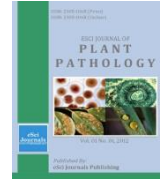




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## WHITEFLY- A STRONG TRANSMITTER OF PLANT VIRUSES

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### ABSTRACT

*Bemisia tabaci* transmit 111 viruses. The silver leaf/sweet potato whitefly prefers 25°C to 30°C for development and rapid generation time while the greenhouse whitefly prefers temperatures of 20°C to 25°C. Eggs hatch in eight to 10 days. Resistance in B- and Q-biotype of *B. tabaci* appears to be linked to enhanced oxidative detoxification of neonicotinoids. Transmission efficiency from infected weeds to tomato varied from 66.7 to 100 percent, whereas, from tomato to these weeds varied from 58.3 to 83.3 percent. Increased mortality of biotype Q females and immature instars with lower rate of fecundity and progeny size compared to biotype B was recorded in such population when reared in single or mixed cultures. Two genetic types of *B. tabaci* were distinguished using RAPD-PCR and cytochrome oxidase I (COI) gene sequence comparisons. One type was assigned to biotype B and the other was genetically dissimilar to the populations described elsewhere and was named Ms. This new genetic type forms a distinct group that is sister to two other groups, one to which the B biotype is a member and Q biotype have similar values of intra population diversity, which were higher than the values shown by populations of biotype B. Epidemics of begomoviruses have been observed in many crops including tomato for which *Tomato yellow leaf curl China virus* (TYLCCNV) and *Tomato yellow leaf curl virus* (TYLCV) have been identified as two major disease-causing agents. The replication of geminiviruses induces micro-structural changes in the nucleus of the host cells. The begomovirus vector *B. tabaci* is an insect species complex that has geographically distinct phenotypic and genotypic variants. Criniviruses are limited to phloem and are transmitted in nature in a semipersistent manner by whiteflies. The genus *Ipomovirus* includes viruses that are transmitted by the whitefly *B. tabaci* in a semipersistent manner. Virus particles occur in the cytoplasm singly or more often in large aggregates which are sometimes banded. The stem necrosis of soybean is caused by a virus of the *Carlavirus* and transmitted by the whitefly *Bemisia tabaci*, also infected beans and identified as *Cowpea mild mottle virus*. The early symptoms of *Tomato torrado virus* are necrotic or dead spots, surrounded by a light green or yellow area at the base of the leaflets. The affected areas may fall out, leaving holes (shot holes) in the leaflets. Necrosis and mottling extend to the remainder of the leaves. The article will bring role of whitefly in development of virus diseases in agricultural crops and management strategies could only be achieved when importance of this pest will be eradicated with non-chemical approach.

**Keywords:** Whitefly, *B.tabaci*, viruses, importance, biotypes, movement, genetic diversity.

### INTRODUCTION

One hundred and eleven viruses are transmitted by silver whitefly (*Bemisia tabaci*) while green house (*Trialetrodes vaporariorum*) and banded winged (*T. abutilonia*) transmit three species, out of 114 virus species transmitted by whiteflies (family Aleyrodidae). Among whitefly transmitted viruses 90% belong to the Begomovirus, 6% Crinivirus and remaining 4% are in the Closterovirus, Ipomovirus and Carlavirus genera.

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(Jones, 2003). The three genera Begomovirus (Geminiviridae), Crinivirus (Closteroviridae) and Ipomovirus (Potyviridae), infect sweet potato (*Ipomoea batatas*) and are transmitted by whiteflies. The *Sweet potato leaf curl virus* (SPLCV) and *Ipomoea leaf curl virus* (ILCV) are Begomovirus and *Sweet potato mild mottle virus* (Ipomovirus) are transmitted by sweet potato whitefly (*Bemisia tabaci*). The *Sweet potato chlorotic stunt virus* (SPCSV) of crinivirus, is transmitted by *B. tabaci* and banded winged whitefly (Valverde *et al.*, 2004). For transmission of these three viruses, reared whiteflies are required, and need two days for

acquisition and transmission feeding period. *Sweet potato leaf curl virus* and *Ipomoea leaf curl virus* were transmitted from single and double infections by *B. tabaci* at rates of 5-10%. Transmission rate for SPLCV by *B. tabaci* was 15-20%. *T. abutilonea* transmitted SPCSV at a rate of 3% but did not transmit *Ipomoea leaf curl virus* or *Sweet potato leaf curl virus*.

The greenhouse whitefly (*Trialeurodes vaporariorum* Westwood) is capable of reducing plant productivity and longevity besides acting as vector of plant virus (Wintermantel, 2004). Two strains of whitefly transmitted *Cowpea mild mottle virus* causing severe (CPMMV-S) and mild (CPMMV-M) disease symptoms in peanuts in two distinct agro-ecological zones in India have been noticed in past. The host-range of these strains was restricted to plants belonging to Leguminosae and Chenopodiaceae with distinguished symptoms incited in different hosts. The 3'-terminal 2500 nucleotide sequence of the genomic RNA of both the strains, 70 percent are identical and contain five ORF. The first three (P25, P12 and P7) overlap to form a triple gene block of proteins, P32 encodes the coat protein, followed by P12 protein located at the 3' end of the genome. Genome organization and pair-wise comparisons of amino acid sequences of proteins encoded by these ORFs with corresponding proteins of known Carla and Potexviruses suggest that CPMMV-S and CPMMV-M are closely related to Carlavirus (Naidu *et al.*, 1998). Ng *et al.* (2011) developed "Vector-enabled metagenomics" (VEM) to investigate the diversity of plant viruses. VEM involves sampling of whiteflies from plants, followed by purification of viral particles and metagenomic sequencing. The VEM approach exploits the natural ability of highly mobile adult whiteflies to integrate viruses from many plants over time and space, and leverages the capability of metagenomics for discovering novel viruses. *Trialeurodes vaporariorum*, *T. abutilonea* and *Parabemisia myricae* other than *B. tabaci* transmitted *Beet pseudo-yellow virus* and have been reported from USA, Europe, Japan and Australia, but so far not from Africa, South America or continental Asia. Virus usually infect Chenopodiaceae, Compositae, Cruciferae, Cucurbitaceae and Solanaceae plants, infection develop chlorotic spots, yellowing or chlorosis, and thickening, brittleness and downward curling of leaves.

Mosaic, leaf curl, and yellowing types are whitefly-transmitted diseases which are recognized on symptoms

of New World begomoviruses, Old World begomoviruses, and Criniviruses, respectively. Mostly whitefly-transmitted viruses are caused by "dimers, or siamese twin particles" (Turina *et al.*, 2007) and predominant among the whitefly-transmitted disease agents. Over the past 20 years or so, begomoviruses have emerged as serious constraints to the cultivation of a variety of vegetable crops (chilli, okra and tomato) especially in the tropics and subtropics. Some devastating begomoviruses have moved to temperate regions, seriously resulting in reduce production of greenhouse crops. The emergence of begomoviruses is associated with changes in crop cultivation, increased global movement of plants, changes in cropping practices and intensive use of insecticides. The spread of begomoviruses by *B. tabaci* has been facilitated by the introduction in many areas of the polyphagous B biotype of *B. tabaci*, which feeds on a wide range of plants and thus has a high probability of acquiring and transmitting a diversity of begomoviruses into potential new hosts. In the mid-1980s, for example, B biotype was introduced into the New World, where it often displaced the local A biotype, which is less polyphagous than B biotype. Begomoviruses have supplanted potyviruses as the group of plant viruses with the largest number of recognized species. *B. tabaci* has also been involved in the emergence of new diseases caused by other groups of viruses, such as Criniviruses (Wisler *et al.*, 1998) or Ipomoviruses (Adkins *et al.*, 2010). *Trialeurodes vaporariorum*, another whitefly is able to transmit some criniviruses restricted to greenhouse crops but it is recently increasingly important as a pest in open-field over the past 20 years in tomato (*Solanum lycopersicum*), cassava (*Manihot esculenta*), cucurbits, and other important crops (Wintermantel, 2004).

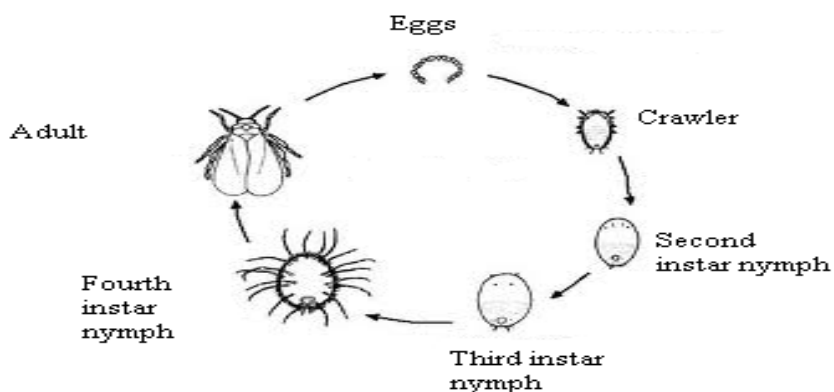
#### WHITEFLY

**Life cycle:** The life cycle of the silver leaf, sweet potato, common whitefly, greenhouse and banded whitefly are similar, although the two species prefer different temperature ranges for optimal development. The silver leaf/sweet potato whitefly prefers temperatures of 25°C to 30°C for development and rapid generation time while the greenhouse whitefly prefers temperatures of 20°C to 25°C. Whitefly eggs are attached to the underside of the leaf surface, usually younger leaves. Eggs hatch in eight to 10 days. There are four immature or nymph stages. Crawlers or first instars nymphs crawl a short distance before settling to feed on plant tissue.

Second and third instars nymphs are stationary and remain attached to the leaf surface where they feed until developing into the fourth and final nymph stage. These fourth instars nymphs stop feeding, pupate and emerge from the pupae case as fully developed adults. The active adult whitefly is largely responsible for virus spread from plant to plant.

The silver leaf whitefly takes 18 to 28 days from egg to adult in warm weather and 30 to 48 days in winter. At 22°C the greenhouse whitefly completes its life cycle in about 28 days. Abdullah and Singh (2004) found effect of

duration on different immature stages. Shorter during August (17.9 days) than September (20 days) was their finding. The survival was maximum (66.7%) during August than in September (59.2%), longevity was higher in November (15.3 and 20 days) for male and female, than June (3.7 and 5.6 days) for male and female. Fecundity was higher during November-December (30.6) than June (17.1). The sex ratio was in favour of females: male (1.03:1) during November-December and 1.85:1 during June on cotton in Ludhiana.



**Life cycle of whitefly**

### BIOTYPES DEVELOPMENT

**(i) Insecticides:** Resistance to neonicotinoid (chloronicotinyls) insecticides has recently been shown to occur, especially in Q type *B. tabaci* in some places in America, Spain, whereas control of B biotype *B. tabaci* in many other intense cropping systems worldwide has remained on high levels. The biochemical mechanisms conferring resistance to neonicotinoids have not yet been elucidated in detail, but synergistic studies suggested a possible involvement of microsomal monooxygenases. However, neonicotinoid resistance is not due to an altered [3H] imidacloprid binding site of nicotinic acetylcholine receptors (Nauen *et al.*, 2002).

Resistance to imidacloprid using [3H] imidacloprid in nicotinic acetylcholine receptor (nAChR) binding assays could not be detected in any of these highly resistant strains. The impact of metabolizing enzymes such as esterases, glutathione S-transferases [glutathione transferase], and cytochrome P450-dependent monooxygenases in neonicotinoid resistance was studied biochemically with artificial substrates. Monooxygenase activity was increased 2-3-fold in moderately resistant strains (RF ~30) and even 5-6-fold in highly resistant strains (RF ~1,000). Only

monooxygenase activity correlated with imidacloprid, thiamethoxam and Acetamiprid resistance and, therefore, monooxygenases seem to be the only enzyme system responsible for neonicotinoid resistance in *B. tabaci* Q and B types. The oxidative degradation of imidacloprid in resistant Q type strains could be confirmed by metabolism studies of [14C] imidacloprid *in vivo* (Rauch and Nauen, 2003).

Efficacy of spiromesifen against insecticide-resistant 'Q' biotypes of *Bemisia tabaci* has been reported from Israel and Spain. Spiromesifen was extremely effective against early instars at LC50s of 0.1-6.2 ppm for 12-day-old nymphs. Spiromesifen was highly effective against pyriproxyfen- and imidacloprid-resistant whitefly. Transovariol effects on oviposition and egg hatch were noticed by Spiromesifen. One Spanish 'Q' type was significantly less susceptible (15-fold) (Guthrie *et al.*, 2003).

The biotype status of whitefly *Bemisia tabaci* survey provided evidence for the occurrence of the *B. tabaci* Q biotype, alongside the more widely distributed B biotype. Both B and Q biotypes are present in Israel (Horowitz *et al.*, 2003). Biotypes of *B. tabaci* resistance to pyriproxyfen in the untreated strains substantially

declined and concurrent with a replacement of Q biotype by B type under non-insecticidal regimes indicated that B biotype was more competitive than the pyriproxyfen-resistant Q-type. Selection under controlled conditions with neonicotinoids on these *B. tabaci* strains which resulted in continued pyriproxyfen resistance, predominantly of Q biotype. Applications of either pyriproxyfen or neonicotinoids may select for biotype Q, which would survive to a greater degree where these insecticides were applied (Horowitz *et al.*, 2005).

Ecdysone agonists (tebufenozide and methoxyfenozide), juvenile hormone mimics (pyriproxyfen and fenoxycarb), and chitin synthesis inhibitors (benzoylphenyl ureas and buprofezin) are compounds which affect the hormonal regulation of molting and developmental processes in insects. Nicotinic acetylcholine receptor such as imidacloprid, Acetamiprid, and thiamethoxam has been introduced for the control of whiteflies and other insects (Ishaaya *et al.*, 2005).

Imidacloprid a neonicotinoid was first time introduced to the market in 1991 later several others belonging of the same chemical class and with the same mode of action were also introduced. Neonicotinoid has provided invaluable new tool for managing aphids, whiteflies, plant hoppers and beetles. Stronger resistance has been confirmed in some populations of whitefly, *Bemisia tabaci*, and *Leptinotarso decemlineata*. Resistance in B- and Q-biotype of *B. tabaci* appears to be linked to enhanced oxidative detoxification of neonicotinoids due to over expression of monooxygenases (Nauen and Denholm, 2005).

**(ii) Host:** Plants viz., *Datura stramonium*, *Solanum nigrum*, *Brassica kaber*, *Capsella bursa-pastoris* and *Malva parviflora*, were evaluated against an isolate of TYLCSV from Murcia, Spain (TYLCSV-ES), using the B, Q and S biotypes of *B. tabaci* as vectors. Both B and Q biotypes transmitted TYLCSV-ES from infected tomato to *S. nigrum* and *D. stramonium* and vice versa. The transmission efficiency from tomato to these weeds varied from 58.3 to 83.3%. Transmission efficiency from infected weeds to tomato varied from 66.7 to 100.0%. The B and Q biotypes did not significantly vary in terms of transmission efficiency from infected tomato to weed plants and from *D. stramonium* to tomato. However, a significant difference in transmission efficiency from infected *S. nigrum* plants to tomato was detected between the B and Q biotypes. No other tested weed

species were infected by TYLCSV-ES. The S-biotype was unable to survive in tomato long enough to acquire or transmit TYLCSV-ES. This biotype could only transmit the virus from *S. nigrum* to *S. nigrum* at a very low efficiency (Jiang *et al.*, 2004). The highest fecundity (eggs) and fertility (pupae and adults) were obtained with *Malva parviflora* L. followed by *Capsella bursa-pastoris* L., *Brassica kaber* (DC) and *Lactuca serriola* L. both B and Q biotypes preferred *Datura stramonium* and *Solanum nigrum* to *Amaranthus retroflexus*, *Chenopodium album* and *Echinochloa crus-galli*. More number of male and female, and more pupae and empty pupa cases per plant were associated on *D. stramonium* than on *S. nigrum*. Very low adult abundance was recorded on *A. retroflexus*, *C. album* and *E. crus-galli*. At a constant temperature of  $26 \pm 1^\circ\text{C}$ , the Q biotype developed significantly faster than the B biotype on *S. nigrum* and *D. stramonium*

**(iii) Environment:** Developmental rates of the B and Q biotypes of *Bemisia tabaci* at 17, 20, 23, 26, 30, 33, and  $35^\circ\text{C}$  on sweet pepper, *Capsicum annum* exhibited that egg incubation period and the times required to complete development at all immature stages decreased with increasing temperature up to  $33^\circ\text{C}$ . The relationships between developmental rate of *B. tabaci* and temperature were influenced by the insect biotype. The simple linear model  $tT = K+ct$  suffices for predicting B and Q biotype phenologies on sweet pepper for the range of temperature ( $17-33^\circ\text{C}$ ). The shortest developmental times as well as the lowest developmental thresholds and thermal constants were mostly obtained with the Q-biotype. Overall, the most favorable temperature range appeared to be  $31-33^\circ\text{C}$ . Mean generation times (adult to adult) ranged from 17 d (Q-biotype) and 18 d (B-biotype) at  $33^\circ\text{C}$  to 49 d (B-biotype) and 46 d (Q biotype) at  $17^\circ\text{C}$  (Muniz and Nombela, 2001).

**(iv) Chemical elicitors:** Chemical elicitors induce plant resistance to insects and other pests in plants. Benzo [1,2,3] thiadiazole-7-carbothioic acid-S-methyl ester (BTH), induced plant resistance to the B and Q biotypes of *Bemisia tabaci* after foliar application of Bion on tomato cv. Marmande. Adult Q-biotype *B. tabaci* significantly preferred control plants to plants sprayed with Bion at 0.2 g/l, number of eggs laid on treated plants was lower, but female fecundity was not affected. After 23 days, a decrease in the number of empty pupal cases was also observed on plants treated

with Bion at 0.2 g/l. The effect produced by Bion applied at 0.1 g/l was not significant. In a no-choice assay, only one leaflet from each tomato plant was treated with either 1 g Bion/litre or water (control plants). A clip-cage containing 5 *B. tabaci* females (biotype B) was attached to each treated leaflet and to another non-treated leaflet from each plant. After 16 days, the total number of immature insects (eggs+L1+L2) on Bion-treated leaflets was significantly lower than on the water-treated leaflets from the control plants. This difference was mostly due to the number of L1 larvae. The acquired resistance seemed to be very localized (LAR) and gave the differences between Bion-treated and non-treated leaflets on the same plants, while no differences were observed between Bion-treated and control plants in the case of non-treated leaflets (Pascual *et al.*, 2003).

**(v) Population:** Pascual and Callejas (2004) collected biotypes B and Q of *Bemisia tabaci* from the islands of Tenerife and Majorca and exposed to competition conditions on tomato (cv. Marmande). They established both biotypes either in single and/ or mixed cultures at different densities. Increased mortality of biotype Q females and immature instars was observed together with a lower rate of fecundity and progeny size compared to biotype B, when reared in single or mixed cultures. The female: male sex ratio of F1 individuals of biotype Q was higher in single than in mixed cultures. However, the sex ratio of F1 individuals of biotype B was the same in single and mixed cultures, suggesting reproductive interference. Whitefly density did not affect inter specific interactions. It had a moderate effect on developmental rate of both biotypes, and on mortality of immature instars and progeny size of biotype B only.

**(vi) Genetics:** Genetic diversity of Iberian populations of *Bemisia tabaci* is based on random amplified polymorphic DNA-polymerase chain reaction. The genetic structure of six Iberian populations of the whitefly *Bemisia tabaci* two of them biotype Q, one biotype B, and the other three a mixture of both. Pair wise number of differences between haplo types showed that biotypes contribute significantly more to the observed variability than populations within biotypes. On average, gene flow between two biotypes of the same population is lower than between populations of identical biotypes. On the basis of these results and the non-detection under natural conditions of a single

hybrid, it is considered that both biotypes are genetically isolated under the ecological conditions prevailing in the south Iberian Peninsula. All populations of biotype Q presented similar values of intra population diversity, which were higher than the values shown by populations of biotype B (Moya *et al.*, 2001).

A new silver leaf whitefly - inducing biotype Ms of *Bemisia tabaci* (Hemiptera: Aleyrodidae) indigenous to the islands of the South-West Indian Ocean has been reported. Two genetic types of *B. tabaci* were distinguished using RAPD-PCR and cytochrome oxidase I (COI) gene sequence comparisons. One type was assigned to biotype B and the other was genetically dissimilar to the populations described elsewhere and was named Ms. This new genetic type forms a distinct group that is sister to two other groups, one to which the B biotype is a member and one to which the Q biotype belongs. The Ms Biotype is thought to be indigenous to the region as it was also detected in Mauritius, the Seychelles and Madagascar. Both B and Ms Populations of *B. tabaci* induced silver leaf symptoms on *Cucurbita* sp. and were able to acquire and transmit TYLCV. Taken together these results indicate that the Ms genetic type should be considered a new biotype of *B. tabaci* (Delatte *et al.*, 2005).

#### **VIRUSES TRANSMITTED BY WHITEFLIES**

Most plant viruses require a vector for plant-to-plant spread number of different type of organisms are vectors for different plant viruses, hemipteroid, phloem-feeding insects (aphids, whiteflies, leafhoppers, and planthoppers) are the most common and transmit the great majority of plant viruses. Two modes of transmission of viruses by whiteflies may be distinguished, semipersistent and persistent (Fig.1). Semipersistent transmission requires minutes to hours for acquisition and has a retention time in the foregut of hours to days. In contrast, persistent transmission requires hours for acquisition, with a retention time in the hemolymph of days to the entire life of the insect. Persistent transmitted viruses give propagative circulative transmission and replicate in the insect (Hogenhout *et al.*, 2008).

**(i) Genus Begomovirus:** Geminiviruses are small plant viruses characterised by a 22 nm, 38 nm geminate particle consisting of two joined incomplete icosahedra encapsidating circular single-stranded (ss) DNA genome molecules of about 2700 nucleotides (Goodman, 1977; Harrison *et al.*, 1977; Francki *et al.*,

1980; Zhang et al., 2001). Geminiviruses transmitted by the whitefly *Bemisia tabaci* are assigned to the genus Begomovirus within the family Geminiviridae (van Regenmortel et al., 2000). Geminiviruses are bi-segmented, circular and ssDNA genome virus, replicates in the host cell nucleus, transmitted in the persistent manner by insect vectors, infect phloem cells. The *Bean golden mosaic virus* (about 200 accepted virus species) is the largest of the four genera in the family *Geminiviridae*. Members of this family are twinned quasi-icosahedral (geminate) virions.

The genera *Mastrevirus*, *Curtovirus*, and *Topocuvirus* differ in genome organization, hosts, and insect vectors are addition to Begomovirus (Fauquet et al., 2008), as with other members of the family *Geminiviridae*, most begomoviruses have a bipartite genome of circular, ssDNA, and both segments (DNA-A and DNA-B) are similar in size (2.5–2.7 kb); in contrast, monopartite begomoviruses contain only one genome component that is homologous to DNA-A (Stanley et al, 2005). A large number of monopartite begomoviruses have been shown to be associated with ssDNA satellites known as

betasatellites. Betasatellites are pathogenicity-determinant molecules completely dependent on the helper component for their replication, encapsidation, and transmission. In addition, some begomovirus-betasatellite complexes associate with a further class of ssDNA components for which the name alphasatellites has been proposed (Nawaz-ul-Rehman and Fauquet, 2009). Begomoviruses are transmitted in a persistent manner by *B. tabaci*, and most are restricted to the phloem of the infected plants. The role of vector-begomovirus-plant interactions in the widespread invasion by some members of the whitefly species complex *Bemisia tabaci* is poorly understood. The invasive B biotype of *B. tabaci* entered China in the late 1990s and had become the predominant or only biotype of the whitefly in many regions of the country. Epidemics of begomoviruses have been observed in many crops including tomato for which *Tomato yellow leaf curl China virus* (TYLCCNV) and *Tomato yellow leaf curl virus* (TYLCV) have been identified as two major disease-causing agents (Liu, et al.,2009).





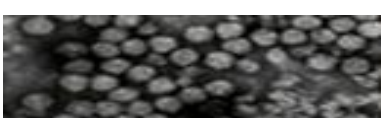
Electron micrographs	Virus	Mode of transmission
	Begomovirus (Geminiviridae)	Circulative ( <i>B. tabaci</i> , <i>T.ricini</i> )
	Ipomovirus (Potyviridae)	Semipersistent ( <i>B. tabaci</i> )
	Crinivirus (Closteroviridae)	Semipersistent ( <i>B. tabaci</i> , <i>B.ofer</i> , <i>T.vipororiorum</i> , <i>T.abutiloneus</i> )
	Carlavirus (Betafelaxiviridae)	Semipersistent ( <i>B. tabaci</i> )
	Torrodovirus (Secoviridae)	Unknown ( <i>B. tabaci</i> , <i>T.vipororiorum</i> )

Fig.1. Structure, viruses and mode of transmission of whitefly transmitted viruses.

**Begomovirus-Whitefly Complex:** The begomovirus vector *B. tabaci* is an insect species complex that has geographically distinct phenotypic and genotypic variants (Bird and Maramorosch, 1978; Perring et al.,

1993; Bedford et al., 1994; Brown et al., 1995; Frohlich et al., 1999). The coat protein (CP) is the only begomoviral gene product that directly interacts with whitefly factors during the circulative transmission of

the virus. Phylogenetic analysis of begomovirus CP sequences resulted in the grouping of the viruses on the basis of geographical origin: 1) New World, 2) Western Mediterranean basin, 3) Middle East, 4) Indian subcontinent, 5) East and Southeast Asia and Australia (Rybicki, 1994; Padidam *et al.*, 1995). Similarly, the *B. tabaci* complex could be resolved into five major groups based on mitochondrial DNA markers, essentially coinciding with the geographical distribution of the begomoviruses (Frohlich *et al.*, 1999; Brown, 2001). This virus vector co-adaptation is likely to be the result of coevolution processes taking place in geographically isolated locations. Independent but converging information suggests that the whitefly-begomovirus interaction may be of long-standing. Geminiviral DNA sequences seem to have integrated into the genome of some tobacco ancestors by illegitimate recombination during *Nicotiana* speciation, about 25 million years ago (Bejarano *et al.*, 1996). The endosymbiotic bacteria that produce the GroEL homologue necessary for the survival of begomoviruses in their insect vector (Morin *et al.*, 1999), have been associated with whiteflies for the last 200 million years (Baumann *et al.*, 1993). With the drift of continents, the initial whitefly-begomovirus complex (es) has developed with time into geographically separated and co-adapted virus-insect combinations (Bradeen *et al.*, 1997). It is inevitable that during this long-lasting virus vector relationship the virus has evolved to ensure both its survival and efficient transmission by the whitefly vector, and the insect also has evolved strategies to safeguard it from possible deleterious effects of the virus. Studying the interactions of transmissible and non-transmissible begomoviruses with vector and non-vector whitefly species may help to identify the viral and cellular determinants involved in transmission and focus some light on the evolutionary history of the begomovirus-whitefly complex. Whitefly cells and organs Involved in the circulative transmission of Begomoviruses In order to identify the position of receptors that are likely to mediate circulative transmission of begomoviruses in their whitefly vector, it is necessary to describe in some detail the insect cells and tissues involved.

The extensive anatomical analysis of the begomovirus non-vector whitefly *Trialeurodes vaporariorum* performed in the 1930s (Weber, 1935) still serves as a reference for analyzing the internal anatomy of whitefly species. Several publications have focussed on the

anatomy of *B. tabaci* mouthparts (Rosell *et al.*, 1995), anterior alimentary canal (Hunter *et al.*, 1996), and digestive tract, filter chamber and salivary glands (Cicero *et al.*, 1995; Harris *et al.*, 1995, 1996; Ghanim *et al.*, 2001a). Molecular studies have helped to define the pathway of begomoviruses in their insect vector (Hunter *et al.*, 1998; Rosell *et al.*, 1999; Ghanim *et al.*, 2001b). Virus particles ingested through the *B. tabaci* stylets enter the oesophagus and the digestive tract, penetrate the gut membranes into the haemolymph, reach the salivary glands and finally enter the salivary duct from where they are egested with the saliva. A schematic drawing can be found in Ghanim *et al.*, (2001b). *B. tabaci* feeds on phloem sap by inserting its stylets into plant tissue and locating the vascular tissue (Pollard, 1955). The stylet bundle is composed of three stylets: the maxillary stylet, which contains the food canal (through which phloem is acquired) and the lateral salivary canal (through which saliva is injected into the plant), and two mandibular stylets (Rosell *et al.*, 1995). The stylet food canal extends into the cibarium and oesophagus, which runs along the dorsal side of the thorax before entering the filter chamber. The internal oesophagus expands within the filter chamber where it is united with the continuous lumen that extends into the connecting chamber, caecae, descending and ascending midguts. Leaving the filter chamber, the descending midgut is composed of thick epithelial cells with large nuclei and microvilli extending into a large lumen. It is prolonged by the ascending midgut, which narrows until it enters the filter chamber. The ascending midgut is formed by very thick epithelial cells with an extensive brush border of microvilli surrounding a rather small lumen. The hindgut terminates with the rectal sac (Ghanim *et al.*, 2001b). The epithelial cells of the whitefly digestive tract separate the gut lumen and the hemocoel, which occupies the entire body cavity. The hemocoel contains the haemolymph, or primitive blood system, which circulates around the body cavity between the various insect organs, bathing them directly. It consists of plasma in which several types of nucleated cells or haematocytes are suspended and contains various inorganic ions, organic substances and proteins. An important function of the haematocyte is phagocytosis of foreign proteins, microorganisms and tissue debris, constituting a nonspecific primitive immune system (Chapman, 1991). Hence, virions face a particularly hostile environment in the haemolymph. Endosymbiotic

bacteria housed in the whitefly mycetocytes seem to have a cardinal role in safeguarding begomoviruses in the haemolymph. *B. tabaci* (biotype B) mycetomes contain two types of endosymbionts: the highly pleiomorphic P-type that constitutes approximately 80% of the total population, and the coccoid C-type (Costa *et al.*, 1995). The C-type endosymbionts produce a GroEL homologue that is released into haemolymph, but not into the digestive tract (Morin *et al.*, 2000). As demonstrated for TYLCV, the GroEL homologue seems to bind to and protect begomoviruses from degradation in the haemolymph (Morin *et al.*, 1999, 2000). A pair of primary salivary glands is located in the prothorax. The paired accessory glands are much smaller and slightly anterior to the primary glands. The primary salivary glands comprise at least 13 nearly symmetrical large cells surrounding a central lumen lined with microvilli, which empties into a duct at the base of the gland. This duct joins the accessory salivary gland duct and the medial duct. Each accessory gland is composed of four, similar, large cells that encircle a central lumen lined with extensive microvilli (Ghanim *et al.*, 2001b). The primary and accessory gland ducts on either side fuse to form the lateral salivary ducts. The two lateral ducts fuse above the hypopharynx to form a single, dual-channelled, medial salivary duct (Harris *et al.*, 1996). The salivary canal is contained almost entirely within one stylet, while the food canal is centrally located and is formed by the opposition of the food grooves in both stylets. The food and salivary canals end at the stylet tip (Rosell *et al.*, 1995).

**Acquisition and transmission of Tomato yellow leaf curl virus by Whitefly:** TYLCV from Israel was one of the first begomoviruses characterised in terms of its relationship with its vector, the B biotype of *B. tabaci*, and its host range (Cohen and Harpaz, 1964; Cohen and Nitzany, 1966). TYLCV has an immense economical impact worldwide (Picó *et al.*, 1996; Nakhla and Maxwell, 1998). Molecular comparisons of virus isolates from distinct geographical regions have revealed that leaf curl disease of tomato is caused by closely- as well as distantly-related monopartite or bipartite begomoviruses (Czosnek and Laterrot, 1997). Minimum time is needed for efficient acquisition and inoculation of TYLCV by *B. tabaci*. Whiteflies develop from an egg, through four nymphal stages (also called instars), to an adult. *B. tabaci* instars are able to ingest and transmit begomoviruses such as TYLCV (Cohen and

Nitzany, 1966) and Tomato yellow leaf curl Sardinia virus (TYLCSV) (Caciagli *et al.*, 1995). However the disease is spread in the field by flying adults. Whitefly-mediated transmission of TYLCV to tomato plants and observation of disease symptoms have indicated that the minimum acquisition access period (AAP) and inoculation access period (IAP) were 15-30 min. Moreover, similar values were obtained with TYLCV isolates from the Middle East (Ioannou, 1985; Mansour and Al-Musa, 1992; Mehta *et al.*, 1994) and from Italy (Caciagli *et al.*, 1995), and with Tomato leaf curl Bangalore virus (ToLCBV) isolates from India (Reddy and Yaraguntaiah, 1981; Muniyappa *et al.*, 2000). However, using PCR TYLCV DNA can be detected in a single insect as early as 5-10 min after the beginning of the AAP (Atzmon *et al.*, 1998; Ghanim *et al.*, 2001a; Navot *et al.*, 1992). Similarly, the viral DNA can be detected at the site of inoculation in tomato after a 5 min IAP (Atzmon *et al.*, 1998).

A single insect is able to infect a tomato plant with TYLCV following a 24 h AAP, although not all plants inoculated in this way will become infected. The efficiency of transmission reaches 100% when five to 15 insects are used (Cohen and Nitzany, 1966; Mansour and Al-Musa, 1992; Mehta *et al.*, 1994). A similar number of insects are necessary to achieve 100% transmission of the New World bipartite geminivirus, Squash leaf curl virus (SLCV) (Cohen *et al.*, 1983). ToLCBV with higher efficiency than males (Cohen and Nitzany, 1966; Muniyappa *et al.*, 2000).

**Geminivirus Replication:** The ssDNA genomes of geminiviruses replicate in the nucleus of infected cells via a rolling circle mechanism using a dsDNA intermediate (Saunders *et al.*, 1991; Stenger *et al.*, 1991). The replication process is analogous to that used by ssDNA phages, such as ØX174 (Kornberg and Baker, 1992) and ssDNA plasmids such as pT181 and pC194 (Gros *et al.*, 1987). Moreover, sequence comparisons have shown that the geminiviral replication-associated proteins are DNA binding proteins and are related to proteins involved in the initiation of replication of some ssDNA plasmids (pMV158 family) (Koonin and Ilyina, 1992). The origin of replication includes a conserved 30 nucleotide putative stem-loop element that is present in all geminiviruses (Revington *et al.*, 1989). A 5'-TAATATTAC-3' motif, present in the stem-loop element, is analogous to the Rep A protein replication cleavage sequence in phage 1X140 (Saunders *et al.*, 1991; Stenger



*et al.*, 1991; Arguello-Astorga *et al.*, 1994). The specific binding site for the replication associated-protein in TGMV and SqLCV has been mapped to a region of about 60 nucleotides upstream of the stem-loop element (Fontes *et al.*, 1994; Lazarowitz *et al.*, 1992). The Rep protein is a multifunctional protein that binds double-stranded DNA, catalyzes cleavage and ligation of single-stranded DNA and forms oligomers (Orozco and Hanley-Bowdoin, 1998). Rep protein initiates the replication cycle by making a single stranded-cleavage of the virion sense strand at the TAATATTAC sequence in the origin of replication. After the DNA cleavage and strand transfer reaction at the origin of replication, the Rep protein becomes covalently linked to the 5' end of the cleaved DNA (Laufs *et al.*, 1995). Laufs *et al.*, (1995) demonstrated that in TYLCV tyrosine-103, located in the stem loop motif initiates DNA cleavage and is the physical link between Rep protein and its origin DNA. Orozco and Hanley-Bowdoin (1998) showed that the DNA binding motif in the Rep protein of TGMV is located between amino acids 1 and 130. The recognition of the origin of replication by the TGMV Rep protein depends on a domain located between amino acids 121 and 200. The transcriptional specificity is conferred primarily by amino acids 1 to 193 (Gladfelter *et al.*, 1997). The synthesis of ssDNA is regulated by the synergistic activity of TrAp and Ren proteins that act as activator of transcription and enhancer of replication respectively (Sunter and Bisaro, 1991). It has been proposed that geminiviruses depend on cellular factors to complete their replicative cycles (Xie *et al.*, 1999). A family of proteins termed GRAB (for geminivirus Rep-A binding) has been shown to bind to the Rep A protein of wheat dwarf geminivirus. Two members of the family, GRAB 1 and GRAB 2, have been characterized (Xie *et al.*, 1999). The N-terminal domain of GRAB proteins exhibit a significant amino acid homology to the NAC domain present in proteins involved in plant development and senescence.

**Cytological effects of geminivirus replication:** The replication of geminiviruses induces micro-structural changes in the nucleus of the host cells. Ultrastructural studies of *Jatropha gossypifolia*, infected with the whitefly-transmitted begomovirus, *Jatropha mosaic virus*, showed fibrillar bodies and virus-like particles in the nuclei of phloem-associated parenchyma cells and sieve elements (Kim *et al.*, 1986). The fibrillar bodies consists of two structural components with different

electron densities: the highly electron-dense beads and the less electrondense matrix (Kim *et al.*, 1986). Light microcopy studies of leaf tissue of plants infected with BGMV and of *lima bean golden mosaic*, *euphorbia mosaic*, *malvaceous chlorosis*, and *rhyncosia mosaic* begomoviruses revealed nuclear inclusions that appear as large blue-violet bodies when the tissue is stained with azure A (Christie *et al.*, 1986). These inclusions consist of aggregated virus particles. Small, ring-shaped blue-violet, inclusions were also observed in the nuclei of the phloem parenchyma cells. The nuclear inclusions were not observed in stained tissues of non-infected host plants (Christie *et al.*, 1986). Pinner *et al.*, (1990) observed four types of cytoplasmic inclusions induced by maize streak virus and serologically related isolates: crystalline, non-crystalline, sheet-like and open lattice. These distinctions enable certain geminiviruses to be identified at the strain level.

**Movement:** The establishment of a virus infection depends upon the spread of the virus through the plant host. The movement of the virus in the plant occurs at two different levels: a) short distance cell- to -cell movement and b) long-distance movement that involve delivery of the virus to distal parts of the plant by the vascular system (Lazarowitz, 1992). The BV1 and BC1 genes encode movement proteins in bipartite geminiviruses. Studies of SqLCV and bean dwarf mosaic virus (Noueiry *et al.*, 1994) have shown that the BV1 and BR1 products act in a cooperative manner to move the viral genome from the nucleus to the cytoplasm and across the wall cell to a contiguous cell. It has been proposed that BV1 is a nuclear shuttle protein. BV1 binds newly replicated ssDNA viral genomes and transports them to the cytoplasm (Sanderfoot *et al.*, 1996). Then, the BV1-genome complexes are directed to the cell periphery through interactions with the BC1 product (Sanderfoot *et al.*, 1996; Sanderfoot and Lazarowitz, 1995). It has been suggested that the BC1 protein allows the movement of BV1-genome complexes from one cell to the next by increasing the exclusion limit of plasmodesmata (Sanderfoot *et al.*, 1996). The synthesis of BV1 is regulated at the transcriptional level by AC2 transactivation (Sunter and Bisaro, 1991).

**Transmission of Geminiviruses, *Bemisia tabaci* (B-biotype):** Begomoviruses are transmitted by the sweetpotato whitefly, *Bemisia tabaci* (Gennadius). *B. tabaci* was first described in the genus *Aleyrodes* in 1889 (Gennadius, 1889), and was first reported as a pest

in 1919 in India (Husain and Trehan, 1933). Since then, *B. tabaci* has been recognized as a pest of crops in tropical and subtropical countries. *B. tabaci* has a very wide host range, consisting of 500 species in 74 plant families (Greathead, 1986). The whitefly is a vector of viruses in the Geminiviridae, Potyviridae and Comoviridae families and the genera Carlavirus and Closterovirus. Approximately 60 different geminiviruses have been reported to be transmitted by *B. tabaci* (Markam *et al.*, 1994). In the New World before 1986, *B. tabaci* was considered a pest of a limited number of crops (tobacco, cotton, potato, bean, soybean), but by 1986 a sudden increase of the whitefly population in ornamentals in Florida was observed (Osborne, 1988). Shortly after that, whiteflies were reported in other crops in Florida (Schuster *et al.*, 1991), in California (Perring *et al.*, 1991), and in Texas, Arizona, Central America and South America (Brown, 1994). In Florida the whitefly infestation was associated with silverleaf of squash and irregular ripening of tomato (Maynard and Cantliffe, 1989). The whitefly population causing these disorders was physiologically, behaviorally, reproductively and genetically different from the population that was present before 1989 in California and Arizona, and was first called the "poinsettia strain". Later, this whitefly became known as the B strain or B biotype. Perring *et al.*, (1991) suggested that A and B strains were separate species, and thus, named the B strain (or B biotype) the "silver leaf whitefly, *B. argentifolii*" (Bellows *et al.*, 1994). The B biotype has a very wide host range, which has contributed to the spread of geminiviruses to new hosts (Bedford *et al.*, 1993) and the outbreak of apparently new geminiviruses (Polston and Anderson, 1997).

**Characteristics of whitefly transmission:** Whitefly-transmitted geminiviruses affect a wide variety of vegetable crops worldwide. In the 1930s, the first transmission of geminiviruses by whiteflies was demonstrated with tobacco leaf curl virus and African cassava mosaic virus in tobacco and cassava, respectively (Storey, 1934; Storey, 1936; Storey and Nichols, 1938). Geminivirus transmission by *B. tabaci* is circulative and non-propagative (Duffus, 1987). Whiteflies can acquire and inoculate bipartite begomoviruses in short periods of time (10 min), but the efficiency of acquisition increases when the feeding period increases up to 24 h. Latent periods of four to 21 h between virus acquisition and the ability of the

whitefly to transmit have been observed (Duffus, 1995). Studies of the transmission of TYLCV, a monopartite begomovirus, showed that whitefly feeding periods of 4 h or longer were necessary to achieve TYLCV transmission rates near to 90% (Zeidan and Czeszcnek, 1991). Hunter *et al.*, (1998) established the location of tomato mottle begomovirus (ToMoV) and cabbage leaf curl egomovirus (CaLCV) in various tissues of *B. tabaci* B biotype by immunofluorescent labeling of viral coat protein in freshly dissected whiteflies. Hunter *et al.*, (1998) proposed the following model for the movement of begomoviruses in the whitefly vector: virus particles are ingested along with plant fluids into the whitefly esophagus and foregut, after which nutrients and begomoviruses are concentrated in the filter chamber. Begomovirus particles adsorb to specific sites on the alimentary membrane or to sites along the anterior region of the midgut. Begomovirus particles move out of these tissues into the hemolymph, eventually invading the salivary glands.

**Impact of Whitefly-Transmitted Geminiviruses:** As early as the 1950s, there were reports of a correlation between the presence of *B. tabaci* and plant diseases characterized by foliar malformation, leaf curling, stunting and yellow mosaic in a variety of crops and weeds in the Americas and the Caribbean basin (Brown and Bird, 1992). Many of those diseases were later determined to be caused by geminiviruses (Brown and Bird, 1992). Until the early 1990s, whitefly-transmitted geminiviruses were primarily a problem in legume production in the Western Hemisphere. Since then, high incidences of geminivirus diseases in tomato-producing areas of Florida, the Caribbean, Mexico, Central America, Venezuela, and Brazil have been reported (Polston and Anderson, 1997). Currently, at least 17 geminiviruses have been reported infecting tomato in the Americas and Caribbean region i. e. chino del tomato virus, tomato leaf crumple virus, pepper huasteco virus, potato yellow mosaic virus, Sinaloa tomato leaf curl virus, Texas pepper virus, pepper jalapeno virus, TYLCV, ToMoV, serrano golden mosaic virus, tomato geminivirus BZ-Ub, tomato geminivirus BZ-Ig, TGMV, tomato yellow mosaic virus, tomato yellow streak virus, Tom GV1 virus, and Tom GV2 virus, with incidences ranging from 20 to 100% and causing crop losses up to 100% (Polston and Anderson, 1997). Tomato geminiviruses have been reported to cause important losses in the tomato producing areas of the Caribbean basin and Florida

(Polston and Anderson, 1997). The crop damage due to geminiviruses in the Dominican Republic between 1988 and 1995 ranged from 5 to 95%, and the economic losses from 1989 to 1995 were estimated at \$50 million (Alvarez and Abud-Antún, 1995). Tomato geminiviruses caused losses estimated at \$ 4.6 million in the Comayagua Valley of Honduras in 1992 (Caballero and Rueda, 1993). In Venezuela, the area of tomato production was reduced by 50% due to losses caused by tomato yellow mosaic virus (Salas and Mendoza, 1995). In central America geminiviruses are thought to be responsible for a significant portion of the crop losses estimated at \$40 million from 1989 to 1995 (Bird *et al.*, 1995). The yields of the tomato crop in Florida have been adversely affected by whitefly-transmitted geminiviruses. In 1990 to 1991, crop losses due to ToMoV were estimated at \$140 million. (Schuster, 1992). In Florida and the Caribbean basin diseases caused by whitefly-transmitted geminivirus diseases are also serious concerns for many different crops such as

beans, cassava, tobacco, potato, cotton, pepper, squash, and cabbage (Polston and Anderson, 1997).

**(ii) Genus *Crinivirus*:** Viruses with a linear, positive-stranded ssRNA genome that is up to ~20 kb and encapsidated in very long and flexuous particles. *Closteroviridae* family includes three genera, *Closterovirus*, *Ampelovirus*, and *Crinivirus* (hair). With the exception of *Potato yellow vein virus*, which has a tripartite genome (Livieratos *et al.*, 2004), the genome of criniviruses is composed of two molecules that are independently encapsidated. RNA-1 encodes proteins involved in replication, and RNA-2 (and RNA-3) encodes proteins involved in viral encapsidation, movement, and vector transmission (Karasev, 2000; Livieratos *et al.*, 2004; Martelli *et al.*, 2002). Criniviruses are limited to phloem and are transmitted in nature in a semipersistent manner by whiteflies (Table 1) of two different genera, *Bemisia* (*B. tabaci*) and *Trialeurodes* (*T. vaporariorum* and *T. abutiloneus*) (Wisler *et al.*, 1998).

Table.1 : Whitefly transmission specificity of criniviruses.

Criniviruses	Whitefly Vector
<i>Abutilon yellows virus</i> (AYV)	Banded wing whitefly ( <i>T. abutilonea</i> ) <sup>1</sup>
<i>Beet pseudo yellows virus</i> (BPYV)	Greenhouse whitefly ( <i>T. vaporariorum</i> ) <sup>2</sup>
<i>Cucurbit yellow stunting disorder virus</i> (CYSDV)	Silverleaf whitefly ( <i>B. tabaci</i> biotype B) <sup>3</sup>
	Sweet potato whitefly ( <i>B. tabaci</i> biotype A) <sup>4</sup>
<i>Lettuce chlorosis virus</i> (LCV)	1
<i>Lettuce infectious yellows virus</i> (LIYV)	4
<i>Strawberry pallidosis associated virus</i> (SPaV)	2
<i>Sweet potato sunken vein virus</i> (SPSVV)	3
<i>Tomato chlorosis virus</i> (ToCV)	1, 2, 3, 4
<i>Tomato infectious chlorosis virus</i> (TICV)	2

**(iii) Genus *Ipomovirus*:** The family *Potyviridae* is the largest group of RNA plant viruses and includes viruses with a linear, ssRNA positive-stranded genome encapsidated in flexuous, filamentous particles. The family includes six genera, which are transmitted by aphids (*Potyvirus*, *Macluravirus*), mites (*Rymovirus*, *Tritimovirus*), plasmodiophorids (*Bymovirus*), or whiteflies (*Ipomovirus*, derived from *Ipomoea*, the sweet potato genus name) (Berger *et al.*, 2005), and a seventh recently proposed genus, *Bramvyvirus*, with no known vector (Carstens, 2010). The genus *Ipomovirus* includes viruses that are transmitted by the whitefly *B. tabaci* in a semipersistent manner (Jones, 2003). This genus has four members: *Cassava brown streak virus* (CBSV), *Cucumber vein yellowing virus* (CVYV), *Squash vein*

*yellowing virus* (SqVYV), and *Sweet potato mild mottle virus* (SPMMV). In cucumber, CVYV causes pronounced vein clearing, chlorosis and finally general necrosis of the affected plant (Cohen and Nitzany, 1966). Light to dark green mosaic is observed on fruit.

Ultramicroscopic observations revealed numerous cylindrical cytoplasmic inclusions in melon and cucumber and inclusions appeared as pinwheels or as bundles (Lecoq *et al.*, 2000). Complementary DNA representing 2108 nucleotides at the 3' end of the genomic RNA of the whitefly-transmitted SPMMV. Sequence analysis revealed an open reading frame of 1 797 nucleotides which codes for a protein of 599 amino acids, followed by a 3' non-coding region of 311 nucleotides. Alignment of the deduced amino acid

sequence with corresponding sequences of other members of the *Potyviridae* demonstrated that part of the presumptive RNA-dependent RNA polymerase and the coat protein coding regions of SPMMV are found at the 3' end of its genome, in that order. Alignment of the amino acid sequence of the core of SPMMV coat protein with those of selected members of the *Potyviridae* showed limited identity, thus demonstrating- with phylogenetic analysis – that SPMMV belongs to a distinct genus of the family *Potyviridae*. (Colinet *et al.*, 1996).

A novel whitefly-transmitted potyvirus isolated from a squash plant (*Cucurbita pepo*) with vein yellowing symptoms has flexuous rod-shaped particles, ~900 nm in length. Koch's postulates were completed by mechanical inoculation of *C. pepo* seedlings with isolated virions (Adkins *et al.*, 2006)). Cucumber vein yellowing virus (CVYV) is widespread in cucurbits; particles are filamentous and transmitted by *Bemisia tabaci* by the semi-persistent mode. The host range are limited to members Cucurbitaceae (squash and watermelon) but excluded in species belonging to Amaranthaceae, Apocynaceae, Asteraceae, Chenopodiaceae, Fabaceae, Malvaceae, and Solanaceae. In above plant species mostly whiteflies transmit the virus but not aphids (*Myzus persicae*). Infection by SqVYV induced inclusion bodies visible by electron and light microscopy that were characteristic of members of the family *Potyviridae*. Comparison of the SqVYV coat protein gene and protein sequences with those of recognized members of the family *Potyviridae* indicate that it is a novel member of the genus *Ipomovirus*. Non-parthenocarpic cucumbers have been reported to be symptomless carriers of CVYV while parthenocarpic cucumbers develop severe symptoms. Symptoms in both cucumber and melon have been described as vein yellowing, vein clearing and stunting with a corresponding yield reduction (Yilmaz *et al.*, 1989). Sudden death (Janssen and Cuadrado, 2001) and occasional splitting of fruits has been observed in melon (Janssen and Cuadrado, 2001).

**(iv) Genus *Carlavirus*:** The genus *Carlavirus* (contraction of *Carnation latent virus*) is one of the six genera in the family *Betaflexiviridae*, which also includes the genera *Capillovirus*, *Citrivirus*, *Foveavirus*, *Trichovirus*, and *Vitivirus* (Carstens, 2010). Members of this family have linear ssRNA positive-stranded genomes encapsidated in flexuous, filamentous virions. Although carlaviruses are primarily transmitted by aphids, two of the 43 accepted species in this genus are transmitted in

a semipersistent manner by the whitefly *B. tabaci*; these two species are *Cowpea mild mottle virus* (CpMMV) (Iwaki *et al.*, 1982) and *Melon yellowing-associated virus* (MYaV) (Nagata *et al.*, 2005). Based on transmission (mechanical, graft, insect vector), purification and serology, electron microscopy and molecular studies the causal agent was determined to be a whitefly-borne carlavirus which is possibly related to *Cowpea mild mottle virus* (CpMMV), virus exhibited stunting and stem necrosis in soybeans (Álvarez *et al.*, 2005) . Slightly flexuous filaments, normally 610-700 nm long and 12-15 nm in diameter, often appearing curved to one side and sedimenting at 147-176 S. The particles are constructed of c. 1600-2000 subunits of a single protein species (M. Wt normally  $3.1-3.4 \times 10^4$ ) arranged as a helix (pitch 3.3-3.45 nm) enclosing the genome which is a single molecule of single-stranded RNA (M. Wt  $2.3-3.0 \times 10^6$ ) and constitutes normally 5-7% of the particle weight. The proteins of some carlaviruses can become partially degraded in the assembled particles (Hollings and Stone, 1972). Thermal inactivation point 55-70°C, longevity in sap a few days, dilution end-point usually  $10^{-3}-10^{-4}$  occasionally up to  $10^{-6}$ . Most carlaviruses have restricted host ranges, but the different viruses occur in a wide range of monocotyledonous and dicotyledonous hosts. Infections in natural hosts are often latent, but sometimes mosaic symptoms are produced. Carlaviruses are transmitted mechanically and usually in the non-persistent manner by aphids. Some are seed-transmitted. Virus particles occur in the cytoplasm singly or more often in large aggregates which are sometimes banded. The stem necrosis of soybean is caused by a virus of the *Carlavirus* and transmitted by the whitefly *Bemisia tabaci*, also infected beans and identified as *Cowpea mild mottle virus* (CpMMV). Periods of access to the acquisition (PAA) of 'Jalo' for 'Jalo', and the effect of periods of access to the inoculation (PAI) had been evaluated. Visually typical symptoms of carlavirus had been evidenced as mosaic, veinclearing, systemic necrosis and reduction of growth. It had transmission of the virus for 'BT-2' of beans and 'BRS-132' of soy with only one insect for plant, being more efficient in this last species. Tax of transmission of the virus was bigger with the increase of the number of insects for plant. PAA was determined 15 min after time for acquisition, and increase with 5 min and increasing the period of access the acquisition and inoculation increased its transmission tax (Marubayashi, 2010).

**(v) Genus *Torradovirus*:** The genus *Torradovirus* (from the type member *Tomato torrado virus*) is one of the genera within the plant picornavirus family *Secoviridae*. It contains viruses reported to be transmitted by whiteflies with three distinct coat protein subunits and an additional ORF at the 5'-end of RNA2 in addition to the polyprotein typical of members of this family. Virions are isometric (icosahedral), not enveloped, about 30 nm in diameter. Bipartite, linear, single stranded positive sense RNA. The 3'- terminus of each RNA has a poly (A) tract and the 5'- terminus has a genome-linked protein (VPg). Each RNA is translated into a polyprotein, which is then processed by a series of steps into functional proteins: RNA1 encodes proteins necessary for replication while the cell-to-cell movement protein and coat proteins are encoded on RNA2. RNA1 (7.8 kb) produces a polyprotein of 241 kDa processed into mature peptides. Cleavage sites have not been determined but these are expected to include a processing regulator, Nucleotide binding protein, VPg (genome-linked protein), Protease and the RNA-dependent RNA polymerase. RNA2 (5.4 kb) has a small (20 kDa) ORF predicted near the 5'-terminus and a polyprotein of 134 kDa in which a movement protein can be identified and three separate coat proteins of about 35, 26 and 23 kDa.

A new plant virus family, *Secoviridae*, has recently been proposed to include a number of plant viruses in the order Picornavirales that were formerly classified in the families *Comoviridae* (*Comovirus*, *Fabavirus*, and *Nepovirus*) or *Sequiviridae* (*Sequivirus* and *Waikavirus*), as well as two previously unassigned genera (*Cheravirus* and *Sadwavirus*) (Sanfacon *et al.*, 2009). Two newly discovered plant viruses, *Tomato torrado virus* (ToTV) and *Tomato marchitez virus* (ToMarV), share properties with members of the proposed family *Secoviridae*, and a new genus in this family, *Torradovirus* (from Spanish torrao or torrado, meaning burnt), has been proposed to include these viruses (Sanfacon *et al.*, 2009). The early symptoms of *Tomato torrado virus* are necrotic or dead spots, surrounded by a light green or yellow area at the base of the leaflets. The affected areas may fall out, leaving holes (shot holes) in the leaflets. Necrosis and mottling extend to the remainder of the leaves. In very susceptible varieties, leaves become necrotic, wither and die. Members of the genus *Torradovirus* have a genome composed of two linear, positive-stranded ssRNA molecules that are encapsidated separately into small

icosahedral particles. ToTV is transmitted by the whiteflies *B. tabaci* and *T. vaporariorum* (Amari *et al.*, 2008 ), but no information about the mode of transmission is available. A newly described entomopathogenic virus was recently discovered in south Florida whitefly populations and was determined to be an iridovirus by DNA analysis. Invertebrate iridescent virus 6 (IIV-6) is known to be pathogenic to insects such as *Bemisia tabaci*, *Diaprepes abbreviatus*, *Trichoplusia ni*, including whiteflies. Mode of transmission for iridovirus has been shown to be through oral ingestion and cuticular wounding (abrasions) (McKenzie, 2001).

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