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A review of geminivirus (begomovirus) diseases in vegetables and other crops in Brazil: current status and approaches for management

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ABSTRACT

Insect-transmitted viruses cause some of the most damaging and economically important diseases of crop plants, especially in tropical and subtropical regions. The geminiviruses, a group of single-stranded DNA viruses with unique twined icosahedral virus particles, are responsible for many of these diseases. Of particular importance are the geminiviruses transmitted by whiteflies (*Bemisia tabaci*), which are in the genus *Begomovirus*. This is the largest genus of plant viruses (in terms of number of species), and some are responsible for devastating diseases in vegetable and fiber crops throughout the world. This review presents the current understanding of begomoviruses, the diseases they cause, and approaches for disease management. An emphasis is placed on the most important begomovirus diseases in Brazil, which are those that affect common bean and tomato. However, because of the wide host range of the vector and the genetic flexibility of begomoviruses, these diseases pose a threat to many other crops. Therefore, the current situation with begomoviruses that infect okra, pepper, potato, sweet potato and soybean in Brazil is also discussed.

Keywords: *Bemisia tabaci*, begomovirus, golden mosaic, integrated pest management, whitefly.

General characteristics of geminiviruses

The worldwide expansion of agriculture has also resulted in the emergence and spread of numerous diseases and insect pests. Of particular importance are insect-transmitted viruses, especially in tropical and subtropical regions. Geminiviruses are insect-transmitted viruses that have emerged, over the past 20 years, as the largest group of plant viruses (in terms of number of species) and one of the most economically important. These viruses cause extremely damaging diseases in a wide range of crops throughout the world, including African cassava

mosaic in Africa; bean golden mosaic (BGM) in the Americas; beet curly top in North America and the Middle East; cotton leaf curl in Asia; maize streak in Africa; and tomato yellow leaf curl in Africa, the Americas, Asia and Europe. In Brazil, BGM (Figures 1A, 2A) and tomato diseases (Figures 1B, 2B, 2C) caused by a complex of geminiviruses are important diseases that lead to substantial yield losses in common bean and fresh market and processing tomato production.

Geminiviruses comprise a biologically and genetically diverse family (*Geminiviridae*) of viruses that share the following characteristics:

RESUMO

Uma revisão de geminiviruses (begomoviruses) em hortaliças e outras culturas: situação atual e estratégias de manejo

Os vírus transmitidos por insetos causam algumas das doenças mais severas e economicamente mais importantes em culturas agrícolas, especialmente em regiões tropicais e subtropicais. Os geminivírus, um grupo único de vírus de DNA de fita simples com partículas icosaédricas e geminadas, são responsáveis por muitas dessas doenças. De particular importância são os geminivírus transmitidos por moscas-brancas (*Bemisia tabaci*), que pertencem ao gênero *Begomovirus*. Esse é o maior gênero de vírus de plantas (em termos de número de espécies), sendo que alguns dos begomovírus causam inúmeras doenças devastadoras em hortaliças e plantas produtoras de fibras em todo o mundo. Esta revisão apresenta o conhecimento atual sobre os begomovírus, as begomoviruses e as estratégias de manejo dessas doenças. Ênfase é colocada nas principais begomoviruses que ocorrem no Brasil, que são aquelas que afetam o feijoeiro e tomateiro. Entretanto, devido ao amplo círculo de hospedeiros do vetor e da flexibilidade genética dos begomovírus, as begomoviruses representam ameaças a diversas culturas. Assim, discute-se também a situação atual das begomoviruses em batata, batata-doce, pimenta, quiabo e soja no Brasil.

Palavras chave: *Bemisia tabaci*, begomovírus, mosaico dourado, manejo integrado de pragas, mosca-branca.

a twinned quasi-icosahedral virus particle (virion) that measures ~18 X 30 nanometers and a small circular single-stranded DNA genome of ~2.9-5.2 kilobases (kb). The family name is derived from the distinctive twinned virions (the Latin word gemini means twin). Based upon genome structure, phylogenetic relationships, insect vector and host range, seven genera have been recognized: *Begomovirus*, *Mastrevirus*, *Curtovirus*, *Topocuvirus*, *Becurtovirus*, *Turncurtovirus* and *Eragrovirus* (Brown *et al.*, 2012). In nature, geminiviruses are transmitted by phloem-feeding insects, including various species of leafhoppers, a treehopper and whiteflies of the

species *Bemisia tabaci* (Figures 3A, 3B). Geminiviruses are not transmitted through seeds, whereas many are graft-transmissible and some are mechanically (sap) transmissible. Plants infected with geminiviruses show a wide range of symptoms including stunting, distorted growth, and leaf streaking and striations in monocotyledonous plants and leaf crumpling, curling, distortion, golden-light green-yellow mosaic/mottle, interveinal yellowing, yellow spots, and vein swelling, purpling, and yellowing in dicotyledonous plants.

Emergence of whitefly-transmitted geminiviruses (begomoviruses)

The whitefly-transmitted geminiviruses are in the genus *Begomovirus*. They comprise the largest number of species (288 of 325 total species) in the family *Geminiviridae* (Brown *et al.*, 2012), and will be the focus of this review. The remarkable emergence of these viruses has been driven by the *B. tabaci* vector, especially the polyphagous biotype B that has spread throughout the world (Gilbertson *et al.*, 2015). Begomoviruses can be subdivided into two major groups: bipartite viruses, those with a genome composed of two ~2.6 kb DNA components (referred to as DNA-A and DNA-B), which are prevalent in the New World (NW, e.g., southern states of the United States of America (USA), Mexico, the Caribbean and Central and South America); and monopartite viruses, those with a genome composed of a single ~2.9 kb genomic DNA, which are prevalent in the Old World (OW, e.g., Europe, Africa, Asia and Australia). Many monopartite begomoviruses are associated with satellite DNAs (alphasatellites and betasatellites), some of which enhance pathogenicity (Zhou, 2013). The bipartite and monopartite begomoviruses reflect an ancestral division that possibly occurred before continental drift. However, more recently the boundaries between these two groups have become less clear. This is because of the introduction and establishment of OW monopartite begomoviruses into the NW, e.g., *Tomato yellow leaf curl virus* (TYLCV) in many regions of the NW (Lefevre

et al., 2010) (although it has not been reported so far in Brazil) and a complex of sweet potato begomoviruses that are widespread in Brazil and other NW regions (Albuquerque *et al.*, 2012a). In addition, indigenous NW monopartite tomato-infecting begomoviruses have been recently identified, e.g., *Tomato leaf deformation virus* (ToLDV) in Peru and *Tomato mottle leaf curl virus* (ToMoLCV; Figure 2B) in Brazil (Gilbertson *et al.*, 2015). In general, begomoviruses cause similar symptoms in plants, including stunting and leaf distortion and some combination of golden-light green-yellow mosaic/mottle, crumpling, curling, distortion, veinal or interveinal yellowing, and yellow spots in leaves. Identification of a specific begomovirus requires the use of molecular methods (e.g., rolling circle amplification [RCA], polymerase chain reaction [PCR] and sequencing).

The whitefly vector of begomoviruses

The vector of begomoviruses, *B. tabaci* (Figure 3), is a complex of morphologically similar, but biologically and genetically distinct populations. The species *B. tabaci* is divided into biotypes (e.g., A, B, Q), which are probably distinct enough to be considered as species (de Barro *et al.*, 2011). This has led to a proposal to elevate some biotypes to the species level, including NW (biotype A), Middle East-Asian Minor 1 (biotype B) and Mediterranean (biotype Q), based on their inability to interbreed and divergence in the mitochondrial cytochrome oxidase 1 (mtCO1) gene (de Barro *et al.*, 2011). However, for this review, we will use biotype designations as they are more familiar and most commonly used in the literature. In Brazil, biotype B is currently the predominant biotype. Biotype A is believed to have been prevalent prior to the introduction of biotype B in the 1990's. Like in other geographical areas, biotype B rapidly displaced the indigenous biotype(s). Today, the *B. tabaci* biotype B is distributed throughout Brazil. Recently, the biotype Q, which possesses resistance to certain insecticides, was reported in the south of

Brazil (Barbosa *et al.*, 2015), and it may be present in other parts of the country.

Effective management of *B. tabaci* is difficult. The most common control method is the application of insecticides, mostly combinations of neonicotinoids, juvenoids and growth regulators. These materials target different stages of the insect, i.e., eggs, nymphs or adults, whereas others block feeding of the insect. Targeting only adults may be one reason for the low control efficiency in some situations. Hence, it is important to monitor fields and be aware of the insect stage(s) present before selecting the insecticide to be applied. Dosage and application volume, mode and timing are other factors that strongly influence the efficiency of insecticide control of whiteflies. In addition, the constant and repeated use of the same active ingredient favors the selection and multiplication of individuals that are resistant to that specific chemistry. Indeed, it is common to hear growers complaining that a certain insecticide no longer kills whiteflies or that a higher dose is needed to be effective; this suggests the selection of a resistant population, often due to excessive and repeated spraying of the same chemical. Finally, the complexity of the Brazilian agricultural system contributes to the difficulty in controlling whiteflies. Because *B. tabaci* biotype B is highly polyphagous, they reproduce on numerous crops, weeds and non-cultivated plants. Thus, in irrigated agricultural production systems, crop hosts of the whitefly are always present and act as bridges to maintain *B. tabaci* populations throughout the year. For example, overlapping of soybean, cotton, potato, tomato, and bean crops in Brazil provides continual host plants for whiteflies in many regions. Whiteflies prefer hot and dry periods, therefore high populations are seen usually from December to March, particularly in the 'veranico' period (periods of at least two weeks without rain in the summer or wet season).

Begomovirus diseases in Brazil

The most important begomovirus diseases in Brazil are BGM (Figure 1A) and a number of diseases of tomato

(Figure 1B) caused by a complex of viruses. In situations where whitefly populations are high and bean or tomato crops are infected with these viruses early in development, entire fields can be destroyed or abandoned due to these diseases (Figure 1B). Other crops (e.g., okra, pepper, potato and sweet potato) can be infected by begomoviruses in Brazil, but economic losses are not substantial or widespread. Weeds in Brazil are commonly infected with begomoviruses and often show striking light green, golden or yellow mosaic symptoms (Figure 2F), and these can serve as progenitors for new crop-infecting begomoviruses (Rocha *et al.*, 2013).

Finally, whereas begomoviruses are the major and perhaps the only type of geminivirus found in Brazil, it is worth noting that a disease with symptoms similar to the curly top of sugar beets and vegetable crops that occurs in the western USA and Asia (Iran and Turkey) has been reported in Argentina and Brazil (Costa, 1952). Although this disease was demonstrated to be leafhopper-transmitted, the causal agent has not been characterized. This disease has not been observed in Brazil for many years, indicating that it is not economically important.

In this review, the major and minor diseases caused by begomoviruses in vegetables and other crops in Brazil (Table 1) are described. In addition, the approaches and challenges faced by growers in managing these diseases are discussed.

Beans (*Phaseolus vulgaris*)

BGM has been one of the most damaging diseases of common beans (and to a lesser extent, lima beans) in Brazil since it emerged in the 1960s (Costa, 1965). The disease is characterized by a striking golden-yellow mosaic/mottle of leaves, as well as blistering, chlorosis, crumpling, and rugosity (Figures 1A, 2A). Infected plants are often stunted, particularly when infected early in development, and yields can be substantially reduced. BGM was the first begomovirus disease that reached epidemic levels in the NW. In Brazil, these epidemics were

associated with massive increases of whitefly populations that developed on vast acreages of soybean. Epidemics of BGM in Brazil typically occur during hot dry weather in the summer months, as well as in dry periods, known as 'veranico', that occur during the rainy season. The occurrence of BGM epidemics has fluctuated over the past decade, but the disease remains a major concern for growers. For example, as recently as 2013, epidemics of BGM in the major bean producing regions caused substantial economic losses (G1 Globo, 2013).

Unlike tomato begomovirus diseases in Brazil, which emerged following the introduction of the *B. tabaci* biotype B in the 1990s, outbreaks of BGM were driven by indigenous *B. tabaci* populations, presumably biotype A. This indicated that the biotype A was an effective vector of *Bean golden mosaic virus* (BGMV) and probably of other begomoviruses, given the extensive infection of weeds with a diversity of begomoviruses prior to the introduction of biotype B in the country. Furthermore, BGM outbreaks continued following the displacement of biotype A by biotype B, indicating that both biotypes are effective vectors of BGMV. This is despite the fact that, in general, beans are less preferred hosts of *B. tabaci* in Brazil compared with cucurbits, soybeans, brassicas or tomatoes. However, because begomoviruses are transmitted in a persistent circulative manner by *B. tabaci*, low populations of viruliferous whiteflies can lead to a high incidence of infection in the field. Thus, the greatest yield losses due to BGM occur when there are high rates of infection early in the growing season, and this is not necessarily correlated with the highest populations of *B. tabaci*.

The causal agent of BGMV is a typical NW bipartite begomovirus (Table 1; Gilbertson *et al.*, 1993). It is the predominant begomovirus associated with BGM in Brazil and Argentina (Faria *et al.*, 2000). Genetic studies have revealed a low level of genetic diversity among BGMV isolates in Brazil (Faria & Maxwell., 1999), which indicates that the virus has undergone

stabilizing selection and is well adapted to the common bean host. In addition to BGMV, other begomoviruses can infect common bean in Brazil, such as *Macroptilium yellow spot virus* (MaYSV), which induces yellow spotting, leaf crumpling and distortion (Ramos-Sobrinho *et al.*, 2014). MaYSV occurs in the North-East region of the country. Recently, an isolate of *Sida micrantha mosaic virus* (SiMMV), a weed infecting begomovirus, was reported infecting common bean in the state of Goiás, where it was associated with golden mosaic, chlorotic spots and leaf distortion (Fernandes-Acioli *et al.*, 2011).

In Mexico and countries of Central America, BGM is also one of the most important diseases of common bean. Here, the disease is caused by a different bipartite begomovirus species, *Bean golden yellow mosaic virus* (BGYMV), with biological (sap transmission and virulence on bean germplasm) and genomic (DNA sequence) properties that are different from those of BGMV (Faria *et al.*, 1994). This was one of the first examples of genetically distinct begomovirus species causing the same type of disease in a crop plant (Gilbertson *et al.*, 1993). This local or parallel evolution of genetically distinct begomoviruses causing a similar disease has proven to be a common phenomenon in the evolution of begomoviruses (Gilbertson *et al.*, 2015). Sources of resistance have been identified for BGYMV and cultivars with some degree of resistance have been released in Central America and Mexico.

The continuing epidemics of BGM in Brazil demonstrate that effective disease management remains a challenge. Resistant cultivars are not commercially available, which reflects a lack of sources of resistance to BGMV in *Phaseolus* germplasm. Management of whitefly populations with insecticides is often not effective, due to the efficiency with which whiteflies transmit the virus and the difficulties in controlling large populations in different crops and weeds.

One approach that can be effective is the implementation of a bean-free period [IN 15, SDA, Ministry of Agriculture,

Livestock and Food Supply (MAPA), Jun 16, 2014], in which growing beans is prohibited for a one month period on a regional basis. For this regulation, the major bean growing regions in central Brazil, which are most severely affected by BGM, were divided into two sub-regions: region 1, comprising the municipalities located in the southern part of the state of Goiás, where the bean-free period is implemented from September 5 to October 5; and region 2, comprising the northern part of Goiás, the Minas Gerais State and the Federal District, where the free period is between September 20 to October 20. This approach takes advantage of the narrow host range of BGMV (primarily common bean and lima bean) and the fact that the virus is not transmitted to the progeny of the whitefly vector. Recent results with a BGMV agroinoculation system has confirmed the narrow host range of BGMV, and supported the use of a bean-free period as a recommended BGM management strategy. Thus, following the host-free period, the inoculum level of the virus is reduced and, hopefully, the whitefly population as well. A similar approach has been effectively used to manage BGM caused by BGYMV in the Dominican Republic.

After the epidemics of BGM in 2013 (G1 Globo, 2013), when growers experienced substantial losses, there was a strong pressure for a response from the Brazilian Ministry of Agriculture. Meetings were held on the local, regional and national levels, and a plan for the implementation of a mandatory bean-free period was agreed upon. Still controversial in many regions, the bean-free period described in the previous paragraph was first implemented in the Federal District in 2013, followed by the states of Goiás and Minas Gerais in 2014. Growers report that since the implementation of the bean-free period, the incidence of BGM has been reduced substantially (Canal Rural, 2015). Therefore, most growers seem to be convinced that the bean-free period is an effective management strategy for BGM, although some remain skeptical. Thus, despite some of the challenges in implementing the bean-free period and the presence of other whitefly

hosts (e.g., soybean, tomato and potato) during this period, it appears that it is a useful management strategy for the disease in Brazil.

Due to the lack of *Phaseolus* germplasm with conventional resistance to BGMV, a transgenic approach has been used to engineer resistance into common bean (Bonfim *et al.*, 2007). Here, a gene silencing (RNA interference) strategy, in which a construct designed to express a double-stranded RNA (dsRNA) corresponding to a portion of the viral gene encoding the replication-associated protein (Rep) was transformed into common bean plants. The expression of the dsRNA triggers silencing of the viral mRNA encoding the Rep, which greatly reduces viral replication. These transgenic plants [Brazilian Agricultural Research Corporation (Embrapa) 5.1 event] are highly resistant to BGMV infection (Aragão *et al.*, 2013). After many years of greenhouse and field testing, followed by biosafety evaluations, these BGMV-resistant transgenic beans were approved for commercial release in 2011. It is expected that seeds of this transgenic bean cultivar will be available for purchase beginning in 2016. However, growers must be aware that the use of the transgenic cultivar represents only one strategy for disease management of BGM, and that this transgenic bean cultivar is not resistant to other bean-infecting viruses, including the whitefly-transmitted *Cowpea mild mottle virus* and, possibly, MaYSV and SiMMV. Thus, other control measures, as part of an integrated pest management (IPM) program (Gilbertson *et al.*, 2011), are needed for effective management of BGM.

Tomato (*Solanum lycopersicum*)

Tomato begomoviruses represent one of the major constraints on tomato production in tropical and subtropical regions of the world. Under high whitefly pressure, yield losses can be as high as 100%. Due to the phenomenon of local evolution, more than 60 species of tomato-infecting begomoviruses have been described worldwide. Indeed, the situation in Brazil is an excellent example of this phenomenon, as at

least 14 distinct indigenous tomato-infecting begomoviruses emerged locally following the introduction of *B. tabaci* biotype B.

The first tomato begomovirus disease in Brazil was tomato golden mosaic (TGM), which was reported in the 1960's (Costa, 1976). The disease was characterized by distorted growth and a yellow to light green mosaic of leaves, and it was shown to be transmitted by whiteflies. As with BGM, it is believed that TGM was transmitted by the indigenous *B. tabaci* biotype A but, in contrast to the situation with BGM, TGM never reached high incidences or caused substantial economic losses. The causal agent of TGM is *Tomato golden mosaic virus* (TGMV; Matyis *et al.*, 1975), a typical NW bipartite begomovirus. Although TGMV never emerged as an economically important virus, it was one of the first begomoviruses to be characterized on the molecular level and it played a key role in studies establishing that some begomoviruses possess a bipartite genome and a number of aspects of viral gene expression and function (e.g., Hamilton *et al.*, 1983). Ironically, these pioneering experiments with TGMV were performed in the laboratory host, *Nicotiana benthamiana*, and it was not until many years later that Koch's Postulates were fulfilled with TGMV in tomato, i.e., reproducing TGM symptoms in tomato with infectious DNA-A and DNA-B clones of the virus (Wyant *et al.*, 2012).

It is believed that one of the reasons that TGM never became an economically important disease in Brazil was that tomato was not a preferred host for *B. tabaci* biotype A. The situation with tomato begomoviruses in Brazil changed dramatically following the introduction of the biotype B, which is highly polyphagous and feeds on tomato, as well as many other crops and non-cultivated plants (e.g., weeds). Indeed, this 'supervector' of plant viruses drove the emergence of new species of tomato-infecting begomoviruses in Brazil (Table 1) and in many other regions of the world (Gilbertson *et al.*, 2015). Moreover, in contrast to the situation in the Caribbean, Mexico

and the southeastern USA, where the invasive OW monopartite TYLCV has emerged as the predominant tomato-infecting begomovirus (Lefeuvre *et al.*, 2010), the viruses emerging in Brazil were unique and emerged from the large and genetically diverse reservoir of indigenous begomoviruses infecting noncultivated plants (weeds) (Rocha *et al.*, 2013).

To date, at least 14 recognized species of tomato-infecting begomoviruses have been described from Brazil (Ribeiro *et al.*, 2003; Fernandes *et al.*, 2006; Castillo-Urquiza *et al.*, 2008; Barbosa *et al.*, 2011; Albuquerque *et al.*, 2012b; Rocha *et al.*, 2013). The disease symptoms induced by these viruses include stunting and distorted growth and golden-light green-yellow mosaic/mottle, crumpling, curling, interveinal chlorosis, rugosity, vein yellowing and purpling, and yellow spotting in leaves (Figures 1B, 2B, 2C). Because these viruses cause similar symptoms in infected tomato plants, molecular tools (RCA, PCR and sequencing) are needed for precise identification. Application of these tools to study Brazilian tomato-infecting begomoviruses has revealed that two viruses are prevalent: *Tomato severe rugose virus* (ToSRV, Figure 2C) and ToMoLCV (Figure 2B). ToSRV is prevalent in central-to-southern tomato growing regions (e.g., the Federal District and states of Minas Gerais, São Paulo and Goiás), whereas ToMoLCV is most common in the north-eastern regions (e.g., the states of Ceará, Piauí and the northern part of Minas Gerais). Interestingly, although most of these viruses are typical NW bipartite begomoviruses, recent studies of ToMoLCV have established that it is another example of an indigenous NW monopartite begomovirus (Gilbertson *et al.*, 2015). Thus, as in many other parts of the world, the invasive *B. tabaci* biotype B has driven the emergence of a diversity of new-tomato infecting begomovirus species via local evolution in Brazil.

Management of diseases caused by tomato-infecting begomoviruses in Brazil requires an IPM strategy (Gilbertson *et al.*, 2011). Unlike the situation in common bean with BGMV,

tomato cultivars with resistance to tomato-infecting begomoviruses are commercially available. These cultivars are hybrids and possess one or more of the begomovirus resistance genes *Ty-1*, *Ty-2*, *Ty-3*, *Ty-4*, *Ty-5*, *ty-5*, *tcm-1*, and *tgr1*. In general, the currently available hybrids are moderately resistant, i.e., they become infected and show mild symptoms of light green mosaic and crumpling of leaves, but they provide acceptable yields in areas where begomovirus disease pressure is high, e.g., states of Goiás, Minas Gerais, Ceará, and São Paulo. It is also important to emphasize that different begomovirus resistance genes do not confer a similar level of resistance to all begomovirus(es); thus, it is critical to evaluate resistant cultivars for their response to the begomoviruses prevalent in a given region before widespread deployment. For example, in Brazil, cultivars with *Ty1/Ty3* genes tend to be resistant, whereas those with the *Ty2* gene are not. It is likely that cultivars with even higher levels of resistance will become available in the future. In Brazil, as in many other tomato-growing regions of the world, it will also be important to combine resistance to begomoviruses and tospoviruses, as the latter are also emerging as major constraints on tomato production (Gilbertson *et al.*, 2015).

A second management strategy that can be very effective for tomato-infecting begomoviruses is the implementation of a tomato- or whitefly host-free period. The underlying basis for the success of this approach is the same as that described for BGM (narrow host range of the virus and no transmission of the virus to the progeny of the whitefly vector). In 2003, a tomato-free period of two months was established for the processing tomato industry by the Ministry of Agriculture in Brazil (IN 024, SDA, MAPA, April 15, 2003). The tomato-free period was officially implemented in the state of Goiás, beginning in 2007 [IN 05/2007; IN 06/2011, Goiás Agency for Agriculture and Livestock Defense (Agrodefesa)]. Tomatoes can be transplanted only from February 1 to June 30 and harvest must be completed by the end of

November. This allows for an annual tomato-free period of at least two months (December and January). The tomato-free period appears to be having a positive effect, delaying the appearance of the virus (helping avoid early infections when plants are most susceptible) and reducing overall disease incidence. For this reason, the tomato-free period is generally accepted by the processing tomato industry and it is being implemented non-officially in other states. Challenges to the effectiveness of the tomato-free period include continuous cropping of indeterminate fresh market tomatoes, which serve as an inoculum source throughout the year, and the apparently wider host range of some tomato-infecting begomoviruses. For example, recent studies have shown that ToSRV can cause a symptomless infection in beans (which can be grown during the tomato-free period) and that whiteflies can acquire the virus from such plants. However, when used as part of an IPM strategy, the tomato-free period is a very effective management strategy.

The worldwide spread of the *B. tabaci* biotype B and plant materials has allowed for the long-distance spread of begomoviruses to new areas (Gilbertson *et al.*, 2015). This is exemplified by the aggressive TYLCV, which has become established throughout the NW and causes severe symptoms of stunting, leaf curling, yellowing and substantial yield loss. Fortunately, TYLCV has not yet been detected in Brazil and efforts to prevent the introduction of this virus should be a priority (e.g., not allowing importation of tomato transplants). In some countries, such as the Dominican Republic, effective management of TYLCV has been accomplished through the use of a three month whitefly-host free period, planting of resistant cultivars (especially late in the season), whitefly management and sanitation, e.g., prompt removal or destruction of plants after harvest (Salati *et al.*, 2002). This IPM strategy has proved to be effective for management of TYLCV and prevented the elimination of the processing tomato industry in the Dominican Republic. In Brazil, although the implementation of a whitefly host-

free period is extremely difficult due to the overlapping cultivation of whitefly hosts (beans, soybeans, cotton, tomatoes and potatoes) in many of the main agricultural areas, it can be helpful as part of an IPM strategy, as discussed in the previous paragraph.

Potato (*Solanum tuberosum*)

Potato is one of the most important crops in Brazilian agriculture. The production is concentrated in the Southeast (e.g., states of Minas Gerais and São Paulo), South (e.g., states of Paraná and Rio Grande do Sul) and Central-West (e.g., state of Goiás) regions of the country. In Brazil, potato has been affected by different viral diseases causing mainly mosaic and leaf rolling symptoms (e.g., *Potato virus Y* - PVY - and *Potato leafroll virus* - PLRV), which often result in yield losses. Whitefly-transmitted begomoviruses have been reported to infect potato in many regions of the world. However, to date, diseases caused by these viruses have not been a major problem for potato production in most regions. In Brazil, begomovirus diseases of potato are not widespread in the main production regions and generally occur at low incidences (Table 1).

The first report of a potato-infecting begomovirus in Brazil was made in the 1980's in the state of Rio Grande do Sul. The disease was referred to as deforming mosaic. Later, it was shown that the disease was caused by an isolate of *Tomato yellow vein streak virus* (ToYVSV), which induces yellow mosaic and leaf distortion symptoms in potatoes (Ribeiro *et al.*, 2006). When the disease was first observed, the incidence was low (3%) and no economic losses were reported. In subsequent surveys, losses as high as 25-40% were attributed to begomovirus infection in some potato fields, indicating that the disease was spreading and started representing a potential threat to potato production (Daniels, 1985). More recently, yellow mosaic disease symptoms (Figure 2D) have re-emerged as a problem on potato in the central-to-south potato producing regions (e.g., states of Goiás, São Paulo, Minas Gerais and the Federal District), and have been shown to be caused by

ToYVSV and ToSRV (Souza-Dias *et al.*, 2008; Lima *et al.*, 2011; Lima & Vieira, 2015). As ToYVSV and ToSRV primarily infect tomatoes, it is believed that tomato plants are the major source for potatoes. Indeed, it was shown that ToYVSV was transmitted to potato plants by whiteflies after short periods of vector feeding on infected tomato plants (Souza-Dias *et al.*, 1996).

Although begomovirus diseases have been detected in some of the main potato producing regions of the country (Table 1), they occur at low incidences. However, as potato is a vegetatively-propagated crop, a major concern is that begomoviruses may be translocated to tubers, producing infected seed tubers, resulting in rapid virus spread and tubers with reduced quality. Lima *et al.* (2012) observed virus transmission rates as high as 80-100% in tubers obtained from begomovirus-infected potato plants. Together with increased whitefly populations on potatoes in tropical and subtropical production regions of Brazil, the potential exists for begomoviruses to become a more important problem for potato production. Moreover, as little is known of the epidemiology of begomovirus diseases of potato in Brazil, it is important to monitor potato production areas for whiteflies and begomovirus disease incidence and species in case these diseases become more important.

Pepper (*Capsicum* spp.)

Pepper is an important crop in Brazil. There is a high level of genetic diversity in the types of pepper grown, and fruits come in a wide range of shapes, sizes, colors and pungency. The predominant species cultivated in Brazil are *Capsicum annuum*, *C. frutescens*, *C. chinense* and *C. baccatum*.

In general, pepper plants are a poor host of *B. tabaci* in Brazil, and other crops such as tomatoes are preferred when grown side-by-side. Consistent with the non-preference of whiteflies for pepper, diseases caused by begomoviruses in pepper are not prevalent or economically important in Brazil. However, over the last decade, the incidence of begomovirus infection in peppers in Brazil has increased. The

first report of a begomovirus infecting sweet pepper in Brazil was in 2001 (Lima *et al.*, 2001) and, in chili pepper, in 2006 (Bezerra-Agassie *et al.*, 2006) when a *C. baccatum* plant with symptoms of virus infection was collected in a survey in the state of Goiás, in 2003. Symptoms in this plant resembled those caused by begomovirus infection in other hosts, e.g., chlorotic spots, rugosity, and mild leaf distortion (Figure 2E), and the bipartite begomovirus ToSRV was detected. *Tomato golden vein virus* and ToYVSV have also been reported in pepper plants in Brazil (Nozaki *et al.*, 2010). In *C. annuum*, yield losses of 28-45% have been attributed to begomovirus infection indicating the potential importance of such diseases in Brazil. At present, no *Capsicum* spp. germplasm with resistance to begomoviruses is available.

Whereas diseases caused by other viruses are clearly more important in pepper in Brazil (e.g., potyviruses such as *Pepper yellow mosaic virus*), it should be noted that pepper-infecting begomoviruses are very important and cause substantial yield losses in other areas of the world, including Mexico and Central America in the NW and Asia (especially India) and Africa in the OW. Mixed infections of begomoviruses and aphid-transmitted viruses are also prevalent in these regions. This demonstrates that pepper can be a suitable host for *B. tabaci* populations in other regions of the world, and that the insect vector is not genetically homogenous, at least in terms of host preference. Thus, the emergence of begomoviruses as economically important viruses of pepper in Brazil is a possibility, and pepper fields in different growing regions of Brazil should be monitored for whitefly populations and appearance of unusual virus symptoms.

Sweet potato (*Ipomoea batatas*)

Sweet potato is a vegetatively propagated crop, and planting of virus-infected cuttings is a serious problem that can lead to high levels of infection, as well as losses in yield and quality. In general, sweet potato plants are commonly infected by multiple viruses in the field, including RNA viruses such

as criniviruses and potyviruses, and DNA viruses such as begomoviruses. Begomovirus symptoms in sweet potato include leaf curling, crumpling and vein yellowing. However, diagnosis of

begomovirus infection in sweet potato based upon symptoms is very difficult, and molecular methods are needed for definitive identification.

Begomoviruses have been detected

infecting sweet potato plants throughout the world, and the presence of some of these viruses in sweet potato plants from multiple continents suggests long-distance spread in association

Table 1. Geminivirus species reported on vegetable and other crops in Brazil, and recognized by the International Committee on Taxonomy of Viruses (espécies de geminivírus relatadas em hortaliças e outras culturas no Brasil e reconhecidas pela Comissão Internacional de Taxonomia de Vírus). Brasília, Embrapa Vegetables, 2015.

Crop	Acronym	Species	Type	Importance
Beans	BGMV	<i>Bean golden mosaic virus</i>	Bipartite	Major importance, widespread
	MaYSV	<i>Macropodium yellow spot virus</i>	Bipartite	Important in North-East
	SiMMV	<i>Sida micrantha mosaic virus</i>	Bipartite	Important in weeds, widespread
Okra	OMoV	<i>Okra mottle virus</i>	Bipartite	Minor importance, one report
	SiMMV	<i>Sida micrantha mosaic virus</i>	Bipartite	Important in weeds, widespread
Pepper	TGVV	<i>Tomato golden vein virus</i>	Bipartite	Minor importance
	ToSRV	<i>Tomato severe rugose virus</i>	Bipartite	Major importance, widespread
	ToYVSV	<i>Tomato yellow vein streak virus</i>	Bipartite	Minor importance
Potato	ToSRV	<i>Tomato severe rugose virus</i>	Bipartite	Widespread, potentially important
	ToYVSV	<i>Tomato yellow vein streak virus</i>	Bipartite	Minor importance
Soybeans	BGMV	<i>Bean golden mosaic virus</i>	Bipartite	Widespread, but minor importance
	SiMMV	<i>Sida micrantha mosaic virus</i>	Bipartite	Minor importance, one report
	SiMoV	<i>Sida mottle virus</i>	Bipartite	Minor importance, one report
	SoCSV	<i>Soybean chlorotic spot virus</i>	Bipartite	Minor importance, one report
Sweet potato	MerLCV	<i>Merremia leaf curl virus</i>	Monopartite	Minor importance, one report
	SPGVV	<i>Sweet potato golden vein virus</i>	Monopartite	Minor importance, one report
	SPLCBRV	<i>Sweet potato leaf curl Brazil virus</i>	Monopartite	Minor importance, one report
	SPLCLaV	<i>Sweet potato leaf curl Lanzarote virus</i>	Monopartite	Minor importance, one report
	SPLCESP	<i>Sweet potato leaf curl Spain virus</i>	Monopartite	Minor importance, one report
	SPLCSPV	<i>Sweet potato leaf curl Sao Paulo virus</i>	Monopartite	Minor importance, one report
	SPLCV	<i>Sweet potato leaf curl virus</i>	Monopartite	Major importance
	SPMV	<i>Sweet potato Malaga virus</i>	Monopartite	Minor importance, one report
	SiMMV	<i>Sida micrantha mosaic virus</i>	Bipartite	Minor importance
	SiMoV	<i>Sida mottle virus</i>	Bipartite	One report
Tomato	TGMV	<i>Tomato golden mosaic virus</i>	Bipartite	Not detected any more
	TGVV	<i>Tomato golden vein virus</i>	Bipartite	Minor importance
	TMiMV	<i>Tomato mild mosaic virus</i>	Bipartite	Minor importance, one report
	ToCmMV	<i>Tomato common mosaic virus</i>	Bipartite	Minor importance
	ToCMoV	<i>Tomato chlorotic mottle virus</i>	Bipartite	Minor importance
	ToICV	<i>Tomato interveinal chlorosis virus</i>	Bipartite	Minor importance, one report
	ToLDV	<i>Tomato leaf distortion virus</i>	Bipartite	Minor importance, one report
	ToMoLCV	<i>Tomato mottle leaf curl virus</i>	Monopartite	Major importance, especially in North-East
	ToRMV	<i>Tomato rugose mosaic virus</i>	Bipartite	Not detected any more
	ToSRV	<i>Tomato severe rugose virus</i>	Bipartite	Major importance, widespread
	ToYSV	<i>Tomato yellow spot virus</i>	Bipartite	Minor importance
ToYVSV	<i>Tomato yellow vein streak virus</i>	Bipartite	Minor/local importance	

with propagative materials (cuttings and roots). Indeed, evidence of the importance of propagative materials as a means of spread for these viruses comes from the observation that many of them are inefficiently transmitted by whiteflies. In Brazil, eight begomovirus species have been reported from sweet potato including *Sweet potato leaf curl virus* (SPLCV), *Sweet potato golden vein virus* (SPGGV), *Sweet potato leaf curl Spain virus* (SPLCESV), *Sweet potato leaf curl Sao Paulo virus*, *Merremia leaf curl virus*, *Sweet potato leaf curl Brazil virus*, *Sweet potato Lanzarote virus* and *Sweet potato Malaga virus* (Paprotka *et al.*, 2010; Albuquerque *et al.*, 2011, 2012a). The genome of these viruses is monopartite and most similar to those of OW begomoviruses. Together with reports of some of these viruses from OW locations, it is likely that these viruses or their progenitors were introduced into Brazil on multiple occasions in association with propagative materials. No information is available regarding begomovirus-resistant germplasm and yield losses caused by these viruses in Brazil. The use of virus-free propagative materials is the best way to control sweet potato viruses. For this reason, many countries have clean stock programs, based on eliminating viruses via meristem tip culture, for providing growers with virus-free sweet potato

planting material.

Okra (*Abelmoschus esculentus*)

Okra (family Malvaceae) is typically grown by smallholder farmers in Brazil. A number of other Malvaceous crops are grown in Brazil, most notably cotton, but also hibiscus. In addition, numerous Malvaceous weeds (e.g., *Malva* spp. and *Sida* spp.) can be found throughout Brazil, and often show symptoms of begomovirus infection (e.g., yellow mosaic and mottle). However, begomovirus diseases have not emerged as economic problems in okra (or cotton or hibiscus). The reason for this is not clear, as these plants are hosts of whiteflies (especially cotton), and a diversity of begomoviruses infect Malvaceous weeds, and these could serve as progenitors for begomoviruses infecting Malvaceous crops in Brazil. In the past, a disease known as okra mosaic was reported in Brazil, and the causal agent was believed to be a begomovirus. However, the disease was apparently effectively controlled by the use of resistant varieties. Thus, it is possible that okra plants are resistant to the major begomoviruses in Brazil. Two begomoviruses have been reported infecting okra plants in Brazil, SiMMV (Aranha *et al.*, 2011) and *Okra mottle virus* (OMoV) (Albuquerque *et al.*, 2013). Not surprisingly, the source of these viruses was believed to be infected

Malvaceous weeds. The symptoms induced in okra by these begomoviruses were mild mottling and chlorotic spots. It is not believed that these viruses reach high incidences of infection or cause economic losses in okra and, thus, may be spill over from infected weeds. As these viruses infect other plants, including common bean, soybean and weeds, it is possible that okra plays a role as a reservoir in some agricultural ecosystems.

Soybean (*Glycine max*)

Soybeans are extensively grown in Brazil and are one of the most important agricultural commodities. Planting is usually done between October and December and the harvest is from January to April. Soybeans are a preferred host of *B. tabaci*, and heavy infestations can be observed in soybean fields, particularly in hot and dry periods (summer months and 'veranico' periods). Growers typically do not manage whitefly populations in soybean as it is believed that this insect causes little or no yield loss. In some cases, growers may try to control whiteflies late in the growing season to prevent damage from sooty mold, but this is usually unsuccessful. Although begomovirus diseases are not economically important, soybeans can be infected with a number of begomoviruses, such as BGMV, SiMMV, *Sida mottle virus* and *Soybean*

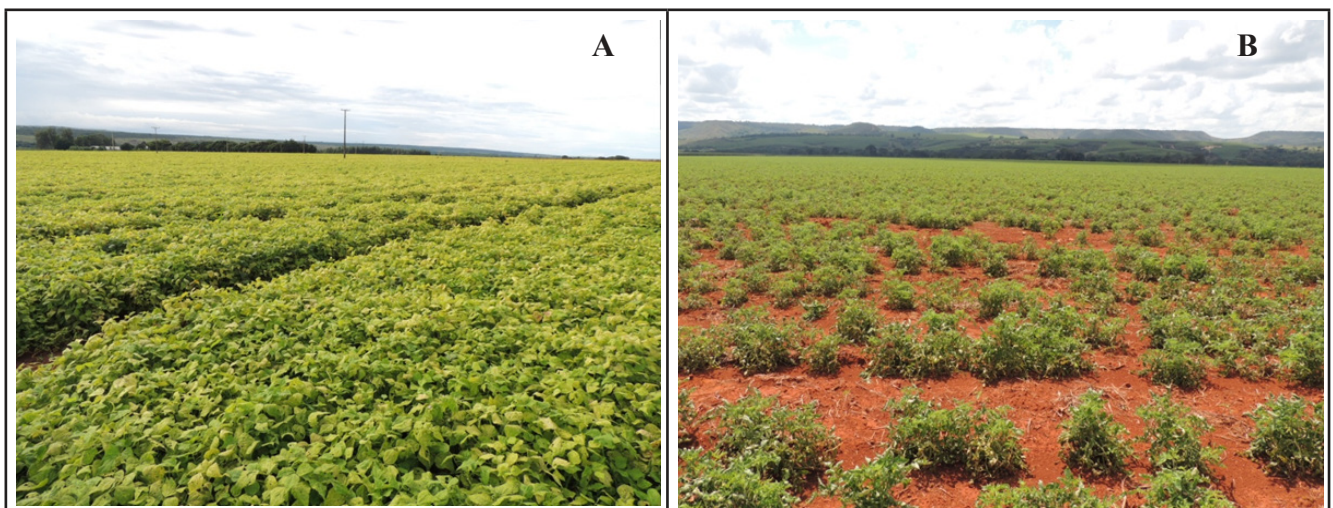


Figure 1. Fields with 100% incidence of begomovirus disease. (A) A common bean field with *Bean golden mosaic virus* (BGMV), and (B) a tomato field with *Tomato severe rugose virus* (ToSRV) {lavouras com 100% de incidência de begomoviruses. (A) Lavoura de feijão com o *Bean golden mosaic virus* (BGMV), e (B) Lavoura de tomate com o *Tomato severe rugose virus* (ToSRV)}. Brasília, Embrapa Vegetables, 2015.

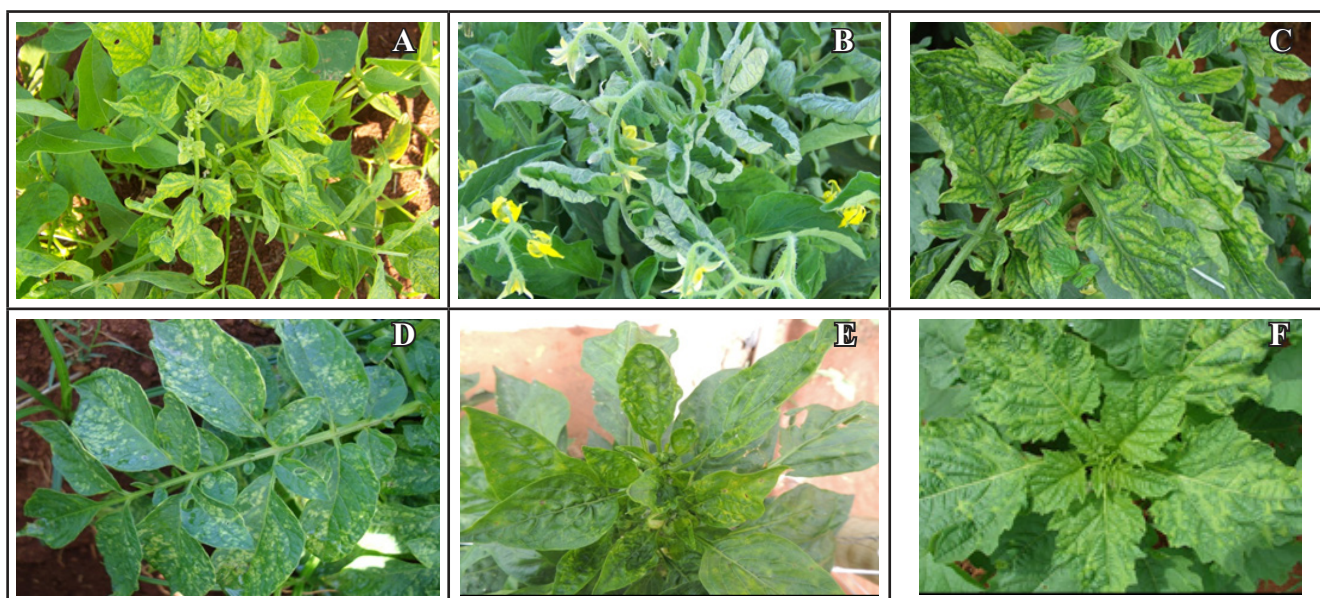


Figure 2. Begomovirus disease symptoms. (A) Common bean infected with BGMV; (B) tomato infected with *Tomato mottle leaf curl virus* (ToMoLCV) and (C) *Tomato severe rugose virus* (ToSRV); (D) potato and (E) pepper with symptoms of begomovirus infection, and; (F) *Nicandra physaloides* infected with ToSRV {sintomas de begomovirose. (A) Feijoeiro infectado por BGMV; (B) tomateiro infectado pelo *Tomato mottle leaf curl virus* (ToMoLCV) e (C) pelo *Tomato severe rugose virus* (ToSRV); (D) batateira e (E) pimenteira com sintomas de infecção por begomovirus e; (F) *Nicandra physaloides* infectada por ToSRV}. Brasília, Embrapa Vegetables, 2015.



Figure 3. Adult of whitefly *Bemisia tabaci* (A) and a tomato leaf infested by adult whiteflies (B) {adulto da mosca branca *Bemisia tabaci* (A) e uma folha de tomateiro infestada por adultos da mosca branca (B)}. Brasília, Embrapa Vegetables, 2015.

chlorotic spot virus (Table 1; Coco *et al.*, 2013; Fernandes *et al.*, 2009). Symptoms of begomovirus infection in soybean include stunting, distorted growth and blistering, chlorotic spots, and light green to golden-yellow mosaic/mottling of leaves. Thus, under high begomovirus

disease pressure it is possible that yield losses could occur and that this could justify a program for managing viruses and whiteflies. Recently, some soybean growers have become aware of the risk posed by begomovirus diseases in soybean production and

whitefly management efforts have been implemented. Such programs would directly benefit soybean growers, as well as indirectly benefit growers of other crops, by reducing the multiplication of whiteflies that migrate out in clouds to other plants.

Concluding remarks

What should be clear from this review is that the begomovirus situation in Brazil has many characteristics that are unique, including the viruses involved (mostly locally evolved) and the crops most heavily impacted (beans and tomato). The lack of begomovirus disease problems in crops such as cotton, okra and pepper, which are heavily impacted by such diseases in other parts of the world, likely reveals differences in properties of the virus progenitors in noncultivated plants (weeds) and the whitefly (host preference). The overlapping and extensive cropping of preferred whitefly hosts in Brazil (beans, soybeans, cotton and tomato) also presents unique challenges for effective and sustainable management of begomovirus diseases. On the other hand, a factor common to Brazil and other regions of the world has been the introduction and establishment of the

B. tabaci B biotype (Figure 3) and the subsequent emergence of economically important diseases caused by tomato-infecting begomoviruses (Table 1). Following the introduction of the biotype B into Brazil, many factors have contributed to the spread and build-up of populations and the level of damage they cause. These include irrigation; intensive cultivation and monoculture of preferred host plants (beans, soybeans, cotton, potato and tomato) throughout the year; greenhouse cultivation, resulting in whitefly propagation during cold periods; lack of effective insecticides and emergence of insecticide-resistant whitefly populations; and the widespread use of transgenic plants resistant to worm pests (cotton, corn, and soybean) that results in reduced application of broad-spectrum insecticides. This means management of whiteflies and the viruses they transmit will continue to be a major challenge for agriculture in Brazil and that the emergence of new whitefly-transmitted virus diseases and changes in the biology of the whitefly should be expected.

It should also be clear that management of whiteflies and begomovirus diseases cannot be accomplished by any single control measure, especially reliance on insecticides, and that an IPM approach is needed (Gilbertson *et al.*, 2011). Indeed, the efficient transmission of begomoviruses by whiteflies has consistently thwarted efforts to manage begomovirus diseases with insecticides. Fortunately, progress is being made and IPM programs for begomovirus diseases in beans and tomatoes are being implemented in Brazil and showing some success. An important tool is begomovirus-resistant cultivars, and these are now available for tomato (conventionally bred hybrids) and should be available soon for common bean (transgenic resistance). The implementation of bean- and tomato free periods are taking advantage of biological properties of the virus and vector (narrow viral host range and lack of transmission of the virus to whitefly progeny) and reducing inoculum levels at the beginning of the growing season, when plants are most vulnerable to virus infection. Management of whitefly

populations with insecticides will continue to be an important tool, but it should be done based on IPM, i.e., only when populations reach defined thresholds and using rotation of different chemistries. The availability of new and improved chemistries for whitefly management should allow for better management, but it will be important to facilitate the registration of these materials in a timely manner so they will be available to growers in Brazil. Unfortunately, biological control of whiteflies in open fields is not effective or practical at the present time.

It is also imperative that efforts to manage the whiteflies and begomovirus diseases are done on a regional basis. In this regard, the capacity of all interested parties (academia, government, and growers) to get together and implement crop-free periods has been very encouraging. This will continue to require careful planning of such periods, including the area and crops to be included in different regions; the crop succession in each area; and the development and implementation of an IPM strategy for each crop. Successful IPM packages will involve some combination of planting virus-free propagative materials (e.g., sweet potato); utilizing resistant cultivars; implementing effective whitefly management strategies; roguing or removing infected plants early in the season; effective sanitation following harvest; management of weeds and volunteers; and implementation of a host-free period.

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