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Mini review

Plant viruses transmitted by whiteflies

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Abstract

One-hundred and fourteen virus species are transmitted by whiteflies (family Aleyrodidae). *Bemisia tabaci* transmits 111 of these species while *Trialeurodes vaporariorum* and *T. abutilonia* transmit three species each. *B. tabaci* and *T. vaporariorum* are present in the European–Mediterranean region, though the former is restricted in its distribution. Of the whitefly-transmitted virus species, 90% belong to the *Begomovirus* genus, 6% to the *Crinivirus* genus and the remaining 4% are in the *Closterovirus*, *Ipomovirus* or *Carlavirus* genera. Other named, whitefly-transmitted viruses that have not yet been ranked as species are also documented. The names, abbreviations and synonyms of the whitefly-transmitted viruses are presented in tabulated form together with details of their whitefly vectors, natural hosts and distribution. Entries are also annotated with references. Whitefly-transmitted viruses affecting plants in the European–Mediterranean region have been highlighted in the text.

Introduction

An indirect effect of feeding by some whiteflies is the transmission of plant viruses, many of which are of economic importance. This review surveys the viruses that are transmitted by whiteflies and provides information on their taxonomic status, hosts and distribution. An annotated list of whitefly-transmitted viruses was originally compiled by the author to guide an analysis of quarantine risks associated with the threat that they may pose to agriculture in the European–Mediterranean region. Continually updated as new information has been published, the list now serves as a testament to the growing importance of whiteflies, especially *Bemisia tabaci*, as vectors of viral plant pathogens.

Whiteflies are insects belonging to the family Aleyrodidae. They occur in warm climates where they are pests of herbaceous and woody plants. In temperate climates, they are usually pests of protected crops. Eggs are laid by winged, mobile adults on leaf surfaces. Upon hatching, a scale-like, 'crawler' stage is followed by three, sessile, immature instars. The last instar or 'pupa' stage undergoes metamorphosis to become an adult (Gill, 1990). Whiteflies damage plants directly by sucking sap from leaves and inducing physiological disorders. 'Silver leaf', a disorder of cucurbits, is caused by the injection of phytotoxins into leaves by some biotypes of *B. tabaci*. Whiteflies can also affect hosts by producing a sticky secretion known as honeydew, which prevents leaves from functioning efficiently, as well as acting as a substrate for fungi (sooty moulds).

Whiteflies as vectors of plant viruses

About 1300 whitefly species in over 120 genera have been described (Anon., 2001a; Mound and Halsey, 1978), but relatively few transmit plant viruses. Only whiteflies in the *Bemisia* and *Trialeurodes* genera are virus vectors. In the genus *Bemisia*, only *B. tabaci* has

been shown to be a vector whereas in the *Trialeurodes* genus, *Trialeurodes vaporariorum*, *T. abutilonea* and *T. ricini* transmit viruses. Whitefly instar nymphs and adults feed by inserting their proboscises into the leaf, penetrating the phloem and withdrawing sap. It is during this feeding process that plant viruses are acquired. Adult whiteflies may disperse and transmit the virus to new plants while feeding.

Two whitefly-associated diseases of unknown etiology are known from Europe. Maple mosaic disease, which affects *Acer negrundo* and *A. pseudoplatanus* in Hungary, is transmitted by *T. vaporariorum* (Szirmai, 1972). Citrus chlorotic dwarf disease, which affects citrus in the eastern Mediterranean area of Turkey is transmitted by *Parabemisia myricae* (Kersting et al., 1996). Neither have been included in the tables in this publication because it is not yet known whether a virus is the causal agent.

Bemisia spp.

B. tabaci has been of increasing importance as a pest and vector of virus diseases of food, fibre and ornamental plants since the early 1980s. This has been due to the emergence of the B biotype and its rapid expansion in geographic distribution and host range. The whitefly, and the viruses it transmits, are now responsible for significant crop losses in many regions with tropical, subtropical, arid and Mediterranean climates. Cassava, cotton, cowpea, cucurbits, crucifers, tobacco, tomato, potato, soybean, sweet potato, okra, lettuce, pea, bean, pepper, poinsettia and chrysanthemum are some of those crops that are vulnerable. In addition to outdoor crops, *B. tabaci* is also a serious pest protected environments, which enable it to survive during the winter in temperate climates in North America and Europe (De Barro, 1995).

A number of biotypes of *B. tabaci*, named with a letter code, have been identified that are morphologically very similar, if not identical. Differentiation has been based on host range, host-plant adaptability, induction of phytotoxic reactions, insecticide resistance, esterase banding patterns, RAPD-PCR and AFLP analysis (Cervera et al., 2000; Martin et al., 2000). To date, 24 distinct populations of *B. tabaci* have been given a biotype designation. The most studied is biotype B, and on the evidence of sexual incompatibility with biotype A, it has been ranked as a different species – *B. argentifolii* (Bellows et al., 1994). However, this separation is not universally supported (Bedford et al., 1994; Martin et al., 2000). One reason is that other biotypes have been found to be sexually incompatible in breeding experiments. The general consensus is that *B. tabaci* forms a species-complex (Martin et al., 2000). This species-complex has recently been reviewed by Perring (2001).

The Indian subcontinent is believed to be the centre of origin of *B. tabaci* because of the numbers and different types of natural enemies found in that region. However, the B biotype has only recently been recorded in the region (Banks et al., 2001). The origin of the B biotype may be the northeastern Africa-Middle East-Arabian peninsula region (De Barro et al., 2000; Frolich et al., 1999).

Differences in plant virus-transmission capabilities between biotypes have been recognized (Bedford et al., 1992; 1994; Sánchez-Campos et al., 1999). Populations of the B biotype have a great capacity to transmit begomoviruses. The appearance of 'new' viruses in areas colonized by the B biotype is thought to be due to the fast development and broad host range of this biotype. Some begomoviruses are also more efficiently transmitted than others.

The global spread of the polyphagous *B. tabaci* biotype B as a 'hitch-hiker' on traded plant material is a major factor in the world-wide increase in whitefly-transmitted diseases. Changes in agronomic practices, which have resulted in irrigated crops being grown for longer overlapping periods of growth of crops in monoculture, and an increase in resistance to insecticides, have also been given as reasons for *B. tabaci* and its associated viruses becoming major problems (De Barro, 1995).

The only other species of *Bemisia* that may transmit a virus is *B. afer*. However, the evidence from East Africa that this whitefly could be a vector of cassava brown streak disease (Bock, 1994), which appears likely to be caused by an ipomovirus (Monger et al., 2001a,b), is circumstantial (Legg and Raya, 1998).

Trialeurodes spp.

T. vaporariorum, the greenhouse whitefly, has been an economically important insect pest for many years. In temperate countries, the most severely affected crops are aubergine, cucumber, beans, sweet peppers, tomatoes and a large number of ornamentals, including chrysanthemum, poinsettia, primula and species of *Fuchsia*, *Gerbera*, *Pelargonium* and *Solanum* (Anon., 2001a). *T. vaporariorum* is cosmopolitan in its

distribution, but is less common in Asia and Australasia (Martin, 1999).

T. abutilonea has only been identified in parts of North America and the Caribbean. It has not been recorded in the European–Mediterranean region.

T. ricini has been reported in parts of the Middle East, Africa, the Indian subcontinent and Southeast Asia (Mound and Halsey, 1978). In the European–Mediterranean region, it has been recorded in the Canary Islands, Egypt and Israel (Anon., 2001a).

Viruses transmitted by *B. tabaci*

B. tabaci is a vector of 111 plant viruses recognized as species in the genera *Begomovirus* (*Geminiviridae*), *Crinivirus* (*Closteroviridae*), *Carlavirus* or *Ipomovirus* (*Potyviridae*). In addition, it is the vector of many other named viruses that are either in the same genera or in unidentified genera (Tables 1–3). These viruses have not been given the rank of species. When fully sequenced, some may be found to be synonyms of known virus species.

Begomoviruses are the most numerous of the *B. tabaci*-transmitted viruses and cause crop yield losses of between 20% and 100% (Brown and Bird, 1992). Symptoms include yellow mosaics, yellow veining, leaf curling, stunting and vein thickening (Anon., 2001a). One million hectares of cotton have been decimated by cotton leaf curl viruses in Pakistan (Mansoor et al., 1993). Damage has also occurred to important subsistence crops, such as cassava, which is affected by a number of different cassava mosaic viruses. Tobacco and tomato crops throughout the world are

Table 1. Names, hosts and distribution of begomoviruses, which are transmissible by *B. tabaci* except where indicated (key: virus names in italics recognized as species by Fauquet et al. (2003); virus names in roman are tentative species)

Virus (abbreviation and other information)	Main natural hosts	Distribution	References
Abutilon mosaic virus: AbMV; West Indian isolate not transmissible by *B. tabaci* in European–Mediterranean region	*Abutilon* spp., *Hibiscus* spp., *Malva* spp., *Sida* spp.	Brazil, West Indies – distributed worldwide in ornamental , 'variagated' *Abutilon* spp.	[19,42,45,68,82–84,88, 102,104,119,149,164, 169,178,215]
Acalypha yellow mosaic virus: AYMV	*Acalypha indica*	India	[68,82–84,169,178, 199,215]
African cassava mosaic virus: ACMV; syn. cassava latent virus	*Hewittia sublobata*, *Jatropha multifida*, *Laportea aestuans*, *Manihot esculenta*, *M. glaziovii*	Burundi, Chad, Kenya, Madagascar; Tanzania, Uganda, West Africa	[42,68,82–84,133,149, 178,200,215]
Ageratum enation virus: AEV	*Ageratum conyzoides*	Nepal	[82]
Ageratum yellow vein China virus: AYVV	*Ageratum conyzoides*	China	[82]
Ageratum yellow vein virus-Pakistan: AgYVV-PK	*Ageratum conyzoides, Zinnia elegans*	India?, Pakistan	[96]
Ageratum yellow vein Sri Lanka virus: AYVSLV	*Ageratum* sp.	Sri Lanka	[82]
Ageratum yellow vein Taiwan virus: AYVTV	*Ageratum* sp.	Taiwan	[82]
Ageratum yellow vein virus: AYVV	*Ageratum conyzoides*	Singapore	[42,68,82–84,149,169, 178,215,223,232]
Asystasia golden mosaic virus: AGMV	*Asystasia gangetica*	Benin, Congo, Côte d'Ivoire, Guinea	[19,82,83,149,169, 178,215]
Bean calico mosaic virus: BCaMV	*Phaseolus lunatus*, *P. vulgaris*, *Malva parviflora*	Mexico	[39,42,82,84,149,164,169, 178,215]
Bean distortion dwarf virus: BDDV	*Phaseolus vulgaris*	China	[42,247]
Bean dwarf mosaic virus: BDMV; incorrectly considered to be a strain of *Abutilon mosaic virus* by some authors	*Phaseolus vulgaris*, *Sida* spp.	Brazil, Colombia	[42,82–84,101,148,163, 164,178,215]
Bean golden mosaic virus: BGMV; syn. bean golden mosaic virus-Brazil	*Phaseolus* spp., *Glycine max.*	Argentina, Brazil, Venezeula	[42,68,78,82–84,92,149, 164,169,178,215,230]

Table 1. (*Continued*)

Virus (abbreviation and other information)	Main natural hosts	Distribution	References
Bean golden yellow mosaic virus: BGYMV; syn. bean golden yellow virus-Puerto Rico	*Phaseolus lunatus*, *P. vulgaris*, *Macroptilium lathyroides*, *Malvastrum coromandelianum*	Colombia, Costa Rica, Cuba, Dominican Republic, El Salvador, Guatemala, Jamaica, Haiti, Honduras, Mexico, Nicaragua, Panama, Puerto Rico, USA	[31,42,75,82–84,92,149, 164,169,178,215]
Bhendi yellow vein mosaic virus: BYVMV; at least one isolate from Pakistan previously called okra yellow vein mosaic virus	*Abelmoschus esculentus*	India, Pakistan	[42,65,82–84,169, 178,215]
Cabbage leaf curl virus: CaLCV; a strain designated CRFA4 is believed to have arisen by recombination between CaLCV and Macroptilium golden mosaic virus	*Brassica oleracae*	USA, Jamaica (CRFA4 strain occurs in Jamaica)	[3,82,83,143,212]
Calopogonium golden mosaic virus: CalGMV	*Calopogonium mucunoides*, *Phaseolus vulgaris*	Costa Rica	[66,205]
Chayote mosaic virus: ChMV; name also given to tymovirus	*Sechium edule*	Nigeria	[82,83,178,181]
Chilli leaf curl virus: ChiLCuV	*Capsicum annuum*	Pakistan	[82]
Chino del tomate virus: CdTV; syn. tomato leaf crumple virus	*Capsicum annuum*, *Datura stramonium*, *Lycopersicon esculentum*, *Malva parviflora*	Mexico, Nicaragua, USA	[42,82–84,149,164,169, 178,180,190,206]
Cotton leaf crumple virus: CLCrV	*Abutilon* spp., *Althaea* spp., *Castanospermum* spp., *Gossypium* spp., *Hibiscus* spp., *Glycine* spp., *Malva* spp., *Phaseolus* spp., *Vigna* spp.	Mexico, USA, Guatemala	[40,42,68,82–84,149,164, 169,170,178,215]
Cotton leaf curl Alabad virus: CLCuAV; syn. cotton leaf curl virus-Pakistan3	*Gossypium hirsutum*	Pakistan	[82,251]
Cotton leaf curl Gezira virus: CLCuGV; syn. cotton leaf curl virus-Sudan	*Gossypium barbadense*	Egypt, Sudan	[68,82,111,149]
Cotton leaf curl Kokhran virus: CLCuKV; syn. cotton leaf curl virus-Pakistan2	*Gossypium hirsutum*	Pakistan	[82,251]
Cotton leaf curl Multan virus: CLCuMV; syns cotton leaf curl virus-Pakistan1; cotton leaf curl virus; note that some references relate to cotton leaf curl viruses in general	*Abelmoschus esculentus, Gossypium hirsutum, Raphanus sativus*	Pakistan	[33,42,82–84,99, 147–149,169,170,178, 215,251]
Cotton leaf curl Rajasthan virus: CLCuRV	*Gossypium* spp.	India	[82]
Cotton leaf curl virus-Malawi: CLCUV-MW	*Gossypium* spp.	Malawi	[41]
Cotton yellow mosaic virus: CYMV	*Gossypium hirsutum*	Brazil, Dominican Republic, Guatemala, USA (Texas)	[41,82]
Cowpea golden mosaic virus: CPGM; syn. cowpea yellow mosaic virus	*Vigna unguiculata*	India, Kenya, Mozambique, Niger, Nigeria, Pakistan, Tanzania, Tunisia	[42,68,82–84,149, 169,178,215]
Croton yellow vein mosaic virus: CYVMN	*Croton bonplandianum*	India	[42,68,82–84,144,169, 178,215]

Table 1. (*Continued*)

Virus (abbreviation and other information)	Main natural hosts	Distribution	References
Cucurbit leaf curl virus: CuLCrV; syn. cucurbit leaf cumple virus	*Cucumis melo*, *Curcubita pepo*	Mexico, USA	[36,37,82,95]
Dicliptera yellow mottle virus: DiYMoV	*Dicliptera sexangularis*	USA	[82,83,139]
Dolichos yellow mosaic virus: DoYMV; syn. Dolichos lab-lab yellow mosaic virus	*Lablab purpurea*	India	[42,68,82–84,149,169, 178,215]
East African cassava mosaic Cameroon virus: EACMCV	*Manihot esculenta*	Cameroon	[82]
East African cassava mosaic Malawi virus: EACMMV	*Manihot esculenta*	Malawi	[82]
East African cassava mosaic virus: EACMV; a severe strain known as the Uganda variant has arisen by recombination between EACMV and *African cassava mosiac virus*	*Manihot esculenta*	Kenya, Madagascar, Malawi, Tanzania, Zimbabwe (Uganda variant in Congo Republic, Democratic Republic of Congo, Kenya, Rwanda, Sudan, Tanzania and Uganda)	[82–84,106,131,133,174, 178,200,215,250]
East African cassava mosiac Zanzibar virus: EACMZV	*Manihot esculenta*	Zanzibar	[82,154]
Eclipta yellow vein virus: EYVV	*Eclipta prostrata*	Pakistan	[82–84,96,169,178,215]
Eggplant yellow mosaic virus: EYMV	*Solanum melongena*	Thailand	[82,83,94,105,169, 178,215]
Eupatorium yellow vein virus: EpYVV	*Eupatorium glehni*, *E. makinoi, Nicotiana tabacum*	Japan	[82–84,169,176,178,215]
Euphorbia mosaic virus: EuMV	*Euphorbia heterophylla*, *E. prunifolia*, *Phaseolus vulgaris*	Brazil, Costa Rica, Puerto Rico, US Virgin Islands, USA, Venezuela	[42,62,68,82–84,164,169, 178,215,230]
Hollyhock leaf crumple virus: HLCrV; syn. Althea (*sic*) rosea enation virus; hollyhock leaf curl virus	*Alcea rosea*	Egypt, Israel, Jordan, Sudan	[1,28,82–84,111, 178,215]
Honeysuckle yellow vein mosaic virus: HYVMV; UK isolate not transmissible by *B. tabaci*	*Lonicera japonica*	Japan – probably widely distributed in ornamental Japanese honeysuckle. Present in UK	[10,19,45,68,82–84,149, 169,176,178,215]
Horsegram yellow mosaic virus: HgYMV	*Cajanus cajan*, *Glycine max*, *Indigifera hirsuta*, *Macrotyloma uniflorum*, *Phaseolus lunatus*, *P. vulgaris*, *Vigna mungo*, *V. radiata*	India	[68,82–84,149,169, 178,215]
Indian cassava mosaic virus: ICMV	*Manihot esculenta*, *M. glaziovii*	India	[42,82–84,106,149,169, 178,207,215,224]
Ipomoea crinkle leaf curl virus: ICLCV	*Ipomoea* spp., but not *I. batatas*	Israel	[53]
Ipomoea yellow vein virus: IYVV; not transmissible by *B. tabaci*	*Ipomoea indica*	Spain	[17,45,82,83]
Jatropha mosaic virus: JMV; syn. Jatropha mosaic virus-Puerto Rico	*Croton lobatus*, *Jatropha gossypifolia*, *J. multifida*, *J. podagrica*, *J. tamnifolia*, *Passiflora edulis*, *P. foetida*	Puerto Rico	[30,41,42,68,82–84,149, 169,178,215]
Kenaf infecting virus: KIGV	*Hibiscus cannabinus*	USA (Texas)	[41]
Leonurus mosaic virus: LeMV	*Glycine max*, *Leonurus sibiricus*	Brazil	[62,78,82–84,178,215]
Limabean golden mosaic virus: LGMV	*Phaseolus vulgaris*	Brazil, Nigeria	[42,78,82–84,149,169, 178,215]

Table 1. (*Continued*)

Virus (abbreviation and other information)	Main natural hosts	Distribution	References
Lupin leaf curl virus: LLCuV	*Lupinus hartwegii*	India	[42,68,82–84,149,169, 178,215]
Macroptilium golden mosaic virus: MGMV; syns MGMV-Jamaica 1; MGMV-Jamaica 2; MGMV-Jamaica 3	*Macroptilium lathyroides*	Dominican Republic, Jamaica	[82–84,178,205,212,215]
Macroptilium mosaic Puerto Rico virus: MaMPRV	*Macroptilium lathyroides*	Puerto Rico	[82,109]
Macroptilium yellow mosaic Florida virus MaYMFV	*Macroptilium lathyroides*	USA (Florida)	[82]
Macroptilium yellow mosaic virus MaYMV	*Macroptilium lathyroides*	Cuba	[82,196]
Macrotyloma mosaic virus: MaMV	*Macrotyloma* spp.	USA	[82–84,149,169,178,215]
Malvaceous chlorosis virus: MCV	*Malva* spp.	Brazil, Puerto Rico	[82–84,149,169,178,215]
Malva infecting virus-Puerto Rico: MIGV-PR	*Malva alceifolia*	Puerto Rico	[41]
Malvastrum yellow vein virus: MYVV	*Malvastrum coromandelianum*	China (Yunnan)	[82]
Melon chlorotic leaf curl virus: MCLCV	*Cucumis melo*	Guatemala	[38,82]
Melon leaf curl virus: MLCV	*Cucumis melo*	USA	[42,68,82–84,149,169, 178,215]
Merremia mosaic virus: MeMV; syn. Merremia mosaic virus-Puerto Rico	*Calonyction acueatum, Lycopersicon esculentum*, *Merremia aegyptia*, *M. quinquefolia*	Puerto Rico	[41,108,164]
Mungbean yellow mosaic India virus: MYMIV	*Cajanus cajan*, *Glycine max*, *Phaseolus vulgaris*, *Vigna aconitifolia*, *V. mungo*, *V. radiata*	India	[42,82,83,179,238]
Mungbean yellow mosaic virus: MYMV; syn. Vigna mungo yellow mosaic virus	*Vigna mungo*, *V. radiata*	Bangladesh, India, Pakistan, Papua New Guinea, Philippines, Sri Lanka, Thailand	[10,42,82–84,149,166, 169,178,215]
Okra leaf curl India virus: OkLCuIV	*Abelmoschus esculentus*	India, Pakistan	[65,82,83]
Okra leaf curl virus: OkLCuV	*Abelmoschus esculentus*	Chad, Côte d'Ivoire, Nigeria, Sudan	[42,82–84,149,169, 178,215]
Okra mosaic Mexico virus: OkMMV; syn. okra yellow mosaic virus-Mexico	*Abelmoschus esculentus*	Mexico	[41,82]
Okra yellow vein mosaic virus: OYVMV	*Abelmoschus esculentus*	Pakistan	[82,251]
Papaya leaf curl virus: PaLCV; syn. tomato leaf curl virus-Panama	*Carica papaya*, *Lycopersicon esculentum*	India, Panama	[82–84,178,215,225]
Papaya mosaic virus: PaMV; name also given to potexvirus	*Carica papaya*	Jamaica	[164,210]
Passiflora leaf mottle virus: PLMV	*Passiflora* spp.	Puerto Rico	[35,149]
Pepper golden mosaic virus: PepGMV; syns Serrano golden mosaic virus, Texas pepper virus, pepper jalapeño virus	*Capsicum annuum*, *C. frutescens*, *Lycopersicon esculentum*, *Nicotiana glaucum*, *Nicotiana tabacum*, *Physalis ixocarpa*	Costa Rica, Guatemala, Mexico, USA	[42,82–84,138,156,164, 169,178,181,190,215]
Pepper hausteco yellow vein virus: PHYVV; pepper hausteco virus	*Capsicum annuum*, *Lycopersicon esculentum*, *Physalis ixocarpa*	Mexico, USA	[42,82–84,156,164, 169,178,190,215]

Table 1. (*Continued*)

Virus (abbreviation and other information)	Main natural hosts	Distribution	References
Pepper leaf curl Bangladesh virus: PepLCBV	*Capsicum annuum*	Bangladesh	[82]
Pepper leaf curl virus: PepLCV	*Capsicum annuum*	Malaysia	[82–84,215]
Pepper mild tigré virus: PepMTV	*Capsicum annuum*	Mexico, USA	[42,82–84,149,164,169, 178,190,215]
Pepper yellow leaf curl virus: PepYLCV	*Capsicum annuum*	Thailand	[220]
Poinsettia leaf curl virus: PLCV	*Euphorbia pulcherrima*	Taiwan	[234]
Potato deforming mosaic virus: PDMV; possible synonymy with tomato yellow vein streak virus	*Solanum tuberosum*, *S. chacoense*, *S. sisymbrifolium*	Argentina?, Brazil	[63,118,239]
Potato yellow mosaic Panama virus: PYMPV; syn. tomato leaf curl virus-Panama	*Lycopersicon esculentum*	Panama	[76,82]
Potato yellow mosaic Trinidad virus: PYMTV; isolates tenatively identified as PYMTV from Antigua and St. Kitts may be strains of *Potato yellow mosaic virus*	*Alternanthera tenella, Abelmoschus moschatus*, *Calopogonium mucunoides*, *Capsicum annuum*, *C. frutescens*, *Euphorbia heterophylla*, *Desmodium frutescens*, *Lycopersicon esculentum*, *Malva alceifolia*, *Rhynchosia minima*, *Sida acuta*, *S. rhombifolia*	Antigua?, St. Kitts?, Trinidad and Tobago	[44,82,190,198,235]
Potato yellow mosaic virus: PYMV; synonymy with tomato yellow mosaic virus is likely, although this has not yet been officially ratified	*Capsicum annum*, *Lycopersicon esculentum*, *Solanum tuberosum*	Dominican Republic, Guadeloupe, Martinique, Puerto Rico, Venezuela	[42,82–84,109,118,149, 164,165,169,178,189, 190,191]
Pseuderanthemum yellow vein virus: PYVV; Yemen isolate not transmissible by *B. tabaci*	*Pseuderanthemum* spp.	Yemen	[19,82–84,149,169, 178,215]
Rhynchosia golden mosaic virus: RhGMV	*Nicotiana tabacum*, *Rhynchosia minima*	Honduras, Mexico	[14,82,192,215]
Rhynchosia mosaic virus: RhMV; syn. Rhynchosia yellow mosaic virus; Rhynchosia mosaic virus-Puerto Rico; pigeon pea golden mosaic virus	*Cajanus cajan, Clitoria falcata*, *Rhynchosia minima*	Puerto Rico	[30,42,68,83,84,110,149, 169,178,204]
Sida golden mosaic Costa Rica virus: SiGMCRV; syn. Sida golden mosaic virus-Costa Rica	*Sida rhombifolia*	Costa Rica	[82–84,89,103,149,169, 178,205,215]
Sida golden mosaic Florida virus: SiGMFV	*Sida rhombifolia*	USA (Florida)	[82,83]
Sida golden mosaic Honduras virus: SiGMHV; syn. Sida golden mosaic virus-Honduras	*Sida rhombifolia*	Honduras	[82,83,89,215]
Sida golden mosaic virus: SiGMV	*Glycine max*, *Sida rhombifolia*	Brazil	[62,82]
Sida golden mosaic Jamaica virus: SiGMJV	*Macroptilium lathyroides*, *Sida rhombifolia*	Jamaica	[82,83,209,211]
Sida golden yellow vein virus: SiGMV	*Sida* sp.	USA (Florida)	82
Sida infecting virus: SIGV	*Alcea rosea*, *Bastardia viscosa*, *Corchorus aestuans*, *Hibiscus brasilensis*, *Sida* spp.	Puerto Rico, USA (Texas)	[41]
Sida mottle virus: SiMoV	*Sida* sp.	Brazil	[82]

Table 1. (*Continued*)

Virus (abbreviation and other information)	Main natural hosts	Distribution	References
Sida yellow mosaic virus: SiYMV	*Sida* sp.	Brazil	[82]
Sida yellow vein virus: SiYVV; syn. Sida golden mosaic Honduras virus-yellow vein	*Sida* sp.	Honduras	[82–84,89,149,169, 178,215]
Solanum apical leaf curl virus: SALCV	*Physalis peruviana*, *Solanum nigrum*, *S. tuberosum*	Peru	[82–84,107,118,149,169, 178,215]
South African cassava mosaic virus: SACMV	*Manihot esculenta*	Madagascar, South Africa	[26,82–84,200,215]
Soybean crinkle leaf virus: SCLV	*Glycine max*	Japan, Thailand	[82–84,149,169,178, 215,221]
Soybean golden mosaic virus: SoyGMV	*Glycine max*	Puerto Rico	[205]
Squash leaf curl China virus: SLCCNV	*Cucurbita* sp.	China	[82]
Squash leaf curl virus: SLCV	*Cucurbita pepo*, *C. maxima*, *C. moschata*, *Cucumis melo*, *Phaseolus vulgaris*	USA	[42,68,82–84,74,149,164, 169,178,215,230]
Squash leaf curl Yunnan virus: SLCCYV	*Cucurbita* sp.	China (Yunnan)	[82]
Squash mild leaf curl virus: SMLCV	*Cucurbita* sp.	USA (California)	[82]
Squash yellow mild mottle virus: SYMMoV	*Carica papaya, Citrullus* sp., *Cucurbita pepo*	Costa Rica	[82,122]
Sri Lankan cassava mosaic virus: SLCMV	*Manihot esculenta*	Sri Lanka	[82,224]
Stachytarpheta leaf curl virus: StaLCV	*Stachytarpheta* sp.	China	[82]
Sweet potato leaf curl Georgia virus: SPLCGV; syn. Ipomoea leaf curl virus	*Ipomoea batatas*	USA (Georgia)	[82,136]
Sweet potato leaf curl virus: SPLCV	*Ipomoea batatas*	Taiwan, USA	[42,82,83,137]
Tobacco apical stunt virus: TbASV	*Nicotiana tabacum*	Mexico	[82,181]
Tobacco curly shoot virus: TbCSV	*Nicotiana tabacum*	China (Yunnan)	[82,248]
Tobacco leaf curl China virus: TbLCCV; syn. squash leaf curl China virus	*Cucurbita pepo*, *C. moschata*, *Cucumis melo*, *Nicotiana tabacum*, *Phaseolus vulgaris*	China	[82–84,178,215]
Tobacco leaf curl India virus: TbLCIV	*Nicotiana tabacum*	India	[81]
Tobacco leaf curl Japan virus: TbLCJV; syn. tobacco leaf curl virus-Japan	*Lycopersicon esculentum*, *Nicotiana tabacum*	Japan	[10,42,68,82–84,105,149, 169,176–178,215]
Tobacco leaf curl Kochi virus: TbLCKoV	*Lycopersicon esculemtum, Nicotiana tabacum*	Japan	[82]
Tobacco leaf curl Yunnan virus: TbLCYV	*Nicotiana tabacum*	China	[82,252]
Tobacco leaf curl Zimbabwe virus: TbLCZWV; syn. tobacco leaf curl virus-Zimbabwe	*Nicotiana tabacum*	Zimbabwe	[82,181–184]
Tobacco leaf rugose virus: TbLRV	*Nicotiana tabacum*	Cuba	[67]
Tomato chlorotic mottle virus: ToCMoV	*Lycopersicon esculentum*	Brazil	[82,203]
Tomato chlorotic vein virus: ToCVV	*Lycopersicon esculentum*	Brazil	[203]
Tomato crinkle virus: ToCrV	*Lycopersicon esculentum*	Brazil	[203]
Tomato curly stunt virus: ToCSV	*Lycopersicon esculentum*	South Africa	[82,188]

Table 1. (*Continued*)

Virus (abbreviation and other information)	Main natural hosts	Distribution	References
Tomato dwarf leaf curl virus: TDLCV	*Capsicum annuum*, *Lycopersicon esculentum*	Jamaica	[82,211,213]
Tomato golden mosaic virus: TGMV	*Lycopersicon esculentum*	Brazil	[42,68,82–84,149,164, 169,178,190,215]
Tomato golden mottle virus: TGMoV	*Lycopersicon esculentum*	Guatemala	[82,155]
Tomato leaf curl Bangalore virus: ToLCBV; syns tomato leaf curl virus-Bangalore1, Indian tomato leaf curl virus Bangalore1; Indian tomato leaf curl virus	*Lycopersicon esculentum*	India	[82–84,168,178,215]
Tomato leaf curl Bangladesh virus: ToLCBDV; syn. tomato yellow leaf curl virus-Bangladesh	*Lycopersicon esculentum*	Bangladesh	[82,83,94]
Tomato leaf curl Barbados virus: ToLCBBV	*Capsicum annuum*, *Cucumis melo*, *Cucurbita maxima*, *Lycopersicon esculentum*, *Phaseolus vulgaris*, *Solanum melongena*	Barbados	[44,208]
Tomato leaf curl Gujarat virus: ToLCGV	*Lycopersicon esculentum*	India	[82]
Tomato leaf curl India virus: ToLCIV	*Lycopersicon esculentum*	India	[82]
Tomato leaf curl Indonesia virus: ToLCIDV	*Lycopersicon esculentum*	Indonesia	[82]
Tomato leaf curl Karnataka virus: ToLCKV; syns tomato leaf curl virus-Bangalore2, Indian tomato leaf curl virus-Bangalore2, Tobacco leaf curl virus-Karnataka 1, Tobacco leaf curl virus-Karnataka 2	*Ageratum conyzoides*, *Datura stramonium*, *Lycopersicon esculentum*, *Nicotiana tabacum*, *Oxalis corniculata*, *Parthenium hysterophorus*, *Solanum nigrum*	India	[48,82–84,178,182, 195,215]
Tomato leaf curl Laos virus: ToLCLV; syn. tomato yellow leaf curl virus-Laos	*Lycopersicon esculentum*	Laos	[82,83,94]
Tomato leaf curl Malaysia virus: ToLCMV	*Lycopersicon esculentum*	Malaysia	[82]
Tomato leaf curl New Delhi virus: ToLCNDV; syns tomato leaf curl virus-New Delhi, tomato leaf curl virus-India, angled luffa leaf curl virus, Solanum yellow leaf curl virus	*Capsicum annuum*, *Lycopersicon esculentum*, *Solanum nigrum* (*Luffa acutangula and Cucumis melo* var. *reliculatus* in Thailand)	India, Pakistan, Thailand	[82–84,96,146,169,178, 215,219,233]
Tomato leaf curl Nicaragua virus: ToLCNV	*Lycopersicon esculentum*	Nicaragua	[82]
Tomato leaf curl Philippines virus: ToLCPV	*Lycopersicon esculentum*	Philippines	[82]
Tomato leaf curl Senegal virus: ToLCSV; syn. tomato leaf curl virus-Senegal	*Lycopersicon esculentum*	Senegal	[82–84,178,215]
Tomato leaf curl Sinaloa virus: ToLCSinV; syns Sinaloa tomato leaf curl virus, Tomato yellow mosaic virus-Costa Rica 2	*Capsicum annuum*, *C. frutescens*, *Lycopersicon esculentum*	Costa Rica, Mexico, Nicaragua, Guatemala	[82–84,123,149,155,164, 178,190,206]

Table 1. (*Continued*)

Virus (abbreviation and other information)	Main natural hosts	Distribution	References
Tomato leaf curl Sri Lanka virus: ToLCSLV	*Lycopersicon esculentum*	Sri Lanka	[82]
Tomato leaf curl Taiwan virus: ToLCTWV; syn. tomato leaf curl virus-Taiwan	*Lycopersicon esculentum*	Taiwan	[82–84,178,215]
Tomato leaf curl Tanzania virus: ToLCTZV; syn. tomato leaf curl virus-Tanzania	*Lycopersicon esculentum*	Tanzania	[82–84,178,215]
Tomato leaf curl Vietnam virus: ToLCVV; syn. tomato yellow leaf curl virus-Vietnam	*Lycopersicon esculentum*	Vietnam	[82,94]
Tomato leaf curl virus: ToLCV; syns tomato leaf curl virus-Australia, Solanum tomato leaf curl virus	*Datura stramonium*, *Lycopersicon esculentum*, *Nicotiana tabacum*, *Solanum melongena*, *Solanum* sp., *Zinnia elegans*	Australia	[22,42,82–84,149,169, 178,190,215]
Tomato mosaic Barbados virus: ToMBV	*Lycopersicon esculentum*	Barbados	[82]
Tomato mosaic Havana virus: ToMHV; syn. Havana tomato virus	*Lycopersicon esculentum*	Cuba, Honduras, Jamaica	[82,83,153,155,164]
Tomato mottle leaf curl virus: ToMoLCV	*Lycopersicon esculentum*	Brazil	[203]
Tomato mottle Taino virus: ToMoTV; syns Taino tomato mottle virus, tomato mottle virus-Taino	*Lycopersicon esculentum*	Cuba	[82–84,164,178,190, 197,215]
Tomato mottle virus: ToMoV; syn. Florida tomato virus	*Lycopersicon esculentum*, *Solanum viarum*	Belize, Mexico, Puerto Rico, USA (Florida)	[42,44,82–84,91,108,149, 164,169,178,190, 215,230]
Tomato rugose mosaic virus: ToRMV	*Lycopersicon esculentum*	Brazil	[82,203]
Tomato severe leaf curl virus: ToSLCV	*Lycopersicon esculentum*	Guatemala, Honduras, Nicaragua	[82–84,155,178,215]
Tomato severe rugose virus: ToSRV	*Lycopersicon esculentum*	Brazil	[82]
Tomato Uberlandia virus: ToUV	*Lycopersicon esculentum*	Brazil	[82]
Tomato yellow dwarf virus: ToYDV	*Lycopersicon esculentum*	Jamaica	[82]
Tomato yellow leaf curl Bangladesh virus: TYLCBV	*Lycopersicon esculentum*	Bangladesh	[94]
Tomato yellow leaf curl China virus: TYLCCV; syn. tomato yellow leaf curl virus-China	*Lycopersicon esculentum*	China	[82–84,178,215]
Tomato yellow leaf curl Gezira virus: TYLCGV; syn. tomato leaf curl virus-Sudan; Tomato leaf curl virus-Gezira1	*Lycopersicon esculentum*	Sudan	[82,112,113]
Tomato yellow leaf curl Kuwait virus: TYLCKWV	*Lycopersicon esculentum*	Kuwait	[82]
Tomato yellow leaf curl Malaga virus: TYLCMV; a recombinant between TYLCV and TYLCSV	*Lycopersicon esculentum*	Spain	[82,159]
Tomato yellow leaf curl Nigeria virus: TYLCNV; syn. tomato yellow leaf curl virus-Nigeria	*Lycopersicon esculentum*	Nigeria	[82–84,178,215]

Table 1. (*Continued*)

Virus (abbreviation and other information)	Main natural hosts	Distribution	References
Tomato yellow leaf curl Sardinia virus: TYLCSV; syn. tomato yellow leaf curl virus-Sardinia	*Lycopersicon esculentum*, *Solanum luteum*, *S. nigrum*	Canary Islands, Italy, Morocco, Spain	[45,82–86,159,169, 178,215]
Tomato yellow leaf curl Saudi Arabia virus: TYLCSAV; syn. tomato yellow leaf curl virus-Southern Saudi Arabia	*Lycopersicon esculentum*	Saudi Arabia (south)	[82–84,178,215]
Tomato yellow leaf curl Tanzania virus: TYLCTZV; syn. tomato yellow leaf curl virus-Tanzania	*Lycopersicon esculentum*	Tanzania	[82–84,178,215]
Tomato yellow leaf curl Thailand virus: TYLCTHV; syn. tomato yellow leaf curl-Thailand	*Lycopersicon esculentum*	Thailand, Myanmar	[82–84,94,149,178,215]
Tomato yellow leaf curl virus: TYLCV; syns tomato yellow leaf curl virus-Israel; tomato leaf curl virus-Gezira 2 (virus also in Table 4)	*Boerhavia erecta, Capsicum annuum*, *Chenopodium murale*, *Cleome viscosa, Convolvulus spp.*, *Conyza sumatrensis*, *Croton lobatus*, *Cuscuta* spp., *Cynanchum acutum*, *Datura stramonium*, *Dittrichia viscosa*, *Eustoma grandiflorum*, *Lycopersicon esculentum*, *Macroptilium* spp., *Malva parviflora*, *M. nicaeensis*, *Mercurialis ambigua*, *Phaseolus vulgaris*, *Physalis* spp., *Sida* spp. *Solanum nigrum*, *Wissadula* spp.	Algeria, Bahamas, Canary Islands, Cuba, Cyprus, Dominican Republic, Egypt, France (under eradication), Georgia, Greece, Haiti, Iran, Israel, Jamaica, Japan, Jordan, Lebanon, Mexico, Morocco, Portugal, Puerto Rico, Reunion, Spain, St. Kitts, Saudi Arabia (north), Sudan, Tunisia, Turkey, USA (Florida, Louisiana, Mississippi), Yemen	[8,13,15,16,27,29,42,44, 45,49,52,54,57,59,68, 82–84,86,112,114,115, 120,141,149,158,159, 164,169,172,173,178, 186,187,189,190,193, 202,215,216,222,228, 230,237]
Tomato yellow leaf curl Yemen virus: TYLCYV	*Lycopersicon esculentum*	Yemen	[82]
Tomato yellow mild mottle virus: ToYMMV: syn. tomato mild mottle virus, but this name already given to tomato virus in *Potyviridae*	*Lycopersicon esculentum*	Honduras, Nicaragua, Guatemala	[83,155,162,206]
Tomato yellow mosaic virus: ToYMoV; synonymy with *Potato yellow mosaic virus* is likely	*Lycopersicon esculentum*, *L. hirsutum*, *L. pimpinellifolium*, *Solanum tuberosum*, *S. quitoense*	Brazil, Venezuela	[11,82–84,42,68,149,164, 165,169,178]
Tomato yellow mottle virus: ToYMoV; syn. tomato yellow mosaic virus-Costa Rica 1	*Lycopersicon esculentum*, *Phaseolus vulgaris*	Costa Rica	[82–84,123,155,164,165, 178,190,215]
Tomato yellow vein streak virus: ToYVSV	*Lycopersicon esculentum*, *Solanum tuberosum*	Argentina, Brazil	[79,82–84,164,178,215]
Triumffeta yellow vein virus: TYVV	*Triumffeta rhomboidiaceae*	India	[97]
Watermelon chlorotic stunt virus: WmCSV	*Citrullus lanatus*, *C. colocynthis*	Iran, Saudi Arabia, Sudan, Yemen,	[42,82–84,127,149,169, 178,215]
Watermelon curly mottle virus: WmCMV	*Citrullus lanatus*, *Cucumis melo* var. *cantalupensis*	USA	[42,82–84,149,169, 178,215]
Wissadula golden mosaic virus: WGMV; syn. Wissadula mosaic virus	*Wissadula amplissima*	Jamaica	[68,82–84,149,169,178, 209,211,215]
Zinnia leaf curl virus: ZiLCV	*Zinnia elegans*	India, Pakistan	[68,82–84,96,215,240]

Table 2. Names, hosts and distribution of *B. tabaci*-transmitted criniviruses (key: all viruses recognized as species by Martelli et al. (2000)

Virus (abbreviation and other information)	Main natural hosts	Distribution	References
Cucurbit yellow stunting disorder virus: CYSDV	*Cucumis melo*, *C. sativus*	Canary Islands, Egypt, Israel, Jordan, Lebanon, Mexico, Morocco, Portugal, Saudi Arabia, Spain, Turkey, United Arab Emirates, USA	[2,8,24,45,46,64,84,100, 121,142,150,214,244]
Lettuce chlorosis virus: LCV	*Beta vulgaris*, *Lactuca sativa* and possibly the same weed hosts as *Lettuce infectious yellows virus*	USA	[71,73,84,150,157]
Lettuce infectious yellows virus: LIYV	*Beta vulgaris*, *Chenopodium murale*, *Citrullus lanatus*, *Cucumis melo*, *Cucurbita pepo*, *C. maxima*, *C. moschata*, *Daucus carota, Lactuca sativa*, *Physalis wrightii*, *Malva parviflora*	Mexico, USA (California – however, not detected recently)	[42,68,69,77,84,150, 159,169,214,230]
Sweet potato chlorotic stunt virus: SPCSV; syn. sweet potato sunken vein virus (virus also in Table 4)	*Ipomoea batatas*	Argentina, Israel, Nigeria, USA	[42,51,84,149,150, 169,226]
Tomato chlorosis virus: ToCV (virus also in Table 4)	*Datura stramonium, Lycopersicon esculentum, Solanum nigrum*	Canary Islands, Italy, Morocco, Portugal, Puerto Rico, Spain, USA	[5,8,12,55,84,98,140,150, 171,243–245]

susceptible to many different species of *Begomovirus* and in most cases exhibit leaf curl symptoms. In the Americas, tomato is affected by a large number of *Begomovirus* species, which can also infect other crops (Polston and Anderson, 1997), and these pose a risk to the agriculture of the European–Mediterranean region. New *Begomovirus* species on tomato are continually being discovered and some may be the result of genetic recombination between viruses present in multiple infections.

After acquisition by whiteflies, begomoviruses are persistent and are retained for periods ranging from a few weeks to life (Duffus, 1987). The interaction between whiteflies and geminiviruses, especially *B. tabaci* and *Tomato yellow leaf curl virus* (TYLCV), has been reviewed by Czosnek et al. (2001).

Eight species of *Begomovirus* have been identified in the European–Mediterranean region. Of these, *Abutilon mosaic virus* (AbMV), *Ipomoea yellow vein virus* (IYVV) and *Honeysuckle yellow vein mosaic virus* (HYMV) are generally no longer transmissible by *B. tabaci* (Anon., 1997; Banks et al., 1999; Bedford et al., 1994). This may have occurred through many years of vegetative propagation of their ornamental host plants (Bedford et al., 1994) that led to changes in the coat protein (Höfer et al., 1997a; Hohnle et al., 2001). Despite their apparent loss of transmissibility, they have been included in Table 1 as it is possible that some undiscovered isolates may still retain the ability to be transmitted by *B. tabaci*. This is certainly true of AbMV, as a Brazilian isolate has been recorded as transmissible (Jeske, 2000). The other five begomoviruses of the eight species recorded in the European–Mediterranean region are transmissible by *B. tabaci*. Tomato is affected by *Tomato yellow leaf curl Sardinia virus* (TYLCSV) and TYLCV (previously TYLCV-Israel) (Accotto et al., 2000), the latter having now spread to the Americas. TYLCSV has caused significant crop losses within the tomato industries of southern Spain, the Canary Islands, Portugal and parts of Italy and has been shown to infect the common weed *Solanum nigrum*, which can act as a reservoir of infection (Bedford et al., 1998). In southern Spain, TYLCV could now be displacing TYLCSV. This may be because TYLCV is more efficiently vectored by the local Q biotype of *B. tabaci* and, unlike TYLCSV, can infect common bean (Sánchez-Campos et al., 1999). TYLCV is the most widespread *B. tabaci*-transmitted virus in the European–Mediterranean region occurring in Algeria, Canary Islands, Cyprus, Egypt, Greece, Israel, Jordan, Morocco, Portugal, Spain, Tunisia and Turkey. A recent outbreak of TYLCV in the Rhone delta area of France was believed to have been eradicated (Bertaux et al., 2001), but there has since been a

Table 3. Names, hosts and distribution of carlaviruses, ipomoviruses and unclassified viruses transmitted by *B. tabaci* (key: virus names in italics are recognized as species by either Brunt et al. (2000) or Berger et al. (2000); virus names in roman are tentative species)

Virus (abbreviation; genus; synonyms)	Main natural hosts	Distribution	References
Cassava brown streak virus: CBSV; a tentative ipomovirus that may be transmitted by *B. tabaci* or/and *B. afer* and causes cassava brown streak disease	*Manihot esculenta*	East Africa	[32,42,132,134,160,161]
Cucumber vein yellowing virus: CVYV; *Ipomovirus*	*Citrullus vulgaris, Convolvulus arvensis, Cucumis sativus, Ecballium elaterium, Malva parviflora, Sonchus asper, S. oleraceus, S. tenerrimus*	Israel, Jordan, Spain, Turkey	[42,56,68,116,130, 149,169]
Cowpea mild mottle virus: CPMMV; *Carlavirus*; syns bean angular mosaic virus, groundnut crinkle virus, Psophocarpus necrotic mosaic virus, tomato pale chlorosis virus, Voandzeia mosaic virus	*Arachis hypogaea*, *Calopogonium mucunoides*, *Canavalia ensiformis*, *Glycine max*, *Lycopersicon esculentum*, *Phaseolus lunatus*, *P. vulgaris*, *Psophocarpus tetragonolobus*, *Mucana pruriens*, *Stylothanthes gracile*, *Vicia faba*, *Vigna. radiata*, *V. unguiculata*, *Voandzeia subterranea*	Asia, Brazil, East and West Africa, Egypt, Israel, Jordan, Oceania, Sudan	[10,42,43,68,84,149]
Frenchbean crinkle stunt virus: FbCSV; unclassified, but possibly synonymous with *Mungbean yellow mosaic India virus*	*Phaseolus vulgaris*	India	[201]
Oxalis leaf curl virus: OxLCV; unclassified	*Oxalis latifolia*, *O. martiana*	India	[227]
Pumpkin yellow vein mosaic virus: PYVMV; unclassified	*Cucurbita moschata*	India	[117]
Squash yellow leaf curl virus: SYLCV; *Ipomovirus*	*Cucurbita pepo*	Oman	[253]
Sweet potato mild mottle virus: SPMMV; *Ipomovirus*	*Ipomoea batatas*	Argentina, Indonesia, Japan, Kenya, Papua New Guinea, Peru, Samoa, Solomon Islands, Tanzania, Tonga, Uganda	[10,25,42,68,84,149,169]
Sweet potato yellow dwarf virus: SPYDV; *Ipomovirus*	*Ipomoea batatas*	Taiwan	[25,42,84,149,169]

second outbreak (Anon., 2002b). Eradication is again being attempted and the situation is being monitored (Anon., 2002b). Both outbreaks have been attributed to the movement of infected tomato plants from Spain. *Tomato yellow leaf curl Malaga virus* is a recombinant between TYLCV and TYLCSV reported from Spain (Monci et al., 2001). *Cowpea golden mosaic virus* and Ipomoea crinkle leaf virus have been found respectively in Tunisia and Israel.

Many other *B. tabaci*-transmitted begomoviruses threaten agriculture in the European–Mediterranean region. New World begomoviruses listed at some time on the European and Mediterranean Plant Protection Organisation (EPPO) Alert List, which is an indication of their possible quarantine significance, are *Pepper golden mosaic virus* (syn. Serrano golden mosaic virus), *Pepper hausteco yellow vein virus* (syn. pepper hausteco virus), pepper mild tigré virus, *Potato yellow mosaic virus*, *Tomato yellow leaf curl Sinaloa virus* (syn. Sinaloa tomato leaf curl virus), *Tomato dwarf leaf curl virus*, *Chino del tomate virus* (syn. tomato golden mosaic virus), *Tomato mosaic Havana virus* (syn. Havana tomato virus), *Tomato mottle Taino virus* (syn. Taino tomato mottle virus), *Tomato yellow mosaic virus*, *Tomato yellow vein streak virus* and *Watermelon chlorotic stunt virus* (Anon., 2001b).

Other *B. tabaci*-transmitted viruses that currently affect European crops are in the *Crinivirus* genus of the *Closteroviridae*. *Cucumber yellow stunting disorder virus* (CYSDV) (Celix et al., 1996) is causing severe damage to cucumbers and melons in Spain, Portugal and the Canary Islands and *Tomato chlorosis virus* (ToCV) also seriously affects tomato crops in these areas (Navas-Castillo et al., 2000; Louro et al., 2000a) and has been detected in southern Italy (Accotto et al., 2001). Criniviruses are carried by whiteflies in a semipersistent manner and are retained after acquisition for periods of only a few days (Duffus, 1987). *B. tabaci*-transmitted criniviruses that have been placed on the EPPO Alert List are CYSDV, ToCV and *Lettuce chlorosis virus* (Anon., 2001b).

Six *B. tabaci*-transmitted viruses are listed as quarantine pests by EPPO. *Euphorbia mosaic virus*, *Bean golden mosaic virus*, *Lettuce infectious yellows virus*, *Squash leaf curl virus* and *Tomato mottle virus* are on the EPPO A1 list of exotic pests. TYLCV is on the EPPO A2 list of quarantine pests present, but not widely distributed, in the EPPO region (Smith et al., 1997). In addition, all plant material that could carry *B. tabaci*-transmitted viruses is subject to quarantine control by the European Community regulations as is *B. tabaci* itself in countries where it has not established (Anon., 2000). In light of recent knowledge on their taxonomic status, some of these pest lists require updating. For example, since Smith et al. (1997) published data sheets on quarantine pests, the original 'bean golden mosaic virus' has been found to be comprized of two distinct virus species and watermelon curly mottle virus and melon leaf curl virus given as synonyms for squash leaf curl virus have become virus species in their own right. 'Tomato yellow leaf curl virus' has also been subdivided into numerous species (Table 1).

The emergence of the B biotype of *B. tabaci*, with its ability to feed on many different host plants, has given whitefly-transmitted viruses the potential to infect new plant species. This has already been shown to have occurred in the Americas (Anon., 2001a).

Viruses transmitted by *Trialeurodes* spp.

Important viruses spread by *T. vaporariorum* in the European–Mediterranean region are *Beet pseudoyellows virus*, which affects cucumber, melon, lettuce and sugar beet, *Tomato infectious chlorosis virus* and ToCV (Table 4). All are in the *Closteroviridae*. The two latter virus species are on the EPPO Alert List (Anon., 2001b).

In Turkmenistan, *T. vaporariorum* has been reported as a vector of a virus causing chlorotic leaf curl symptoms in tomato and it was suggested that this virus could be TYLCV (Vlasov and Teploukhova, 1997). However, this virus–vector relationship is unlikely given that *T. vaporariorum* has not been recorded as a vector of TYLCV elsewhere. For this reason, this virus–vector combination has not been included in Table 4.

T. abutilonea has been shown to transmit *Sweet potato chlorotic stunt virus* and ToCV. Both of these viruses are present in the European–Mediterranean region though, in the absence of *T. abutilonea*, they are spread by other whitefly vectors (see Tables 2 and 4).

Although *T. ricini* has been documented as a vector of TYLCV in experiments in Egypt (Idriss et al., 1997), this whitefly has not yet been confirmed as a vector of TYLCV in transmission studies currently being undertaken in the UK (I. Bedford, John Innes Centre, UK, pers. comm.). However, despite the present uncertainty over the validity of *T. ricini* as a vector, this virus–vector combination has been included in Table 4.

Information sources

The information presented in Tables 1–4 has been compiled from various sources. The starting point in the investigations was those *B. tabaci*-transmitted begomoviruses listed by Markham et al. (1994) and the *B. tabaci*-transmitted viruses of all genera listed by Duffus (1987) and Brunt et al. (1996). All named begomoviruses have been included in Table 1 because, by definition, they are considered capable of transmission by *B. tabaci*, despite a few exceptions (Rybicki et al., 2000). Geminiviruses that have not been shown to be in the *Begomovirus* genus and which are not known to be whitefly-transmitted have not been included.

The decision to rank begomoviruses as species and place their names in italics was made after reference to Fauquet et al. (2003). It has been suggested that the full nucleotide sequence of the DNA A component of the genome should be the main taxonomic indicator. Begomoviruses with full sequence similarities above 89% should be considered isolates/strains of the same species, whereas those with full sequence similarities below 89% should be taken to be different species (Fauquet, 2002a).

Problems associated with correctly documenting the natural host range and distribution of viruses were

Table 4. Names, hosts and distribution of viruses transmitted by *Trialeurodes* spp. (key: virus names in italics recognized as species by either Martelli et al. (2000) or Fauquet (2002); virus names in roman are tentative species)

Virus (abbreviation; genus; synonyms; vector)	Main natural hosts	Distribution	References
Abutilon yellows virus: AbYV; *Crinivurus*; *T. abutilonea*	*Abutilon* spp.	USA	[24,42,68,69,84,150]
Beet pseudoyellows virus: BPYV; *Closterovirus*; syns cucumber chlorotic spot virus, cucumber yellows virus, melon yellows virus; *T. vaporariorum*	*Beta vulgaris*, *Lactuca sativa*, *Cichorum endiva*, *Cucumis melo*, *C. sativus*, *Capsella burse-pastoris*, *Taraxacum officinalis*, *Conium maculatum*	Australia, France, Greece (Crete), Japan, the Netherlands, Spain, UK, USA	[42,45,50,68,84,135,149, 150,169,175,214,222, 229,246,249]
Diodia vein chlorosis virus: DVCV; *Closterovirus*; syn. Diodia yellow vein virus; *T. abutilonea*	*Diodia virginiana*	USA	[42,68,69,84,129,149,169]
Potato yellow vein virus: PYDV; *Crinivirus*; *T. vaporariorum*	*Catharanthus roseus*, *Lycopersicon* spp., *Polygonium* spp., *Rumex obtusifolium*, *Solanum nigrum*, *S. tuberosum*, *Tagetes* spp.	Colombia, Ecuador, Peru, Venezuela	[217,218]
Sweet potato chlorotic stunt virus: SPCSV; *Crinivurus;* syn. sweet potato sunken vein virus; *T. abutilonea* (virus also in Table 2)	*Ipomoea batatas*	Israel, Nigeria, USA	[42,51,84,149,150, 169,226]
Tomato chlorosis virus: ToCV; *Crinivirus*; *T. abutilonea*, *T. vaporariorum* (virus also in Table 2)	*Datura stramonium, Lycopersicon esculentum, Solanum nigrum*	Canary Islands, Italy, Morocco, Portugal, Puerto Rico, Spain, USA	[5,8,12,55,84,98,140,150, 171,243–245]
Tomato infectious chlorosis virus: TICV; *Crinivirus*; *T. vaporariorum*	*Callistephus chinensis*, *Cynara cardunculus*, *C. scolymus*, *Lactuca sativa*, *Lycopersicon esculentum*, *Nicotiana glauca*, *Petunia hybrida*, *Physalis ixocarpa*, *Picris echioides*, *Ranunculus* spp.	Czech Republic, Italy, Mexico, Spain (Castellón), USA (California, North Carolina)	[42,45,55,70,72,84,87, 150,236,244]
Tomato yellow leaf curl virus: TYLCV; *Begomovirus*; *T. ricini* (virus also in Table 1)	See under *Tomato yellow leaf curl virus* in Table 1	See under *Tomato yellow leaf curl virus* in Table 1	See under *Tomato yellow leaf curl virus* in Table 1

encountered. Some viruses originally thought to be one species have been split into different species as more sequence information has become available. Examples of this are the groups of viruses now known to cause cotton leaf curl and tomato yellow leaf curl diseases. Information on hosts and distribution recorded when a disease was thought to be caused by a single virus agent may no longer be valid. What is needed is the same information for the different virus species that are now recognized. However, this information is not always available. Therefore, the data presented in some cases is tentative.

Some virus pathogens, which have been recorded as being transmitted by *B. tabaci*, were reported in early publications (Brunt et al., 1996; Duffus, 1987; Markham et al., 1994), but have not reappeared recently in the literature. Furthermore, they have not been included in the most recent official lists of plant virus names (Rybicki et al., 2000; Fauquet et al., 2003). Their authenticity must now be in doubt and some of the more obscure have not been included in this publication. An example is tomato necrotic dwarf virus, which was thought to be a possible whitefly-transmitted nepovirus (Duffus, 1987; Larson et al., 1984; Markham et al., 1994). The viruses in this category that have been included are bean distortion dwarf virus (Markham et al., 1994; Xi et al., 1982) and Passiflora leaf mottle virus (Brown et al., 1993; Markham et al., 1994), which are tentative begomoviruses.

Because decisions were taken to include or exclude whitefly-transmitted viruses that have not been referenced in recent years by virus taxonomists

and to exclude unnamed begomoviruses listed on GeminiNet (Fauquet, 2002b), other unnamed begomoviruses (e.g. Amin et al., 2002; De Mello et al., 2001; Khan et al., 2002a,b; Mansoor et al., 2001a; Raj et al., 2000; Royas et al., 2000) plus other unconfirmed virus reports (e.g. Vidal et al., 2000), the virus tables presented here are subjective. New begomoviruses are also being described on a regular basis and additional species will undoubtedly be recognized in the near future. However, this document does represent most of what is known at the time of writing and should serve as a guide to the number and range of viral pathogens that are transmitted by whiteflies and the risks they pose to agriculture particularly in the European–Mediterranean region.

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