Tribune

METHODS AND CRITERIA FOR ASSESSING THE TRANSMISSION OF PLANT VIRUSES BY LONGIDORID NEMATODES

David L. TRUDGILL *, Derek J.F. BROWN * and David G. MCNAMARA**

* *Scottish Crop Research Institute, Invergowrie, Dundee, Scotland and*
** *East Malling Research Station, Maidstone, Kent, England.*

Since Hewitt, Raski and Goheen (1958) first showed that *Xiphinema index* is a vector of grapevine fanleaf virus more than forty plant virus/nematode vector combinations have been reported. Many of these reports have not been confirmed, but among those that have been substantiated a pattern of specificity between the viruses and their longidorid nematode vectors is apparent. Harrison, Mowat and Taylor (1961) observed that the degree of similarity between the different viruses seemed to parallel the degree of systematic relationship between their nematode vectors. This relatedness of specificity may be partly due to virus particles with particular protein coat properties (Harrison, 1964 ; Harrison *et al.*, 1974) becoming attached to the lining of the feeding apparatus at specific sites within their vectors. These are the inner surface of the odontophore and oesophagus in vector species of *Xiphinema* (Taylor & Robertson, 1970 ; McGuire, Kim & Douthit, 1970 ; Raski, Maggenti & Jones, 1973) and the inner surface of the odontostyle and between the odontostyle and the guiding sheath in *Longidorus* spp. (Taylor & Robertson, 1969 & 1973 ; Taylor, Robertson & Roca, 1976). Further evidence for the "narrowness" of specificity between viruses and their nematode vectors is provided in several reports of nematode populations differing in their ability to transmit isolates of a virus (Dalmasso, Munck-Cardin & Legin, 1972 ; Van Hoof, 1966 ; Brown & Taylor, 1981). In contrast to the above, the results of some laboratory experiments have indicated nematode transmission of viruses contrary to the pattern of specificity proposed by Harrison (1964). For example, six species of longidorid nematode have been reported as vectors of arabis mosaic virus (AMV ; specific field vector *X. diversicaudatum ;* Jha & Posnette, 1959 ; Harrison & Cadman, 1959). Similarly transmission of raspberry ringspot virus English strain (RRV-E ; specific field vector *Longidorus macrosoma ;* Harrison, 1962 ; Debrot, 1964) has been reported for seven species of longidorid nematodes (Tab. 1). If all these reports of transmission are true then it would seem that nematode species other than those with which these viruses are specifically associated with in the field can also act as vectors. In this connection, Taylor and Robertson (1969) found unattached particles of AMV in the buccal capsule of *L. elongatus* which suggested that some transmission may result from non-specific retention of virus.

McNamara (1978) offered another explanation for apparent non-specific transmissions. He suggested that, in laboratory experiments, contamination of the outside of bait plant root systems may occur either from virus coming from bodies of nematodes entangled in, or in nematode faeces adhering to the outside of, the roots. He reached these conclusions after attempting to substantiate the claim by Valdez (1972) that RRV-E could be transmitted by *X. diversicaudatum*. McNamara (1978) found that, although he could recover this virus from the roots of bait plants exposed to *X. diversicaudatum*, none of these plants was systemically infected, all the RRV-E detected apparently coming from external contamination of the roots. In contrast, when he used *L. macrosoma*, the natural vector of RRV-E, many bait plants eventually became systemically infected. McNamara (1978) concluded that evidence for nematode transmission "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 nematodes have not had direct access".

Table 1

Longidorus, *Paralongidorus* and *Xiphinema* species reported as vectors for arabis mosaic virus (AMV) and the English strain of raspberry ringspot virus (RRV-E)

Virus	*Field vector*	*Other vectors*	
AMV	*X. diversicaudatum*	*X. coxi*	(Fritzsche, 1964)
		X. bakeri	(Iwaki & Komuro, 1974)
		X. index	(Fritzsche & Thiele, 1979)
		L. caespiticola	(Valdez, 1972)
		P. maximus	(McElroy *et al.* 1976)
RRV-E	*L. macrosoma*	*L. elongatus*	(Taylor & Murant, 1969)
		L. profundorum	(Fritzsche & Kegler, 1968)
		L. caespiticola	(Valdez, 1972)
		L. leptocephalus	(Valdez, 1972)
		X. diversicaudatum	(Fritsche & Kegler, 1968)
		P. maximus	(McElroy *et al.* 1976)

More than two-thirds of the reports of longidorid nematodes transmitting virus fail to satisfy this requirement. Also, many of these reports give inadequate descriptions of the methods used or describe tests that did not have adequate controls or in which the nematode and/or virus used were not adequately identified.

In this paper we consider the criteria by which the results of a virus transmission test with longidorid nematodes should be judged and describe a test procedure which, modified where necessary to suit the nematode/virus combination being tested, should give results which satisfy those criteria. Our experience has been limited to European species of virus vector nematodes but we believe that the procedure we describe can also give information about the efficiency with which a virus is transmitted and, within the limits of the numbers of nematodes tested, useful evidence of the inability of a nematode to transmit a virus.

The criteria for evaluating the results of transmission tests

To demonstrate that a particular virus is transmitted by a given species of longidorid nematode we consider that the following criteria must be satisfied :

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.

In the following section each of these criteria is considered in more detail.

Identification of the virus and the nematode

Only one nematode species should be tested at any one time, unless controls with other nematodes are required. The virus to be transmitted should be characterised by serology and, where possible, its relationship with other viruses be established. Any virus transmitted must be identified serologically and, where appropriate, shown to be serologically identical to that in the source plant. The nematodes tested should be from one population and, except where they are from naturally infected field soil, shown to be initially virus-free by bait-testing with appropriate control plants. Details of the source of nematodes should be given, as it is known that populations of a species may differ in their ability to transmit strains of a virus, and those transmitting virus must be identified and permanent mounts kept. Where necessary they should be compared with paratypes or similar specimens and any deviations from these noted.

EVIDENCE THAT THE BAIT PLANT IS INFECTED WITH VIRUS

This evidence is best provided by demonstrating that the bait plant is systemically infected. This is most readily accomplished by recovering virus from the hypocotyl or aerial parts but, in some instances, production of leaf symptoms may suffice. If testing of the root system is unavoidable, infection must be unequivocally demonstrated. In all tests infection of either the bait or assay plants due to contamination or by alternative vectors must be excluded.

THE NEMATODE MUST BE SHOWN TO BE THE VECTOR

In preliminary tests inhibition of transmission by nematicides or by air-drying the soil may be used to indicate that a nematode may be the vector. In definitive tests nematodes must be extracted after exposure to the virus infected source plants and individually transferred to the roots of the bait plants which should be grown in containers and a medium which have previously been partially sterilized to ensure freedom from potential vectors. The sievings from which the nematodes have been removed must be tested for alternative vectors and appropriate controls should be used to check for possible transmission by stray arthropods or wind-borne fungal spores. Where possible, these organisms should also be rigorously excluded. The control plants should be numerous, and be an integral part of the bait and assay tests, and should also be used to demonstrate that the source, bait and assay plants and the nematodes (unless they were from around a virus-infested plant in the field) were all initially virus-free.

Demonstrating the inability of a nematode to transmit a virus

It cannot be completely proved that a particular species of nematode is completely unable to transmit a virus. It is known that populations of a species may differ in their ability to transmit strains of a virus. However, if good techniques are used, much circumstantial evidence can be obtained that the population under study is not a vector. Likely causes of failure to transmit due to poor experimental procedures are :

UNSUITABLE VIRUS SOURCE OR BAIT PLANTS

Douthit and McGuire (1978) recovered tobacco ringspot virus from only 25 of 38 species of bait plants exposed to viruliferous *X. americanum s. lat.* (1) and found that in those plant species to which virus was transmitted the frequency of infection varied greatly. Similarly Trudgill and Brown (1979) and Trudgill, Brown and Robertson (1981) found that *L. macrosoma* transmitted RRV-E to *Petunia hybrida* and *Fragaria ananassa* but not to *Chenopodium quinoa* whereas *X. index* could acquire grapevine fanleaf virus from, but not transmit it to *Gomphrena globosa.*

UNSUITABLE VIRUS ISOLATE OR STRAIN

Differences in ability to transmit virus have been shown to occur within a nematode species, different populations transmitting different isolates of the same virus (Van Hoof, 1966 ; Dalmasso, Munck-Cardin & Legin, 1972 ; Brown & Taylor, 1981). Viruses also differ in their ability to become systemically distributed in source plants and in manually inoculated plants and may therefore vary in their availability to feeding nematodes.

UNFAVOURABLE ENVIRONMENT

An unfavourable distribution of soil particle sizes, or too high, too low, or rapidly fluctuating soil moistures or temperatures may be unsuitable to the nematodes and prevent their moving and feeding. Toxins, pathogens, rough handling or extreme conditions may result in the nematodes being adversely affected or killed. Also some viruses or strains may be adapted for a particular temperature or host range.

Suggested test procedure

The most suitable procedure for testing the ability of a longidorid nematode to transmit a particular virus isolate depends on the nematode/virus combination being tested but, as already indicated, there are certain basic requirements. A test procedure which is a development of that described by Valdez (1972) and Trudgill and Brown (1978) and satisfies these requirements is given in Figure 1. It minimises the possibility of contamination, uses only small

(1) *X. americanum s. lat.* is a complex of species and *X. americanum sensu stricto* has a geographical distribution restricted to the eastern part of North America (Lamberti & Bleve-Zacheo, 1979).

numbers of nematodes, and demonstrates that the nematodes have fed on and ingested virus from the source plants, and have fed on the bait plants. In this procedure virus-free nematodes are placed around the roots of virus-infected source plants growing in small pots which are plunged in a bed of moist peat or sand. McNamara (1978) used porous pots without drainage holes but plastic pots may be used provided they are maintained in a humid atmosphere as described by Taylor and Brown (1974). Ideally only adult nematodes should be added to source plants so as to eliminate the possibility of negative results being obtained because of the nematodes moulting during the test. After an appropriate period of access to the source plants, the nematodes are carefully extracted, counted and about half their number are transferred in small groups, by hand-picking, to virus-free bait plants growing in similar conditions. At the same time a few nematode heads are taken and processed for electronmicroscopy of thin sections, as described by Taylor and Robertson (1970), to determine the proportion of nematodes retaining virus particles within their feeding apparatus. Further nematodes and the bodies from which the heads were removed are tested directly for virus in their intestine. This can be done in one of two ways.

1) If the virus in the nematode remains infective it can be tested for by slash-testing (breaking-up small numbers of nematodes in phosphate-buffer (pH 6.9) and inoculating virus indicator plants with the suspension ; Taylor, 1964).

2) A more sensitive technique, which has been used successfully where the virus particles could not be detected by slash-testing, is immunosorbent electron microscopy (ISEM). This technique involves attaching virus particles on electron microscope grids using the appropriate antiserum (Roberts & Brown, 1980).

The nematodes that were placed on bait plants are allowed to feed for a sufficient period to enable

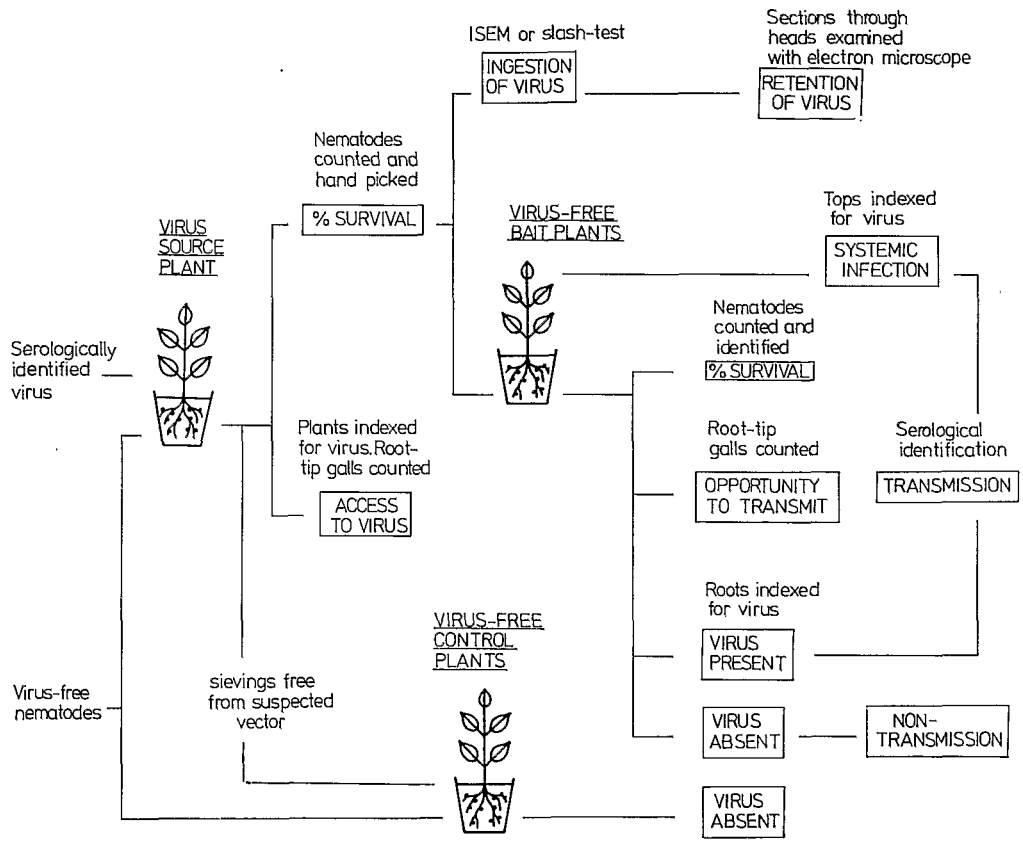

Fig. 1. The suggested procedure for establishing the ability of longidorid nematodes to transmit plant viruses.

virus to be transmitted and then to spread systemically within the plant, after which the nematodes are re-extracted and counted and the carefully washed roots and hypocotyl or tops of the plants tested for virus infection.

From the results of the ISEM, slash and bait tests the proportions of nematodes acting as sources of virus can be estimated using the Maximum Likelihood formula (Gibbs & Gower, 1960) provided that the experiments are extensively replicated and that the proportion of infected plants is neither too small nor too large.

Evidence that the nematodes fed on the source and bait plants can be obtained by showing that the nematodes developed and reproduced or by examining the plant roots for feeding damage (galls, etc.). Controls must be numerous, randomised within the bait-test and not evident to those conducting the final assay. In addition to testing for alternative vectors the controls should also test the nematodes, the source, bait and assay plants for initial freedom from virus. Virus that is transmitted and the nematodes transmitting that virus must be re-identified at the end of the test.

Conclusions

Accurate information about the capacity of longidorid nematodes to transmit viruses causing plant diseases is a pre-requisite for effective disease control measures. Inaccurate or misleading information delays progress and causes confusion and difficulties for nematologists involved in regulatory matters (i.e. production of virus-free planting stocks). Because of the complexity of the trans-

Table 2

Viruses and their specific *Longidorus* or *Xiphinema* vectors for which the evidence for nematode transmission is considered adequate

Virus	*Vector*	*Reference*
Grape fanleaf virus	*X. index*	Hewitt *et al.*, 1958
Grape fanleaf virus	*X. italiae*	Cohn *et al.* 1970 *
Arabis mosaic virus	*X. diversicaudatum*	Jha & Posnette, 1959 Harrison & Cadman, 1959
Strawberry latent ringspot virus	*X. diversicaudatum*	Lister, 1964 Harrison, 1967
Tobacco ringspot virus	*X. americanum sensu lato* **	Fulton, 1962 Griffin *et al.*, 1963
Tomato ringspot virus	*X. americanum sensu lato*	Breece & Hart, 1959
Peach rosette mosaic virus	*X. americanum sensu lato*	Klos *et al.*, 1967
Cherry rasp leaf virus	*X. americanum sensu lato*	Nyland *et al.*, 1967
Tomato black ring virus (E)	*L. attenuatus*	Harrison, 1964
Tomato black ring virus (S)	*L. elongatus*	Harrison *et al.*, 1961
Raspberry ringspot virus (E)	*L. macrosoma*	Harrison, 1962 Debrot, 1964
Raspberry ringspot virus (S)	*L. elongatus*	Taylor, 1962
Raspberry ringspot virus (S)	*L. macrosoma*	Harrison, 1964
Artichoke Italian latent virus	*L. apulus* ***	Rana & Roca, 1975
Mulberry ringspot virus	*L. martini*	Yagita & Komuro, 1972

* This result has been questioned by Martelli (1975) ; ** See footnote p. 135 ; *** *L. attenuatus* redescribed as *L. apulus* by Lamberti and Bleve-Zacheo (1977).

Table 3

Virus and vector combinations for which the evidence for nematode transmission is considered to be inadequate

Virus	*Described vector*	*Reference*	*Reason* *
	NEPOVIRUSES		
Arabis mosaic	*X. coxi*	Fritzsche, 1964	1, 2
	L. caespiticola	Valdez, 1972	1
	X. bakeri	Iwaki & Komuro, 1974	1
	P. maximus	McElroy *et al.*, 1976	1
	X. index	Fritzsche & Thiele, 1979	2
Strawberry latent ringspot	*X. coxi*	Putz & Stock, 1970	1
	P. maximus	McElroy *et al.*, 1976	1
Cherry leaf roll	*X. diversicaudatum*	Fritzsche & Kegler, 1964	1, 2
		Flegg, 1969	1, 2
	X. coxi	Fritzsche & Kegler, 1964	1, 2
	X. vuittenezi	Flegg, 1969	1, 2
Tobacco ringspot	*X. coxi*	Van Hoof, 1971	1, 2
Tomato ringspot	*X. brevicolle*	Fritzsche & Kegler, 1968	1, 2
Euonymus ringspot	*Xiphinema* spp	Puffinberger & Corbett, 1973	2
Raspberry ringspot	*L. profundorum*	Fritzsche & Kegler, 1968	1, 2
	X. diversicaudatum	Fritzsche & Kegler, 1968	1, 2
	L. caespiticola	Valdez, 1972	1
	L. leptocephalus	Valdez, 1972	1
	P. maximus	McElroy *et al.*, 1976	1
Artichoke Italian latent	*L. attenuatus*	Rana & Roca, 1975	3
Grape chrome mosaic	*X. index*	Mali *et al.*, 1975	2
	OTHER VIRUSES **		
Brome mosaic	*X. diversicaudatum*	Schmidt *et al.*, 1963	1, 2
	X. coxi	Schmidt *et al.*, 1963	1, 2
	L. macrosoma	Fritsche, 1968	1, 2
Carnation ringspot	*X. diversicaudatum*	Fritzsche & Schmelzer, 1967	1, 2
	L. macrosoma	Fritzsche, 1968	1, 2
	L. elongatus	Fritzsche *et al.*, 1979	2
Prunus necrotic ringspot	*L. macrosoma*	Fritzsche, 1968	1, 2
Euonymus mosaic	*L. euonymus*	Mali & Hooper, 1973	1, 2
Cowpea mosaic	*X. ifacolum* ***	Caveness *et al.*, 1975	2
Pear stony pit	*L. macrosoma*	Kegler *et al.*, 1976	1, 2, 3

* 1 : No systemic infection, contamination of roots possible ; 2 : Inadequate description of methods or inadequate or inappropriate control ; 3 : Vector and/or virus not adequately identified.

** Rumbos *et al.* (1977) have reported *X. index* may be a vector of a rickettsia-like organism associated with yellows disease of grapevines. However they do not provide any experimental evidence for this suggestion.

*** *X. basiri* reported by Caveness *et al.* (1975) is *X. ifacolum* (M. Luc, in litt.).

mission process accurate information can be provided only by careful experimentation and there is now a need for a generally accepted set of criteria by which the results of transmission tests can be judged. Below we list the criteria we consider should be satisfied to demonstrate that a plant virus is transmitted by a species of longidorid nematode.

1) It must be shown that the virus has infected the bait plant.

2) The test should be conducted with hand-picked nematodes and with such controls that the nematode is shown to be the vector.

3) The nematodes transmitting the virus should be identified, preferably by an authority on the genus, noting any differences from type specimens.

4) The virus isolate must be identified before and after the transmission test.

Using these guidelines we have listed in Table 2 the nematode/virus associations for which we consider there is sufficient evidence to substantiate the authors' claim that the virus is transmitted by a particular nematode species. Interestingly most of these associations have been reported causing economically important disease outbreaks in the field. The much greater number of associations for which we consider the evidence insufficient are listed in Table 3. Some of the associations reported in Table 3 may be correct but for those not involving nepoviruses, viruses such as carnation ring spot virus which may be transferred from plant to plant in soil water (Kleinhempel, Gruber & Kegler, 1980), or those contrary to the pattern of specificity previously observed we consider that unequivocal evidence is required before they are accepted as valid.

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Addendum (5 may 1983)

Further reports of virus transmission by longidorid nematodes are :

1) Artichoke Italian latent virus transmitted by *L. fasciatus* (Roca & Lamberti, 1981, *Nematol. medit.*, 9 : 175-179 ; Roca, Rana & Kyriakopoulou, 1982, *Nematol. medit.*, 10 : 65-69). This association is accepted as valid with the reservation that the virus status of the controls was not reported.

2) Tomato ringspot virus transmitted by *X. rivesi* (Forer, Hill & Powell, 1981, *Phytopathology*, 71 : 874, Abstract). The published evidence for this association is regarded as inadequate (2, 1 (see foot-note to Table 3)).

3) Description of *X. diadecturus* n. sp. (Nematoda : Longidoroidea), a vector of the peach rosette mosaic virus in peach orchards in south-western Ontario, Canada (E.S. Eveleigh & W.R. Allan, 1982, *Can. J. Zool.*, 60 : 112-115). No evidence is presented to support this association and therefore it cannot be regarded as acceptable (2) (see foot-note Table 3).

4) *L. vuittenezi* (Nematoda : Dorylaimidae). Virusüberträger bei Reben ? (Maria Rudel, 1980, *Die Wein-Wissenschaft*, 35 : 117-194). The author of this paper expresses reservations, with which we agree, regarding the transmission of grape fanleaf virus by *X. vuittenezi*.