Fundam. appl. Nematol., 1998, **21** (1), 1-11

Forum article

SPECIFICITY, EXCLUSIVITY AND COMPLEMENTARITY IN THE TRANSMISSION OF PLANT VIRUSES BY PLANT PARASITIC NEMATODES: AN ANNOTATED TERMINOLOGY [1]

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Accepted for publication 5 March 1997.

Summary – Eighteen species in the plant-parasitic nematode genera *Longidorus*, *Paralongidorus* and *Xiphinema* are vectors of twelve nepoviruses and in the genera *Paratrichodorus* and *Trichodorus* thirteen species are vectors of all three tobraviruses. A characteristic of these vector nematode and virus associations is that serologically distinct nepoviruses and virus strains are transmitted by different, but related, longidorid species. The viruses are referred to as having "specific" vector species, and the terminology has been adopted by researchers who refer to "specificity" of transmission of viruses by vector nematodes. Further research has confirmed that specificity of transmission extends to populations of vector species and to minor serological variants of nepoviruses. It has also been shown to extend to tobraviruses and their vector species. We describe the possible mechanisms which determine the association between vector nematodes and their viruses and provide and explain definitions of several terms and concepts used in vector nematode research.

Résumé – ***Spécificité, exclusivité et complémentarité dans la transmission des virus par les nématodes phytoparasites : une terminologie annotée*** – Dix-huit espèces de nématodes phytoparasites appartenant aux genres *Longidorus*, *Paralongidorus* et *Xiphinema* sont vectrices de douze nepovirus, tandis que treize espèces des genres *Paratrichodorus* et *Trichodorus* sont vectrices de trois tobravirus. Une caractéristique de ces nématode vecteurs et de leurs associations avec les virus avait été rapidement reconnue lorsque des nepovirus sérologiquement distincts et des souches différentes de virus avaient été reconnus transmis par des espèces de Longidorides différentes, mais proches. Les virus avaient donc été considérés comme ayant des espèces vectrices "spécifiques", ce qui avait conduit à adopter une terminologie suivant laquelle les chercheurs faisaient référence à la "spécificité" de la transmission des virus par les nématodes vecteurs. En outre, la spécificité de la transmission avait été confirmée par des recherches ultérieures et démontrée s'étendre au niveau des populations des espèces vectrices et à celui de variants sérologiques mineurs des nepovirus. Il a été également démontré que ce phénomène s'applique aux tobravirus et à leurs vecteurs. Sont décrits dans cet article les mécanismes qui pourraient déterminer l'association entre les nématodes vecteurs et leurs virus. Sont également données et expliquées les définitions d'un certain nombre de termes et concepts utilisés lors des recherches sur les vections par les nématodes.

Key words : *Longidorus*, nematode, nepovirus, *Paralongidorus*, *Paratrichodorus*, tobravirus, *Trichodorus*, *Xiphinema*.

Interest in nematodes as possible vectors of plant viruses was stimulated with the publication of unequivocal evidence that *Xiphinema index* present in vineyards in California, USA, was the natural vector of grapevine fanleaf nepovirus (GFLV) (Hewitt *et al.*, 1958). Identification of further associations between soil-borne plant viruses and plant-parasitic nematode species quickly followed and it became apparent that successful nematode-virus interactions were limited to two distinct nematode groups and to two groups of viruses. Whilst the Longidoridae are considered to have originated in the northern part of Gondwanaland in association with the *Glossopteris*-flora (Coomans, 1996) it was probably not until the nematodes subsequently spread into Laurasia, in association with more diverse flora, that they came into contact with, and some species began to coevolve with, plant viruses.

Of the approximately 3500 phytonematode species described only 31 (less than 1%) are virus-vectors. Eighteen of approximately 350 species belonging to the genera *Longidorus, Paralongidorus* and *Xiphinema* (Family Longidoridae, Order Dorylaimida) are vectors of twelve of the 36 viruses comprising the nepovi-

[1] This paper has been developed from a talk "Virus and Vector Interactions" presented at a seminar on Nematode Interactions at the 3rd International Nematology Congress, Gosier, Guadeloupe, 7-12 July 1996.

rus group (Taylor & Brown, 1997). Thirteen of approximately 70 species in the genera *Trichodorus* and *Paratrichodorus* (Family Trichodoridae, Order Triplonchida) transmit the three tobraviruses: pea early-browning (PEBV), pepper ringspot (PRV) and tobacco rattle (TRV).

An obvious and intriguing aspect of vector research is why so few nematode species are apparently capable of transmitting plant viruses and, equally, why such a restricted range and number of viruses have nematodes as their natural vector. A principal feature of these relationships is the apparent specificity between the virus and its vector. Features of this specificity of association are transmission exclusivity, in which there is an apparent unique association between a virus or virus strain and its vector species, and transmission complementarity whereby a virus/virus strain may have several vector species or a species may transmit several viruses/virus strains (Tables 1, 2). We describe the mechanisms which determine these associations between nematodes and viruses, and explain and define several terms frequently used in nematode vector research.

The nematode-virus association

An ability by viruses and nematodes, which are relatively immobile, to utilise an extensive range of potential hosts provides a distinct advantage for survival. Nepo- and tobraviruses are transmitted through seed, and in some instances through pollen, but the existence of a vector provides the only pathway for a virus to be exposed to potential new host species (Brown & Trudgill, 1989). The nematode transmitted viruses (NTV's) and their vector species are natural pathogens and parasites, respectively, of wild (uncultivated) plants, and usually have extensive host ranges (Murant, 1970; Weischer, 1975; Weischer & Almeida, 1995). Whilst the presence of a vector is advantageous for a virus there is no information available to suggest that a NTV, when present in a host, provides any advantage for its vector.

The transmission process

Transmission of a virus by a vector nematode involves several discrete but inter-related processes (Table 3). However, these processes are poorly defined and the terms used to describe them are frequently used interchangeably and thus may be misleading.

Ingestion

Any plant parasitic nematode feeding on a virus-infected plant has the potential to ingest virus particles but for this to be successfully accomplished the virus must be present in the cell(s) being fed upon. Ingested virus particles may be adsorbed (see below) but most are likely to enter directly into the nematode gut where they can remain viable (infective).

> **Virus ingestion** may be defined as: **"The intake of virus particles during feeding".**

Infective tobra- and nepoviruses have been recovered from comminuted bodies of their associated vector nematodes, *e.g.*, TRV from *Trichodorus* sp., *P. pachydermus* and *P. allius* (Sanger *et al.*, 1962; Sol *in* Raski & Hewitt, 1963; Ayala & Allen, 1968); GFLV from *X. index* (Raski & Hewitt, 1963; Das & Raski, 1968); raspberry ringspot nepovirus (RRSV) from *L. macrosoma* (Trudgill & Brown, 1978); and RRSV and tomato black ring nepovirus (TBRV) from *L. elongatus* (Taylor, 1964; Yassin, 1968; Taylor & Murant, 1969). Arabis mosaic (ArMV) and strawberry latent ringspot (SLRSV) nepoviruses were not recovered from *X. diversicaudatum* but were recovered from *L. elongatus,* although this species is not a vector of either of these viruses (Taylor & Thomas, 1968)

Acquisition

A plant parasitic nematode feeding on a virus-infected plant will passively ingest virus particles which pass through the oesophagus into the intestine where they may be digested or simply defecated and thereby lost for transmission. With virus-vector species a proportion of ingested virus particles are retained in the feeding apparatus and thus there is a potential for them to be transmitted.

> **Virus acquisition** may be defined as: **"The act of ingesting virus particles, some or all of which are retained in the feeding apparatus".**

Unattached virus particles have been observed in the stoma of *Longidorus* and *Xiphinema* species and it was suggested that non-specific transmission of these particles might occasionally occur, especially if the nematodes were transferred quickly between virus infected and healthy plants (Taylor & Robertson, 1969, 1975). However, this type of transmission will occur rarely under field conditions. The apparent transmission, in laboratory experiments, of peach rosette mosaic nepovirus (PRMV) by one of 52 groups of two *L. breviannulatus* and by one of 46 groups of ten *L. elongatus* was concluded to result from this type of non-specific transmission (Allen, 1986; Allen & Ebsary, 1988).

Adsorption

Virus particles may be actively or passively retained during acquisition in the nematode feeding apparatus.

Table 1. *Complementarity and exclusivity of* Longidorus, Paralongidorus *and* Xiphinema *vector transmission of nepoviruses.*

Virus	Serotype	Vectors
Vector and virus/virus strain transmission exclusivity		
artichoke Italian latent	Italian	*L. apulus*
	Greek	*L. fasciatus*
cherry rosette	Switzerland	*L arthensis*
mulberry ringspot	Japan	*L. martini*
raspberry ringspot	English	*L. macrosoma*
	German grapevine	*P. maximus*
tomato black ring	German/English	*L. attenuatus*
Vector transmission complementarity		
cherry rasp leaf	North America	*X. americanum*
peach rosette mosaic	North America	
tobacco ringspot	North America	
tomato ringspot	North America	
cherry rasp leaf	North America	*X. californicum*
tobacco ringspot	North America	
tomato ringspot	North America	
arabis mosaic	English Barley	*X. diversicaudatum*
strawberry latent ringspot	English	
	Italian olive	
	Italian peach	
	Italian raspberry	
cherry rasp leaf	North America	*X. rivesi*
tobacco ringspot	North America	
tomato ringspot	North America	
raspberry ringspot	Scottish	*L. elongatus*
tomato black ring	Scottish	
tobacco ringspot	North America	*X. intermedium*
tomato ringspot	North America	
tobacco ringspot	North America	*X. tarjanense*
tomato ringspot	North America	
Virus/virus strain transmission complementarity		
arabis mosaic	English Barley	*X. diversicaudatum*
cherry rasp leaf	North American	*X. americanum*
		X. californicum
		X. rivesi
grapevine fanleaf	North American	*X. index*
		X. italiae
peach rosette mosaic	North American	*L. diadecturus*
		X. americanum s.l.
strawberry latent ringspot	English	*X. diversicaudatum*
	Italian olive	
	Italian peach	
	Italian raspberry	
tobacco ringspot	North American	*X. americanum*
		X. californicum
		X. intermedium
		X. rivesi
		X. tarjanense
tomato ringspot	North American	*X. americanum*
		X. bricolense
		X. californicum
		X. intermedium
		X. rivesi
		X. tarjanense

Table 2. *Complementarity and exclusivity of* Paratrichodorus *and* Trichodorus *vector transmission of tobraviruses.*

Virus	Serotype	Vectors
	Vector and virus/virus strain transmission exclusivity	
tobacco rattle	Portugal	*P. hispanus*
tobacco rattle	Italy	*P. tunisiensis*
	Vector transmission complementarity	
pea early-browning	English	*P. anemones*
tobacco rattle	PaY4	
pea early-browning	Dutch	*P. pachydermus*
tobacco rattle	PRN	
	PaY4	
pea early-browning	Dutch	*P. teres*
tobacco rattle	Oregon	
pea early-browning	English	*T. cylindricus*
tobacco rattle	RQ	
	TcB2-8	
pea early-browning	English	*T. primitivus*
tobacco rattle	RQ	
pea early-browning	English	*T. viruliferus*
tobacco rattle	RQ	
pepper ringspot	Brazil	*P. minor*
tobacco rattle	USA	
tobacco rattle	Ts Belgium	*T. similis*
	Ts Netherlands	
	Ts Greek	
	Virus/virus strain transmission complementarity	
pea early-browning	English	*P. anemones*
		T. cylindricus
		T. primitivus
		T. viruliferus
pea early-browning	Dutch	*P. pachydermus*
		P. teres
tobacco rattle	North America	*P. allius*
		P. minor
		P. porosus
tobacco rattle	PaY4	*P. anemones*
		P. pachydermus
tobacco rattle	PRN	*P. pachydermus*
		P. nanus
tobacco rattle	RQ	*T. cylindricus*
		T. primitivus
		T. viruliferus

Virus adsorption may be defined as: **"The active process by which virus particles adhere to specific sites of retention in the nematode feeding apparatus".**

In vector nematodes, particles of the associated virus(es) are specifically adsorbed to discrete parts of the oesophagus. In *Longidorus*, and probably also in *Paralongidorus*, they associate with the inner surface of the oesophageal guiding sheath and the interior surface of the odontostyle (Taylor & Robertson, 1969; Taylor & Brown, 1997). In vector *Xiphinema* species virus particles are adsorbed to the cuticular lining of the odontophore and of the oesophagus (Taylor & Robertson, 1970 *a*), with the maximum concentration of particles usually occurring in the anterior part of the odontophore (Martelli & Taylor, 1989). When examining the transmissibility of different strains of SLRSV by *X. diversicaudatum*, Brown and Trudgill (1983) found that lack of transmission was associated

Table 3. *Probable interactions between vector nematodes, viruses and host plants required for successful tranmission of virus to occur.*

	Nematodes	Viruses	Plants
Ingestion	+		+
Acquisition	+	+	
Adsorption	+	+	
Retention	+	+	
Release	+	+	(+?)
Transfer	+	+	+
Establishment		+	+

with an absence of particles adsorbed at the sites of retention. In trichodorid vectors, tobravirus particles are adsorbed to the cuticle lining the lumen of the entire oesophagus, but not to the onchiostyle (Taylor & Robertson, 1970 *b*).

RETENTION

Virus particles, after acquisition and adsorption by the nematode, are retained in the vector.

> **Retention (time)** may be defined as: **"The period during which specifically adsorbed virus particles remain attached to the site of retention in the nematode feeding apparatus".**

Some authors have used the term "persistence" to refer to the length of time a vector has retained virus which it has subsequently transmitted. Therefore, to prevent confusion we suggest that "persistence" should be used to refer to the time a virus is present at a field site.

Although little information is available of the retention period for actively feeding nematodes it probably is shorter than with specimens stored in plant-free soil, where vector nematodes can apparently retain virus for weeks, months, and even years. In contrast, a diminution of retained virus particles can occur at each occasion a nematode feeds. However, during a prolonged feeding-cycle on an individual root the nematode will initially only transfer virus (see below) but subsequently, after virus establishment and replication in the host, the nematode will both ingest and transfer virus particles whilst feeding.

Substantial differences have been reported between retention times for the vector genera *Longidorus*, *Paratrichodorus* and *Xiphinema* when the nematodes have been denied access to a host plant. Transmission of RRSV by *L. elongatus* kept in fallow soil for 8 weeks decreased rapidly after 3 weeks, whereas under similar conditions *X. diversicaudatum* transmitted SLRSV and ArMV after almost three and four months, respectively (Lister & Murant, 1967; Taylor, 1968; Taylor & Thomas, 1968). Buser (1990) identified RRSV in serological tests using ELISA from comminuted bodies of *L. macrosoma* after the nematodes had been stored at 4°C for 60 months in soil without plants. Also, Bitterlin (1986) reported that *X. rivesi* transmitted tomato ringspot nepovirus (ToRSV) after the nematodes had been kept for 2 years in soil without plants. *Xiphinema index* kept in moist soil transmitted GFLV after 8 months (Taylor & Raski, 1964) and in a laboratory experiment, *X. americanum sensu lato* kept at 8°C transmitted tobacco ringspot nepovirus after 9 months starvation (McGuire, 1973). There is little information available on retention of viruses by their vectors when the nematodes have been allowed access to a non-host of the virus. However, *X. index* transmitted GFLV after 3 months access to fig, a non-host for the virus (Das & Raski, 1968); *X. diversicaudatum* transmitted ArMV after 8 months access to the immune raspberry cultivar Malling Jewel (Harrison & Winslow, 1961) and *L. elongatus* did not transmit RRSV after 2 weeks access to a virus immune host (Taylor, 1970). Van Hoof (1970) reported that *P. pachydermus* from the rhizosphere of TRV infected plants transmitted the virus after being kept in soil in a refrigerator for 2 years. Similarly, *P. allius,* from the rhizosphere of TRV infected plants, kept in soil without access to host plants for 20 weeks, and other specimens allowed access to virus-immune sweet pea, transmitted the virus (Ayala & Allen, 1968).

RELEASE

For transmission to occur, virus particles retained by a vector must dissociate from the specific site(s) of retention in the nematode feeding apparatus.

> **Release** may be defined as: **"The dissociation of virus particle(s) from the specific sites of retention in the nematode feeding apparatus".**

The dissociation of virus particles from their sites of retention within the vector nematode is believed to occur during feeding when secretions from the oesophageal glands in the basal bulb of the nematode pass anteriorly through the oesophagus and feeding apparatus into the plant cell. It has been speculated that the gland secretions modify the pH within the lumen and alters the surface charge of the virus particles (Taylor & Robertson, 1977; Martelli & Taylor, 1989) or that the dissociation may be mediated by an enzymic effect of the gland secretions on the bonding of the virus particles to the cuticular surface of the nematode (Taylor & Brown, 1997). However, it is probable that not all adsorbed virus particles are released during a single feeding process. For example,

individual viruliferous *X. diversicaudatum* and *P. pachydermus* were able to transmit SLRSV and TRV, respectively, to three successive bait plants (van Hoof, 1965; Harrison, 1967).

The mechanism of release can determine specificity. *Longidorus macrosoma* transmits the English but only rarely the Scottish strain of RRSV, although both strains are retained at apparently identical sites within the vector. Therefore, it appears that only the English strain of RRSV dissociates whereas the Scottish strain remains attached during the feeding process (Taylor & Robertson, 1973; Trudgill & Brown, 1978).

TRANSFER

Transfer can simply refer to the active relocation of virus particles from point "A" to point "B". Such a simplistic definition is not appropriate in relation to the transmission process. When referring to nematode transmission of viruses, dissociated virus particles released from the specific sites of retention have to move forward through the nematode's feeding apparatus to the external environment and then must enter a living plant cell for transmission to be concluded.

> **Transfer** may be defined as: **"The placement of virus particle(s) in a live plant cell".**

Whilst attempting to substantiate a claim made by Valdez (1972), that *X. diversicaudatum* was a vector of RRSV, McNamara (1978) obtained evidence that the external surface of plant roots could become contaminated with particles of the virus (RRSV) present in nematode faeces adhering to the external surface of the roots. As these virus particles proved to be viable McNamara concluded that evidence for nematode transmission of a virus "can only be fully acceptable if virus is translocated from the roots of the bait plant after transmission and infection is shown to be present in the leaves, hypocotyl or in other regions to which the nematodes have not had access".

ESTABLISHMENT

Transfer of virus particles into a live plant cell can result in non-propagation of the virus (immune-host), or, successful disassembly, reassembly and replication of the virus. Thereafter, the virus may colonise new cells, thus successfully infecting the plant.

> **Establishment** may be defined as: **"The successful colonisation (infection) of the plant by a virus following transfer (= transmitted virus)".**

The nematode-virus-plant interaction

Virus transmission involves acquisition of the virus by the nematode ingesting it from a plant cell(s), thereafter followed by adsorption, retention, release, transfer and finally establishment of the virus in a new plant host. Interruption to any of these processes will prevent transmission. The ingestion of virus involves an interaction between the nematode, virus and plant; acquisition, adsorption, retention and release probably only involve an interaction between the nematode and virus; transfer involves a nematode-virus-plant interaction; and establishment involves a virus-plant interaction (Table 3). Each of these interactions can be described in terms of efficiency, frequency and effectiveness and are subject to the influence of several environmental factors (Table 4).

Table 4. *The principal influence of some environmental factors on nematode/virus/plant interactions.*

	Nematodes	Viruses	Plants
Occurrence (distribution)	+	+	+
Temperature	+	+	+
Soil moisture	+		+
Soil particle size	+		+
Plant species or cultivar	+	+	

Much of our knowledge of virus transmission by nematodes is based on laboratory experiments. These experiments, using specialised techniques, rely on the recovery of virus from bait plants as the principal evidence of transmission having occurred. Data collected from these experiments are often used to describe "frequency" or "efficiency" or "rates of transmission" by the vector nematode. However, these terms are frequently used interchangeably and without clear definition when applied to vector nematode research.

To ameliorate such misunderstanding and misinterpretation of virus transmission data we provide an explanation and definition of these terms as applicable to laboratory-based research on nematode transmission of plant viruses.

FREQUENCY

Laboratory experiments used to investigate transmission of viruses by nematodes involve allowing nematodes access to virus infected plants, subsequently recovering the nematodes and then giving groups of variable numbers of nematodes access to bait plants. The results of these experiments are primarily expressed as the proportion of bait plants from which virus is recovered.

Frequency may be defined as: **"The number of bait plants from which virus is recovered as a proportion of the total number of bait plants".**

EFFICIENCY

Transmission (= vector) efficiency can be described in terms of numbers of feeds on virus source plants, number of feeds on bait plants, and duration of individual feeds on virus source and/or bait plants. However, the final results are invariably based on the number of nematodes given access to bait plants and the proportion of bait plants from which virus is recovered.

Efficiency may be defined as: **"Relation between number of nematodes given access to a bait plant and the number of bait plants from which virus is recovered".**

Application of the maximum likelihood equation of Gibbs and Gower (1960) to experiment data provides an estimate of the probability that a single nematode transmitted virus. The probability can be calculated in experiments in which groups of nematodes are added to pots containing bait plants. This probability can be referred to as the efficiency of transmission of the nematode population or species. The equation used to calculate the probability is :

$$P = 1 - \sqrt[n]{Q}$$

In the equation, P is the probability that a single nematode transmitted virus, Q is the proportion of bait plants uninfected with virus to those from which virus was recovered when n nematodes were added to each pot containing a bait plant.

RATE OF TRANSMISSION

The number of bait plants infected with virus (= frequency, see above) or the proportion of individual nematodes calculated to have transmitted virus (= efficiency, see above) have each been used to describe the rate of transmission by a vector. However, a rate involves both time and quantity and this term should only be used when referring to aspects of the transmission process involving both these elements.

Rate of acquisition may be defined as: **"The proportion of individual nematodes estimated to have acquired virus during a given period of access to a virus source plant".**

Rate of retention may be defined as: **"The proportion of individual nematodes estimated to have retained virus particles in a given period of time from when the nematodes are removed from the virus source plant to the time they are given access to a bait plant".**

Rate of transfer may be defined as: **"The proportion of individual nematodes estimated to have transferred virus during a given period of access to a bait plant".**

Rate of transmission may be defined as: **"The proportion of individual nematodes estimated to have acquired, retained and transferred virus during a given period from when the nematodes were given access to a virus source plant to their removal from the bait plant".**

The distinction between efficiency and rate of transmission is that the former is the proportion of individual nematodes calculated to have transmitted virus whereas the latter is the proportion of individual nematodes calculated to have acquired, retained and transmitted virus in a given period of time.

EFFECTIVENESS

Xiphinema diversicaudatum, which has an extensive natural host range, transmits ArMV and SLRSV to a wide range of cultivated and uncultivated plant species, whereas, *X. index*, which has a very restricted host range, transmits GFLV only to grapevine. Thus, *X. diversicaudatum* may be regarded as a very effective vector species as it is capable of exposing its associated viruses to a wide range of potential hosts for the viruses. Conversely, *X. index* may be regarded as being an ineffective vector as it does not expose its associated virus to many potential hosts.

Effectiveness may be defined as: **"A vectors ability to successfully provide a pathway for its associated virus to infect new host species".**

Specificity of transmission

THE NEMATODES

Harrison *et al* (1961) observed that the degree of similarity between different nematode transmitted viruses resembled the degree of systematic relationship between their vectors and concluded by stating that "this apparent specificity still needs confirmation by experiment". This initial observation was expanded by Cadman (1963) who reported that whereas different viruses have different vectors it was also apparent that serologically distinct strains of the same virus are transmitted by different but closely related species of

the same genus. However, it was Harrison (1964) who referred to specific nematode vectors for serologically distinct forms of viruses. Thereafter, researchers adopted the phrase "specificity" as referring to the associations between nematode species and different viruses and virus strains. This specificity of transmission has subsequently been confirmed by further research. Furthermore, the level of specificity between virus and vector has been shown to extend to populations of vector species and minor serological variants of several of the viruses (Brown *et al.*, 1995). Specificity of transmission has also been shown to occur with tobraviruses and their associated vector species (Brown & Ploeg, 1989; Ploeg *et al.*, 1992)

> **Specificity of transmission** may be defined as: **"The specific relationship between a plant virus and its vector nematode *viz.* likely a recognition event between the virus and the site of retention in the vector".**

Taylor and Brown (1981) and Brown *et al.* (1994) speculated that positively charged virus particles ingested by *Longidorus* nematodes were attracted to the negatively charged surface of the odontostyle. Different strains of one virus could then have different surface charge densities, thus requiring different vector species. Correspondingly, two different viruses transmitted by the same vector would then have similar charge densities, *e.g.*, RRSV and TBRV, both transmitted by *L. elongatus* (Taylor & Brown 1981).

Experiments with *Xiphinema* and *Paratrichodorus* species revealed that adsorption of virus particles to specific sites of retention probably involves a recognition process between the particles and a layer in the cuticular lining of the oesophagus which stains for carbohydrate. This layer appears to be continuous in *Paratrichodorus* but was observed as a discontinuous layer in *X. diversicaudatum* and *X. index* (Robertson & Henry, 1986). However, in different virus-vector combinations the mechanism of recognition may differ between vector genera as well as between different viruses transmitted by the same nematode species (Brown, 1986; Brown & Robertson, 1990).

THE VIRUSES

The nematode-transmitted plant viruses, both tobra- and nepoviruses, have bipartite genomes with the RNA-2 segment containing the genetic determinants conferring vector transmissibility. Harrison *et al.* (1974) was first to identify that the RNA-2 of RRSV contained the determinants for transmissibility by *L. elongatus*. Similarly, Harrison and Murant (1978) reported that transmissibility of TBRV by *L. elongatus* was determined by the RNA-2 segment of the virus. Ploeg *et al.* (1993) reported that the RNA-2 of TRV contained the determinants of vector transmissibility.

The RNA-2 of nematode transmissible isolates of TRV and PEBV contain three or four Open Reading Frames (ORF's), including the viral coat protein. MacFarlane *et al.* (1995) reported that nematode transmissibility of PEBV was not determined exclusively by the coat protein and subsequently demonstrated that all three ORF's were required for vector transmission of this virus (MacFarlane *et al.*, 1996). Hernandez *et al.* (1997) reported that the coat protein and a 29 kDa protein were required for vector transmissibility.

Differences in polypeptide sequences adjacent to the N-terminal of the coat proteins could also account for some aspects of specific association between nepoviruses and their longidorid vectors (Block *et al.*, 1992). In tobraviruses "finger-like" structures at the end of the coat protein sub-units of particles of tobacco rattle tobravirus could be involved in the specific association with the vector (Legorboru, 1993).

Vector and virus exclusivity and complementarity

Exclusivity and complementarity are reflections of the specificity of the association between vectors and viruses. In Europe, several nepoviruses, or serologically distinct strains of virus, are transmitted only by one *Longidorus* or *Paralongidorus* species, which is not the vector of another virus/virus strain (Table 1). However, in America the four nematode transmitted nepoviruses each have more than one vector species and conversely most vector nematode species in America can transmit more than one virus (Halbrendt, 1993) (Table 1). Similarly, in Europe there is transmission complementarity between vector *Xiphinema* species and their associated nepoviruses and also between *Paratrichodorus* and *Trichodorus* vector species and tobraviruses (Table 2),

> **Vector and virus exclusivity** may be defined as: **"The case where a nematode species transmits one virus, or one serologically distinct virus strain, and the virus/virus strain has only a single vector".**

> **Vector and virus complementarity** may be defined as: **"The case where a nematode species transmits two or more viruses, or serologically distinct strains of a virus, and where two or more viruses/virus strains share the same vector species."**

The *X. americanum*-group is considered to represent a discrete evolutionary line within the genus as

the North American species appear to have only three juvenile development stages and these nematodes do not induce root-tip galling when feeding. Most of the *X. americanum*-group species associated with nepoviruses in North America are widespread and are vectors of two or more distinct viruses. For example, populations of *X. americanum sensu stricto* from Pennsylvania, Arkansas and California transmit cherry rasp leaf, tobacco ringspot and tomato ringspot nepoviruses (Brown *et al.*, 1994). In contrast, the vector longidorids in Europe mainly have restricted or localised distributions and are vectors of only one virus or serologically distinct virus strain, *i.e.*, *L. apulus* and *L. fasciatus* are vectors of Italian and Greek strains, respectively, of artichoke Italian latent nepovirus (Brown & Trudgill, 1989, 1997; Taylor & Brown, 1997).

Factors affecting specificity, exclusivity and complementarity in vector transmission

Successful transmission of a virus by a nematode involves numerous complex and subtle interactions between the nematode, virus, plant host and the environment. The most important of these are presented in Table 4 and their ability to affect the nematode/virus/plant interactions are indicated.

Nepo- and tobraviruses have developed highly specific relationships with the nematode species which function as their vectors. Nematode species occur as localised populations, usually in restricted geographical areas. Their limited mobility imposes prolonged and continuous association with their host plants which provides the opportunity for developing specific associations with plant pathogens such as viruses. Also, this is a dynamic process as under these conditions their isolated occurrence will result in a reduced gene flow so that homozygosity increases which can result in speciation. Similarly, the nematode transmitted viruses have restricted geographical distributions, usually reflecting that of their vector, and they too can mutate to form new virus strains or viruses. Thus, specific associations between nematodes and viruses are constantly evolving possibly resulting in some viruses losing their vector transmissibility, some vectors losing their ability to transmit viruses whilst concurrently new virus and vector associations are becoming established.

Acknowledgements

Research at the Scottish Crop Research Institute is grant-aided from the Scottish Office Agriculture, Environment and Fisheries Department.

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