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AN APPRAISAL OF SOME ASPECTS OF THE ECOLOGY OF NEMATODE VECTORS OF PLANT VIRUSES

by
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Summary. Eight *Longidorus*, one *Paralongidorus* and seven *Xiphinema* species are natural vectors of nepoviruses and seven *Paratrichodorus* and four *Trichodorus* species are vectors of tobraviruses. Nematode transmitted viruses and their vector nematodes are restricted in their distribution to regions with temperate or Mediterranean climates with the natural distributions of the viruses reflecting that of their vectors. In Europe the occurrence of a virus and vector frequently are localised within a relatively small area whereas in North America the viruses and/or their vectors are widespread. Specificity of transmission is indicative of a long association between virus and vector which has been determined and maintained by the range of factors influencing the complex nematode-virus-plant interactions. The influence of several ecological factors which may affect these interactions and the geographic distributions of the nematode/virus associations are reviewed and discussed.

Among the many groups of nematodes that are parasites of plants, only a relatively few species of Dorylaimida and Triplonchida are vectors of plant viruses (Jairajpuri and Ahmad, 1992; Hunt, 1993). Currently seven *Xiphinema*, eight *Longidorus* and one *Paralongidorus* species are natural vectors of nepoviruses and four *Trichodorus* and seven *Paratrichodorus* of tobraviruses (Table I). Most vector species are indigenous to Europe and North America, an exception being *L. martini* which is associated with mulberry ringspot virus in Japan. Several *Longidorus* and *Xiphinema* species, and their associated viruses, have inadvertently been transported by man's activities from their areas of origin to other regions such as Australasia and North America, e.g. *X. diversicaudatum* with arabis mosaic virus (AMV) and *X. index* with grapevine fanleaf virus (GFLV). Trichodorid nematodes are also widely distributed in Europe and North America with several species associated naturally with tobacco rattle virus (TRV), the most widespread of the tobraviruses. Again, these viruses and vectors have been dispersed by man to other countries such as Japan, New Zealand and Brazil. However, pepper ringspot virus (PRV) appears to be unique to Brazil, where it is vectored by *P. minor*, and the remaining tobravirus, pea early-browning (PEBV), occurs only in localised areas in northern Europe and North Africa (Taylor and Brown, 1981; Brown, 1989).

It is now generally accepted that nepo- and tobraviruses are naturally associated with wild plants and have developed specific relationships with nematode species that function as their vectors. Because of their limited mobility, nematode populations tend to be localised in discrete territorial enclaves in which they become specifically associated with viruses through interdependent ecological facotrs. Wider distribution occurs when viruses and vectors become associated with cultivated plants, which provide the means for their long distance dissemination in plant material and soil through man's activities. In most situations nepo- and tobra-virus infections in the field are apparent only in crop plants in which symptoms are relatively severe and, in some instances, plant death may occur. By contrast, infection of wild plants is usually symptomless, indicating an ecologically balanced association. Likewise, many longidorid and trichodorid vector species have a wide host range among wild plants but apparently their feeding causes little appreciable damage whereas the growth of crop plants is often impaired by nematode feeding.

Whilst agricultural activities have resulted in the widespread dissemination of several vector species, the geographical distributions of most longidorid and trichodorid nematodes are nevertheless established relative to ecological facotrs, on a geological timescale. Concurrently, specific associations became established between some of the species and their respective nepo-and tobra-viruses. Some of the ecological factors pertaining to the establishment of virus and vector associations are discussed here.

Geographical distribution

Nematode taxa which are recognized today are considered to have been derived from a widespread taxon which split as the continents separated to their present geographical position (Ferris, 1983). From a comparison of taxonomic characteristics of longidorid genera, Coomans (1954) concluded that *Xiphinema* originated in Gondwana and before the breakup of Pangaea had spread to Laurasia. *Longidorus* and *Paralongidorus* are considered to have originated in Southeast Africa and India, when these two areas were still united, and a later spread to Laurasia was followed by a main speciation of *Longidorus* in the holarctic region, especially Europe. Although taxonomic characteristics have been used to identify distinct groupings of trichodorid species (Loof, 1975; De Waele *et al.*, 1982) these do not indicate evolutionary directions or centres of origin. However, the present distribution of trichodorids is broadly the culmination of the influence of changing geological events. Man's influence on the geographical distribution of species is relatively small, probably being mainly manifest in outlier populations, and the dispersal of a species over large distances, such as world wide dissemination of *X. index* with grapevine from its presumed centre of origin in Iran (Persia).

The most recent major geological event that has influenced nematode distribution is the quaternary glaciation which occurred *c.* 40,000 years ago. In Europe there is a marked decrease, south to north, in species richness (Topham and Alphey, 1985) and the present northern limit of several species is clearly demarcated. For example *L. macrosoma* is uniformly distributed throughout France and the low countries but does not extend northwards beyond southern England. This northern boundary has been correlated with the mean July 15° isotherm, implying that the species has certain ecological temperature requirements (Boag *et al.*, 1991). Also, it has been suggested (Dalmasso, 1970; McNamara and Flegg, 1981) that *L. macrosoma* populations which survived the period of glaciation were unable to spread northwards because of the destruction of the deciduous forests, which provided hosts for the species, during the bronze and iron ages. *Xiphinema diversicaudatum* is another example of a longidorid species which is widely distributed in Europe but with a clearly demarcated northern boundary in Scotland for which there are no obvious climatic or edaphic reasons (Topham and Alphey, 1985); the frequency of occurrence of the species suggests that its slow northerly diffusion has not yet been completed. Although these interpretations of geographical distribution are highly conjectural they nevertheless indicate some of the ecological parameters that influence speciation within the broad ranges of ancestral species. Unfortunately, little is known about the ecological requirements of the majority of longidorid and trichodorid nematodes and elucidation of speciation and species diversity has currently to be approached on the groupings of morphometric characters.

Western Europe appears to be a region of well established nematode species and with relatively gradual change in distribution and speciation. However, the eastern Mediterranean countries present a complexity of longidorid and trichodorid species that possibly reflects the geological history of the region, with the formation, during the Miocene, of microcontinents movement between the major plates of Africa and Eurasia (McKenzie, 1970 in Topham and Alphey, 1985).

The present geographical distribution of *Xiphinema* and *Longidorus* species in Europe and the Mediterranean region (Alphey and Taylor, 1986; Brown and Taylor, 1987) has been quantitatively analyzed by Navas *et al.*, (1990). They recognized two main groups of species, the European-Atlantic and the Mediterranean. Furthermore, they considered the distribution of *Xiphinema* species to be a relatively recent dispersion process, with the pleisochoric limits of the genus in the southern Mediterranean region and that of *Longidorus*, with a relatively early dispersal, in the northern Mediterranean and southern European countries. In a more detailed appraisal of the distribution of *Longidorus* species in Euromediterranea, Navas *et al.* (1993) identified the centres of distribution of 32 species within distinctive geographical regions (chorological units). They hypothesized, *inter alia*, that after glaciation the founder species *L. intermedius*, *L. africanus* and *L. congoensis* were the origin of dispersive speciation throughout much of Euromediterranea.

Longidorids and trichodorids present in North America are largely distinct from those species present in Europe and other continents. Also, there is an apparent paucity of *Longidorus* species in North America; of the ten species reported only seven are probably indigenous, the three others having been introduced with planting material. This compares with more than 50 species reported from Europe. In contrast, 38 species of *Xiphinema* have been identified in North America of which more than half have probably been introduced compared with at least 60 species in Europe (Robbins and Brown, 1991; Robbins, 1993). However, the apparent paucity in North America of the large *Xiphinema* and *Longidorus* species has been partly attributed to inappropriate nematode extraction procedures being employed there and it seems probable that many new species will be discovered in the future (Robbins and Brown 1991; Robbins, 1993). For example, for 60 years the most widespread longidorid occurring in North America was identified as *Xiphinema americanum*. However, a taxonomic reappraisal of populations previously identified as *X. americanum* resulted in fifteen new species being described to give a complex of 25 morphologically similar, parthenogenetic species (Lamberti and Bleve-Zacheo,

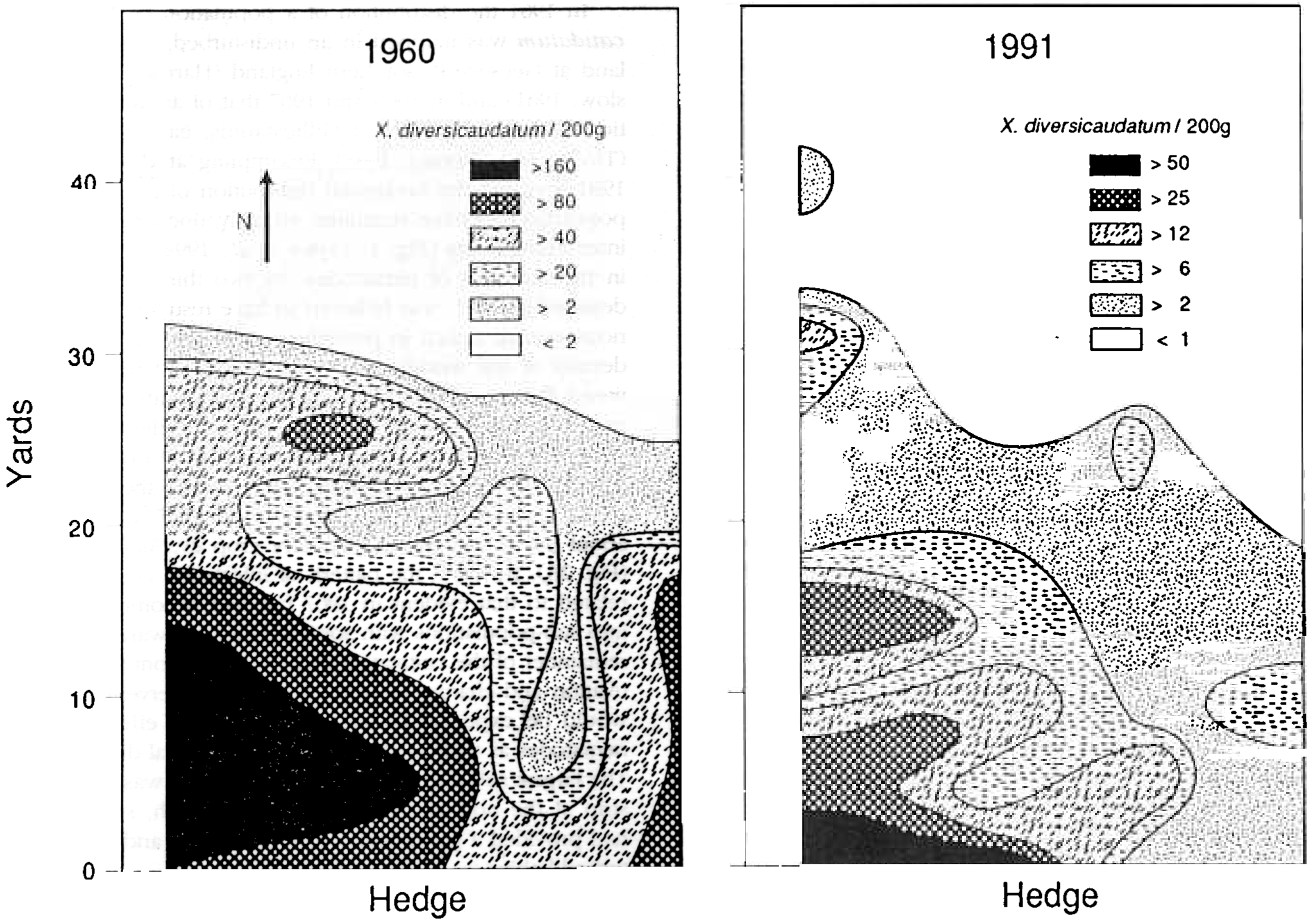

Fig. 1 - The distribution of *Xiphinema diversicaudatum* in a mixed woodland at Geesecroft, southern England. A, in 1960 (data from Harrison and Winslow, 1961); B, in 1991 (after Taylor *et al.*, 1994).

1979). Currently 20 of the 39 *X. americanum*-group species have been described from specimens originating from North America (Robbins and Brown, 1991; Robbins, 1993).

Halbrendt and Brown (1992, 1993) recently reported that several *Xiphinema americanum*-group species from Europe have four juvenile stages, which is considered normal for Nematoda, but that populations from North America have only three such stages. These North American populations are vectors of three North American nepoviruses (Brown *et al.*, 1993, 1994b). Using Restriction Fragment Length Polymorphism with 16 populations of *X. americanum*-group nematodes Vrain (1993) distinguished four groups of populations representing *X. americanum*, *X. rivesi*, *X. pacificum*/*X. californicum* and *X. bricolense*. Lamberti and Ciancio (1993) studied the morphometrics of 49 populations of 39 species attributed to the *X. americanum*-group and by hierarchical cluster analysis placed the populations into five subgroups. Their *X. americanum* subgroup consisted primarily of North American species; *X. pachtaicum* subgroup mainly of European species; *X. lambertii* subgroup mainly of Asian species; *X. brevicolle* subgroup, comprising seven species has a cosmopolitan distribution and the *X. taylori* subgroup containing only two species, one each from Europe and North America.

The species of *Xiphinema* and *Longidorus* indigenous to Africa, Europe and North America form distinct continental groups. This also applies to the nematode transmitted nepoviruses indigenous to Europe and North America. Indigenous species of *Trichodorus* and *Paratrichodorus* differ between North America and Europe, and although tobacco rattle virus occurs in both continents and is transmitted by some of the species, the North America strains of the virus are serologically distinct from those in Europe (Oswald and Bowman, 1958; Cadman, 1963).

The apparent effectiveness with which some species have been widely dispersed by man or by natural means indicates that they have genetic and ecological flexibility e.g. wide host range, adaptability to a range of soil types, and reproduction sustained over a broad temperature range. It may be expected that isolation of populations in diverse biotopes would result in reproductive isolation and hence the establishment of new species. When Brown and Topham (1985) examined *X. diversicaudatum* specimens that were obtained from populations widely distributed throughout the world they found morphological and morphometric differences between populations, but they did not regard these differences as sufficient to distinguish populations as separate species. Subsequently, this conclusion was validated when it was demonstrated that many of these populations could interbreed successfully with a population from Scotland (Brown, 1986a).

Dalmasso and Berge (1983) presented a hypothetical model to explain evolution in the Longidoridae in which populations of ancestral amphimictic forms (species) could be affected by inbreeding resulting in complete homozygosity, subsequent facultative meiotic parthenogensis with a resulting loss of males, and finally mutations giving rise to "clonal" species. These "clonal" species would be morphologically similar within species complexes. Several such groups are evident today, for example, populations of *X. coxi* from Florida, USA, were recognized as distinct from those in Europe (Dalmasso, 1970; Taylor and Brown, 1976) to the extent that Sturhan (1984) recognized two species, *X. pseudocoxi* and *X. coxi*, with the latter divided into two sub-species (Brown and Taylor, 1987). Morphometric differences between dispersed populations have also been noted in *L. elongatus*, *L. profundorum* and *L. vineacola*. Such differences should also be considered in relation to their effect on the efficiency of virus transmission, as it has been demonstrated with populations of *X. diversicaudatum* (Brown and Taylor, 1981; Brown and Trudgill, 1983; Brown, 1985, 1986b) and in populations of *X. americanum sensu lato* (Griesbach and Maggenti, 1989). However, there is no evidence that differences in the ability to transmit viruses provide a basis for distinguishing species or populations of a vector.

Persistence of Nematode Populations and Viruses

A characteristic of nematode transmitted viruses is their persistence at sites for long periods, even in the absence of virus infectible crop hosts. This is dependant both on the survival of the vector population, particularly in situations where the soil is cultivated and where crops are rotated, and on the presence of virus-infected weed seeds and/or perennial plants. A study of two populations of *X. diversicaudatum* spanning 30 years provided data on some of the ecological factors involved.

In 1961 the distribution of a population of *X. diversicaudatum* was mapped in an undisturbed, mixed woodland at Geesecroft, southern England (Harrison and Winslow, 1961) and in 1966 and 1967 that of another population in an arable field at Gilliesfaulds, eastern Scotland (Taylor and Thomas, 1968). Resampling at Geesecroft in 1991 revealed the horizontal distribution of the nematode population to have remained virtually unchanged in the intervening years (Fig. 1; Taylor *et al.*, 1994). A reduction in the numbers of nematodes, by two thirds from levels detected in 1961, was believed to have resulted from a serious rainfall deficit in preceding years and the increased density of the woodland canopy which had reduced the weed flora and hence the hosts for nematodes in the upper soil layers which were sampled. At Gilliesfaulds, the nematode infestation was presumed to have originated in a hedge bordering the eastern perimeter of the field and when sampled in 1966, and again in 1967, had spread about 35 metres into a raspberry crop cv. Malling Jewel (Fig. 2A). By 1991, the pattern of infestation could still be related to that evident in 1967 but had become scattered into sub-populations with some spread westwards into the remainder of the cultivated area (Fig. 2B). Continuous cultivation and change in crops during the intervening years would be expected to have some adverse effect on the nematodes as well as affecting their horizontal distribution. The largest sub-population recorded in 1991 was in a grass strip at the northern part of the field which, since 1986, had provided a good host for the nematode and an undisturbed habitat.

In 1966 the raspberry crop at Gilliesfaulds was infected with SLRV but not AMV, to which it is immune, although the latter virus was detected in several weed species. In 1991, after several crop rotations including the planting of SLRV-immune raspberry cv. Glen Moy, in 1987, only AMV was detected in soil samples and in some weed species (Taylor *et al.*, 1994). The virus was present as two strains, differing in the severity of symptoms induced in herbaceous plants, indicating that the natural weed bank is an efficient reservoir for preserving nepoviruses and their variants that occur naturally. Weed seed transmission of nepo- and tobra-viruses has been well documented as providing an alternative strategy for virus persistence in nature with up to 100% of seed from an infected mother plant being infected and capable of survival in soil for many years (Murant, 1983).

The existence of two variants of AMV with a population of *X. diversicaudatum* is an example of a strategy for the survival of nematode transmitted viruses in nature. Other examples of several variants of a virus occurring naturally together with a vector population have been reported for AMV and *X. diversicaudatum* from strawberry in Norway; RRV and *L. elongatus* from raspberry in eastern Scotland (Jones *et al.*, 1989) and TRV with *T. cylindricus*

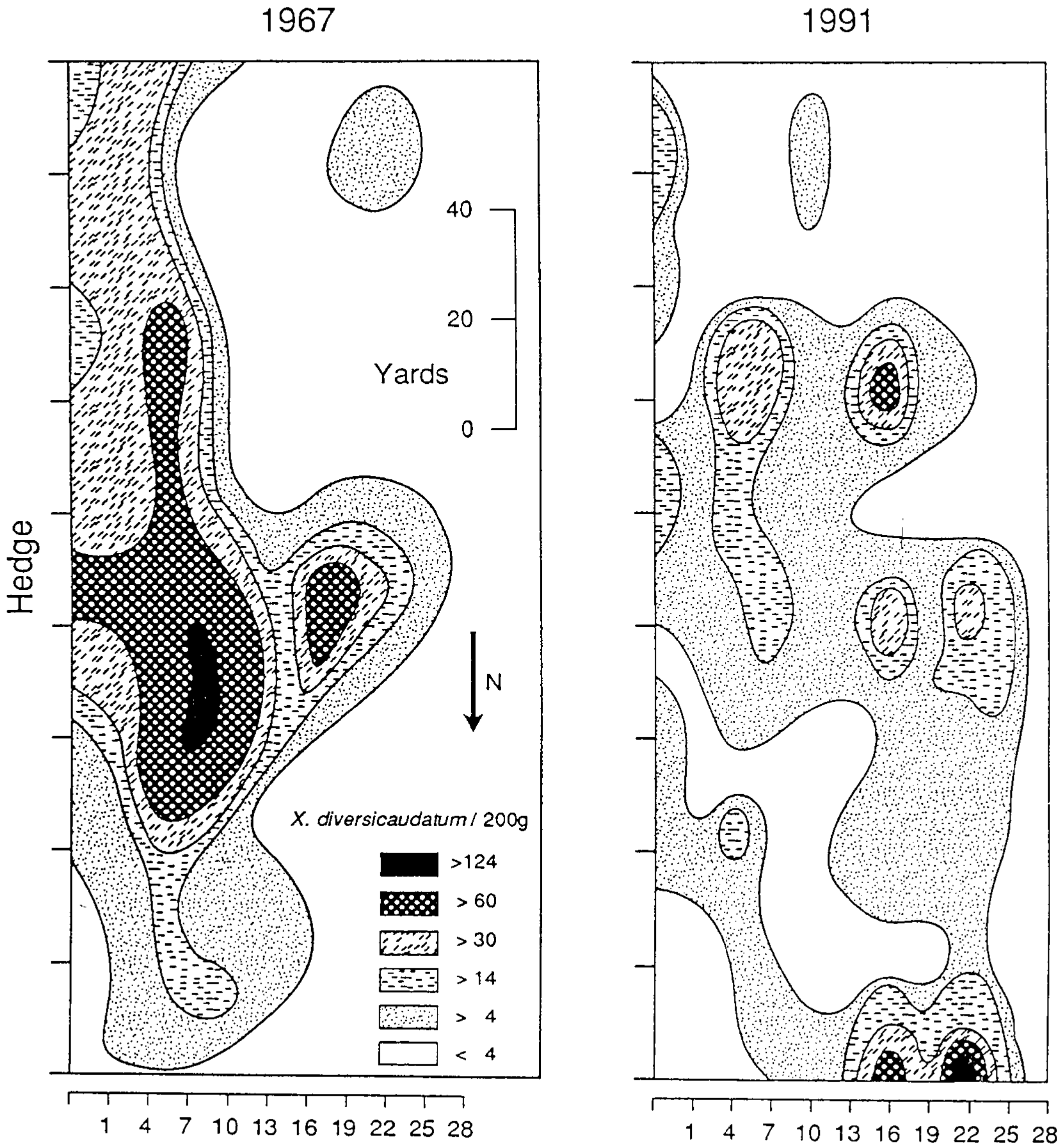

Fig. 2 - The distribution of *X. diversicaudatum* in a raspberry plantation at Gilliesfaulds, eastern Scotland. A, in 1967 (data from Taylor and Thomas, 1968); B, in 1991 (after Taylor *et al.*, 1994).

and *P. pachydermus* in pasture in eastern Scotland (Ploeg *et al.*, 1992). The appearance of resistance-breaking strains of a virus in new crop cultivars is also an indication of the reservoir of virus variants that exist in nature allowing viruses to adapt to a changing ecological environment e. g. the MX and Lloyd George strains of RRV can infect Malling Exploit and Lloyd George raspberry cultivars, respectively, which are immune to the type strain of the virus (Murant *et al.*, 1968; Jones *et al.*, 1989).

Virus and Vector Associations

The soil environment imposes many constraints on the behaviour of nematodes. It effectively isolates populations which are relatively immobile, and which extend at the rate of only a few centimetres each year. As a result there is considerable inbreeding with the consequence of increased homozygosity within the population. In such a conserved environment, viruses would tend to develop

TABLE I - *Specific associations between* Longidorus, Paralongidorus, Paratrichodorus, Trichodorus *and* Xiphinema *virus-vector nematode species and nepo- and tobra-viruses.*

Vector species	Viruses	Acronym	Reference
	NEPOVIRUSES		
L. apulus	artichoke Italian latent (Italian strain)	AILV	Rana and Roca, 1973
L. arthensis	cherry rosette disease	CRDV	Brown *et al.*, 1994a
L. attenuatus	tomato black ring (German/English strain)	TBRV	Harrison, 1964
L. diadecturus	peach rosette mosaic	PRMV	Eveleigh and Allen, 1982
L. elongatus	raspberry ringspot (Scottish strain)	RRV	Taylor, 1962
	tomato black ring (Scottish strain)	TBRV	Harrison *et al.*, 1961
L. fasciatus	artichoke Italian latent (Greek strain)	AILV	Roca *et al.*, 1982
L. macrosoma	raspberry ringspot (English strain)	RRV	Harrison, 1964
L. martini	mulberry ringspot	MRV	Yagita and Komuro, 1972
P. maximus	raspberry ringspot (German grapevine strain)	RRV	Jones *et al.*, 1994
X. americanum (*sensu lato*[*])	cherry rasp leaf	CRLV	Nyland *et al.*, 1969
	peach rosette mosaic	PRMV	Klos *et al.*, 1967
	tobacco ringspot	TobRSV	Fulton, 1962
	tomato ringspot	TomRSV	Breece and Hart, 1959
X. americanum (*sensu stricto*[**])	cherry rasp leaf	CRLV	Brown and Halbrendt, 1992
	tobacco ringspot	TobRSV	Brown and Halbrendt, 1992
	tomato ringspot	TomRSV	Brown and Halbrendt, 1992
X. bricolense	tomato ringspot	TomRSV	Brown and Halbrendt, 1992
X. californicum	cherry rasp leaf	CRLV	Brown and Halbrendt, 1992
	tobacco ringspot	TobRSV	Brown and Halbrendt, 1992
	tomato ringspot	TomRSV	Hoy *et al.*, 1984
X. diversicaudatum	arabis mosaic	AMV	Jha and Posnette, 1959
	strawberry latent ringspot	SLRV	Lister, 1964
X. index	grapevine fanleaf	GFLV	Hewitt *et al.*, 1958
X. italiae	grapevine fanleaf	GFLV	Cohn *et al.*, 1970
X. rivesi	cherry rasp leaf	CRLV	Brown and Halbrendt, 1992
	tobacco ringspot	TobRSV	Brown and Halbrendt, 1992
	tomato ringspot	TomRSV	Forer *et al.*, 1981
	TOBRAVIRUSES		
P. anemones	pea early-browning	PEBV	Harrison, 1967
	tobacco rattle	TRV	Hoof, 1968
P. minor (syn. *christiei*)	pepper ringspot	PRV	Salomao, 1973
	tobacco rattle	TRV	Walkinshaw *et al.*, 1961
P. nanus	tobacco rattle	TRV	Cooper and Thomas, 1970
P. pachydermus	pea early-browning	PEBV	Hoof, 1962
	tobacco rattle	TRV	Gibbs and Harrison, 1964b

Vector species	Viruses	Acronvm	Reference
P. tansaniensis (syn. *allius*)	tobacco rattle	TRV	Ayala and Allen, 1968
P. teres	pea early-browning	PEBV	Hoof, 1962
	tobacco rattle	TRV	Hoof, 1964
P. tunisiensis	tobacco rattle	TRV	Roca and Rana, 1981
T. cylindricus	tobacco rattle	TRV	Hoof, 1968
T. primitivus	pea early-browning	PEBV	Gibbs and Harrison, 1964a
	tobacco rattle	TRV	Sanger, 1961
T. similis	tobacco rattle	TRV	Cremer and Schenk, 1967
T. viruliferous	pea early-browning	PEBV	Gibbs and Harrison, 1964a
	tobacco rattle	TRV	Hoof *et al.*, 1966

* Unequivocal identification of species not available or prior to the review of the *X. americanum*-group (Lamberti and Bleve-Zacheo, 1979).

** Species identification determined by using individual nematodes in virus transmission studies (Brown and Halbrendt, 1992; Brown *et al.*, 1994b).

highly specific associations with their vectors. Specificity of transmission is most evident in the European context, where a particular virus, or a serologically distinct strain, can be transmitted by one species but not by another. For example, AMV is transmitted by *X. diversicaudatum* but not by any other species tested, Scottish strains of RRV and TBRV are transmitted by *L. elongatus* but English strains of these viruses by *L. macrosoma* and *L. attenuatus*, respectively, and a strain from grapevine in Germany (Jones *et al.*, 1994) by *P. maximus* but not by *L. macrosoma*. Specificity of transmission is also evident with TRV with many of the strains associated with different vector species (Ploeg *et al.*, 1992).

In North America, *X. americanum* has been implicated as a natural vector of CRLV, PRMV, TobRSV and TomRSV (Breece and Hart, 1959; Fulton, 1962; Klos, *et al.*, 1967; Nyland *et al.*, 1969) and *X rivesi* and *X. californicum* as vectors of TomRSV (Forer *et al.*, 1981; Hoy, *et al.*, 1984; Table I). This indicates little specific transmission of TomRSV by several members of the *X. americanum*-group and that *X. americanum* is unusual in being a vector of each of the four indigenous North American nematode transmitted nepoviruses. Some of this apparent lack of specificity may be a result of uncertainty in species identification prior to a reappraisal of the taxonomy of the *X. americanum*-group (Lamberti and Bleve-Zacheo, 1979) and of the characterisation of the specific virus strains transmitted. However, Brown and Halbrendt (1992) and Brown *et al.* (1993, 1994b) using individual nematodes from three populations of *X. americanum sensu stricto*, *X. bricolense*, *X. californicum* and *X. rivesi* showed that *X. americanum*, *X. californicum* and *X. rivesi* transmitted CRLV, TobRSV and two strains of TomRSV but that *X. rivesi* transmitted the viruses more frequently. *Xiphinema bricolensis* transmitted only TomRSV. These data confirm a relative lack of specificity between North American nematode transmitted nepoviruses and some of their vectors.

Martelli and Taylor (1989) speculated that vector populations widely separated geographically might be expected to differ in their ability and efficiency to transmit viruses. This could result from ecological pressure on the virus to adapt to its plant host, whereby if the dominant host were an annual, or short term perennial, selection pressure for frequent (= efficient) transmission would be selected to ensure survival of the virus; whereas with long term perennials, such as fruit trees, such pressure would be much less and relatively infrequent (= inefficient) transmission by vectors might result. Ecologically driven selection pressure can be presumed to be more likely in disturbed (cultivated) than in undisturbed habitats. Viruses are also subject to selection pressure because of the changing flora, as well as biological modifications in the nematodes, and evidence for this may be assumed from the range of virus strains which occur. Thus, the type British strain of SLRV is efficiently transmitted by several geographically disparate populations of *X. diversicaudatum* but only infrequently by populations from France, Italy and Spain, whereas serologically distinguishable strains of SLRV from Italy were transmitted consistently only by a population of the vector from Italy, and then only infrequently (Brown and Taylor, 1981; Brown and Trudgill, 1983; Brown, 1985, 1986b).

Recently, specificity of transmission of serologically distinguishable strains of tobraviruses with trichodorid nematodes has been demonstrated (Ploeg *et al.*, 1992). Tobraviruses occur naturally as a range of serotypes which in Europe have been shown to be transmitted each by a different nematode species e.g. isolates of the PRN serotype of TRV from Britain, Sweden and the Netherlands are transmitted only by *P. pachydermus*. In North America, where only *Paratrichodorus* species have been reported as vectors of TRV, it is uncertain if specificity of transmission occurs with TRV isolates and populations/species of (para)trichodorid nematodes.

Mechanisms Involved in Virus and Vector Associations

Electron microscopy has provided evidence for the sites of virus retention in nematode vectors. In *Longidorus* species the virus particles are apparently adsorbed in a single layer to the inner surface of the odontostyle, and in *L. elongatus* particles of RRV or TBRV may also be located between the odontostyle and the guiding sheath (Taylor and Robertson, 1969). In contrast *Xiphinema* vectors have nepovirus particles specifically associated with the cuticular lining of the odontophore and the oesophagus (Taylor and Robertson, 1970a). In trichodorid vectors TRV particles are retained in association with the lining of the food canal from the anterior region of the oesophostome to the oesophago-intestinal valve, but are not attached to the onchiostyle (Taylor and Robertson, 1970b).

Experiments with pseudo-recombinant isolates of some nepo- and tobraviruses have demonstrated that the association between vector and virus is determined by the RNA-2 of the bipartite virus genome (Harrison *et al.*, 1974; Harrison and Murant, 1977; Ploeg *et al.*, 1993). As RNA-2 also determines the production of the virus protein coat, it seems reasonable to assume that the specific association between virus and vector involves some properties of the protein coat and the cuticular surfaces at the sites of retention within the nematode vector. However, the precise nature of this association has still to be determined and there is some circumstantial evidence that this may not be the same for virus/vector associations.

In *Longidorus* vectors a strong negative charge is present on the exterior surface of the odontostyle and it is speculated that positively charged virus particles ingested by the nematode with plant sap are attracted to the negatively charged surface of the odontostyle. It is further speculated that different strains of the same virus would have different surface charge densities, thus requiring different vector species, but that two different viruses transmitted by the same vecotr species, e. g. RRV and TBRV by *L. elongatus*, would have similar charge densities (Taylor and Brown, 1981). In *Xiphinema* it has been shown that a discontinuous layer of carbohydrate lines the odontophore and oesophagus and virus particles attach only in these zones (Robertson and Henry, 1986). Similarly, in *P. pachydermus* and presumably in other trichodorid vectors, the total wall of the food canal stains for carbohydrates and the mechanism of virus retention is similar to that for *Xiphinema* species. The nature of the attachment of the virus particles is believed to involve the interaction of complementary molecules at their point of contact, such as occurs in many host-pathogen systems and in other biological situations where "self" and "non-self" have to be recognized.

There is some evidence of "finger-like" structures at the end of TRVparticles that may be involved in the specific association with the vector (Legorboru, 1993). Biochemical evidence from nepoviruses indicates differences in polypeptide sequences adjacent to the N-terminal side of the coat proteins which could account for some aspects of specific association between virus and vector species (Block *et al.*, 1992).

Specificity of the virus/vector association, which probably developed during a long association of the vectors with their associated viruses, implies at its simplest a "gene for gene" type of recognition process. Although in many instances the same part of the coat protein appears to be crucial for both specificity of retention and antibody recognition, this is not so for all nematode and virus associations. For example, a population of *L. attenuatus* from Britain transmitted two serologically distinguishable British isolates of TBRV much more efficiently than two isolates from Germany (Brown *et al.*, 1989), implying that efficienciy of transmission is correlated more strongly with geographic origin than antigenic relatedness. Nevertheless, more substantive serological differences are usually associated with differences in the vector species. Thus two serologically distinct strains of artichoke Italian latent nepovirus from Italy and Greece are transmitted by *L. apulus* and *L. fasciatus*, respectively (Table I). Similarly, the German and Scottish serotypes of TBRV are transmitted specifically by *L. attenuatus* and *L. elongatus*, respectively. The Scottish and English serotypes of RRV are transmitted most efficiently by *L. elongatus* and *L. macrosoma*, respectively, but each species can transmit the other virus, albeit less efficiently.

Conclusion

In Europe, vector species and their associated viruses are considered to have developed a high degree of specificity of virus transmission. In North America there is evidence of much less specificity of transmission at the species level, but differences have been recorded between populations. Thorough taxonomic reappraisal of the group and further precise transmission experiments will help to elucidate the nature of the associations between North American nepo- and tobra-viruses and their associated vectors.

It may be concluded that a close association has developed between virus and vector that is nevertheless capable of adjustment to the changing ecological selection pressures that influence the different components of the nematode-virus-plant interaction. Although generalisations may be made about nematode transmission of plant viruses each virus and vector association has elements of uniqueness that are a constant reminder of the gaps in our knowledge and the inevitability of change in biological situations, due to nature itself or to man's activities.

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