *B. tabaci* adults by molecular hybridization with two specific probes. In symptomatic resistant cultivars, the average ratio TYLCV-Is/TYLCV-Sar was 18, while the same ratio was 12 in asymptomatic resistant plants. The 80% of the *B. tabaci* adults collected on resistant crops gave positive signal with the TYLCV-Sar probe and the above ratio was less than one. When the symptomatic and asymptomatic susceptible cultivars were sampled, the average ratio TYLCV-Is/ TYLCV-Sar was 8 and 4.5 respectively. On these plants, more than the 75% of the *B. tabaci* adults carried the virus and the above ratio was more than one. The proportion of insects carriers of TYLCV-Sar is much higher than expected according to its proportion on the resistant and susceptible plants. This finding needs an explanation. At the same time, the prevalence of TYLCV-Is on the resistant cultivars is evident, suggesting a certain selection process which could increase in the future, as the use of these cultivars is becoming widespread.

Acquisition and transmission of TYLCV from tomato fruits by *Bemisia tabaci*

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TYLCV is one of the most damaging viruses transmitted by the whitefly *Bemisia tabaci*. This virus, that causes severe symptoms on tomato culture, had spread for about 10 years in several parts of the world. To date, the possible transport of the virus by the way of imported and exported tomato fruits had never been considered. In this study, we report that TYLCV is present in tomato fruits at high titre. The virus can be acquired by 5 to 15 % of whiteflies that fed on tomato fruits, depending on the acquisition access period, and then be transmitted up to 8 % to tomato plants. The potential risk of causing new outbreaks of TYLCV via infected tomato fruits as a virus source is discussed.

Diversity of *Bemisia tabaci* (Gennadius) in Morocco and its potential to be vector of Tomato yellow leaf curl virus

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Since 1998, Tomato yellow leaf curl virus was detected on tomato in Morocco. The virus was first detected near Casablanca and was later discovered in several regions particularly in the south near Agadir and in the north east near Berkane (DPVCTFR, personal communication). Economic losses ranged between 20 and 100%. In 1999, Tomato yellow leaf curl Sardinia virus was detected from Agadir. High populations of *Bemisia tabaci*, the vector of these viruses, were observed on tomato, other crops and weeds. Only biotype Q was identified in *B. tabaci* populations from Agadir. No sample were analysed so far from the north of the country. Since biotype B was reported from several Mediterranean countries, it was assumed that this cosmopolitan biotype could be present in Morocco. Therefore a survey of *B. tabaci* was undertaken in several regions to determine which are the biotypes present in Morocco and particularly in the north. Samples were collected from the north eastern Mediterranean coast (Saïdia, Berkane, Nador), from the north western region (Gharb region, Fez, Meknès) and from Agadir. Based on RAPD, cytochrome oxydase I gene sequencing and microsatellite markers biotype Q was detected in all the regions. Biotype B was only detected in the north eastern region. To our knowledge, this the first molecular detection of biotype B in Morocco. Following the severe outbreaks of tomato yellow leaf curl disease in tomato crops, several growers from Agadir developed techniques to reduce the impact of this new disease, particularly by the use of insect proof shelters. In spite of this careful physical control to prevent whiteflies to have access to the tomato plants, there are often a significant percentage of TYLCV infected plants. This suggests that TYLCV is efficiently transmitted by *B. tabaci*. To investigate this efficiency several experiments were carried out in a tomato farm in the region of Agadir. Natural populations of whiteflies have been trapped during a 3 month period. The flight activities recorded at different height of a trapping mast were studied according to the temperature. The ratio *B. tabaci*/*Trialeurodes vaporariorum* was assessed on batches of tomato plants that were placed around the trapping mast and weekly changed. These plants were also used to monitor the infectivity of *B. tabaci* in relation to the flight activity. Finally the proportion of competent vector i.e. those which have the ability to transmit, were determined for males and females in a natural population of *B. tabaci*.

Preliminary epidemiological studies of two whitefly-transmitted viruses in Spain: Tomato chlorosis virus and Tomato infectious chlorosis virus

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Weeds have been reported to be important reservoirs of whitefly-transmitted viruses and play a significant role in the epidemiology of some virus species. Tomato chlorosis virus (ToCV) and Tomato infectious chlorosis virus (TICV) are whitefly-transmitted, phloem-limited criniviruses infecting tomato in several countries worldwide. ToCV is transmitted by *Bemisia tabaci* (Gennadius), *Trialeurodes vaporariorum* (Westwood) and *T. abutilonea* (Haldeman), whereas TICV is transmitted only by *T. vaporariorum*. In tomato (*Lycopersicon esculentum* Mill), ToCV and TICV cause interveinal yellowing on leaves that often develop into red or necrotic flecks, and brittle and rolling lower leaves. In Spain ToCV was first detected in 2000 infecting tomato crops which were collected during 1997 in Malaga and Almeria (southern Spain). TICV was first detected in 2001 in greenhouse- and field-grown tomatoes in the Castellón province (eastern Spain). Nowadays, the geographical distribution of these diseases in Spain is the following: ToCV has been detected in the provinces of Murcia, Alicante, Castellón (eastern Spain) and also in the islands of Mallorca, Tenerife and Gran Canaria, whereas TICV has only been detected in two provinces of eastern Spain: Castellón and Alicante. In order to understand the epidemiological cycle of ToCV and TICV, specific studies of the flora of the affected regions have been attained, analysing the role that different weeds play as natural hosts of these viruses and their vectors. Tomato plants and weeds were collected in and around tomato fields (during the growing season) or fields that had tomato production (during the host-free period). Weeds were usually collected from areas directly bordering fields and 1 to 2 m from the edge of the field. Forty-one common weed species were sampled at several locations adjacent to commercial tomato plantings, affected by ToCV and TICV. A total of 100 plants were sampled. Total RNA was extracted from leaf tissue (about 0.1 g) and used as template for RT-PCR. ToCV- and TICV-specific primers were used for the reliable diagnosis of ToCV and TICV in samples. RT-PCR was performed using the One Step RT-PCR System (Invitrogen). The RT-PCR products were separated by electrophoresis in 1.5% agarose gels. ToCV and TICV were detected in several weed species that therefore might be new hosts for ToCV and TICV.

Occurrence of Tomato yellow leaf curl disease (TYLCD) and Cucurbit yellow stunting disorder virus (CYSDV) in the Canary Islands

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Bemisia tabaci (Gennadius, 1889) (Hemiptera: Aleyrodidae) is considered one of the most widespread and economically damaging pest in the Canary Islands, mainly due to heavy incidence of viruses transmitted by this whitefly in several horticultural crops. Since the first detection of the geminivirus Tomato yellow leaf curl disease (TYLCD) in the Canary Islands, this disease has been causing great economic damage and nowadays it could be considered the major limiting factor for production of tomato in the archipelago. Together with TYLCD, the closterovirus Cucurbit yellow stunting disorder virus (CYSDV) is an emergent and economically important problem of different cucurbit crops in the Canary Islands. A preliminary survey has been carried out to evaluate the incidence of TYLCD and CYSDV in the major tomato and cucurbit production areas. A number of 17 farms (both outdoors and protected-crops) were visited. The identification of the virus infection was made by ELISA-TAS tests and hybridisation with (DIG)-labeled probes; evaluation of the disease severity was made by symptom observation in the field. Surveys since 2000 have been also undertaken in order to identify weed hosts of *B. tabaci* that could be potential reservoirs of TYLCD and CYSDV and may play a role in the epidemiology of both diseases. At the same time, studies on the dynamic of the populations of *B. tabaci* were carried out on tomato and cucurbits. In the case of Tomato yellow leaf curl disease, which is associated with different species of the genus Begomovirus, samples of infected plants were collected and analysed by PCR to determine which virus species were involved in the epidemics as well as their distribution in the field. Results of these studies will be presented.

Investigation of virus interactions and putative cross-protection through grafting and transmission studies with *Bemisia tabaci*

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A study was conducted to investigate interactions between Cassava mosaic geminiviruses (CMGs) and establish whether 'mild' strains of East African cassava mosaic virus (EACMV-Ug) confer immunity against infection by 'severe' strains of the same virus. Both whitefly transmission and bud grafting were carried out in a greenhouse to achieve transmission. Whiteflies raised on cassava plants infected with EACMV-Ug 'severe', EACMV-Ug 'mild' and African cassava mosaic virus (ACMV)+EACMV-Ug were used to inoculate CMD-free and EACMV-Ug 'mild'-infected plants raised in a separate insect-proof greenhouse. More whitefly transmission was achieved with EACMV-Ug 'severe' and ACMV+EACMV-Ug in comparison to EACMV-Ug 'mild'. Eighty percent, 90% and 50% of CMD-free plants got infected when inoculated with EACMV-Ug 'severe', ACMV+EACMV-Ug and EACMV-Ug 'mild' respectively. The most severe symptoms were shown by ACMV+EACMV-Ug and EACMV-Ug 'severe' transfers to CMD-free plants whilst EACMV-Ug 'severe' to EACMV-Ug 'mild' infected plants had the least severe symptoms. All newly emerged shoots from the grafts showed CMD symptoms and at 5 months after grafting symptoms in the grafted buds were the same as those in the stock plants in all cases. Results suggested that there is evidence that mild strains protect against infection by severe strains where the natural vector *Bemisia tabaci* is used but not where transmission is by artificial grafting. Previous research has indicated that there is some interaction when the method of inoculation of the severe strain is the whitefly vector but none is observed when grafting is used. The implications of these findings towards establishing whether cross-protection occurs in cassava are discussed.

Cassava mosaic begomoviruses and *Bemisia tabaci* in Uganda: current status and control options

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Cassava mosaic disease (CMD) occurs throughout Africa wherever cassava is grown and epidemic, endemic and benign states of the disease have been described. Under epidemic conditions, there is rapid spread by the vector *Bemisia tabaci*, CMD is prevalent, symptoms are severe, associated losses are serious and control measures are necessary to restore production. This is the situation in the current pandemic of CMD in the Great Lakes region of Africa, first observed in Uganda in 1988. A natural recombinant variant of East African cassava mosaic virus (EACMV-UG) was isolated in Uganda and associated with the pandemic. Other cassava-infecting begomoviruses (CMGs) reported in Uganda are; African cassava mosaic virus (ACMV), non-recombinant EACMV and a pseudo-recombinant involving EACMV-UG. Diverse symptoms including 'light green mosaic', 'green mosaic', 'yellow mosaic' and varying degrees of leaf distorting and plant stunting are caused by the CMGs and some CMGs incite more than one symptom type, even in the same field. More CMGs than already reported are thought to be present in the CMD pathosystem in Uganda. Another key feature of the CMD pandemic is the previously unseen high numbers of *B. tabaci*. The large populations persist in areas where epidemic 'front' conditions have passed, especially on some of the CMD-resistant varieties introduced to control the disease, causing serious concerns. Use of CMD-resistant varieties constitutes the core of control strategies, other practices are phytosanitation and varietal mixtures. Options being considered for the control of *B. tabaci* are host plant resistance and biological control using parasitoids.