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NEMATODE-VIRUS PLANT INTERACTIONS¹

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Nematode transmission of plant viruses is remarkable in involving only two distinct groups of viruses, nepo and tobra, and being limited to longidorid and trichodorid nematodes. Further, only a small proportion of species in the virus vector genera have been shown to be capable of transmitting and these are mainly located in Europe and North America. In a survey of virus vector nematodes in Britain, Taylor and Brown (1976) found that very few vector populations were viruliferous. The association between viruses and vector nematodes possibly originated independently in the two continents as the viruses and vectors are quite distinct between each (Taylor and Brown, 1981; Lamberti and Roca, 1987). Some of the vectors and viruses have been disseminated to other geographical areas e.g. arabis mosaic virus (AMV) and *Xiphinema diversicaudatum* from Europe to New Zealand (Thomas and Proctor, 1972); grapevine fanleaf virus (GFV) and *Xiphinema index* from Ancient Persia to Europe and North America (Hewitt, 1968). Also, several of the nepoviruses have been disseminated in planting material e.g. strawberry latent ringspot virus from Europe to California, USA (Hanson and Campbell, 1979); tomato black ring virus (TBRV) from Europe to Kenya, Africa (Kaiser *et al.*, 1978); tomato ringspot virus (TomRSV) from North America to Europe (Martelli, 1975). Some nepoviruses appear to have evolved from transmission by vector nematodes to alternative methods for their efficient transmission e.g. pollen transmission of cherry leaf roll virus (Jones *et al.*, 1981).

Much of the accumulated experimental evidence indicates that viruses are transmitted in a specific manner by their vector nematodes (Taylor and Brown, 1981). Thus although serologically unrelated nepoviruses may share a common vector species e.g. AMV and strawberry latent

ringspot virus (SLRV) are both transmitted by *X. diversicaudatum*, strains of a virus that are serologically distinct may be transmitted by different, although closely related, species of the same nematode genus. For example the Scottish serotypes of raspberry ringspot (RRV) and the unrelated tomato black ring (TBRV) viruses are transmitted by *Longidorus elongatus*, but the English serotypes of the viruses have *L. macrosoma* and *L. attenuatus*, respectively, as vectors (Harrison, 1964).

Evidence of vector specificity in the transmission of tobamoviruses is less clear. In America and Europe there are serologically distinguishable isolates of tobacco rattle virus (TRV). In Europe different isolates are associated with different trichodorid species in the genera *Trichodorus* and *Paratrichodorus*. However, in North America where both genera are present only *Paratrichodorus* species have thus far been reported to transmit TRV (Lamberti and Roca, 1987). In the Netherlands, Hoof (1968) compared transmission of TRV by nine *Trichodorus* or *Paratrichodorus* species and found that transmission occurred only when the nematode and virus came from the same locality. Conversely, in Britain Kurppa *et al.* (1981) found that a population of trichodorids, including *T. primitivus*, from eastern Scotland transmitted the spinach yellow mottle strain of TRV, originally isolated from spinach growing in southern England.

The *Xiphinema americanum* complex has been reported to comprise several species (Lima, 1965), or to represent a number of geographically isolated, morphologically variable populations (Tarjan, 1969). More recently Lamberti and Bleve-Zacheo (1979) separated populations previously identified as *X. americanum*, into 25 discrete species. *X. americanum sensu lato* has been reported as the vector of tobacco ringspot, tomato ringspot, cherry rasp leaf and peach rosette mosaic viruses in North America. However, Lamberti and Roca (1987) speculated that several of the

¹ Full text of an invitational lecture presented at the 5th International Congress of Plant Pathology, Kyoto, Japan, 20-27 August 1988

species described by Lamberti and Bleve-Zacheo (1979), formerly identified as *X. americanum*, could be vectors of viruses in several geographically separated areas in North America (Table I). Differential transmissibility has been reported of isolates of serologically distinct strains of tomato ringspot virus by species or populations belonging to the *X. americanum* complex, but, a comprehensive investigation is required to facilitate an understanding of such relationships (Hoy *et al.*, 1984). Peach rosette mosaic virus is also transmitted by *L. diadecturus*, the only vector species of *Longidorus* indigenous to North America (Allen *et al.*, 1982). Consequently, peach rosette mosaic virus presents a unique situation as being the only nepovirus having vectors belonging to separate genera. It is not known whether either vector can transmit the virus isolate that is naturally associated with the other nematode.

In Europe recent progress in understanding the transmission of viruses by nematodes has resulted from improved techniques (Trudgill and Brown, 1978a). These have also led to a comprehensive evaluation of previous records of virus transmission with the proposed rejection of about two thirds of published virus and vector associations (Trudgill *et al.*, 1983; Brown *et al.*, 1989b).

Methodology for virus transmission studies

Most of the records of virus transmission have been obtained by transferring relatively large numbers of a vector nematode, or of a nematode believed to be a vector, from pots containing plants systemically infected with a specific virus to pots containing herbaceous bait plants, susceptible to the virus. The number of transmissions obtained in such experiments is affected by many factors, including the soil

mixture in the test pots, the size of the test pots, the age, size and species of bait plants used, and the moisture content and temperature of the soil (Taylor, 1972). If conditions are not optimal intrinsic differences in efficiency of transmission by vector species or between populations can be masked. Similarly if appropriate controls are lacking or systemic infection of the bait plants is not demonstrated misleading results may be obtained (Trudgill *et al.*, 1983; Brown and Trudgill, 1984; Brown *et al.*, 1989b).

McElroy (1978) recognised that if the vector status of a nematode is to be established with any certainty, several criteria must be met. These include: the virus must be available to the nematode; the test conditions must be suitable for transmission to occur, and the possibility of virus contamination of the bait plant must be avoided. These criteria were further developed and refined by Trudgill *et al.* (1983) as 1) the virus and nematode must be fully and correctly identified; 2) bait plant tissues must be shown to be infected with the virus under test; 3) the nematode under test must be shown to be the only possible vector in that experiment.

Test procedures have been developed to meet these criteria (McElroy, 1978; Trudgill and Brown, 1978b; Taylor and Brown, 1981). That of Trudgill *et al.* (1983); (Fig. 1) is the most refined and sufficiently sensitive to detect small differences in efficiency of virus transmission. Using such a technique, the efficiency can be determined of each process in the acquisition, retention and transmission of a virus. For example, in an experiment with *L. macrosoma* and RRV-E the number of root-galls indicated that the majority of nematodes had probably fed on the virus source and bait plants (Fig. 1). From slash-tests and examination by electron microscopy it was shown that most of the nema-

Table I - Possible geographical associations between North American nepoviruses and nematode species belonging to the *Xiphinema americanum sensu lato complex* (after Roca and Lamberti, 1987)

Nematode species	Virus	Area	Reference
<i>X. americanum</i>	Tomato ringspot	Eastern USA	Forer and Stouffer, 1982
<i>X. americanum</i>	Tobacco ringspot *	Eastern USA	Hibben and Walker, 1971
<i>X. americanum</i>	Peach rosette mosaic	Michigan, USA	Klos <i>et al.</i> , 1967
<i>X. americanum</i>	Peach rosette mosaic	Ontario, Canada	Allen <i>et al.</i> , 1984
<i>X. californicum</i>	Cherry rasp leaf	California, USA	Nyland <i>et al.</i> , 1969
<i>X. californicum</i>	Tomato ringspot	California, USA	Hoy <i>et al.</i> , 1984
<i>X. occiduum</i> / <i>X. thornei</i>	Tomato ringspot	British Columbia, Canada	Jones <i>et al.</i> , 1981
<i>X. rivesi</i>	Tomato ringspot	Eastern USA	Forer <i>et al.</i> , 1981
<i>X. rivesi</i>	Tomato ringspot	Ontario, Canada	Ebsary <i>et al.</i> , 1984
<i>X. utahense</i>	Tomato ringspot	Oregon, USA	Converse and Ramsdell, 1982
<i>X. incognitum</i>	Tomato ringspot	Japan	Iwaki and Komuro, 1971

* Roca and Lamberti (1987) do not consider *X. americanum sensu stricto* to be a vector of tobacco ringspot virus. Fulton (1967) reported dual transmission of tobacco ringspot and tomato ringspot virus by a single specimen of *X. americanum sensu lato* from Arkansas, USA but the specific identity of this species requires to be confirmed.

todes had ingested virus and retained virus particles in their odontostyle. However, only a relatively small proportion of the nematodes appeared to transmit the virus. This could be due to either the bait plants resisting infection, or infection not being detected, or to a failure by the nematodes, during feeding, to release and pass into the plant infective virus particles.

Virus transmission by (Para) *Trichodorus* nematodes is more difficult to study than that by longidorids. However, Brown *et al.* (1989b) have developed techniques to meet similar criteria for determining virus transmission by trichodorid nematodes. The test procedure of Trudgill *et al.* (1983) utilises small plastic pots (25 cc) enclosed in controlled temperature boxes (Taylor and Brown, 1974) to reduce soil moisture and temperature fluctuations. The system developed by Brown *et al.* (1989b) is similar to that of Trudgill *et al.* (1983) but the bait plants are grown in 0.5 cc plastic capsules. As yet, it has not proved possible to reliably assess the extent of feeding or the proportion of nematodes ingesting virus. Nevertheless, the technique does enable study of the transmission of virus by individual nematodes.

Variability of transmission among vector populations

Populations of *X. diversicaudatum* were reported to differ in their ability to transmit AMV (Martelli, 1975; Dalmaso *et al.*, 1972), *X. coxi* to transmit tobacco ringspot virus (Hoof, 1971) and *L. elongatus* to transmit RRV and TBRV (Brown and Taylor, 1981). Differences between vector species in efficiency of transmission of their specific viruses have also been reported. Using the experimental procedures referred to above (Fig. 1), Trudgill *et al.* (1978c) demonstrated that *X. diversicaudatum* was an efficient vector of AMV whereas *L. elongatus* and *L. macrostoma* were comparatively inefficient vectors of RRV (Scottish) and RRV (English) respectively.

The efficiency with which populations of *X. diversicaudatum* from several different countries transmitted strains of AMV and SLRV has been investigated (Brown and Trudgill, 1983; Brown, 1985; 1986). Of ten populations of *X. diversicaudatum* tested, seven efficiently transmitted two serologically distinct strains of AMV but very few transmissions of either strain were obtained with populations from Italy, France or Spain (Table II). These three populations were also inefficient vectors of the type-

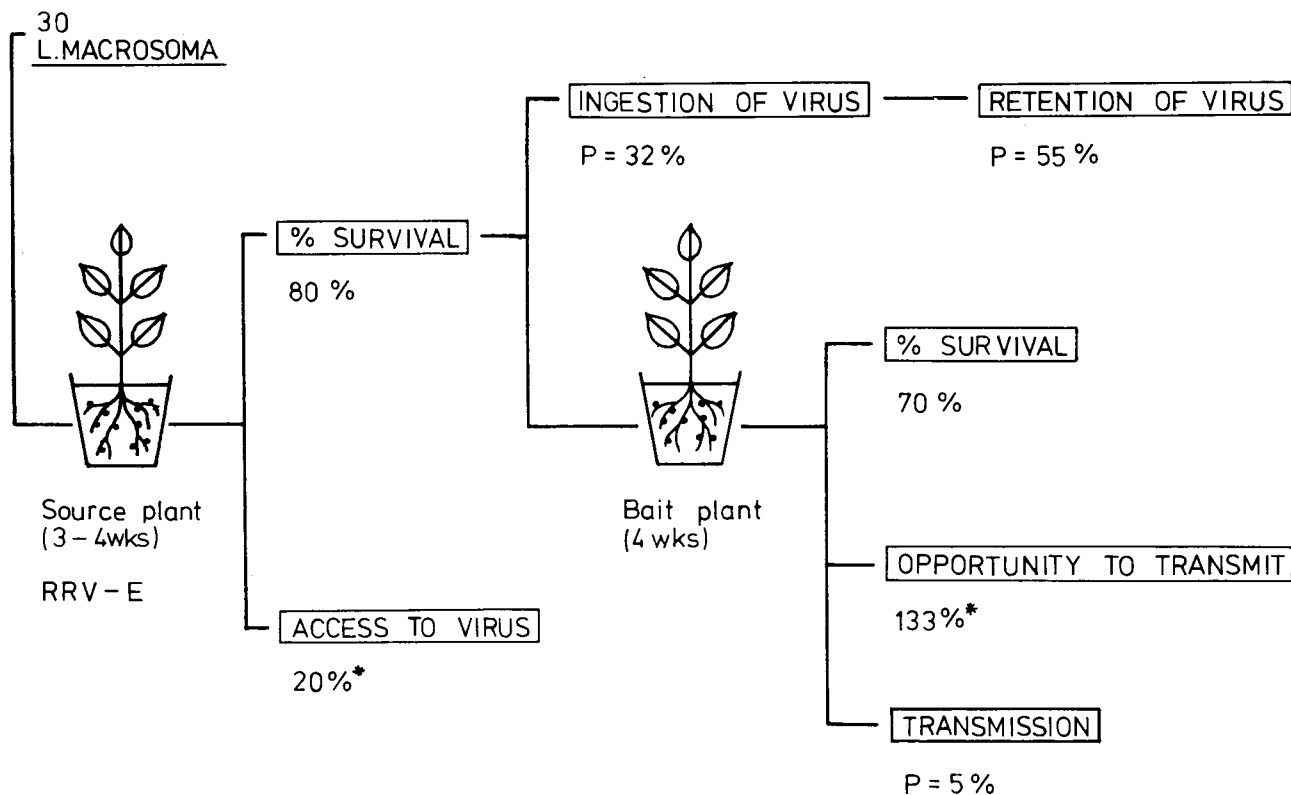


Fig. 1 - Procedure for assessing transmission of nepoviruses by longidorid nematodes (Trudgill *et al.*, 1983). The numerical data are from an experiment examining the transmission by *Longidorus macrostoma* of raspberry ringspot virus - English serotype (RRV - E). Thirty nematodes were added to virus source plants and after 3-4 wks. 80% of the nematodes were recovered. It was estimated that 20% of the nematodes had fed on the plant roots (assuming one root gall per nematode), 32% were found to have ingested virus and 55% had virus particles specifically retained in their feeding apparatus. Of the nematodes added to the bait plants 70% were recovered after 4 wks., it was estimated that 133% had fed on the bait plants (assuming one root gall per nematode; or all nematodes had fed, each producing 1-3 root galls). It was estimated that only 5% of the nematodes recovered from the bait plants had transmitted virus.

British strain of SLRV (Table II). When these populations were exposed to a strain of SLRV recovered from *Prunus persica* L. in Italy most populations did not transmit but a few transmissions were obtained with Italian, French and Spanish populations (Table III). In other tests, virus free populations of *X. diversicaudatum* from Scotland and Italy were exposed to two Italian strains of SLRV, from *P. persica* and *Rubus idaeus* L., and the type-British strain of the virus. The Scottish populations readily transmitted the type strain of the virus, but neither of the Italian strains; whereas the Italian population transmitted all three strains but at a very low frequency.

Differences in specificity and efficiency of transmission also occur between *Longidorus* vectors. A Scottish population of *L. elongatus* transmitted three isolates of TBRV and of RRV (all similar to the type strains of the viruses) more frequently than an English population and neither population transmitted the German potato bouquet strain of TBRV, which is a distinct serotype and is considered to be vectored by *L. attenuatus* (Brown and Taylor, 1981). Using nematodes recovered directly from field soil from Germany, Brown *et al.* (1989a) found that 10% of the *L. attenuatus* transmitted the isolate of TBRV with which they were naturally associated whereas 56% of individuals in field soil from England transmitted TBRV. In laboratory tests Brown *et al.* (1989a) found that an English population of *L. attenuatus* transmitted potato bouquet and two other isolates of TBRV from Germany less frequently than several English isolates including the celery yellow vein isolate. With antiserum to the potato bouquet isolate, celery yellow vein and potato bouquet isolates were serologically distinguishable from one another and from all the other

isolates tested. The estimated proportion of *L. attenuatus* that transmitted the English isolates ranged from 0.26 to 0.78, whereas only 0.01 to 0.03 transmitted the German potato bouquet isolate, and 0.03 to 0.15 transmitted the other two German TBRV isolates.

Little is known about the natural association between tobacco rattle viruses and their vector trichodorids. In a study with field soils from eastern Scotland containing mixed populations of trichodorids, Brown *et al.* (1989b) found that only a few individuals of the vector species present transmitted virus. The numbers of nematodes transmitting virus was considerably increased in laboratory tests by first allowing the nematodes access for four weeks to TRV infected *Petunia hybrida* plants.

Association of virus and vector

The specific association between virus and vector appears to involve the protein coat of the virus which interacts with the cuticular site of virus retention within the feeding apparatus of the nematode. Electron microscopic examination of individual *X. diversicaudatum* which had fed on plants infected with British strains of AMV or SLRV (Table II) revealed that nematodes from Italian and French populations, which were poor vectors, had very few or no particles associated with the odontophore and oesophagus. However, virus particles were present in nematodes from the Scottish population, which was an efficient vector, but particles of the Italian *P. persica* strain of SLRV were not present in any of the populations (Brown and Trudgill, 1983). In all nematodes examined by immunosorbent electron microscopy (Roberts and Brown, 1980) virus

Table II - Transmission of two strains of Arabis mosaic and the type-British strain of strawberry latent ringspot viruses by ten populations of *Xiphinema diversicaudatum* (after Brown, 1985, 1986; Brown and Trudgill, 1983)

Nematode populations	Percentage number of transmissions		
	AMV-T ²	AMV-W	SLRV-T
Bulgaria	100	38	48
England	96	36	60
New Zealand	96	60	60
Norway	96	52	40
Scotland	92	36	68
Switzerland	96	40	56
USA	48	36	36
France	10	4	10
Italy	4	4	2
Spain	0	0	15

¹ Using groups of 2 nematodes per test pot; 25 replicates of each test.

² AMV-T, type-British strain; AMV-W strain from woodland at High Hailstow, England, transmitted by *X. diversicaudatum*.

TABLE III - Transmission of an Italian strain (*Prunus persica*) of strawberry latent ringspot virus by ten populations of *Xiphinema diversicaudatum* (after Brown, 1985).

Nematode populations	No. of transmissions		Estimated percentage nematodes transmitting ¹	
	No. nematodes per replicate			
	2	5	2	5
Bulgaria	0/19 ²	0/4	<3	<6
England	0/24	1/10	<2	2
New Zealand	0/22	0/10	<2	<2
Norway	0/24	0/8	<2	<3
Scotland	—	0/20	—	<2
Switzerland	0/20	1/10	<3	<2
USA	1/23	0/10	2	<2
France	0/40	—	<2	—
Italy	2/35	2/16	2	<3
Spain	0/20	1/10	<3	2

¹ Calculated from the equation of Gibbs and Gower (1960)

² Numerator is the number of bait plants infected, denominator is the number tested.

particles of AMV and SLRV were present in the intestine and had therefore been ingested by the nematodes. Thus, it is assumed that in those populations of *X. diversicaudatum* which failed to transmit virus the particular feature of the virus particle protein coat and cuticular lining of the nematode's food canal associated with retention of virus were not compatible and hence little or no specific retention occurred. It has been speculated that specific virus retention involves the carbohydrate layer which discontinuously lines the odontophore and oesophagus in *X. diversicaudatum* and which may recognise lectin-like molecules on the protein coat of the virus (Robertson and Henry, 1986). Whatever the particular nematode feature involved, it was shown that by interbreeding *X. diversicaudatum* from Italy (inefficient vector) with *X. diversicaudatum* from Scotland (efficient vector) the ability to transmit viruses is inherited and possibly controlled by a single gene (Brown, 1986b).

Substantial differences in efficiency of virus transmission between nematode populations suggests the possibility of biological differences within the species. This applies especially where the nominal species is widely distributed, such as *X. diversicaudatum*. Brown and Topham (1985) showed that geographically separate populations of *X. diversicaudatum*, which differed in ability to transmit virus, could be grouped on the basis of their morphometrics but, apart from a Spanish population - which appeared to be distinct, the differences were not considered sufficient to designate new species. Brown (1986c) subsequently demonstrated that several of these populations, including that from Spain, could readily interbreed with a Scottish population. Hence, it is considered that all the populations examined belonged to the same biological species. Other vector species recognised as species complexes include *L. elongatus*, *L. attenuatus* and *X. americanum sensu lato* (Brown and Taylor, 1987) the latter redefined as being several distinct morphological species (Lamberti and Blevé-Zacheo, 1979). These species have parthenogenetic mode of reproduction and thus interbreeding techniques are inapplicable.

The ability of a vector species to transmit has also to be considered in relation to the taxonomy of the viruses. It is generally assumed that both serological distinctness and specificity of transmission are conferred by the properties of the virus protein coat, genetically encoded for by the RNA-2 of the bipartite genome. However, differences in the ability of German and English populations of *L. attenuatus* and the transmission of possibly minor serological variants of TBRV suggest that other factors may be involved in the specific association of virus with its vector.

The association of virus/vector/plant is a dynamic and interactive process which probably confers ecological evolutionary selection pressures resulting in subtle differences in the specific relationships developing between some virus strains and virus vector populations at a particular time. Brown *et al.* (1989b) found that in eastern Scot-

land mixed species populations of trichodorid nematodes were naturally associated with TRV. In some populations two of the species present were each associated with serologically distinct isolates of the virus. Furthermore, in a Scottish raspberry plantation infested with *L. elongatus* transmitting RRV two serologically distinct isolates of the virus were detected (Brown and Jones, unpublished data). At another field site *X. diversicaudatum* transmitted two serologically identical isolates of AMV which caused markedly different symptoms in *Chenopodium quinoa* test plants.

The evolutionary processes applying to vector nematodes and their associated viruses in response to changing environmental conditions results in a continuous flux in the interrelationships between virus/vector and host plants. The occurrence of several virus isolates at a particular field site in association with a vector nematode species may, therefore, have resulted from selection processes related to differences in plant hosts and vector biology. Consequently, it is likely that new virus and vector nematode associations will continue to be identified, as research into such associations progresses, especially with the advent of new and more advanced techniques for virus and nematode identification.

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