

TRANSMISSION SPECIFICITY OF PLANT VIRUSES BY VECTORS

P. Andret-Link¹ and M. Fuchs^{1,2}

¹Laboratoire de Virologie, Institut National de la Recherche Agronomique et Université Louis Pasteur, Unité de Recherche 'Santé de la Vigne et Qualité des Vins', 28 rue de Herrlisheim, 68021 Colmar, France

²Department of Plant Pathology, Cornell University, New York State Agricultural Experiment Station, Geneva, NY 14456, USA

SUMMARY

Most plant viruses are transmitted by vectors from one host to another. Virus transmission by a vector is often characterized by some degree of specificity. Numerous studies suggest the involvement of a virus-ligand interaction in transmission specificity. The coat protein (CP) and its derivatives (readthrough CP and minor CP), and nonstructural proteins, such as a helper component (HC) or a transmission factor, are major viral determinants of transmission specificity. A number of virion-binding vector proteins have been identified as potential receptors. This article reviews the literature on the molecular aspects of virus transmission with a major emphasis on the specificity of transmission. It highlights recent advances in the field and identifies areas of desirable progress.

Key words: Plant virus, vector, transmission, specificity, virus-ligand interaction.

INTRODUCTION

Plant viruses can cause severe yield losses to the cereal, vegetable, fruit, and floral industries, and substantially lessen the quality of crop products. Due to virus infection, losses of over \$1.5 billion are reported in rice in South-East Asia (Hull, 2002), and estimates of losses have been calculated as \$63 million in apple in the United States (Cembali *et al.*, 2003), and over \$20 million in potato in the United Kingdom (Hull, 2002). *Tomato spotted wilt virus* (TSWV) alone is responsible for losses of over \$1 billion in vegetable and ornamental crops. TSWV is transmitted by thrips and has the largest host range of any plant virus infecting more than a thousand plant species from 84 families (Parella *et al.*, 2003). Similarly, *Grapevine fanleaf virus* (GFLV), which is transmitted by the ectoparasitic nematode *Xiphinema index*,

is causing \$1 billion losses to the grapevine industry in France (Andret-Link and Fuchs, unpublished). Also, Tomato yellow leaf curl virus (TYLCV) and its whitefly vector *Bemisia tabaci* have been of increasing importance recently in many regions with tropical, subtropical, and arid Mediterranean climates due to a rapid expansion in geographic distribution and host range of the virus and its vector (Pico *et al.*, 1996).

Plant viruses are transmitted from host to host through budwood, seeds or tubers, or by arthropods, nematodes, fungi, or plasmodiophorid vectors. Transmission is an important step in the biological cycle of viruses because it ensures their maintenance and survival. Most plant viruses are transmitted by vectors from one host to another, although they are efficiently disseminated by human activities such as vegetative plant propagation, grafting, global exchange of infected material, changes in cropping systems, and the introduction of novel crops in existing or new agricultural areas. Vector-virus transmission consists of several successive steps: acquisition of virions from an infected source, stable retention of acquired virions at specific sites through binding of virions to ligands, release of virions from the retention sites upon salivation or regurgitation, and delivery of virions to a site of infection in a viable plant cell. Each step of this sequence is needed for transmission to be successful.

Extensive information is available on viral determinants of transmissibility but limited information is available yet on viral determinants of transmission specificity. The coat protein (CP), or its derivatives (readthrough CP and minor CP), and nonstructural proteins, including a helper component (HC) or a transmission factor (Pirone and Blanc, 1996), are involved in transmission specificity. Numerous comprehensive reviews have been recently published on virus transmission by arthropods (Gray and Banerjee, 1999), including aphids (Ng and Perry, 2004), *Olpidium* and plasmodiophorid vectors (Campbell, 1996; Kanyuka *et al.*, 2003; Rochon *et al.*, 2004), and nematodes (McFarlane, 2003). This article reviews the literature on the molecular aspects of virus transmission with a major emphasis on the specificity of transmission. It highlights recent advances in the field and points out areas of significant progress. It also identifies topics for which more research would be

Table 1. Virus species cited in this review article.

Name	Acronym	Genus	Family
<i>Abutilon mosaic virus</i>	AbMV	<i>Begomovirus</i>	<i>Geminiviridae</i>
<i>African cassava mosaic virus</i>	ACMV	<i>Begomovirus</i>	<i>Geminiviridae</i>
<i>Alfalfa mosaic virus</i>	AMV	<i>Alfamovirus</i>	<i>Bromoviridae</i>
<i>Arabidopsis mosaic virus</i>	ArMV	<i>Nepovirus</i>	<i>Comoviridae</i>
<i>Barley mild mosaic virus</i>	BaMMV	<i>Bymovirus</i>	<i>Potyviridae</i>
<i>Barley yellow dwarf virus</i>	BYDV	<i>Luteovirus</i>	<i>Luteoviridae</i>
<i>Barley yellow mosaic virus</i>	BaYMV	<i>Bymovirus</i>	<i>Potyviridae</i>
<i>Beet curly top virus</i>	BCTV	<i>Curtovirus</i>	<i>Geminiviridae</i>
<i>Beet western yellows virus</i>	BWYV	<i>Polerovirus</i>	<i>Luteoviridae</i>
<i>Bean golden mosaic virus</i>	BGMV	<i>Begomovirus</i>	<i>Geminiviridae</i>
<i>Beet leaf curl virus</i>	BLCV	unassigned	<i>Rhabdoviridae</i>
<i>Beet necrotic yellow vein virus</i>	BNYVV	<i>Benyvirus</i>	unassigned
<i>Beet soil-borne virus</i>	BSBV	<i>Furovirus</i>	unassigned
<i>Beet western yellow virus</i>	BWYV	<i>Polerovirus</i>	<i>Luteoviridae</i>
<i>Brome mosaic virus</i>	BMV	<i>Bromovirus</i>	<i>Bromoviridae</i>
<i>Cauliflower mosaic virus</i>	CaMV	<i>Caulimovirus</i>	<i>Caulimoviridae</i>
<i>Cucumber mosaic virus</i>	CMV	<i>Cucumovirus</i>	<i>Bromoviridae</i>
<i>Cucumber necrosis virus</i>	CNV	<i>Tombusvirus</i>	<i>Tombusviridae</i>
<i>Cucurbit aphid-borne yellows virus</i>	CABYV	<i>Polerovirus</i>	<i>Luteoviridae</i>
<i>Cacao swollen shoot virus</i>	CSSV	<i>Badnavirus</i>	<i>Caulimoviridae</i>
<i>Grapevine fanleaf virus</i>	GFLV	<i>Nepovirus</i>	<i>Comoviridae</i>
<i>Grapevine leafroll-associated viruses</i>	GLRaV	<i>Ampelovirus</i>	<i>Closteroviridae</i>
<i>Grapevine virus A</i>	GVA	<i>Vitivirus</i>	<i>Flexiviridae</i>
<i>Grapevine virus B</i>	GVB	<i>Vitivirus</i>	<i>Flexiviridae</i>
<i>Groundnut ringspot virus</i>	GRSV	<i>Tospovirus</i>	<i>Bunyaviridae</i>
<i>Iris yellow spot virus</i>	IYSV	<i>Tospovirus</i>	<i>Bunyaviridae</i>
<i>Lettuce infectious yellow virus</i>	LIYV	<i>Crinivirus</i>	<i>Closteroviridae</i>
<i>Pea early browning virus</i>	PEBV	<i>Tobravirus</i>	unassigned
<i>Pepper ringspot virus</i>	PepRSV	<i>Tobravirus</i>	unassigned
<i>Potato leafroll virus</i>	PLRV	<i>Polerovirus</i>	<i>Luteoviridae</i>
<i>Potato mop top virus</i>	PMTV	<i>Furovirus</i>	unassigned
<i>Rice dwarf virus</i>	RDV	<i>Phytoreovirus</i>	<i>Reoviridae</i>
<i>Rice ragged stunt virus</i>	RRSV	<i>Oryzavirus</i>	<i>Reoviridae</i>
<i>Soil-borne wheat mosaic virus</i>	SBWMV	<i>Furovirus</i>	unassigned
<i>Southern bean mosaic virus</i>	SBMV	<i>Sobemovirus</i>	unassigned
<i>Strawberry latent ringspot virus</i>	SLRV	<i>Sadwavirus</i>	unassigned
<i>Tobacco mosaic virus</i>	TMV	<i>Tobamovirus</i>	unassigned
<i>Tobacco rattle virus</i>	TRV	<i>Tobravirus</i>	unassigned
<i>Tobacco ringspot virus</i>	TRSV	<i>Nepovirus</i>	<i>Comoviridae</i>
<i>Tomato black ring virus</i>	TBRV	<i>Nepovirus</i>	<i>Comoviridae</i>
<i>Tomato bushy stunt virus</i>	TBSV	<i>Tombusvirus</i>	<i>Tombusviridae</i>
<i>Tomato chlorotic spot virus</i>	TCSV	<i>Tospovirus</i>	<i>Bunyaviridae</i>
<i>Tomato golden mosaic virus</i>	TGMV	<i>Begomovirus</i>	<i>Geminiviridae</i>
<i>Tomato yellow leaf curl virus</i>	TYLCV	<i>Begomovirus</i>	<i>Geminiviridae</i>
<i>Tomato spotted wilt virus</i>	TSWV	<i>Tospovirus</i>	<i>Bunyaviridae</i>
<i>Velvet tobacco mosaic virus</i>	VTMV	<i>Sobemovirus</i>	unassigned
<i>Wheat streak mosaic virus</i>	WSMV	<i>Tritimovirus</i>	<i>Potyviridae</i>

desirable. A summary list of the virus species cited in this article is given in Table 1.

PLANT VIRUS VECTORS AND SPECIFICITY OF TRANSMISSION

Vectors of plant viruses. Vectors of plant viruses are taxonomically very diverse and can be found among

arthropods, nematodes, fungi, and plasmodiophorids (Froissart *et al.*, 2002; Hull, 2002). Arthropod vectors that transmit most plant viruses are aphids, whiteflies, leafhoppers, thrips, beetles, mealybugs, mirids, and mites (Spence, 2001), the most common being aphids with more than 200 vector species identified (Ng and Perry, 2004). More than half of the nearly 550 vector-transmitted virus species recorded so far are disseminated by aphids (55%), 11% by leafhoppers, 11% by bee-

bles, 9% by whiteflies, 7% by nematodes, 5% by fungi and plasmodiophorids, and the remaining 2% by thrips, mites, mirids, or mealybugs (Astier *et al.*, 2001).

Characteristics of a virus-vector interaction. The transmission of a virus by a vector is often characterized by some degree of specificity. Transmission specificity can be broad or narrow but it is a prominent feature for numerous viruses and vectors. Specificity of transmission is defined as the specific relationship between a plant virus and one or a few vector species but not others. For instance, a virus transmitted by aphids is not transmitted by nematodes or, among arthropod vectors, a virus transmitted by leafhoppers is not transmitted by beetles. An extreme case of transmission specificity is exclusivity, when a vector transmits one virus or one serologically distinct virus strain, and this virus or virus strain has a single vector. As examples of the different degrees of specificity, GFLV is naturally transmitted by a single nematode species, *Xiphinema index* (Andret-Link *et al.*, 2004), while some potyviruses are transmitted by more than 30 aphid species (Jeger *et al.*, 2004). Also, the whitefly *Bemisia tabaci* transmits numerous viruses from various genera and families, while the beat lace bug *Pisema quadratum* transmits only Beet leaf curl virus (BLCV). In contrast, closteroviruses are transmitted by aphids, mealybugs, or whiteflies, whereas tobamoviruses are transmitted only by trichodorid nematodes. The specificity of transmission is explained by several characteristics, including a recognition event between the virion, or a viral protein motif, and a site of retention in the vector (Brown and Weischer, 1998).

Mode of virus transmission by vectors. Different modes of virus transmission have been characterized depending on the retention time, sites of retention, and internalization of virions by vectors. Nonpersistent viruses are retained by their vectors for less than a few hours whereas semipersistent viruses are retained for days, weeks, or even years. Viruses in these two categories are acquired from infected plants and inoculated within seconds or minutes to recipient plants. In addition, they do not require a latent period, e.g. time interval between acquisition and transmission, and do not replicate in the vector. Nonpersistent and semipersistent viruses are specifically associated with the epicuticle that lines the stylets (mouthparts) or the foreguts of their arthropod vectors, respectively, or the cuticle lining of the feeding apparatus of their nematode vectors. Since the cuticle, including the lining of the mouthparts and foregut, is shed during molting, acquired viruses are lost at each molt. Collectively, the nonpersistent and semipersistent viruses are referred to as noncirculative because they are not internalized by vectors. In other words, they do not enter the hemocoel (vector body cavity) or cross any vector cell membrane (Gray and Banerjee, 1999).

Persistent viruses, once acquired from infected plants, are associated with the vector for the remainder of their lifetime. They require long acquisition times (hours to days) and long latent periods (one day to several weeks). Successful transmission of persistent viruses requires an internalization of the ingested viruses that are actively transported across several cell membranes. Thus, they are found in the hemocoel of vectors and retained by vectors after molting. Ultimately, they must associate with the vector salivary system to be transmitted into a new host. Persistent viruses are referred to as circulative. They can be further divided into propagative, e.g. viruses that replicate in their arthropod vectors in addition to their plant hosts, and nonpropagative viruses, e.g. viruses that replicate only in their plant hosts but not in their vectors (Gray and Banerjee, 1999).

A single mode of transmission is characteristic of most viruses. Features of the different modes of virus transmission are important for transmission specificity.

VIRAL DETERMINANTS INVOLVED IN THE SPECIFICITY OF VIRUS TRANSMISSION BY VECTORS

Extensive information is available on viral determinants of transmissibility but limited information is available on viral determinants of transmission specificity. The CP, or its derivatives (readthrough CP and minor CP), in the case of luteoviruses, *Cucumber mosaic virus* (CMV), *Cucumber necrosis virus* (CNV), and GFLV, and a HC or a transmission factor in the case of potyviruses, caulimoviruses, and waikaviruses have a profound role in transmission specificity.

Determinants of noncirculative nonpersistent viruses. Plant viruses transmitted by aphids in a noncirculative nonpersistent manner include members of the genera *Alfavirus* (family *Bromoviridae*), *Carlavirus* (family *Flexiviridae*), *Cucumovirus* (family *Bromoviridae*), *Fabavirus* (family *Comoviridae*), *Machlomovirus* (family *Tombusviridae*), *Macluravirus* (family *Potyviridae*), and *Potyvirus* (family *Potyviridae*) (Hull, 2002; Pirone and Perry, 2002) (Table 2). They represent over 130 distinct virus species (Astier *et al.*, 2001; Ng and Perry, 2004).

There is limited information on the viral determinants involved in the transmission of *Alfalfa mosaic virus* (AMV) or members of the genera *Fabavirus*, *Carlavirus*, *Machlomovirus*, and *Macluravirus*. The transmission of carlaviruses involves the CP encoded by a 1.3 kb subgenomic RNA but apparently no HC (Brunt *et al.*, 1996). For CMV, the CP is the only virus-encoded protein involved in transmission (Chen and Francki, 1990). A prominent feature on the surface of CMV virions is a negatively charged loop structure termed the BH-BI loop. Six of eight amino acids in this CP loop are highly conserved among CMV strains and other cucu-

moviruses (Liu *et al.*, 2002). Interestingly, distinct CP motifs are responsible for the transmission of CMV by different aphid species. The amino acids in position 25, 129, 162, 168, and 214 of the CP are critical for efficient transmission by *Myzus persicae*, whereas those in position 129, 162, and 168 are critical for efficient transmission by *Aphis gossypii* (Perry *et al.*, 1998). Structural analyses show that the amino acids in position 129 and 162 are exposed on the surface of virions and buried in the folded CP, respectively (Wikoff *et al.*, 1997). Mutation of these CP residues affects CMV transmission indirectly through a destabilization effect or conformational changes (Liu *et al.*, 2002; Ng *et al.*, 2005).

For potyviruses, not only is the motif DAG, which is located near the surface-exposed CP N-terminus and conserved among several isolates, required for virus transmission by aphids but also the context within which the DAG motif occurs is of considerable importance (Dombrovsky *et al.*, 2005). In addition, potyvirus transmission requires the acquisition of the viral non-structural HC protein by aphids. A KITC motif and a PTK motif are highly conserved at the N- and C-terminus of HCs, respectively. It has been hypothesized that, to bridge virions to the aphid alimentary tract, the HC could act as a dimer, its KITC motif interacting with the aphid stylet and its PTK motif interacting with the DAG motif of the CP (Pirone and Perry, 2002; Llave *et al.*, 2002). HC plays a critical role in vector specificity, as shown by the differential transmissibility of homologous and heterologous combinations of HC-virions (Pirone and Perry, 2002). A lower proclivity for heterologous virion-HC interactions and/or a differential effect of the saliva of distinct aphid species on HC activity could explain the differential virus transmissibility (Martin *et al.*, 1997). Interestingly, HC and virions can be acquired sequentially (Froissart *et al.*, 2002).

Determinants of noncirculative semipersistent viruses.

Plant viruses transmitted by vectors in a noncirculative semipersistent manner include members of the genera *Ampelovirus* (family *Closteroviridae*), *Badnavirus* (family *Caulimoviridae*), *Caulimovirus* (family *Caulimoviridae*), *Closterovirus* (family *Closteroviridae*), *Crinivirus* (family *Closteroviridae*), *Ipomovirus* (family *Potyviridae*), *Nepovirus* (family *Comoviridae*), *Sadwavirus* (unassigned family), *Sequivirus* (family *Sequiviridae*), *Trichovirus* (family *Flexiviridae*), *Tobravirus* (unassigned family), *Vitivirus* (family *Flexiviridae*), and *Waikavirus* (family *Sequiviridae*) (Hull, 2002) (Table 2). They represent over 80 distinct virus species (Astier *et al.*, 2001).

For *Cauliflower mosaic virus* (CaMV), the CP, protein P2, which is an aphid transmission factor, and protein P3, which bridges protein P2 and virions, are all necessary for virus transmission (Drucker *et al.*, 2002; Haas *et al.*, 2002). For *Lettuce infectious yellow virus* (LIYV), the minor capsid protein (CPm), which is lo-

cated at one end of virions, forming a short tail-like structure (Brown and Czosnek, 2002), is a major determinant of transmissibility (Tiam *et al.*, 1999). No information is available on the specificity of CaMV or LIYV transmission.

Mealybugs transmit virions of badnaviruses, including *Cacao swollen shoot virus* (CSSV), ampeloviruses (family *Closteroviridae*), including Grapevine leafroll-associated viruses (GLRaV) -1, -3, -5 and -9, vitiviruses (family *Flexiviridae*), including *Grapevine virus A* (GVA) and *Grapevine virus B* (GVB) (Plumb, 2002). However, no information is available on the molecular determinants of transmissibility or of transmission specificity.

Previous work with pseudorecombinant isolates indicated that RNA2 carries the determinants for transmission of the nematode-borne nepoviruses (Harrison *et al.*, 1974; Harrison and Murant, 1978) and tobnaviruses (Ploeg *et al.*, 1993). These results were confirmed by the use of full-length infectious chimeric cDNA clones of *Pea early browning virus* (PEBV) (Brown *et al.*, 1995a; MacFarlane and Brown, 1995). For nepoviruses, the CP seems to be the sole determinant of transmission specificity, as shown for GFLV (Belin *et al.*, 2001; Andret-Link *et al.*, 2004). The retention of virions at specific sites on the walls of the nematode's food canal could explain the specificity of transmission (Belin *et al.*, 2001). Homology modeling of the GFLV CP subunits and capsid structure with the 3.5 Å resolution crystal structure of *Tobacco ringspot virus* (TRSV) (Chandrasekar and Johnson, 1997), the type member of the genus *Nepovirus*, was further used to examine the surface topography of the capsid structure. Putative sites of interaction with a vector receptor were identified in a depression at the bottom of pronounced protrusions near the icosahedral fivefold axis (Andret *et al.*, 2003). Interestingly, the receptor-binding site for poliovirus is also located in a deep invagination of the virus surface (Hogle, 2002). Mutagenesis experiments are on going in our laboratory to validate the GFLV 3D model and determine the functional significance of the putative CP sites responsible for transmission specificity.

For tobnaviruses, one or two nonstructural proteins, in addition to the CP, are involved in transmission (MacFarlane *et al.*, 1995). The nonstructural proteins 2b and/or 2c may facilitate retention of virions in the nematode feeding apparatus in a manner similar to the HC-bridge of poty- and caulimoviruses (MacFarlane *et al.*, 2002). Protein 2b of *Tobacco rattle virus* (TRV) can interact with the CP, as shown by yeast-2-hybrid binding data, and removal of the CP C-terminal domain abolishes this interaction (Visser and Bol, 1999). Furthermore, immunogold localization studies show *in vivo* binding of the TRV and PEBV 2b proteins to virions (Vellios *et al.*, 2002).

Determinants of noncirculative undetermined non-persistent or semipersistent viruses. Members of the genera *Aureusvirus* (family *Tombusviridae*), *Carmovirus* (family *Tombusviridae*), *Dianthovirus* (family *Tombusviridae*), *Necrovirus* (family *Tombusviridae*), *Ophiovirus* (unassigned family), *Tombusvirus* (family *Tombusviridae*), and *Varicosavirus* (unassigned family) can be transmitted by vectors in a noncirculative, either nonpersistent or semipersistent, manner (Hull, 2002; Rochon *et al.*, 2004) (Table 2). They represent at least 10 distinct

virus species (Astier *et al.*, 2001). Vectors in this category include the fungi *Olpidium bornovanus* and *O. brassicae*. Vectored virions are attached to the surface of *Olpidium* zoospores whereas nonvectored virions fail to bind physically to the outer membrane of zoospores, indicating a direct and specific CP-zoospore interaction. Reciprocal CP exchanges between the *Olpidium*-transmissible CNV and the *Olpidium*-nontransmissible *Tomato bushy stunt virus* (TBSV) demonstrate that specificity of transmission resides with the CNV CP (MacLean *et al.*, 1994).

Table 2. Vectors of plant viruses and transmission mode.

Vector	Noncirculative		Circulative persistent	
	Nonpersistent	Semipersistent	Nonpropagative	Propagative
Aphids	<i>Alfamovirus</i> <i>Carlavirus</i> <i>Cucumovirus</i> <i>Fabavirus</i> <i>Macluravirus</i> <i>Potyvirus</i>	<i>Caulimovirus</i> <i>Closterovirus</i> <i>Sequivirus</i> <i>Trichovirus</i> <i>Waikavirus</i>	<i>Enamovirus</i> <i>Luteovirus</i> <i>Nanovirus</i> <i>Polerovirus</i> <i>Umbravirus</i>	<i>Cytorhabdovirus</i> <i>Nucleorhabdovirus</i>
Beetles	<i>Machlomovirus</i>		<i>Bromovirus</i> (?) <i>Carmovirus</i> (?) <i>Comovirus</i> (?) <i>Sobemovirus</i> (?) <i>Tymovirus</i> (?)	
Fungi	<i>Carmovirus</i> <i>Necrovirus</i> <i>Tombusvirus</i>			<i>Benyvirus</i> <i>Bymovirus</i> <i>Furovirus</i> <i>Varicosavirus</i>
Leafhoppers		<i>Badnavirus</i> <i>Waikavirus</i>	<i>Curtovirus</i> <i>Mastrevirus</i>	<i>Cytorhabdovirus</i> <i>Fijivirus</i> <i>Marafivirus</i> <i>Nucleorhabdovirus</i> <i>Oryzavirus</i> <i>Phytoreovirus</i> <i>Tenuivirus</i> <i>Phytoreovirus</i>
Mealybugs		<i>Ampelovirus</i> <i>Badnavirus</i> <i>Trichovirus</i> <i>Vitivirus</i>		
Mirids			<i>Sobemovirus</i>	
Mites		<i>Trichovirus</i>	<i>Rymovirus</i>	
Nematodes		<i>Nepovirus</i> <i>Tobravirus</i> <i>Sadwavirus</i>		
Plasmodiophorids	<i>Aureusvirus</i> <i>Dianthovirus</i> <i>Ophiovirus</i> <i>Varicosavirus</i>			
Thrips	<i>Machlomovirus</i>			<i>Tospovirus</i>
Whiteflies		<i>Crinivirus</i> <i>Ipomovirus</i>	<i>Begomovirus</i>	

(?) Limited information is available on virus-vector interactions, raising some uncertainty on the transmission mode.

Transmission is directly related to the quantity of virions absorbed on the zoospore plasmalemma (Temminck *et al.*, 1970). Mutations within the CNV CP shell domain decrease surface binding of virions to zoospores and consequently reduce transmission efficiency (Robbins *et al.*, 1999). In addition, binding of virions to zoospores is saturable and subject to competitive inhibition. The differential ability to transmit viruses was substantiated by using single sporangial isolates of the fungus showing distinct transmission abilities (Campbell *et al.*, 1995). Thus, virus binding to zoospores depends upon a specific receptor site in the zoospore plasmalemma and this receptor is not necessarily the same for all viruses that are transmitted (Robbins *et al.*, 1999). Sequences required for CP binding to the zoospore have been investigated but the determinants of transmission specificity have not been identified yet (Adams, 2002).

Determinants of circulative, persistent, nonpropagative viruses. Viruses transmitted by vectors in a circulative, persistent, nonpropagative manner include members of the genera *Begomovirus* (family *Geminiviridae*), *Bromovirus* (family *Bromoviridae*), *Carmovirus* (family *Tombusviridae*), *Comovirus* (family *Comoviridae*), *Curtoovirus* (family *Geminiviridae*), *Enamovirus* (family *Luteoviridae*), *Luteovirus* (family *Luteoviridae*), *Mastrevirus* (family *Geminiviridae*), *Nanovirus* (unassigned family), *Polerovirus* (family *Luteoviridae*), *Rymovirus* (family *Potyviridae*), *Sobemovirus* (unassigned family), *Tymovirus* (family *Tymoviridae*), and *Umbravirus* (unassigned family) (Hull, 2002) (Table 2). They represent close to 150 distinct virus species (Astier *et al.*, 2001). Vectors in this category are aphids, beetles, leafhoppers, whiteflies, and mirids.

Members of the family *Luteoviridae* circulate in aphid vectors with no evidence of replication and virions are transported across the gut epithelium and plasmalemma of accessory salivary glands (Reavy and Mayo, 2002). Distinct Barley yellow dwarf virus (BYDV) isolates are specifically transmitted by different aphid species although the degree of specificity can change following heterologous encapsidation. Vector receptors at salivary gland cells and luteovirus particles determine the specificity of transmission (Reavy and Mayo, 2002). Luteovirus capsids are composed of two CPs, a major CP and a less abundant CP generated by a readthrough (RT) mechanism of the major CP's stop codon. The minor CP (RT protein) is required for aphid transmission (Gray and Banerjee, 1999), as shown by the use of infectious chimeric cloned cDNA of different luteovirus genomes and the recovery of virions from infectious transcripts following either transfection of protoplasts or agroinfiltration of plants. For *Potato leafroll virus* (PLRV), the C-terminal end of the RT domain is important for aphid transmission (Jolly and Mayo, 1994) as well as a surface loop (Lee *et al.*, 2005). In the case of *Beet western yellows virus* (BWYV) and *Cucurbit aphid-borne yellows virus* (CABYV), vector specificity is clearly driven

by the nature of the RT (Brault *et al.*, 2005). It is to be noted that the N-terminal part of the RT component interacts with a specific domain of symbionin, the GroEL homolog of the bacterial endosymbiont *Buchnera*, which acts as chaperonin, in the aphid vector (Brown, 2001). This interaction seems important for virion stability but is probably not involved in transmission specificity since it is present in aphid vectors and nonvectors.

In the family *Geminiviridae*, members of the genera *Mastrevirus* and *Curtoovirus* are transmitted by leafhoppers, whereas those of the genus *Begomovirus* are transmitted by whiteflies (Power, 2000). The CP is a major determinant of vector specificity (Zeidan and Czosnek, 1991). A functional CP gene is required for the transmission of *Bean golden mosaic virus* (BGMV) (Azzam *et al.*, 1994) and exchanging the CP gene of the whitefly-transmitted *African cassava mosaic virus* (ACMV) with that of the leafhopper-transmitted *Beet curly top virus* (BCTV) produces a leafhopper-transmitted ACMV, confirming a major role of the CP in the specificity of transmission (Briddon *et al.*, 1990). Most begomoviruses have genomes composed of two DNA molecules but TYLCV has both monopartite and bipartite species, all of them transmitted by *Bemisia tabaci*. By studying defective genomic DNAs of the monopartite TYLCV, amino acids essential for transmission have been mapped between positions 129 and 134 of the CP (Noris *et al.*, 1998). Also, the N-terminus of the CP of *Abutilon mosaic virus* (AbMV) is a critical determinant of whitefly-mediated transmission (Azzam *et al.*, 1994; Wu *et al.*, 1996). However, the CP does not solely determine the transmission phenotype of all geminiviruses. Both genomic components of the whitefly-transmitted *Tomato golden mosaic virus* (TGMV) are essential for transmission. The CP is required for acquisition of the virus, DNA B is essential for the accumulation of TGMV in the whitefly, and DNA A is required for the successful inoculation of plants by viruliferous insects (Liu *et al.*, 1997).

Mites, mainly *Eriophyidae*, transmit viruses of cereal and fruit crops very likely in a circulative nonpropagative manner (Plumb, 2002). Most of the eriophyid vectors transmit members of the genus *Rymovirus* but no molecular motif has been yet associated with transmissibility (Plumb, 2002). *Wheat streak mosaic virus* (WSMV) has been detected in the salivary glands of its vector (Paliwal and Sinha, 1970) but *Brome mosaic virus* (BMV), which is not transmitted by mites but accumulates in mites fed on BMV-infected plants, was not. This observation indicates that, like for persistently aphid-transmitted viruses, the gut and salivary gland membranes are likely the sites of vector specificity (Reavy and Mayo, 2002).

Beetles transmit sobemoviruses after acquiring them from drops of purified preparations (Gergerich *et al.*, 1991), suggesting no requirement of a HC for efficient transmission. Nevertheless, reassembled virions with the

CP of a beetle-transmissible virus, e.g. *Southern cowpea mosaic virus* (SBMV), and the RNA of a beetle non-transmissible virus, e.g. the cowpea strain of *Tobacco mosaic virus* (TMV), are transmitted by beetles, although the latter are not natural vectors of TMV (Mahmood *et al.*, 1993). These experiments suggest that the recognition, at either the vector or host level, which enables a virus to be efficiently transmitted by a beetle vector, is mediated by the CP properties.

Determinants of circulative, persistent, propagative viruses. Viruses transmitted by vectors in a circulative, persistent, propagative manner include members of the genera *Cytorhabdovirus* (family *Rhabdoviridae*), *Fijivirus* (family *Reoviridae*), *Marafivirus* (family *Tymoviridae*), *Nucleorhabdovirus* (family *Rhabdoviridae*), *Oryzavirus* (family *Reoviridae*), *Phytoreovirus* (family *Reoviridae*), *Tenuivirus* (unassigned family), and *Tospovirus* (family *Bunyaviridae*) (Hull, 2002) (Table 2). They represent at least 60 distinct virus species (Astier *et al.*, 2001). Vectors in the category include thrips, aphids, leafhoppers, and whiteflies.

Tospovirus transmission by thrips is highly specific. *Thrips tabaci* transmits most isolates of TSWV and *Iris yellow spot virus* (IYSV) (Cortes *et al.*, 1998) but not *Tomato chlorotic spot virus* (TCSV) and *Groundnut ringspot virus* (GRSV) (Wijkamp *et al.*, 1995). Also, *Frankliniella occidentalis* transmits numerous tospoviruses but not IYSV (Nagata and Almeida, 1999). Compelling evidence for transmission specificity involving an interaction between viral proteins and a potential receptor is provided by the relationship between thrips and TSWV (Medeiros *et al.*, 2000). A 50-kDa midgut protein from *F. occidentalis* selectively binds to the structural glycoproteins GP1 and GP2 of TSWV in gel overlay (Bandla *et al.*, 1998) and immunoprecipitation assays (Medeiros *et al.*, 2000). In contrast, midgut proteins from a related thrips species that does not transmit TSWV do not bind TSWV glycoproteins.

Leafhoppers transmit *Rice dwarf virus* (RDV) for which the P2 and P8 components of the outer CPs are likely receptor binding sites on the virion surface, as they are crucial for vector infection and transmission (Omura and Yan, 1999).

Determinants of circulative, persistent, propagative or nonpropagative viruses. Some viruses are transmitted in a circulative propagative or nonpropagative manner (Power, 2000; Hull, 2002) (Table 2). Members of the genera *Benyvirus* (unassigned family), *Bymovirus* (family *Potyviridae*), *Furovirus* (unassigned family), and *Varicosavirus* (unassigned family) are transmitted by the plasmodiophorids *Polymyxa graminis*, *Polymyxa betae*, and *Spongospora subterranean* (Rochon *et al.*, 2004) (Table 2). These viruses represent 20 distinct species (Astier *et al.*, 2001) with filamentous or rod-shaped par-

ticles and multipartite RNA genome, which are internally borne and carried within the cytoplasm of resting spores and presumably also within zoospores (Adams *et al.*, 2001; Campbell and Fry, 1996). The *Potato mop top virus* (PMTV) and *Beet necrotic yellow vein virus* (BNYVV) CP RT product, which is present as a few copies per virion at one end of the particles (Haeberle *et al.*, 1994), is required for transmission (Reavy *et al.*, 1998; Tamada and Kusume, 1991). It was proposed that a KTER motif within the C-terminal region of the BNYVV RT domain is important for successful transmission (Tamada *et al.*, 1996). However, the lack of a similar motif in the CPs of other plasmodiophorid-transmitted viruses, except KTEIR in the *Soil-borne wheat mosaic virus* (SBWMV) RT, suggests that linear amino acid sequences may be less important in transmission than higher order amino acid arrangements.

Recently, conserved hydrophobic residues in protein P2 of *Barley yellow mosaic virus* (BaYMV) and *Barley mild mosaic virus*, and the RT of SBWMV, PMTV, and BNYVV (Dessens and Meyer, 1996), and conserved hydrophilic residues flanked by two hydrophobic regions in the RT of PMTV, *Beet soil-borne virus* (BSMV), SBWMV, and BNYVV (which include the KTER motif in BNYVV) (Reavy *et al.*, 1998) have been identified and suspected to be important for transmission, perhaps as transmembrane domains. Recent computer predictions suggest that RTs and P2 proteins contain two regions that not only show strong evidence of transmembrane activity but also of compatibility between their amino acids, suggesting that they could be closely paired within a membrane and with the region between them aligned on the inside of the membrane (Diao *et al.*, 1999; Adams *et al.*, 2001). Nontransmissible deletion mutants lack the second of these regions. In the light of these findings, the lack of transmission of a BNYVV mutant in which KTER was replaced by ATAR (Tamada *et al.*, 1996) can be explained because the substitution is expected to affect the alignment of the polypeptide at a crucial point and interfere with the compatibility between the two domains since the KTER motif is adjacent to the second transmembrane domain. It therefore seems possible that the two transmembrane regions are involved in attachment to the zoosporangial plasmalemma, and assist virions to move between the cytoplasm of the plant host and that of the plasmodiophorid vector (Adams, 2002). No information is available on determinants of transmission specificity.

VECTOR LIGANDS INVOLVED IN THE SPECIFICITY OF VIRUS TRANSMISSION

Interaction between viral determinants and vector receptors. The specificity of vector-mediated transmission of plant viruses may involve a ligand-receptor inter-

action. Binding between a virion and a cell surface receptor provides the initial physical association required for virus entry and/or retention into vectors. By analogy to virus entry into animal cells, viruses can enter vector cells either by receptor-mediated endocytosis, generally through clathrin-coated vesicles, as has been proposed for luteoviruses (Gildow, 1987), or by direct fusion of the viral envelope with the cell membrane (Marsh and Helenius, 1989). Based on electron microscopy observations, the latter mechanism has been proposed for bunyaviruses for which glycoproteins present in the envelope membrane have been suggested to mediate attachment (Ludwig *et al.*, 1991; Bandla *et al.*, 1998; Kikkert *et al.*, 1998). Ligands may be individual protein receptors that mediate virion uptake via endocytosis or may prove to be complex surfaces including components of the cuticular lining of the stylet and foregut, a matrix of carbohydrates, proteins, or lipids.

Vector proteins that could act as receptor. Virus overlay assays reveal vector proteins with a virus-binding capacity. Anti-idiotypic antibodies mimicking the glycoproteins of TSWV specifically label a 50-kDa band in extracts from thrips in western blots and on the plasma membrane of the larval thrips midgut (Bandla *et al.*, 1998). As purified virus displays affinity for a similar-sized protein in an overlay assay of thrips proteins, the 50-kDa protein might be a cellular receptor (Bandla *et al.*, 1998). A second thrips protein (~94 kDa) that has a TSWV-binding capacity has also been identified (Kikkert *et al.*, 1998). This protein firmly binds the TSWV G2 glycoprotein, which contains the highly conserved motif RGD near the N-terminus. This sequence is an important determinant for cellular attachment of several mammalian viruses and pathogens, including foot-and-mouth disease virus (Berinstein *et al.*, 1995), human coxsackievirus A9 (Roivainen *et al.*, 1996), and the spirochete *Borrelia burgdorferi* (Coburn *et al.*, 1998), which is the causal agent of Lyme disease. Owing to the protease sensitivity of TSWV G2 and the high concentration of proteolytic enzymes that probably occur in the gut lumen, G2 is not expected to be involved in cellular attachment in the midgut of thrips (Kikkert *et al.*, 1998; van den Heuvel *et al.*, 1999).

A 32 kDa leafhopper membrane protein has been identified as potential receptor for virions of *Rice ragged stunt virus* (RRSV) (Zhou *et al.*, 1999).

It has been postulated that luteoviruses are transported transcellularly through epithelial cell linings in the aphid vector's gut and salivary glands by receptor-mediated endocytosis-exocytosis (Gildow, 1987). Upon contact with the basal lamina of the accessory salivary gland, virions can be transported through this gland (Peiffer *et al.*, 1997), eventually arriving in the salivary duct, from which they are excreted with the saliva when the aphid feeds (Gildow and Gray, 1993). Vector specificity seems

to be determined at the level of the accessory salivary gland (Gildow and Gray, 1993; Peiffer *et al.*, 1997). A BYDV-MAV-like isolate from China displays a strong affinity for two proteins of 31 and 44 kDa from the aphid vectors *Sitobion avenae* and *Schizaphis graminum* but not from *Rhopalosiphum padi*, which is unable to transmit BYDV-MAV (Wang and Zhou, 2003). Antisera raised against P31 and P44 react specifically with extracts of the accessory salivary glands of aphid vectors, suggesting an involvement in luteovirus-specific recognition at the accessory salivary glands. Also, proteins SaM35 and SaM50 (with Mr of 35,000 and 50,000, respectively) that bind specifically to purified BYDV-MAV particles have been identified in the vector aphid *S. avenae*. The fact that these two nonGroEL homologue proteins are detected only in head extracts from vector aphids and not from nonvector aphids suggest that they may be potential receptors of BYDV-MAV virions associated with the accessory salivary glands (Li *et al.*, 2001). Recently, the proteins Rack-1, GAPDH3, and acting of *Myzus persicae* have been shown to bind *in vitro* purified virions of BWYV. Rack-1 could interact directly with a specific motif of the RT protein, eventually through a membrane receptor that includes GAPDH3, to facilitate transcytosis of BWYV in the aphid vector. Transcytosis of BWYV has been hypothesized to occur via macropinocytosis, rather than clathrin-mediated endocytosis, by direct interaction of virions and actin (Seddas *et al.*, 2004).

In vitro binding of CNV virions to zoospores of the fungus *O. bornovanus* is saturable, and vector zoospores bind CNV more efficiently than nonvector zoospores (Kishore *et al.*, 2003). Also, CNV binding to zoospores treated with periodate and trypsin is reduced, suggesting the involvement of glycoproteins in zoospore attachment. CNV binds to several proteins in virus overlay assays whereas CNV transmission mutants either fail to bind or bind at significantly reduced levels. Incubating CNV with zoospores in the presence of various sugars suggest the possible involvement of specific oligosaccharides in attachment. Binding of CNV to zoospores is mediated by specific mannose and/or fucose-containing oligosaccharides (Kishore *et al.*, 2003). Interestingly, CNV undergoes conformational changes upon zoospore binding (Kakani *et al.*, 2004). It has been hypothesized that CNV particles could recognize a glycoprotein receptor on the surface of zoospores via the virion quasi-threefold axis, which contains sugar recognition elements. This binding initiates a swelling of virions with subunits at the quasi-threefold axis migrating away from each other, two arms translocating out of particles, and the hydrophobic portion of the arm domain interacting with the zoospore plasmalemma, thus stabilizing the virus-receptor interaction and contributing to the release of viral RNAs.

Other vector ligands that could act as receptor. In addition to proteins, other ligands have been identified

as potential vector receptors of virions. In the case of nematode vectors, the site of virus retention is the inner surface of the odontostyle in *Longidorus* species whereas it is the oesophageal tract, extending from the anterior end of the odontophore posteriorly into the oesophageal bulb, in *Xiphinema*, *Paratrichodorus*, and *Trichodorus* species. For *Xiphinema* and trichodorid nematodes, a discontinuous layer of carbohydrate-staining material is identified lining the oesophageal tract. In *X. diversicaudatum*, particles of *Arabid mosaic virus* (ArMV) and *Strawberry latent ringspot virus* (SLRV) are absorbed only where this layer accumulates. Consequently, virus retention in *Xiphinema* and trichodorids could involve interactions between carbohydrate moieties in the nematode's oesophageal tract and surface structures of the virus capsid. An alternative hypothesis is that surface charges on virions interact with oppositely charged areas associated with the cuticle lining the nematodes' feeding apparatus. Fundamental differences occur in the morphology of the cuticle associated with the odontostyle region in nematodes, which is similar to the external cuticle, compared to that of the oesophageal tract, which represents the internal cuticle. These two cuticle types have differential isoelectric points and labeling of the odontostyle region in *L. elongatus* with cationized ferritin reveals a strong negative charge associated with the surface of the odontostyle and the wall of the lumen. Therefore, particularly with *Longidorus* species, surface charges may determine virus retention. Studies on the accumulation of *Tomato black ring virus* (TBRV) show that, late in infection or after purification, the CP in virions is reduced in size. This change results from the removal of nine amino acids at the C-terminal end, suggesting that this region is exposed at the surface of the protein where it could be available for interaction with nematode surfaces during vector transmission. However, not all nepovirus CPs possess a protruding C-terminal peptide (MacFarlane *et al.*, 2002).

The CP subunits of tobnaviruses form a tight helical array with their N- and C-termini located on the external surface of virions. Nuclear magnetic resonance studies of *Pepper ringspot virus* (PePRSV) reveal that the C-terminal region of the CP is unstructured and presumably extends away from the surface of virions (MacFarlane *et al.*, 2002). This protruding flexible domain could be involved in the specific attachment of virions to sites of retention within nematode vectors. Electron microscopy studies show a gap of 5-7 nm between the surface of TRV particles and the cuticle lining the oesophageal lumen (MacFarlane *et al.*, 2002). This space is too large to be bridged by a CP C-terminal peptide of only 22 (TRV-PpK20) to 38 (PepRSV) amino acids. However, the observed gap might be bridged by one or more of the additional nonstructural (2b and 2c) proteins encoded by the tobnavirus RNA2, and these helper proteins might link the C-terminal peptide with the car-

bohydrate-staining material lining the nematodes' oesophageal tract.

CONCLUSION AND PROSPECTS

Transmission from host to host by vectors is an important step in the biological cycle of plant viruses to ensure their maintenance and survival. Most plant virus species (88%) use an arthropod vector as a mean of transportation from one host to another. The remaining vector-transmitted plant viruses (12%) use fungi, plasmiodiophorids, and nematodes.

Significant progress has been made over the last two decades on the interaction between viruses and their vectors through biological, biochemical, and molecular studies. For some viruses, new advances have been possible through the development of pseudorecombinant isolates that have one RNA from one virus isolate combined with the RNA of a different isolate of the same virus or a different virus. Also, hybrid isolates have been developed with some genes derived from one virus or isolate and other genes from another virus or another isolate from the same virus. Recent advances have also been possible through molecular studies based on reverse genetics and mutagenesis, or by comparative sequence analysis of vector transmissible viruses and transmission deficient mutants.

Transmission mechanisms are remarkably different between plant viruses, with no correlation with genome type, particle morphology, or strategy of viral protein expression (Table 2). Transmission is often characterized by some degree of specificity and numerous findings indicate the possible involvement of a specific ligand/receptor interaction. Extensive information is available on viral determinants of transmissibility but limited information is available on viral determinants of transmission specificity. The CP, and its derivatives, e.g. RT product or CPm, and nonstructural proteins, including a HC or a transmission factor, have been clearly shown to be involved in transmission specificity. More information is likely to be obtained in the future on virus sites involved in attachment to vector ligands. Little is known about vector receptors, except for *Olpidium bornovianus*, *Frankliniella occidentalis*, and *Myzus persicae*, for which several virus-binding proteins have been identified. The functional role of these proteins in the specificity of the transmission process remains to be elucidated. In spite of these findings, more vector receptor sites need to be identified. Also, the attachment and release of virions to and from specific vector receptors need to be investigated. Remarkably, attachment of icosahedral plant viruses to vector receptor sites has similar features to poliovirus cell interactions. Poliovirus binding to its host cell receptor initiates a series of conformational changes of virions that triggers attachment to the mem-

brane, forming a pore in the membrane, and releasing viral RNA from the capsid (Hogle, 2002). Interestingly, the structural states associated with the various transitions of poliovirus particles are analogous to the expanded states of structurally similar plant viruses, in particular CNV (Kakani *et al.*, 2004) and CMV (Ng *et al.*, 2005).

Unraveling the biological and molecular interaction between a virus and its vector is important to identify opportunities for the development of novel control measures. Control strategies against viruses are usually designed to mitigate the considerable losses viruses can cause by reducing the sources of infection and limiting the spread by vectors (Lecoq *et al.*, 2004). Roguing and removal of infected plants can contain viral diseases but seldom achieve a complete eradication. Chemical control of vectors can reduce the spread of plant viruses but the effectiveness of agrochemicals against vectors is highly variable and there may be adverse biological and environmental consequences related to their use (Perring *et al.*, 1999). Given the limitations of the current control strategies against viruses, there is a need for efficient and environmentally sound alternatives for sustainable agricultural production. Although gene silencing offers new and promising avenues (Voinnet, 2001, 2005; Prins, 2003; Ritzenthaler, 2005), understanding the transmission process and the intimate relationship between a virus and its vector can facilitate the development of novel opportunities for designing control strategies against plant viruses, including the genetic manipulation of vectors and the expression of recombinant proteins in transgenic plants to neutralize the transmission process.

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