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-205.
M., Laket, M.F., Parkin, W.E.,
J.K., 1984, *Amblyomma ameri-*
in New Jersey, *Science* **224**:601–

Shisler, J.K., Charette, D.J., and
of infection by the Lyme disease
ides dammini and *Amblyomma*
akteriol. Mikrobiol. Hyg. **263**:72–

ies sur la fièvre récurrente et son
algérienne, *Ann. Inst. Pasteur*

Ristic, M., 1978, Pathobiology of
oophilus microplus, J. Invertebr.

.., Hirschl, A.M., Aberer, E.,
988, European Lyme borrelioses,

kers, G.J., 1971, *Borrelia theileri*
, *Tijdschr. Diergeneesk.* **96**:1028–

g bei *Ornithodorus moubata* und
Acta Trop. **15**:118–168.
, G.S., and Benach, J.L., 1989,
ment of acute inflammation in the
gland, midgut, and spirochetal

r Spirochaeta des Rückfallfiebers,

I., 1977, An experimental study of
ticks. 2. Transstadial survival and
3:213–223.

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Distribution of Viruses and Their Nematode Vectors

Giovanni P. Martelli and Charles E. Taylor

Introduction

There are several landmarks on the pathway of our expanding knowledge of nematode transmissiom of plant viruses. The initial discovery of *Xiphinema index* as vector of grapevine fanleaf virus (GFLV) (51) stimulated the search for nematode vectors of other soil-borne viruses, and this was accompanied by research on many aspects of the biology, ecology, and taxonomy of both nematodes and viruses. Early investigations established that plant viruses specifically associate with their nematode vectors, and the mechanism of this association began to emerge when it was discovered that the virus coat protein was a key factor in the adsorption of particles at virus retention sites within the nematodes. The importance of wild hosts for both viruses and vectors, the perennation of viruses in weed seeds, and the insight into the feeding behavior of vector nematodes improved our understanding of how viruses survive and spread in nature, and a basis for their control in commercial crops.

In recent years, improved technology has provided detailed information on the characteristics of viruses of the Nepovirus and Tobravirus groups. Members of both groups have a bipartite genome made up of two functional and separately encapsidated RNA species, which may recombine under both experimental and natural conditions to give rise to pseudo-recombinant strains (48, 108).

Now that the physicochemical composition of nepoviruses and their hydrodynamic and serological properties are known, subgroups that are broadly consistent with the geographical distribution and presumed origin of the different viruses have been established. Interest in the taxonomy of the virus vectors longidorids and trichodorids continues, as the number of

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species known increases and the role of nematodes as vectors is better understood (63, 139).

There have been numerous reviews on many aspects of nematode transmission of viruses (47, 63, 68, 69, 83, 86, 122, 124, 125, 127, 128, 132, 133). In this most recent review, here, we consider the geographical distribution of the nepoviruses and tobraviruses as an approach to understanding the ecological and biological association between these viruses and their vectors.

Nematode-Transmitted Viruses as Plant Pathogens

Diseases Induced by Nepoviruses

Nepoviruses are reported to infect wild plants, annual crops, and perennial crops. The natural host range varies greatly with individual viruses, as does the severity of the diseases they induce. Some nepoviruses are pathogens of primary economic importance, since they affect and damage major crops. Other nepoviruses are restricted to a single or a few hosts; thus, they are, for the most part, only of scientific interest. Grasses and cultivated cereals do not appear to be hosts to nepoviruses, and the only gymnosperm host so far reported is *Cycas revoluta* in Japan (39, 61).

The diseases caused by nepoviruses have been reviewed repeatedly, and most recently by Murant et al. (89) and Stace-Smith and Ramsdell (122). Thus, they will only be summarized here, with a few selected examples in the following plant categories.

Vegetables

The artichoke (*Cynara scolymus*) seems to be one of the vegatables most frequently attacked by nepovirus. Three different viruses, viz., artichoke Italian latent (AILV), artichoke yellow ringspot (AYRV), and artichoke vein banding (AVBV) viruses, are named after this host (36, 73, 95). Two additional members of the group, strains of raspberry ringspot (RRV) and of tomato black ring (TBRV) viruses, have been recovered from artichoke plants in the eastern Mediterranean area (96) and in France (80), respectively.

Depending upon the cultivar and, perhaps, growing conditions, nepovirus-infected artichokes may either be symptomless (AILV, RRV) or exhibit symptoms ranging from mild chlorotic discolorations (AVBV, RRV, TBRV) to generalized yellowing and stunting (AILV), scattered yellow blotches (RRV), and intense chrome yellow rings and line patterns accompanied by necrosis and stunting (AYRV). The yield is variously affected, but no estimates of crop loss have been made (94).

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Potato (*Solanum tuberosum*) has its own nepoviruses in Peru, such as potato black ringspot (PBRV), potato virus U (PVU), and arracacha virus B (AVB) (55, 56, 112), of which only PBRV induces a field syndrome characterized by necrotic spotting or generalized yellowing of the leaves (112). In Europe, potato is affected by TBRV, the cause of "bouquet" and "pseudo-aucuba" diseases, the symptoms of which are necrotic spots, rings and malformations of the leaves, and stunting. Crop losses of up to 30% have been estimated in secondarily infected plants (5).

Cucurbits (melon, watermelon, squash, cucumber) are seriously affected by tobacco ringspot virus (TobRSV) in the United States. Infected plants have mottled and malformed leaves, ringspotting, stunting and poor fruit set (122). In Europe, arabis mosaic virus (ArMV) induces mottling, ringspotting and stunting of field-grown cucumbers (84).

Five different nepoviruses, ArMV, chicory yellow mottle (CYMV), grapevine chrome mosaic (GCMV), strawberry latent ringspot (SLRV), and TBRV have been associated in Europe with diseases of celery (*Apium graveolens*), in which they cause bright yellow mottling (GCMV, CYMV) or chlorotic mottling, distortion and crinkling of the leaves, stunting, and necrosis (ArMV, SLRV, TBRV) (72, 84, 85, 93).

Interestingly, of the three nepoviruses named after tomato, that is, TBRV, tomato ringspot (TomRSV), and tomato top necrosis (TTNV) viruses, none seems to be of economic importance to this crop.

Small Fruits

The consensus is that grapevine (*Vitis vinifera*), raspberry (*Rubus idaeus*), and strawberry (*Fragaria* × *ananassa*) are affected by nepoviruses more than any other small fruit species.

No less than twelve different nepoviruses have been found associated with two major grapevine disorders known as "grapevine degeneration" and "grapevine decline." These viruses are ArMV, AILV, blueberry leaf mottle (BBLMV), grapevine Bulgarian latent (GBLV), GCMV, GFLV, peach rosette mosaic (PRMV), RRV, SLRV, TobRSV, TBRV, and TomRSV.

Grapevine degeneration is typically caused by GFLV in the Mediterranean basin and all other viticultural areas, except for Central Europe and the Balkans where several other nepoviruses (ArMV, GCMV, RRV, SLRV, and TBRV), either alone or in association with GFLV, are able to induce a comparable disease. Grapevine degeneration consists of three distinct syndromes, characterized either by deformations of the leaves, shoots, and canes; chlorotic mottling; reduced vigor and poor fruit setting (fanleaf); or by bright yellow discolorations of the foliage (yellow mosaic) or chrome yellow flecks along the main veins, which sometimes spread into the interveinal tissues (vein banding) (10). The crop may be drastically affected, with average losses up to or above 60% (110).

Grapevine decline typically occurs in *V. vinifera* and *Vitis labrusca* grown in the northern United States and Canada. It shows leaf and cane symptoms comparable to those of fanleaf, but affected vines die more frequently, especially when they are European cultivars. Tomato ringspot virus is the main cause of grapevine decline, together with three additional American nepoviruses [BBLMV, PRMV, and TobRSV (71)].

Raspberry has been reported to be a host to seven different nepoviruses: ArMV, cherry leafroll (CLRV), cherry rasp-leaf (CRLV), RRV, SLRV, TBRV, and TomRSV, all of which are pathogenic, except for CRLV whose infections are latent (122).

The field syndromes induced in raspberry by nepoviruses vary with the agent, or association of agents, and the cultivar. There are cultivars that are resistant or immune to individual viruses (ArMV, RRV, SLRV, TBRV) or some of their isolates (ArMV). Susceptible cultivars react to viral infections with a variety of foliage changes (chlorotic mottling, vein yellowing, yellow speckling, yellow or chlorotic ringspotting, curling), reduced vigor, stunting, and reduction and deformation of fruit (89).

Although, compared with raspberry, fewer nepoviruses (ArMV, RRV, SLRV, TBRV, and TomRSV) have been found to infect strawberry plants, their effects on this crop are equally destructive. Except for TomRSV, which rarely causes a natural infection in strawberry (26), all other viruses are major pathogens, especially in Great Britain and Central Europe, where mixed infections (e.g., ArMV and SLRV; RRV and TBRV) are common.

Symptoms consist of chlorotic spots, rings, and/or yellow blotches of the leaves, which may also be twisted, cupped, or crinkled. With mixed infections, the symptoms are usually more severe; the plants are stunted and often die (89).

Fruit Trees

Nepovirus-induced diseases of pome fruit trees are rare, apple (*Malus sylvestris*) being the only species known to be affected. Two disorders of apple have been described, both in North America: "flat apple" and "union necrosis and decline," which are induced by CLRV and TomRSV, respectively (123).

Flat apple derives its name from the flattened appearance of the fruit borne by diseased plants. The affected plants become progressively weaker, stunted, and densely bushy.

In apple decline, the infected trees develop a necrosis of the woody cylinder at the graft union, possibly due to the hypersensitive reaction of the scion to the virus, which leads to a progressive decline.

Several nepoviruses cause diseases of economic importance in stone fruits.

Cherry (*Prunus avium*) is reported to be susceptible to six different nepoviruses two of which (CLRV and CRLV) are named after it. A typical, nepovirus-induced disease of cherry is rasp-leaf, which is characterized by enations on the underside of the leaves. Rasp-leaf syndromes are reported from western North America and Europe, but the causal agents differ. Rasp-leaf is caused by a single virus (CRLV) in North America (121), whereas in Europe it originates from mixed infections of nepoviruses (ArMV or RRV) and viruses of the prunus necrotic ringspot type (29).

Stem pitting and decline is another serious disease of cherry caused by TomRSV. Affected trees have reduced vigor and yield, with extensive pitting of the vascular cylinder. A similar disease, induced by the same agent (TomRSV), affects peach (*Prunus persica*) in North America. With this disease, known as yellow bud mosaic, stem pitting is accompanied by different patterns of yellow discoloration and severe distortion of the leaves (119).

Other economically important diseases of peach caused by nepoviruses are peach rosette mosaic, caused by PRMV in North America (58), and peach willow leaf rosette, caused by SLRV in Europe (28). In both disorders, there are various degrees of mottling and distortion of the leaves and a progressive decline of the tree.

A high incidence of CLRV infections has been found in English walnut (*Juglans regia*) in Europe and North America. The effect of the virus differs dramatically, depending on whether the host is on its own roots or is grafted to rootstocks of species other than *J. regia,* or their hybrids (e.g., Paradox = *J. regia* × *Juglans hindisii*). Self-rooted English walnuts are tolerant of infection; most plants are symptomless or, at most, show chlorotic ringspots and line patterns, or an occasional bright yellow blotching (117). Grafted walnuts, however, go into a severe decline, a condition known as "black line," which, in several areas, constitutes a limiting factor to walnut production. This disease depends upon CLRV hypersensitivity of walnut rootstocks, the tissues of which, when invaded by the virus, necrotize to give rise to a black line of dead cells at the graft union (89).

Finally, the olive (*Olea europaea*) should be briefly mentioned as a natural host of nepoviruses. A long debate, started in 1938 on whether olive was affected by virus diseases, ended some 10 years ago with the detection of virus particles in developing pollen grains (91). So far, seven different viruses have been recovered, mostly from symptomless olive trees, by sap inoculation (70). Of these viruses, four are nepoviruses, viz., olive latent ringspot virus (OLRV), ArMV, CLRV, and SLRV. None of them, however, causes a specific disease, except for SLRV, which has been found to be associated with striking malformations of leaves and fruits of cv. Ascolana tenera (67).

Diseases Induced by Tobraviruses

Among the tobraviruses, tobacco rattle virus (TRV) has the widest natural host range. This range includes herbaceous weeds and wild, woody perennials, as well as annual and perennial crops (44–46).

In naturally infected plants, TRV tends to remain localized in the roots—the initial site of infection. In certain hosts, however, the virus moves to the above-ground parts, as in the case of pepper (*Capsicum annuum*), in which TRV induces bright yellow ring and line patterns in the leaves and yellow blotching, puckering, and malformation of the fruit (25).

Limited TRV systemic infection also occurs in potato plants originating from tubers affected by spraing disease—a severe disorder characterized by areas of corky tissues in the tuber flesh and mottled foliage (21).

Pea early-browning virus (PEBV) has a natural host range restricted to Leguminosae. Pea (*Pisum sativum*), French bean (*Phaseolus vulgaris*), broad bean (*Vicia faba*), and alfalfa (*Medicago sativa*) are the only plants from which the virus has been recovered. The infection is usually systemic and the symptoms shown by the foliage range from mild mottling and deformation to yellow chevrons and bands to extended necrosis (46).

Pepper ringspot virus (PRV) has been reported only from Brazil, where it systemically invades crops like tomato, pepper, and artichoke, to produce various patterns of bright yellow rings, lines, and bands on the foliage (46).

Causal Agents

Nepoviruses

The nepovirus group is one of the most rapidly expanding taxonomic groups of plant viruses. Its initial membership of eight, inclusive of definitive and possible members (47), had already grown to twenty-six in 1982 (79), and currently numbers thirty-four (Table 6.1). Of these, only eleven have a recognized nematode vector (see also Table 6.4). The rest owe their present taxonomic assignment to the possession of specific biological characteristics (i.e., host range responses, transmission through seeds) and physicochemical and other properties such as the type of intracellular behavior that conform those typical of the group.

Although all nepoviruses have isometric particles ~30 nm in diameter and a bipartite genome with two functional RNA species (42), wide differences exist in the physicochemical and hydrodynamic properties of individual members. Their serological properties, geographical distribution, vectors, and means of natural spread also differ. Such differences may be used to subdivide the group into smaller coherent clusters.

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Grouping on a Molecular Basis

Nepoviruses differ with respect to their physicochemical properties and hydrodynamic behavior. Normally, these viruses contain three types of particles, corresponding to centrifugal component T, empty protein shells; M, nucleoproteins containing one molecule of the smaller genomic RNA (RNA-2); and B, nucleoproteins containing one molecule of the larger RNA (RNA-1). However, a few members (six in all), contain a different type of particle that encapsidates two molecules of RNA-2. This determines whether the B component yields one (homogeneity) or two (heterogeneity) buoyant density classes when centrifuged at equilibrium.

Nepoviruses with a homogeneous B component also exhibit clear-cut differences in the molecular weight of RNA-2, which influences the sedimentation behavior and, hence, the sedimentation coefficient of the M particles.

Finally, the protein coat of eight members of the group, rather than having a single polypeptide with a molecular weight of ~55,000 daltons, is made up of two or three smaller polypeptides (e.g., AVBV) with a different molecular weight (21,000–29,000 daltons and 42,000 to 47,000 daltons, respectively).

Taking these differences in physical properties into account, Martelli and coworkers (68, 74) divided the Nepovirus group into four distinct clusters; Murant and Taylor (87) however, divided the group into three clusters. These subdivisions were questioned by Francki et al. (33), since the properties of some nepoviruses are incompletely known and since many of the published values of particle sedimentation and RNA molecular weight may not be correct. They (33) proposed instead two subgroups, based on whether RNA-1 and RNA-2 differed significantly in size.

These two ways of subgrouping both have their merits. The scheme shown in Table 6.1 delineates the complexity of the group as a whole; it separates definitive from tentative members, except for TTNV, which is not fully characterized; and it is consistent with serological clustering, in that related viruses fall into the same subgroup. In no case is there serological cross-reactivity between members of different clusters.

The presence of two kinds of coat proteins seems to constitute the major single criterion whereby some nepoviruses are still regarded as tentative members of the group. In fact, except for lucerne Australian symptomless virus (LASV) and rubus Chinese seed-borne virus (RCSV), in which nucleoproteins apparenly sediment as a single component (4, 99), all other tentative nepoviruses, including SLRV (35), have two nucleoprotein centrifugal components, as do the definitive members of the group.

The importance of the difference in protein coat composition in the separation of definitive and tentative nepoviruses has been questioned by Francki et al. (33). They pointed out that the smaller polypeptides

TABLE 6.1. Grouping of nepoviruses according to their physicochemical properties.

Protein coat with one polypeptide			Protein coat with two polypeptides
B component homogeneous (one molecule of RNA-1)		B component heterogeneous (one molecule of RNA-1 or two molecules of RNA-2)	Arracacha virus B (AVB) Artichoke vein banding virus (AVBV) Cherry raspleaf virus (CRLV) Lucerne Australian symtomless virus (LASV) Lucerne Australian latent virus (LALV) Rubus Chinese seed-borne virus (RCSBV) Satsuma dwarf virus (SDV) Strawberry latent ringspot virus (SLRV)
M component with $S_{20,w}$ up to 100;MW of RNA-2, $\sim 1.5 \times 10^6$	M component with $S_{20,w}$ above 110; MW of RNA-2, above 2×10^6	Arabis mosaic virus (ArMV) Grapevine fanleaf virus (GFLV) Olive latent ringspot virus (OLRV) Potato black ringspot virus (PBRV) Raspberry ringspot virus (RRV) Tobacco ringspot virus (TobRSV)	
Arracacha virus A (AVA) Artichoke Italian latent virus (AILV) Cocoa necrosis virus (CNV) Crimson clover latent virus (CCLV) Cycas necrotic stunt virus (CNSV) Grapevine chrome mosaic	Artichoke yellow ringspot virus (AYRV) Blueberry leaf mottle virus (BBLMV) Cassava green mottle virus (CGMV) Cherry leafroll virus (CLRV) Chicory yellow mottle virus (CYMV)		

M component with $S_{20,w}$ up to 100;MW of RNA-2, $\sim 1.5 \times 10^6$	M component with $S_{20,w}$ above 110; MW of RNA-2, above 2×10^6	Arabis mosaic virus (ArMV) Grapevine fanleaf virus (GFLV) Olive latent ringspot virus (OLRV) Potato black ringspot virus (PBRV) Raspberry ringspot virus (RRV) Tobacco ringspot virus (TobRSV)	Rubus Chinese seed-borne virus (RCSBV) Satsuma dwarf virus (SDV) Strawberry latent ringspot virus (SLRV)
Arracacha virus A (AVA) Artichoke Italian latent virus (AILV) Cocoa necrosis virus (CNV) Crimson clover latent virus (CCLV) Cycas necrotic stunt virus (CNSV) Grapevine chrome mosaic virus (GCMV) Mulberry ringspot virus (MRV) Tomato black ring virus (TBRV) Tomato top necrosis virus (TTNV)	Artichoke yellow ringspot virus (AYRV) Blueberry leaf mottle virus (BBLMV) Cassava green mottle virus (CGMV) Cherry leafroll virus (CLRV) Chicory yellow mottle virus (CYMV) Grapevine Bulgarian latent virus (GBLV) Hibiscus latent ringspot virus (HLRV) Lucerne Australian latent virus (LALV) Myrobalan latent ringspot virus (MyLRV) Peach rosette mosaic virus (PRMV) Potato virus U (PVU) Tomato ringspot virus (TomRSV)		

detected in protein coat preparations of viruses like satsuma dwarf (SDV) may just be dimers and trimers of the true coat protein subunit, which is estimated to have a molecular weight of 14,500 daltons, that is, a value comparable to that calculated for the smallest polypeptides observed in dissociated virus protein preparations of TomRSV, TobRSV, and OLRV. This polypeptide is thought to be the basic unit of the tetrameric coat protein (55,000–60,000 daltons) typical of the group (23, 24, 115).

Different views are held by other workers (99), who consider some of the tentative nepoviruses with more than one coat polypeptide to be sufficiently distinct from the rest to warrant classification either as a true taxonomic subgroup of nepoviruses or as a new group with SLRV as the type member; they propose the name Slaterivirus for this new group.

This controversy results from the fact that it is not known whether the two polypeptides originate from (a) a *Comovirus*-like translational strategy of RNA-2, whereby a single large polyprotein precursor, produced in vivo, cleaves by internal proteolysis to form two smaller capsid proteins (for a review, see ref. 38) or (b) the originally single, large subunit, simply cleaves during chemical dissociation of the protein coat for electrophoretic analysis.

Serological Grouping

The taxonomy of nepoviruses, that is, the establishment of individual "species" within the group, is largely based on serology, which, as indicated in the preceeding section, is in turn linked with their physicochemical properties.

Most of the nepoviruses (22 out of 34 definitive and possible members) are serologically distinct and are apparently not related to any other member of the group. Their identification as separate entities is, therefore, unambiguous.

Serological stability seems to be highest with viruses infecting a single host or a narrow range of hosts. A primary example of this is GFLV, the populations of which, regardless of their geographical origin, their host (species or cultivars of *Vitis*), and the type of symptomatological responses they induce in host plants, exhibit a remarkable serological uniformity (69). A naturally occurring serological variant of GFLV was only recently discovered in Tunisia (116) after a long search.

A possible explanation offered for the striking serological uniformity of GFLV—which may be applicable to comparable cases with other viruses—is the low selection pressure to which the virus has been subjected in nature because of its strict adaptation to a single host (*V. vinifera* in particular) (69).

Nepoviruses with a wide natural host range apparently vary much more serologically and often give rise to distinct "species." Here, the distinction between close and distant relationship is arbitrary, and, therefore, it

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3.	Raspberry ringspot virus
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	Artichoke strain
4.	Strawberry latent ringspo
	Rubus Chinese seed-born
5.	Blueberry leaf mottle viru
	(blueberry and grapevine
	Grapevine Bulgarian late
6.	Tobacco ringspot virus (T
	Eucharis mottle strain
	Potato black ringspot viru

may be hard to decide whether virus isolates are best considered different viruses or different strains of the same virus.

A conservative approach has been used with CLRV, for which many serologically distinguishable variants have been regarded as strains of the type virus, rather than as different viruses, even though American and European strains form two distinct clusters (54). However, the eucharis mottle isolate of TobRSV has been considered either a distant serological variant of the type virus (86) or a separate entity worthy of its own name (120, 122).

A comparable situation exists with the RRV "strain" recoverd from artichoke in the eastern Mediterranean area. This virus, of which minor serological variants from Greece and Turkey are known, differs from Scottish and English serotypes of RRV by a serological differentiation index of 3 to 6 (96), that is, a value equal to or above that separating GFLV from ArMV, or TBRV from GCMV or cocoa necrosis virus (CNV). When the geographical origin of the virus and the fact that the host it infects is a typical Mediterranean species are considered, it would seem appropriate to regard the artichoke strain of RRV as a distinct nepovirus. This possibility appears to be strongly supported by recent information indicating that although the Greek isolate has only a 9% sequence homology with the English serotype of RRV, it shares 73% of its sequence with the Turkish isolate (105).

An intriguing aspect of serological clustering of nepoviruses is that it is largely consistent with the geographical distribution of the viruses (Table 6.2 and 6.3) and hence, with their possible centers of origin. For instance,

TABLE 6.2. Grouping of nepoviruses according to serological relatedness.

Serological clusters	Geographical origin
1. Arabis mosaic virus (ArMV) (type and hop strain)	Europe
Grapevine fanleaf virus (GFLV)	Mediterranean–Near East
2. Tomato black ring virus (TBRV) (type and beet ringspot strain)	Europe
Grapevine chrome mosaic virus (GCMV)	Europe
Cocoa necrosis virus (CNV)	Africa
3. Raspberry ringspot virus (RRV) (Scottish, English, grapevine, and cherry strains)	Europe
Artichoke strain	Mediterranean–Near East
4. Strawberry latent ringspot virus (SLRV)	Europe
Rubus Chinese seed-borne virus (RCSBV)	Far East
5. Blueberry leaf mottle virus (BBLMV) (blueberry and grapevine strain)	North America
Grapevine Bulgarian latent virus (GBLV)	Europe
6. Tobacco ringspot virus (TobRSV) (type strain)	North America
Eucharis mottle strain	South America
Potato black ringspot virus (PBRV)	South America

TABLE 6.3. Grouping of nepoviruses according to presumed geographical origin.

Presumed origin and viruses	Natural host range[a]	Present distribution[a]
1. *Europe*		
Arabis mosaic virus (ArMV)	Very wide (fruits, vegetables, ornamentals)	Very wide
Cherry leafroll virus (CLRV)	Very wide (fruits, shrubs)	Very wide
Crimson clover latent virus (CCLV)	Crimson clover	Wide
Grapevine Bulgarian latent virus (GBLV)	Grapevine	Wide
Grapevine chrome mosaic virus (GCMV)	Grapevine, celery	Wide
Raspberry ringspot virus (RRV)	Very wide (especially small fruits)	Wide
Strawberry latent ringspot virus (SLRV)	Very wide (fruits, vegetables, ornamentals)	Wide
Tomato black ring virus (TBRV)	Very wide (fruits, vegetables, ornamentals)	Wide
2. *Mediterranean—Near East*		
Artichoke Italian latent virus (AILV)	Narrow (vegetables, grapevine)	Wide
Artichoke vein banding virus (AVBV)	Artichoke	Restricted
Artichoke yellow ringspot virus (AYRV)	Narrow (vegetables)	Restricted
Chicory yellow mottle virus (CYMV)	Narrow (vegetables)	Restricted
Grapevine fanleaf virus (GFLV)	Grapevine	Ubiquitous
Myrobalan latent ringspot virus (MyLRV)	Narrow (fruits)	Restricted
Olive latent ringspot virus (OLRV)	Olive	Restricted
Raspberry ringspot virus, artichoke strain	Artichoke	Restricted
3. *North America*		
Blueberry leaf mottle virus (BBLMV)	Blueberry, grapevine	Restricted
Cherry rasp leaf virus (CRLV)	Narrow (fruits)	Restricted
Peach rosette mosaic virus (PRMV)	Narrow (fruits)	Restricted
Tobacco ringspot virus (TobRSV)	Very wide (fruits, vegetables, ornamentals)	Wide
Tomato ringspot virus (TomRSV)	Very wide, (fruits, vegetables, ornamentals)	Very wide
Tomato top necrosis virus (TTNV)	Tomato	Restricted
4. *South America*		
Arracacha virus A (AVA)	Arracacha	Restricted
Arracacha virus B (AVB)	Arracacha, ocra, potato	Restricted
Potato black ringspot virus (PBRV)	Potato	Restricted

TABLE 6.3. *Continued*

Presumed origin and
Potato virus U (PVU)
Tobacco ringspot virus, e strain
5. *Africa*
Cocoa necrosis virus (CN
Hibiscus latent ringspot v (HLRV)
6. *Australia*
Cassava green mottle viru (CGMV)
Lucerne Australian latent (LALV)
Lucerne Australian symp virus (LASV)
7. *Far East*
Cycas necrotic stunt virus
Mulberry ringspot virus (M
Rubus Chinese seed-borne (RCSBV)
Satsuma dwarf virus (SDV

[a] Ubiquitous, occuring in all m countries in two or more co restricted, recorded from a sin

North Americam To part of the continent European ArMV, RF further south: RRV area, and CNV in A serologically interrel ancestor. The fact t though separated regi have developed in th

GEOGRAPHICAL ORIG

There is a consensus plants and thus depe ments (as opposed tc nation by nematode v reviews, refs. 40 and

TABLE 6.3. *Continued*

Presumed origin and viruses	Natural host range[a]	Present distribution[a]
Potato virus U (PVU)	Potato	Restricted
Tobacco ringspot virus, eucharis strain	Eucharis	Restricted
5. Africa		
Cocoa necrosis virus (CNV)	Cocoa	Restricted
Hibiscus latent ringspot virus (HLRV)	Hibiscus	Restricted
6. Australia		
Cassava green mottle virus (CGMV)	Cassava	Restricted
Lucerne Australian latent virus (LALV)	Alfalfa, white clover	Restricted
Lucerne Australian symptomless virus (LASV)	Alfalfa	Restricted
7. Far East		
Cycas necrotic stunt virus (CNSV)	Cycas	Restricted
Mulberry ringspot virus (MRSV)	Mulberry	Restricted
Rubus Chinese seed-borne virus (RCSBV)	*Rubus*	Restricted
Satsuma dwarf virus (SDV)	Satsuma mandarin	Restricted

[a] Ubiquitous, occuring in all major areas of cultivation of the host plant; very wide, recorded from many countries in two or more continents; wide, recorded from many countries in the same continent; restricted, recorded from a single or two adjacent countries.

North Americam TobRSV has serological counterparts in the southern part of the continent (TobRSV eucharis strain and PBRV), and, similarly, European ArMV, RRV, and TBRV have serologically related "species" further south: RRV artichoke strain and GFLV in the Mediterranean area, and CNV in Africa. The viruses within each of these clusters are serologically interrelated, which indicates evolution from a common ancestor. The fact that these viruses occur in physically contiguous, though separated regions, is therefore in line with the likelihood that they have developed in these regions.

GEOGRAPHICAL ORIGIN AND DISTRIBUTION

There is a consensus that nepoviruses are primarily pathogens of wild plants and thus depend for their survival and spread in natural environments (as opposed to man-made agricultural environments) on dissemination by nematode vectors and host plant seeds that they may infect (see reviews, refs. 40 and 86). It follows that these viruses have little natural

mobility, so they tend to be localized in specific territorial enclaves in which they become firmly established.

It is therefore conceivable that the geographical distribution of nepoviruses broadly corresponds to their areas of origin or differentiation, in which their hosts, primary and alternative (usually crop plants), and vectors are readily available.

The notion that nepoviruses may have differential geographical origins, first put forward with reference to viruses infecting grapevines in Europe and North America (68, 69) and recently extended to other nematode-borne viruses of the American continent (122), seems tenable and is consistent with the distribution of vectors. Therefore it seems reasonable to hypothesize a presumed geographical origin of currently recognized nepoviruses, as shown in Table 6.3. From this table, it is evident that nepoviruses that generally infect a wide range of hosts have a much wider distribution, especially if the hosts are vegetatively propagated perennial crops, than have viruses with a few or a single host. Such viruses, as would be expected, have a restricted distribution.

A remarkable exception to the latter is GFLV, which although a highly specialized pathogen has the widest geographical distribution of the nepoviruses. Uncontrolled marketing of infected budwood and rooted cuttings have greatly facilitated the spread of GFLV and its major vector, *X. index,* to virtually all the viticultural areas of the world. This also applies to records of European nepoviruses such as SLRV, TBRV and ArMV, from grapevines in eastern Mediterranean regions (Turkey and Israel) and Japan (9); from grapevines, cherry, rhubarb and parsley in North America (122), as well as the American TomRSV, from a shrub in Australia (24). No plausible explanation is presently available for the records of ArMV from a native shrub in the United States (122) and of TobRSV from soybean in the People's Republic of China (144).

Another widely distributed virus, CLRV, is recorded from cultivated and native plant species in Europe and North America. Simple dissemination through infected propagative material may not account for the widespread occurrence of CLRV outside Europe, its presumed area of origin, since there is serological evidence that strains of CLRV may have independently arisen in Europe and North America. This is compatible with the notion that, in nature, CLRV spreads by air-borne pollen rather than by nematodes (54, 122) (Table 6.4).

Tobraviruses

Tobraviruses constitute the other recognized taxonomic group of plant viruses transmitted by nematodes (*Trichodorus* and *Paratrichodorus*). These viruses have rigid, rod-shaped particles that vary in length: very short, ~45 nm.; short (S), 50 to 110 nm; and long (L), 185 to 200 nm. Their

TABLE 6.4. Grouping of

Virus
1 *Transmitted by nematodes*
Arabis mosaic virus (ArMV)
All strains
Artichoke Italian latent viru (AILV)
Italian strain
Greek strain
Cherry rasp leaf virus (CRLV)
Grapevine fanleaf virus (GFLV)
Mulberry ringspot virus (MRSV)
Peach rosette mosaic virus (PRMV)
Raspberry ringspot virus (RRV)
Scottish strain
English strain
Strawberry latent ringspot virus (SLRV)
All strains
Tobacco ringspot virus (TobRSV)
All strains
Tomato black ring virus (TBRV)
Type strain
Beet ringspot strain
Tomato ringspot virus (TomRSV)
Type strain
Grapevine yellow vein strai
2. *Transmitted by pollen to mother plants, no vector found*
Cherry leafroll virus (CLRV)
Blueberry leaf mottle virus (BBLMV)
Artichoke yellow ringspot virus (AYRV)
3. *Vector unknown*
Arracacha virus A (AVA)
Arracacha virus B (AVB)

TABLE 6.4. Grouping of nepoviruses according to means of natural spread.

Virus	Seed transmission in naturally and/or artificially infected hosts	Vector
1. *Transmitted by nematodes*		
Arabis mosaic virus (ArMV)	Yes	
All strains		*Xiphinema diversicaudatum*
Artichoke Italian latent virus (AILV)	Not detected	
Italian strain		*Longidorus apulus*
Greek strain		*Longidorus fasciatus*
Cherry rasp leaf virus (CRLV)	Yes	*Xiphinema americanum*
Grapevine fanleaf virus (GFLV)	Yes	*Xiphinema index*, *Xiphinema italiae*
Mulberry ringspot virus (MRSV)	Yes	*Longidorus martini*
Peach rosette mosaic virus (PRMV)	Yes	*Xiphinema americanum*, *Longidorus diadecturus*, *Longidorus elongatus*
Raspberry ringspot virus (RRV)	Yes	
Scottish strain		*Longidorus elongatus*
English strain		*Longidorus macrosoma*
Strawberry latent ringspot virus (SLRV)	Yes	
All strains		*Xiphinema diversicaudatum*
Tobacco ringspot virus (TobRSV)	Yes	
All strains		*Xiphinema americanum*
Tomato black ring virus (TBRV)	Yes	
Type strain		*Longidorus attenuatus*
Beet ringspot strain		*Longidorus elongatus*
Tomato ringspot virus (TomRSV)	Yes	
Type strain		*Xiphinema americanum*, *Xiphinema rivesi*
Grapevine yellow vein strain		*Xiphinema californicum*
2. *Transmitted by pollen to mother plants, no vector found*		
Cherry leafroll virus (CLRV)	Yes	
Blueberry leaf mottle virus (BBLMV)	Yes	
Artichoke yellow ringspot virus (AYRV)	Yes	
3. *Vector unknown*		
Arracacha virus A (AVA)	Yes	
Arracacha virus B (AVB)	Yes	

TABLE 6.4. *Continued*

Virus	Seed transmission in naturally and/or artificially infected hosts	Vector
Artichoke vein banding virus (AVBV)	Not tested	
Cassava green mottle virus (CGMV)	Not tested	
Chicory yellow mottle virus (CYMV)	Yes	
Cocoa necrosis virus (CNV)	Yes	
Crimson clover latent virus (CCLV)	Yes	
Cycas necrotic stunt virus (CNSV)	Yes	
Grapevine Bugarian latent virus (GBLV)	Not tested	
Grapevine chrome mosaic virus (GCMV)	Not tested	
Hibiscus latent ringspot virus (HLRV)	Not detected	
Lucerne Australian latent virus (LALV)	Yes	
Lucerne Australian symptomless virus (LASV)	Yes	
Myrobalan latent ringspot virus (MyLRV)	Not tested	
Olive latent ringspot virus (OLRV)	Not tested	
Potato black ringspot virus (PBRV)	Not detected	
Potato virus U (PVU)	Yes	
Rubus Chinese seed-borne virus (RCSBV)	Yes	
Satsuma dwarf virus (SDV)	Yes	
Tomato top necrosis virus (TTNV)	Not tested	

bipartite genome has two functional RNA species, their S particles encapsidate one molecule of the smaller RNA (RNA-2), and their L particles contain one molecule of the larger RNA (RNA-1). Coat protein subunits are of a single type and have a molecular weight of 21,000-23,000 daltons.

In contrast with nepoviruses, tobraviruses have increased very little in number: The two members constituting the group when it was first established (47) are now three (46) (Table 6.5).

The classification of tobraviruses is based on molecular hybridization, that is, the extent of sequence homology between RNA-1 species, rather

TABLE 6.5. Tobravirus group: Members, host range, vectors, and geographical distribution.

Geographical distribution

Vectors

TABLE 6.5. Tobravirus group: Members, host range, vectors, and geographical distribution.

Virus	Natural Host Range	Seed transmission	Vectors	Geographical distribution
Tobacco rattle virus (TRV)	Very wide (vegtables, ornamentals, woody perennials, shrubs)	Yes	*Trichodorus cylindricus, T. hooperi, T. primitivus, T. similis, T. viruliferus; Paratrichodorus allius, P. anemones, P. christiei, P. minor, P. nanus, P. pachydermus, P. porosus, P. teres, P. tunisiensis*	Very wide (Europe, Mediterranean, North America, Japan, New Zealand)
Pea early-browning virus (PEBV)	Narrow (legumes only)	Yes	*Trichodorus primitivus, T. viruliferus; Paratrichodorus anemones, P. pachydermus, P. teres*	Wide (Europe, Mediterranean)
Pepper ringspot virus (PRV)	Narrow (vegetables)	Yes	*Paratrichodorus christiei*	Restricted (Brazil)

than on serology. This led to the recognition of three distinct viruses, each with its own separate gene pool: TRV, PEBV, and PRV (106).

Isolates belonging to any given virus or "species" have strongly conserved RNA-1 genes, whereas their RNA-2 genes vary. Therefore, serology is, at most, only useful for separating strains within each "species." For example, broad bean yellow band virus (BBYBV) was originally considered to be a possible new member of the group because it is not apparently related serologically to the English or Dutch strains of PEBV (111). However, it was later demonstrated that its RNA-1 has substantial sequence homology with PEBV RNA-1, and, therefore, despite its lack of serological relatedness, it was synonymized with PEBV as a new serotype (107).

The use of serology to identify certain tobraviruses can be misleading. In fact, since sequences of a gene pool of a tobravirus "species" may be captured in nature by a gene pool of a different "species", new pseudo-recombinants arise in which the RNA-2 (i.e., the part of the genome responsible for serological specificity as it codes for the coat protein) of a given virus becomes dependent for its replication on the RNA-1 of another virus, conferring upon it the serological characteristics of the former virus (108).

The geographical distribution of tobraviruses seems to differentiate, to a certain extent, individual members of the group from one another, thus justifying the concept of the existence of gene pools.

Vectors

Many species of nematodes ingest viruses when they feed on the roots of virus-infected plants, but it is now well established that the natural transmission of nepoviruses is only by longidorid nematodes, and of tobraviruses by trichodorid nematodes. However, of the 157 species of *Xiphinema* and 82 species of Longidorus described to date (early 1989), relatively few have been implicated as vectors and, indeed, not all nepoviruses require nematode vectors for their survival and dissemination (Table 6.4). So far, at least 14 of about 50 described species of *Trichodorus* and *Paratrichodorus* are vectors of the tobraviruses TRV and PEBV, but each species may only transmit a particular strain. A third tobravirus, PRV, has been described from Brazil and *P. christiei* has been implicated as a vector (22, 113) (Table 6.5).

Distribution of *Xiphinema* and *Longidorus*

Xiphinema and *Longidorus* have been reported from most parts of the world where nematode surveys have been undertaken. Individual species mostly occur as discrete populations in a particular region, and analyses

of their distribution have been made in an attempt to deduce their phylogenetic relationships. From a comparison of several morphological characteristics of different longidorid genera, Coomans (27) concluded that *Xiphinema* originated in Gondwanaland and, before the break-up of Pangaea, the genus spread to Laurasia. The main speciation occurred in Africa, from where the majority of species have been described, with South American regarded as another important speciation area.

Longidorus, with *Paralongidorus* and *Longidoroides,* is considered to have originated in Southeast Africa and India when these areas were still united, and a later spread to Laurasia was accompanied, and followed, by a main speciation of Longidorus in the holarctic region, especially Europe.

In their analysis of the European longidorid fauna, Topham and Alphey (135) relate the relative impoverishment of species in the northern regions to Quaternary glaciation and attribute the highly diverse fauna of the eastern Mediterranean countries of Israel, Italy, and Malta to Miocene plate tectonic activity in that area. The distribution of longidorid species in the Americas also provides evidence of the effect of changing latitude on species richness and diversity.

Much of the present distribution of longidorid species can, in broad terms, be related to paleoecology (16, 30, 78, 98, 135), but in relatively recent times, many species, especially those associated with crop plants, have been disseminated from their centers of origin by man's activities. Examples include *X. index,* the vector of GFLV, which has been distributed throughout Europe and the areas of the world where grapevines are grown from its center of origin in ancient Persia (50, 82). *Xiphinema rivesi,* a vector of TomRSV in the eastern United States, has probably been exported to Europe where it occurs in scattered localities particularly in western France, but so far without association with the virus. Among *Longidorus* species, there is evidence that *L. elongatus* and *L. vineacola* have been introduced into the Scottish Western Islands with garden planting material (7, 16) and that *L. apulus* has been distributed in Apulia (southern Italy) on soil adhering to artichoke sprouts used for propagation (109).

Species that have been widely dispersed survive in new biotopes because of their genetic adaptability. With time, many of the geographically separated populations may change sufficiently in their taxonomic characteristics to be considered new species. Certainly there is much evidence of morphometric variation within widely dispersed species of *Xiphinema* and *Longidorus,* and this has caused problems not only in terms of taxonomy but also in the identification of their role in virus transmission.

Brown and Topham (17) found that populations of *Xiphinema diversicaudatum* from different countries were distinguishable morphometrically, as well as by certain aspects of their biological behavior, including

their reproductive ability and their ability to transmit virus. However, although populations could be grouped morphometrically, the differences were not considered to be sufficient to establish new species. Morphometric differences between dispersed populations have also been noted in *Xiphinema coxi, L. elongatus, L. profundorum,* and *L. vineacola,* and these species, together with *X. diversicaudatum,* may be regarded as species complexes in which the biological characteristics of the populations also differ to some degree. *Xiphinema americanum* was recognized as a species complex by Lima (62), who concluded that it comprised seven parthenogenetic species, four of which he described as new. Other workers (52, 123) supported this view, although they thought the demarcation of these species were problematical and unsatisfactory. However, Lamberti and Bleve-Zacheo (62) divided *X. americanum sensu lato* into six groups of species, totaling 25 in all, with 15 of them new. They thought that *X. americanum sensu stricto* is restricted in its geographical distribution to the eastern part of North America, and they designated *Xiphinema californicum* a new species to define the morphologically distinct group of the western seaboard of the United States. Apart from some outstanding queries, records of *X. americanum* in European countries have been assigned to *Xiphinema pachtaicum* of *Xiphinema brevicolle,* neither of which species has been shown to be a vector in field situations(16).

Because of the taxonomic reconstruction of *X. americanum* (62) many of the records of its association with TomRSV or TobRSV in North America need to be reconsidered. *Xiphinema americanum senus stricto* remains as the vector of some strains of TomRSV, and so far it is the only recognized vector of TobRSV, although the geographical distribution of the virus is not entirely coincident with that of the vector; however, *X. californicum* is established as the vector of California-type strains of TomRSV (53) and is presumed to be the vector of CRLV (62, 90). Similarly, *X. rivesi* is the vector of strains of TomRSV in eastern Canada and Pennsylvania (USA) (34), and *X. utahense* and *X. occidum* are also considered to be potential vectors of some strains of TomRSV (62, 144).

Records of virus transmission of *X. americanum* or derived species outside North America may be authentic but at most are associated with outlier populations of the nematode that have been dispersed, through man's agency, from the center of origin of both the vector and the virus in North America.

The other species in North America that have been associated with the transmission of nepoviruses in field situations are *X. index,* which was introduced from Europe, and which is unique in its association with GFLV, and *Longidorus diadecturus,* which is a vector of PRMV in Ontario (Canada), with *X. americanum* also being recorded as a less efficient vector of the virus (1, 2). In a recent paper (2a), an Ontario population of *L. elongatus* was also recorded as a vector of PRMV but only at a low transmission level.

Longidorus diadecturi
in Japan (143), are unk
Longidorus species in ce

Distribution of *Tricho*

Trichodorid nematodes a
have been recorded fr
relatively isolated island
that different species are
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In a survey of trichodor
and *Trichodorus primiti*
countries, whereas *Para*
in Italy, and *Trichodor*
Trichodorid species des
to be localized, but sur
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Although groupings o
65), their taxonomy doe
of origin. However, the
occurrence of several sp
active speciation is occ

Some species are c
Paratrichodorus minor
been distributed by ma
mechanical injury as oc
are unlikely to survive
However, they may be
(6, 114), and their abilit
exploit new environme

Most of the records
are from Europe and N
research interest in the
associations may be ex
Currently, there are is
and New Zealand, and

Isolates of TRV from
are transmitted by di
geographical separatio
vector. So far, PEBV h
have been indentified
implicated as vectors.

Longidorus diadecturus and *Longidorus martini*, the vector of MRSV in Japan (143), are unknown in Europe; they are distinct from other *Longidorus* species in certain morphological details (11).

Distribution of *Trichodorus* and *Paratrichodorus*

Trichodorid nematodes are widespread in North America and Europe and have been recorded from many parts of the world, including some relatively isolated islands. Most species appear to be locally distributed so that different species are present in different landmasses, although within a geographical region some species may be more widespread than others. In a survey of trichodorids in Europe (3), *Paratrichodorus pachydermus* and *Trichodorus primitivis* were found to occur in most of the northern countries, whereas *Paratrichodorus tunisiensis* has so far been found only in Italy, and *Trichodorus hooperi* only in the southwest of England. Trichodorid species described from Africa, India, and Japan also appear to be localized, but surveys in those regions have been insufficient to establish the extent of their geographical distribution.

Although groupings of trichodorids species have been recognized (31, 65), their taxonomy does not indicate evolutionary directions and centers of origin. However, the abundance of species in Europe, and the usual occurrence of several species in a single soil sample (64, 90), suggests that active speciation is occurring and new biotopes are being invaded.

Some species are cosmopolitan in their distribution, for example, *Paratrichodorus minor* and *Paratrichodorus porosus* (66), and may have been distributed by man, although trichodorids are susceptible to such mechanical injury as occurs in the rough handling of soil samples (8), and are unlikely to survive casual transportation from one region to another. However, they may be successfully dispersed in flood or irrigation waters (6, 114), and their ability to reproduce rapidly allows them to invade and exploit new environments quickly (59).

Most of the records of tobravirus transmission by trichodorid species are from Europe and North America (63, 127, 140), but this reflects the research interest in these regions, and, in due course, more virus–vector associations may be expected to be identified in other parts of the world. Currently, there are isolated records of TRV transmissions from Japan and New Zealand, and of PRV from Brazil.

Isolates of TRV from North America differ from those from Europe and are transmitted by different species, which supports the view that geographical separation is associated with differentiation of virus and vector. So far, PEBV has been found only in Europe, but several strains have been indentified and at least five trichodorid species have been implicated as vectors.

Virus–Vector Associations

Much of the accumulated experimental evidence of nematode transmission of plant viruses indicates that there is a high degree of specificity in the association between virus and vector. Thus, although serologically unrelated nepoviruses may share a common vector species (e.g., *X. diversicaudatum* transmits ArMV and SLRV), strains of a virus that are serologically distinct are transmitted by different, although closely related species of the same nematode genus. For example, the Scottish strains of RRV and the unrelated TBRV are transmitted by *L. elongatus,* but the English strains of these viruses have *Longidorus macrosoma* and *Longidorus attenatus,* respectively, as vectors. Further, the division of *X. americanum* species complex into several discrete species (62) now supposes the association of serologically distinct strains of TomRSV with different vector species (63).

Evidence of the specific association between tobraviruses and trichoroid vectors is less clear. American and European isolates of TRV are serologically distinguishable (see earlier section) and, in nature, are associated with different species of *Trichodorus* and *Paratrichodorus;* indeed, only species of the latter genus have been recorded as vectors in North America.

In comparing the transmission of TRV by nine species of *Trichodorus* and *Paratrichodorus* from the Netherlands, van Hoof (141) found that transmission occurred only when the nematode and virus came from the same locality. A high level of specificity is also apparent with the transmission of PEBV, different isolates of which are transmitted by several trichodorid species (37, 142). Other evidence suggests that specificity of transmission is not well developed. In Britain, the spinach yellow mottle strain of TRV was transmitted by a mixed population of *Trichodorus* and *Paratrichodorus* species (60); in Belgium, five trichoroid species transmitted TRV, infecting a potato crop (92), although in this case it was not recorded whether a single virus strain was involved.

A recent study in eastern Scotland (19) showed that a close relationship may be established between different species of trichodorid nematodes and serologically distinct isolates of TRV. At two field sites, *P. pachydermus* transmitted the majority of the several isolates of TRV (PRN serotype) that were present, but *Trichodorus cylindricus* transmitted isolates of a previously uncharacterized serotype.

For some years, it has been recognized that if the vector status of a nematode is to be established with any certainty, several criteria must be met in experimental work (75, 127, 136). These include (a) the virus must be available to the nematode; (b) test conditions must be suitable for transmission to occur; (c) the possibility of virus contamination of the bait plants must be avoided. To these criteria, Trudgill et al. (139) added (d) the virus and nematode must be correctly identified; (e) bait plant

tissues must be shown t
(f) the nematode being
vector in that experimen
meet these criteria, and
differences in efficiency
longidorids and trichodo
rated into the procedure
anomalous results previ
unsupported by field e
contamination (77) and t
vector associations are i

Efficient extraction of
virus transmission tests.
virus–vector nematodes,
canting and sieving tec
satisfactory procedure fo

Variation in Transmiss

Although the authenticity
established, the different
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transmission; but becaus
has been difficult to subst
were used, it was demo
vector of ArMV, whereas
vectors of RRV (Scottish
(134, 138).

Recent experiments ha
widely separated geograp
sion of the virus with w
populations of *X. diversic*
and SLRV, Brown (12, 1
rarely transmitted the vir
were all efficient vectors
to the British strains of t
exposed to an Italian str
not improve. In another
Italy was exposed to tw
SLRV. The Scottish pop
virus, but did not trans
transmitted all three viru
sorbent electron microsc
they had ingested the
electron microscopy of

tissues must be shown to be infected with the virus being tested; and (f) the nematode being tested must be shown to be the only possible vector in that experiment. Test procedures have now been developed to meet these criteria, and they are sufficiently sensitive to detect small differences in efficiency of transmission between different species of longidorids and trichodorids (19, 138). Further, the refinements incorporated into the procedures have led to the conclusion that some of the anomalous results previously obtained in laboratory experiments and unsupported by field evidence (127, 132) might have been due to contamination (77) and that two-thirds of the published results of virus–vector associations are invalid (139).

Efficient extraction of nematodes from the soil is a prerequisite for virus transmission tests. In a comparison of methods used to extract virus–vector nematodes, Brown and Boag (18a) concluded that a decanting and sieving technique, with 200-g soil samples, is the most satisfactory procedure for longidorid and trichodorid nematodes.

Variation in Transmission

Although the authenticity of many of the virus–vector associations is well established, the different results of transmission tests obtained by different workers suggest that vector species differ in their efficiency of transmission; but because of the different experimental conditions, this has been difficult to substantiate. However, when precise test procedures were used, it was demonstrated that *X. diversicaudatum* is an efficient vector of ArMV, whereas *L. elongatus* and *L. macrosoma* are inefficient vectors of RRV (Scottish strain) and RRV (English strain), respectively (134, 138).

Recent experiments have also shown that vector populations that are widely separated geographically may differ in their efficiency of transmission of the virus with which they are normally associated. Comparing populations of *X. diversicaudatum* from 10 countries as vectors of ArMV and SLRV, Brown (12, 14) found that those from France, Italy, and Spain rarely transmitted the viruses, whereas populations from other countries were all efficient vectors (Table 6.6). These populations had been exposed to the British strains of the viruses, but when the Italian population was exposed to an Italian strain of SLRV, the efficiency of transmission did not improve. In another test (18), *X. diversicaudatum* from Scotland and Italy was exposed to two Italian strains and the type (British) strain of SLRV. The Scottish population readily transmitted the type strain of the virus, but did not transmit the Italian strains; the Italian population transmitted all three virus strains but at a very low frequency. Immunosorbent electron microscopy (100) of the nematodes demonstrated that they had ingested the viruses to which they had been exposed, but electron microscopy of sections of the odontophore, the site of virus

TABLE 6.6. Transmission of the type strains of arabis mosaic (ArMV) and strawberry latent ringspot (SLRV) viruses by 10 populations of *Xiphinema diversicaudatum*.[a]

	Percentage number of transmissions[b]	
Nematode Population	ArMV	SLRV
Bulgaria	100	48
England	96	60
New Zealand	96	60
Norway	96	40
Scotland	92	68
Switzerland	96	56
United States	48	36
France	10	10
Italy	4	2
Spain	0	15

[a] Compiled from Brown (12, 14) and Brown and Trudgill (18).
[b] Using groups of two nematodes per test pot; 25 replicates of each test.

retention in *Xiphinema* vectors, revealed that few or no virus particles were present in those populations that failed to transmit. Although no significant morphometric differences were apparent between the populations of *X. diversicaudatum* from the 10 countries (17), the marked difference in transmission efficiency of the Italian, and possibly also the French and Spanish, populations could be considered to indicate putative new species. However, it is interesting to note that the Scottish and Italian *X. diversicaudatum* were capable of cross-breeding and that the resulting progeny were intermediate between the parents in efficiency of transmission (13).

Differences in efficiency of transmission have also been shown to occur among *Longidorus* vectors. A Scottish population of *L. elongatus* transmitted the type strains of TBRV and RRV more frequently than the English population, and neither population transmitted the German potato bouquet strain of TBRV, which is a distinct serotype and is considered to have as a vector *L. attenuatus* (15).

In laboratory tests, potato bouquet and two other isolates of TBRV were transmitted less frequently by an English population of *L. attenuatus* then were several English isolates of the virus, including an isolate associated with celery yellow vein disease (20). This, and similar evidence for other vectors, supports the contention that local populations of a vector species are most efficient at transmitting local virus isolates, and, thus, geographical separation tends to lead to high levels of specificity between virus and vector.

Nematode–Virus Interactions

Electron microscopy of thin sections of nematode vectors has identified the virus retention sites within each of the vector genera. In *Longidorus*

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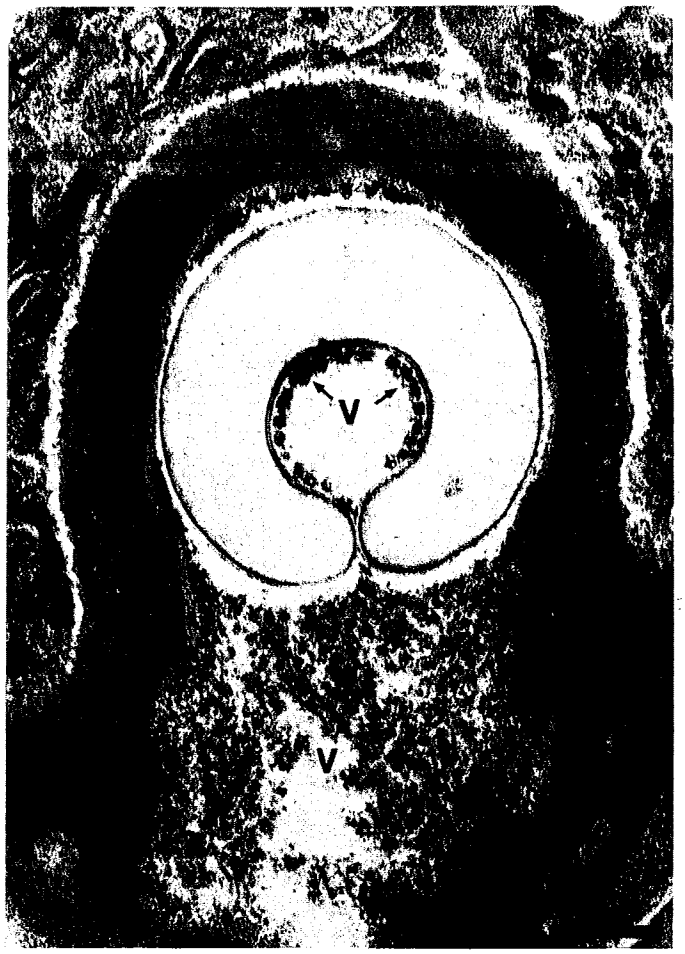


FIGURE 6.1. Transverse section of the odontostyle and guiding sheath of *Longidorus elongatus* reared on a plant infected with raspberry ringspot virus. Particles of the virus (V) are present in association with the inner surface of the odontostyle and between the odontostyle and the guiding sheath (bar, 200 nm). Courtesy of W.M. Robertson.

species, virus particles are adsorbed to the inner surface of the odontostyle (129, 132, 138), and in *L. elongatus,* particles of RRV and TBRV may also be located between the odontostyle and the guiding sheath (129) (Figure 6.1). In *X. diversicaudatum* carrying ArMV or SLRV (130), *X. americanum* carrying TomRSV (76), or *X. index* carrying GFLV (97, 130), virus particles are specifically associated with the cuticular lining of the odontophore, the slender esophagus, and the esophageal pump; the maximum concentration of particles usually occurs in the anterior region of the odontophore.

In trichodorid vectors, TRV particles have been found to be retained in association with the lining of the food canal from the anterior region of the esophastome to the esophagointestinal valve (131) but not attached to the onchiostyle. The tubular particles may be attached by their sides or their ends: the long particles tend to line up parallel to the long axis of the food canal, whereas the short particles tend to adhere by their ends (104, 132).

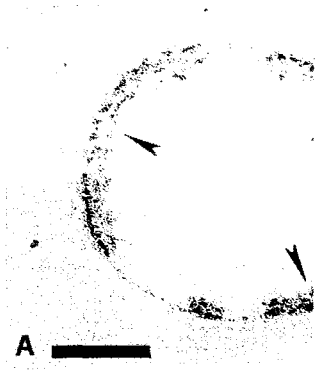
Experiments with pseudo-recombinant isolates of RRV and TBRV have indicated that the specific association of a nepovirus with its vector is determined by the RNA-2 of the virus genome, which carries the coat protein cistron (41, 43, 49). Thus, association between virus and vector appears to depend on some feature of the protein coat that interacts specifically with the retention site within the nematode.

The tobraviruses also have RNA genomes in two pieces. Pseudo-recombinants of TRV strains have been produced (46), and although they have not been used in transmission experiments with trichodorid vectors, it seems likely that the mechanism of specific association between virus and vector is similar to that of nepoviruses.

The mechanism whereby virus particles are adsorbed specifically at the retention site within the nematode vector has been a subject for speculation for some time (127, 133). Recent investigations indicate that specific recognition between virus and vector may involve the interaction of complementary molecules at their point of contact, as occurs in a variety of host–pathogen systems (118). In *X. diversicaudatum,* a discontinuous layer of carbohydrates lines the odontophore and esophagous, and ArMV and SLRV particles attach only to the carbohydrate zones (101, 102, 103) (Figure 6.2). In *P. pachydermus,* a vector of TRV, the total lining of the wall of the esophagous also stains for carbohydrates (102). Thus, virus retention in *Xiphinema* and trichodorid vectors may involve an interaction between carbohydrate moieties on the food canal wall and complementary lectin-like molecules on the protein coat of the virus.

Carbohydrates have not been detected on the guiding sheath or the odontostyle in *L. elongatus* (101). However, by labeling the odontostyle with cationized ferritin, a strong negative charge was shown to be present on the exterior surface of the adontostyle and on the wall of the lumen, and this may account for the retention of positively charged virus particles (101).

Dissociation of virus particles from the retention site is thought to occur when the pH of the lumen is changed by the passage of secretions from the esophageal glands during the initial stages of feeding (127, 133). In Longidorus vectors, specificity and efficiency of transmission may be determined in some cases, if not in all, by the mechanism of dissociation of the virus particles from the retention site (127). For example, when *L. macrosoma* was exposed to the English and Scottish strains of RRV, the former was transmitted, but not the latter, as expected, although virus particles were found to be adsorbed to the inner surface of the odonto-



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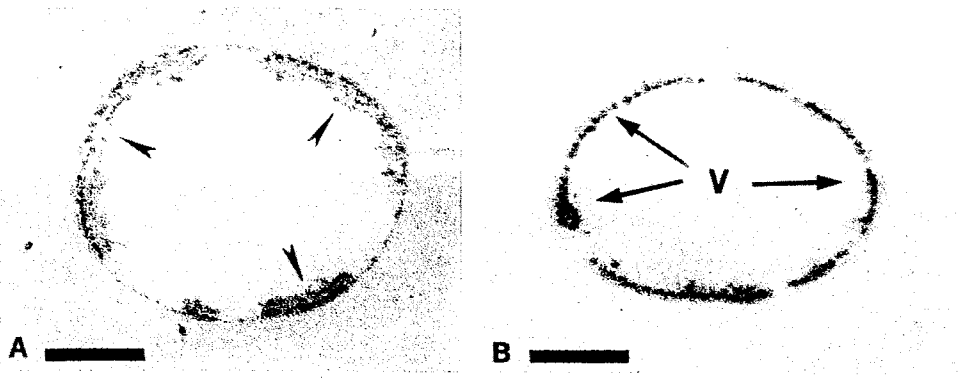

FIGURE 6.2. (A) Transverse section of the lumen of the odontophore of *Xiphinema diversicaudatum* reared on a plant infected with arabis mosaic virus. The section is stained to show the thin discontinuous carbohydrate layer in association with cloud-like areas (arrows). The unstained virus particles are within the cloud-like areas. (B) Transverse section of the lumen of the odontophore of *X. diversicaudatum* reared on a plant infected with arabis mosaic virus and stained with uranyl acetate and lead citrate to show virus particles (V) (bars, 200nm). Courtesy of W.M. Robertson.

style in both sets of nematodes (132, 137). In terms of surface charge density, this was considered to indicate that the change in pH brought about by the esophageal gland secretions altered the surface charge of the particles of the English strain and resulted in detachment and transmission but that it did not have a similar effect on the virus particles of the Scottish strain (127).

The assumed difference in the mechanism of transmission in *Longidorus* vectors, compared with *Xiphinema* and trichodorid vectors, also reflects other observed differences between the two groups of nematodes. Viruses are retained for only a few weeks, at most, in *Longidorus* vectors and transmission is inefficient; in *Xiphinema* and trichodorid vectors, however, associated viruses may be retained for several months and transmission is efficient.

Discussion

The survival and dissemination of plant viruses depends on their effective transmission and their access to suitable host plants for their multiplication. Tobraviruses and nepoviruses are dispersed over short distances by their nematode vectors, that is, to the extent of the area occupied by the local population, but dissemination to new sites may occur through the distribution of infected week seeds or pollen. Thus, nematodes may not

appear to be essential for the maintenance and spread of tobraviruses and nepoviruses, and, indeed, some of the nepoviruses are not associated with nematode vectors (Table 6.4). However, the interaction between virus, nematode, and host plant is a dynamic process, which, at various stages, offers opportunities for genetic selection to the advantage of the virus.

The nematode-transmitted viruses are essentially parasites of wild plants and usually infect them without causing obvious symptoms of infection. However, when crop plants are infected, symptoms are almost invariably severe and, in some cases, may cause the death of the plants, as RRV in some raspberry cultivars and TomRSV and CLRV in union necrosis in apple and walnut, respectively. Similarly, most of the longidorid and trichodorid vectors have wide host ranges among wild plants with which they are compatible enough as not to cause excessive injury by their feeding; but when the roots of crop plants are attacked, they are often severely galled and the growth of the plant is affected (127).

The feeding apparatus of *Longidorus* and *Xiphinema* nematodes is a long tubular odontostyle with which they pierce the young roots and feed on the cell contents. Feeding commences with the penetration of a column of cells near the root apex, and each cell may be fed on progressively until the tip of the odontostyle is located at the feeding site some five to seven cells distant from the rhizodermis. Secretions from the esophageal glands induce a hypertrophic reaction in the root cells around the feeding site, and the coenocyte or cisternum that is formed, depending on the species, provides a rich and readily accessible food source for the nematode. The high metabolic activity of the cells presumably is also conducive to the multiplication and translocation of viruses within the root tissues.

In trichodorid nematodes, the feeding apparatus is in the form of a solid tooth, or onchiostyle, which is used to penetrate the rhizodermal cells of the root tip. Secretions from the esophageal glands are injected into the cell soon after the wall has been penetrated and the contents of the cell are usually ingested within a few seconds, after which the nematode moves to another rhizodermal cell. It is thought that virus particles are also injected into the cell with the secretions of the esophageal glands, and that the virus quickly passes to adjacent cells, or possibly that virus transmission occurs on those occasions when the nematode fails to ingest the total contents of the cell on which it is feeding.

Seemingly, nematodes are passive carriers of the viruses with which they are associated, in the sense that the viruses do not invade the nematode tissues or have any obvious effect on their biological behavior. Nevertheless, the vectors may affect the transmission of the viruses. For instance, vector species vary from being efficient to highly inefficient in their ability to transmit virus. Populations of *X. diversicaudatum* from Britain are efficient vectors of ArMV and SLRV, whereas Italian popula-

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tions only infrequently transmit these viruses. Thus, the same viruses may be disseminated at different rates in different regions. Also, the adsorption of virus particles at the site of retention within the vectors involves the interaction of the virus coat protein with particular features of the cuticular lining of the nematode food canal, and this in itself may have a selective effect on the virus.

Because of the requirement of compatibility between virus and vector to ensure the survival of the virus, it might be expected that the coat protein would be a relatively invariant property of each virus. There is, however, increasing evidence that, in field situations, several minor antigenic variants of a virus may be present together. Such variants have often been revealed when cultivars that are considered to be immune to a particular virus are planted and become infected.

Variants of RRV and ArMV that broke the resistance of raspberry cultivars in Scotland were revealed in this way (88, 134), and, more recently, further isolates of both viruses were found to infect raspberry cultivars that had been shown to be immune to the viruses in graft-inoculation tests (57). Crops constitute a large monoculture area that can apply a selection pressure to the viruses, but the new isolates may have characteristics that are unfavorable in an ecological environment outside of the crop. Such characteristics include poor seed transmissibility and lack of virulence (40), which are conferred by RNA-1, and thus are not believed to be influenced by nematode transmission.

In the above examples, the viruses have wide host ranges that include wild herbaceous species, and the genetic variation displayed by these viruses contrasts with the lack of variation of GFLV, which in nature has so far been found only in association with *Vitis* spp.

The genome of nepoviruses is bipartite, with RNA-1 and RNA-2 located in separate particles, but because these viruses have a similar coat protein, it is assumed that each type is equally ingested and transported by the nematode vector. However, although there is good circumstantial evidence for linking transmission with the properties of the virus coat protein, and hence linking it with the antigenic characteristics of the virus, there remains the possibility that the regions in the coat protein that are important for the attachment and release of particles at retention sites in the nematode vector are not involved in the immunological reaction (20). Further, some properties determined by RNA-1 may affect transmissibility by the vector, as suggested to explain the poorer transmissibility of a pseudorecombinant isolate of TBRV compared to that of the parental source of its RNA-2 (43).

The RNA-1 and RNA-2 of tobraviruses are located in particles of different lengths, and these are readily visualized by electron microscopy of thin sections of the vector species. In the limited number of observations so far made, short and long particles of TRV are randomly distributed at the site of retention in the nematode. Different isolates of

the virus, however, cannot be identified in thin sections of the nematodes and the experimental evidence is inconclusive about specific transmission by trichodorid vectors.

The RNA-1 of tobraviruses is strongly conserved, and the RNA-2 is variable; in nepoviruses, however, both parts of the genome diverge more or less in parellel (32). The RNA-2 nucleotide sequence seems to differ markedly between isolates. Harrison and Robinson (46) suggest that the variation in the tobravirus particle protein indicates that there is no selection pressure for its conservation, and hence it does not play a key role in determining vector transmissibility and specificity. A wide range of naturally occurring strains of both tobraviruses and nepoviruses has been found, but the processes by which these variants are produced remain a matter of speculation.

Nepoviruses and tobraviruses have two complementary methods of dispersion that ensure their survival in a particular location and their distribution to new areas. The nematode vectors are usually static populations, and the spread of virus is slow, but this slow spread is compensated for by the long period of retention of the viruses in the vectors, which, in the case of *Xiphinema* and trichodorid nematodes, may ensure survival between plantings of susceptible crops or through periods when plants are absent in natural situations. Infection of the seeds of weed hosts provides a means of perennation of the viruses over long periods of time and a means of spread to new sites. Weed seed infection is more prevalent among *Longidorus* vectors, which retain viruses for only a few weeks, compared with retention for several months in *Xiphinema* and trichodorid nematodes.

In the past, dispersal of viruses to new areas was probably attained solely through infected week seeds, and continued existence of viruses would depend on their coming into contact with suitable vector species. In more recent times, man has been responsible for the distribution of virus and vector with commercial vegetative material, examples of which are *X. diversicaudatum* and ArMV and *X. index* and GFLV. However, only the less vulnerable of the nematode vector species have been widely distributed, and most species remain in relatively limited ares. Thus, it is not surprising that surveys continue to record more and more species in the genera associated with virus transmission. If nematode vectors apply some selection pressure on the viruses they carry, then it seems likely that there will be a continuing genetic drift of both viruses and vectors to establish new associations.

References

1. Allen, W.R., Van Schagen, J.G., and Eveleigh, E.S:, 1982, Transmission of peach rosette mosaic virus to peach, grape and cucumber by *Longidorus diadecturus* obtained from diseased orchards in Ontario, Can. J. Pl. Pathol. **4**:16–18.

2. Allen, W.R., Van S
transmission of the p
Longidorus diadectur
dae), *Can. J. Pl. Pat*
2a. Allen, W.R., and Eb
tomato black ring and
of *Longidorus elonga*
3. Alphey, T.J.W., and
and Trichodoridae, *S*
4. Barbara, D.J., Asht
purification and som
Appl. Biol. **107**:45–5
5. Beemster, A.B.R.,
and symptoms, in d
ruses of Potato and
113.
6. Boag, B., 1986, Dete
R., Ruesink, B., an
Modelling and Predi
119–145.
7. Boag, B., and Brown
in Scotland with no
15:51–57.
8. Bor, N.A., and Kui
Trichodorus pachyde
ouwetensch. Gent. 3
9. Bovey, R., and Marte
grapevine. A bibliogr
10. Bovey, R., Gartel, W
Virus and virus-like
11. Brown, D.J.F., 198
Europe and variation
Xiphinema diversica
University, Milton K
12. Brown, D.J.F., 1985
ringspot virus by pc
Dorylamoidea), *Nem*
13. Brown, D.J.F., 198
between *Xiphinema*
and Scotland, *Rev. N*
14. Brown, D.J.F., 1986
from England by pc
Dorylamoidea) from
15. Brown, D.J.F., and
tra popolazioni di ne
Soc. ital. Nematol.,
16. Brown, D.J.F., and
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17. Brown, D.J.F., and

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eigh, E.S:, 1982, Transmission of
ɔe and cucumber by *Longidorus*
ds in Ontario, Can. J. Pl. Pathol.

2. Allen, W.R., Van Schagen, J.G., and Ebsary, B.A., 1984, Comparative transmission of the peach rosette mosaic virus by Ontario populations of *Longidorus diadecturus* and *Xiphinema americanum* (Nematoda:Longidoridae), *Can. J. Pl. Pathol.* **6**:29–32.

2a. Allen, W.R., and Ebsary, B.A., 1988, Transmission of raspberry ringspot, tomato black ring and peach rosette mosaic viruses by an Ontario population of *Longidorus elongatus, Can. J. Plant. Pathol.* **10**:1–5.

3. Alphey, T.J.W., and Taylor, C.E., 1987, European Atlas of Longidoridae and Trichodoridae, *Scott. Crop Res. Inst., Dundee, Scotland,* 35 p.

4. Barbara, D.J., Ashby, S.C., and McNamara, D,G., 1985, Host range, purification and some properties of rubus Chinese seed-borne virus, *Ann. Appl. Biol.* **107**:45–55.

5. Beemster, A.B.R., and de Bokx, J.A., 1987, Survey of properties and symptoms, in de Bokx, J.A., and Van der Want J.P.H. (eds): Viruses of Potato and Seed-Potato Production, Pudoc, Wageningen, pp. 84–113.

6. Boag, B., 1986, Detection, survival and dispersal of soil vectors, in Garret, R., Ruesink, B., and G. McLean (eds): Virus Epidemics: Monitoring, Modelling and Predicting Outbreaks, New York, Academic Press, pp. 119–145.

7. Boag, B., and Brown, D.J.F., 1987, The occurrence of *Longidorus vineacola* in Scotland with notes on its distribution in Europe, *Nematol. Medit.* **15**:51–57.

8. Bor, N.A., and Kuiper, K., 1966, Gevoilighed van *Trichodorus teres* en *Trichodorus pachydermus* voor uitvendige invloeden, *Meded. Rijks Landouwetensch. Gent.* **31**:609–616.

9. Bovey, R., and Martelli, G.P., 1986, The viroses and virus-like disease of the grapevine. A bibliographic report 1979–1984, *Vitis* **25**:227–275.

10. Bovey, R., Gartel, W., Hewitt, W.B. Martelli, G.P., and Vuittenez, A, 1980, Virus and virus-like diseases of grapevine, Lausanne, Payot, 181 p.

11. Brown, D.J.F., 1983, The distribution of Longidoridae (Nematoda) in Europe and variation in the morphology, biology and virus transmission of *Xiphinema diversicaudatum* (Micol.) Thorne, 1939 Ph.D. Thesis, Open University, Milton Keynes, England, 303 p.

12. Brown, D.J.F., 1985., The transmission of two strains of strawberry latent ringspot virus by populations of *Xiphinema diversicaudatum* (Nematoda: Dorylamoidea), *Nematol. Medit.* **13**:217–223.

13. Brown, D.J.F., 1986a, Transmission of virus by the progeny of crosses between *Xiphinema diversicaudatum* (Nematoda:Dorylamoidea) from Italy and Scotland, *Rev. Nematol.* **9**:71–74.

14. Brown, D.J.F., 1986b, The transmission of two strains of arabis mosaic virus from England by populations of *Xiphinema diversicaudatum* (Nematoda: Dorylamoidea) from ten countries, *Rev. Nematol.* **9**:83–87.

15. Brown, D.J.F., and Taylor, C.E., 1981, Variazioni nella trasmissione di virus tra popolazioni di nematodi vettori Longidoridae, *Atti Giornate Nematol., Soc. ital. Nematol., Firenze 1981,* pp. 191–204.

16. Brown, D.J.F., and Taylor, C.E., 1987, Comments on the occurrence and geographical distribution of longidorid nematodes in Europe and the Mediterranean region, *Nematol. Medit.* **15**:333–373.

17. Brown, D.J.F., and Topham, P.B., 1985, Morphometric variability between

populations of *Xiphinema diversicaudatum* (Nematoda:Dorylamoidea), *Rev. Nematol.* **8:**15–26.
18. Brown, D.J.F., and Trugdill, D.L., 1983, Differential transmissibility of arabis mosaic and strawberry latent ringspot viruses by three populations of *Xiphinema diversicaudatum* (Nematoda:Dorylamoidea), *Rev. Nematol.* **6:**229–238.
18a. Brown, D.J.F., and Boag, B., 1988, An examination of methods used to extract virus–vector nematodes (Nematoda:Longidoridae and Trichodoridae) from soil samples, *Nematol. Medit.* **16:**93–99.
19. Brown, D.J.F., Ploeg, A.T., and Robinson, D.J., 1988, Transmission of viruses by trichodorid nematodes, *Ann. Rpt. Scott. Crop Res. Inst. 1987:* 130–131.
20. Brown, D.J.F., Murant, A.F., and Trudgill, D.L., 1988, Transmission of serotypes of tomato black ring virus (TBRV) by *Longidorus attenuatus, Ann. Rpt. Scott. Crop. Res. Inst. 1987:*131–132.
21. Cadman, C.H., 1959, Potato stem-mottle disease in Scotland, *Eur. Potato J.* **2:**165–175.
22. Chagas, C.M., and Silberschmidt, K., 1972, Virus da faixa amarela da alcachofra no Estado de Sao Paulo, *O Biologico,***38:**35–40.
23. Chu, P.W.G., and Francki, R.I.B., 1979, The chemical subunit of tobacco ringspot virus coat protein, *Virology* **93:**398–412.
24. Chu, P.W.G., Francki, R.I.B., and Hatta, T., 1983, Some properties of tomato ringspot virus isolated from *Penta lanceolata* in South Australia, *Pl. Pathol.* **32:**353–356.
25. Conti, M., and Masenga, V., 1977, Identification and prevalence of pepper viruses in Northern Italy, *Phytopathol. Z.* **90:**212–222.
26. Converse, R.H., 1981, Infection of cultivated strawberries by tomato ringspot virus, *Phytopathology* **71:**1149–1152.
27. Coomans, A., 1985, A phylogenetic approach to the classification of the Longidoridae (Nematoda:Dorylaimida), *Agricult. Ecosystems Environ.* **12:**335–354.
28. Corte, A., 1968, D. Soil-borne viruses associated with a peach disease occurring in North Italy, *Tagunsgber. Dal.* **97:**187–194.
29. Cropley, R., 1961, Viruses causing rasp-leaf and similar diseases in sweet cherry, *Ann. Appl. Biol.* **49:**530–538.
30. Dalmasso, A., 1970, Influence directe de quelques facteurs écologiques sur l'activité biologique et la distribution des espèces françaises de la famille Longidoridae (Nematoda:Dorylaimida), *Ann. Zool. Ecol. Anim.* **2:**163–200.
31. DeWaele, D., Mancini, G., Roca, F., and Lamberti, F., 1982, *Trichodorus taylori* sp n. (Nematoda:Dorylaimida) from Italy, *Nematol. Medit.* **10:**27–37.
32. Dodd, S.M., and Robinson, D.J., 1984, Nucleotide sequence homologies among RNA species of strains of tomato black ring virus and other nepoviruses, *J. Gen. Virol.* **65:**1731–1740.
33. Francki, R.I.B., Milne, R.G., and Hatta, T., 1985, *Atlas of Plant Viruses* II, Boca Raton, FL, CRC Press, pp. 23–38.
34. Forer, L.B., Hill, N., and Powell, C.A., 1981, *Xiphinema rivesi,* a new tomato ringspot vector, *Phytopathology* **71:**874.
35. Gallitelli, D., Savino, V., and Martelli, G.P., 1982, The middle component of strawberry latent ringspot virus, *J. Gen. Virol.* **55:**169–172.

36. Gallitelli, D, Marte
virus, CMI/AAB D
Mycological Institu
England.
37. Gibbs, A.J., and H
found in Britain, *A*
38. Goldbach, R., and
expression of the bi
(ed): Molecular Pl
120.
39. Hanada, K., Kusu
particles, nucleic ac
Phytophathol. Soc.
40. Harrison, B.D., 19
vectors, *Ann. Rev.*
41. Harrison, B.D., and
of raspberry ringsp
31:455–457.
42. Harrison, B.D., a
Descriptions of Pl
stitute/Association
43. Harrison, B.D., a
pseudo-recombinan
86:209–212.
44. Harrison, B.D., and
23:25–77.
45. Harrison B.D., an
Handbook of Plant
dam, Elsevier/Nort
46. Harrison, B.D., a
mortel, M.H.V., an
2, New York, Plen
47. Harrison, B.D., Fi
Valenta, V., and W
45:356–363.
48. Harrison, B.D., M
raspberry ringspot
17:137–141.
49. Harrison, B.D., M
Distribution of dete
tode transmissibilit
virus, *J. Gen. Viro*
50. Hewitt, W.B., 196
Mycol. **47:**433–455.
51. Hewitt, W.B., Ras
soil-borne fanleaf v
52. Heyns, J., 1974, T
group (Nematoda:D
53. Hoy, J.W., Mirce

36. Gallitelli, D, Martelli, G.P., and Rana G.L., 1984, Artichoke vein banding virus, CMI/AAB Descriptions of Plant Viruses, No. 285, Commonwelath Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
37. Gibbs, A.J., and Harrison, B.D., 1964, A form of pea early browning virus found in Britain, *Ann. Appl. Biol.* **54**:1–11.
38. Goldbach, R., and Van Kammen, A., 1985, Structure, replication and expression of the bipartite genome of cowpea mosaic virus, in Davies J.W. (ed): Molecular Plant Virology, Boca Raton, FL, CRC Press, pp. 83–120.
39. Hanada, K., Kusunoki, M., and Iwaki, M., 1986, Properties of virus particles, nucleic acid and coat protein of cycas necrotic stunt virus, *Ann. Phytophathol. Soc. Japan* **52**:422–427.
40. Harrison, B.D., 1977, Ecology and control of viruses with soil-inhabiting vectors, *Ann. Rev. Phytopathol.* **15**:331–360.
41. Harrison, B.D., and Hanada, K., 1976, Competitiveness between genotypes of raspberry ringspot virus is mainly determined by RNA-1, *J. Gen. Virol.* **31**:455–457.
42. Harrison, B.D., and Murant, A.F., 1977, Nepovirus group, CMI/AAB Descriptions of Plant Viruses No. 185, Commonwealth Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
43. Harrison, B.D., and Murant A.F., 1977, Nematode transmissibility of pseudo-recombinant isolates of tomato black ring virus *Ann. Appl. Biol.*, **86**:209–212.
44. Harrison, B.D., and Robinson, D.J., 1978, The tobraviruses, *Adv. Virus Res.* **23**:25–77.
45. Harrison B.D., and Robinson, 1981, Tobraviruses, in Kuzstak, E. (ed): Handbook of Plant Viruse Infections and Comparative Diagnosis, Amsterdam, Elsevier/North Holland, pp. 516–540.
46. Harrison, B.D., and Robinson, D.J., 1986, Tobraviruses in Van Regenmortel, M.H.V., and Fraenkel-Konrat, H. (eds): The Plant Viruses, Volume 2, New York, Plenum Press, pp. 339–369.
47. Harrison, B.D., Finch, J.T., Gibbs, A.J., Hollings, M., Shepherd, R.J., Valenta, V., and Wetter, C., 1971, Sixteen groups of plant viruses, *Virology* **45**:356–363.
48. Harrison, B.D., Murant, A.F., and Mayo, M.A., 1972, Two properties of raspberry ringspot virus determined by its smaller RNA, *J. Gen. Virol.* **17**:137–141.
49. Harrison, B.D., Murant, A.F., Mayo, M.A., and Roberts, I.M., 1974, Distribution of determinants for symptom production, host range and nematode transmissibility between two RNA components of raspberry ringspot virus, *J. Gen. Virol.* **22**:233–247.
50. Hewitt, W.B., 1968, Viruses and virus disease of grapevine, *Rev. Appl. Mycol.* **47**:433–455.
51. Hewitt, W.B., Raski, D.J., and Goheen, A.C., 1958, Nematode vector of soil-borne fanleaf virus of grapevine, *Phytopathology* **48**:586–595.
52. Heyns, J., 1974, The genus *Xiphinema* in South Africa. I. *X. americanum* group (Nematoda:Dorylaimida), *Phytophylactica* **6**:157–164.
53. Hoy, J.W., Mircetich, S.M., and Lownsbery, B.F., 1984, Differential

transmission of prunus tomato ringspot virus strains by *Xiphinema californicum, Phytopathology* **74:**332–335.
54. Jones, A.T., 1985, Cherry leafroll virus, AAB Descriptions of Plant Viruses, No. 306, Association of Applied Biologists, Warwick, England.
55. Jones, R.A.C., and Kenten, R.H., 1983, Arracacha virus B, CMI/AAB Descriptions of Plant Viruses, No. 270, Commonwealth Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
56. Jones, R.A.C., Fribourg, C.E., and Koenig, R., 1983, A previously undescribed nepovirus isolated from potato in Peru, *Phytopathology* **73:**195–198.
57. Jones, A.T., Mitchell, M.J., and Brown, D.J.F., 1989, Infectibility of some new raspberry cultivars with arabis mosaic and raspberry ringspot viruses and further evidence for variation in British isolates of these two nepoviruses. *Ann. appl. Biol.* **114** (in press).
58. Klos, E.J., 1976, Rosette mosaic, in Virus Diseases and Noninfectious Disorders of Stone fruits in North America, Agric. Handbook 437, USDA, Washington D.C., pp. 135–138.
59. Kuiper, K., and Loof, P.A.A., 1962, *Trichodorus flavensis* n. sp. (Nematoda:Enoplida). A plant nematode from new polder soil, *Versl. Pl. Ziekt. Dienst. Wageningen* **136:**193–200.
60. Kurppa, A, Jones, T.A., Harrison, B.D., and Bailiss, K.W., 1981, Properties of spinach yellow mottle, a distinctive strain of tobaco rattle virus, *Ann. Appl. Biol.* **98:**243–254.
61. Kusunoki, M., Hanada, K., Iwaki, M., Chang, M.U., Doi, Y., and Yora, K., 1986, Cycas necrotis stunt virus, a new member of nepoviruses found in *Cycas revoluta*. Host range, purification, serology and some other properties, *Ann. Phytopathol. Soc. Japan* **52:**302–311.
62. Lamberti, F., and Bleve-Zacheo, T., 1979, Studies on *Xiphinema americanum sensu lato* with descriptions of fifteen new species (Nematoda:Longidoridae), *Nematol. Medit.* **7:**51–106.
63. Lamberti, F., and Roca, F., 1987, Present status of nematodes as vectors of plant viruses, in Veech, J., and Dickson, D.W. (eds): Vistas on Nematology, Soc. Nematol., Hattsville, pp. 321–328.
64. Lima, M.B., 1965, Studies on species of the genus *Xiphinema* and other nematodes, Ph. D. Thesis, University of London, 163 p.
65. Loof, P.A.A., 1973, Taxonomy of the *Trichodorus-aequalis* complex (Diphtherophorina), *Nematologica* **19:**49–61.
66. Loof, P.A.A., 1975, Taxonomy of Trichodoridae, in Lamberti, F., Taylor, C.E., and Seinhorst, J.W. (eds): Nematode Vectors of Plant Viruses, New York, Plenum Press, pp. 103–127.
67. Marte, M., Gadani, F., Savino V., and Rugini, E., 1986, Strawberry latent ringspot virus associated with a new disease of olive in Central Italy, *Pl. Disease* **70:**171–172.
68. Martelli, G.P., 1975, Some features of nematode-borne viruses and their relationships with the host plants, in Lamberti, F., Taylor, C.E., and Seinhorst, J.W. (eds): Nematode Vectors of Plant Viruses, New York, Plenum Press, pp. 223–252.
69. Martelli, G.P., 1978, Nematode-borne viruses of grapevine, their epidemiology and control, *Nematol. Medit.* **6:**1–27.

70. Martelli, G.P., a
122(2):150–156.
71. Martelli, G.P., a
122(2):201–228.
72. Martelli, G.P., an
CMI/AAB Descri
gical Institute/Ass
73. Martelli, G.P., Ra
virus, CMI/AAB
Mycological Insti
England.
74. Martelli, G.P., Qu
1978, A tentative
75. McElroy, F.D., 1
review, *Proc. Am*
76. McGuire, J.M., K
nematode *Xiphine*
77. McNamara, D.G.
divesicaudatum (N
in plant-free soil,
78. McNamara, D.G.
nematodes in Gre
Thresh, J.M. (ed)
225–235, 977.
79. Matthews, R.E.F
virology **17:**1–199
80. Migliori, A., Marz
black ring virus (T
81. Mircetich, S.M.,
graft transmission
topathology **70:**96
82. Mojtahedi, H., St
species in Iranian
83. Murant, A.F., 19
nematode-transmi
84. Murant, A.F., 19
Viruses, No. 16,
plied Biologists, K
85. Murant, A.F., 19
tions of Plant Vi
Association of Ap
86. Murant, A.F., 19
Virus Infections a
Holland, pp. 197–
87. Murant, A.F., ar
nepovirus RNA s
naturing condition
88. Murant, A.F., Ta
ships and transm

70. Martelli, G.P., and Gallitelli, D., 1985, Virosi dell'olivo, *Italia Agric.* **122(2):**150–156.
71. Martelli, G.P., and Prota, U., 1985, Virosi della vite, *Italia Agric.* **122(2):**201–228.
72. Martelli, G.P., and Quacquarelli, A., 1972, Grapevine chrome mosaic virus, CMI/AAB Descriptions of Plant Viruses, No. 103, Commonwealth Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
73. Martelli, G.P., Rana, G.L., and Savino, V., 1977, Artichoke Italian latent virus, CMI/AAB Descriptions of Plant Viruses, No. 176, Commonwealth Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
74. Martelli, G.P., Quacquerelli, A., Gallitelli, D., Savino, V., and Piazzolla, P., 1978, A tentative grouping of nepoviruses, *Phytopath. Medit.* **17:**147–147.
75. McElroy, F.D., 1977, Nematodes as vectors of plant viruses. A current review, *Proc. Am. Phytopathol. Soc.* **4:**1–10.
76. McGuire, J.M., Kim, K.S., and Douthit, L.M., 1970, Tobacco ringspot in the nematode *Xiphinema americanum, Virology* **42:**212–216.
77. McNamara, D.G., 1978, Studies on the ability of the nematode *Xiphinema divesicaudatum* (Micol.) to transmit raspberry ringspot virus and to survive in plant-free soil, Ph.D. Thesis, University of Reading, England, 280 p.
78. McNamara, D.G., and Flegg, J.J.M., 1981, The distribution of virus–vector nematodes in Great Britain in relation to past and present vegetation, in Thresh, J.M. (ed): Pests, Pathogens and Vegetation, London, Pitman, pp. 225–235, 977.
79. Matthews, R.E.F., 1982, Classification and nomenclature of viruses, *Intervirology* **17:**1–199.
80. Migliori, A., Marzin, H., and Rana, G.L., 1984, Mise en evidence du tomato black ring virus (TBRV) chez l'artichaut en France, *Agronomie* **4:**683–686.
81. Mircetich, S.M., Sandborn, R.R., and Ramos, D.E., 1980, Natural spread, graft transmission and possible etiology of walnut blackline disease, *Phytopathology* **70:**962–968.
82. Mojtahedi, H., Sturhan, D., Akhiani, A., and Barooti, S., 1980, *Xiphinema* species in Iranian vineyards, *Nematol. Medit.* **8:**165–170.
83. Murant, A.F., 1970, The importance of wild plants in the ecology of nematode-transmitted viruses, *Outlook Agric.* **6:**114–121.
84. Murant, A.F., 1970, Arabis mosaic virus, CMI/AAB Descriptions of Plant Viruses, No. 16, Commonwelath Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
85. Murant, A.F., 1974, Strawberry latent ringspot virus, CMI/AAB Descriptions of Plant Viruses, No. 126, Commonwealth Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
86. Murant, A.F., 1981, Nepoviruses, in Kurstak, E. (ed): Handbook of Plant Virus Infections and Comparative Diagnosis, Amsterdam, Elsevier/North Holland, pp. 197–238.
87. Murant, A.F., and Taylor, M., 1978 Estimates of molecular weights of nepovirus RNA species by polyacrylamide gel electropphoresis under denaturing conditions, *J. Gen. Virol.* **41:**53–61.
88. Murant, A.F., Taylor, C.E., and Chambers J., 1968, Properties, relationships and transmission of a strain of raspberry ringspot virus infecting

rasberry cultivars immune to the common Scottish strain, *Ann. Appl. Biol.* **61:**175–186.
89. Murant, A.F., Jones, A.T., Martelli, G.P., and Stace-Smith, R., 1990, Nepoviruses: Diseases and virus identification, in Harrison, B.D., and Murant, A.F. (eds): The Plant Viruses, Volume 5, New York, Plenum Press, (in press).
90. Nyland, G., Lownsbery, B.F., Loew, S.K., and Mitchell, J.F., 1969, The transmission of cherry rasp-leaf virus by *Xiphinema americanum, Phytopathology* **59:**1111–1112.
91. Pacini, E., and Cresti, M., 1977, Viral particles in developing pollen grains of *Olea europaea, Planta* **137:**1–4.
92. Pelmaeker, M. de, and Coomans, A., 1986, Virusvectornematoden in Aadeppelvelden, *Parasitica* **42:**11–16.
93. Quacquarelli, A., Martelli, G.P., and Vovlas, C., 1974; Chicory yellow mottle virus, CMI/AAB Descriptions of Plant Viruses, No. 132, Commonwealth Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
94. Rana, G.L., and Martelli, G.P., 1983, Virosi del carciofo, *Italia Agric.* **120(1):**27–38.
95. Rana, G.L., Kyriakopoulou, P.E., and Martelli, G.P., 1983, Artichoke yellow ringspot virus, CMI/AAB Descriptions of Plant Viruses, No. 271, Commonwealth Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
96. Rana, G.L., Castrovilli, S., Gallitelli, D., and Kyriakopoulou, P.E., 1985, Studies on two serologically distinct raspberry ringspot virus strains from artichoke, *Phytopathol. Z.* **112:**222–228.
97. Raski, D.J., Maggenti, A.R., and Jones, N.O., 1973, Location of grapevine fanleaf and yellow mosaic virus particles in *Xiphinema index, J. Nematol.* **5:**208–211.
98. Rau, J., 1975, Das Vorkommen Virusubertragender Nematoden in ungerstorten Biotopen Niedersachsens, Diss. Techn. Univ. Hannover, 169 p.
99. Remah, A., Jones, A.T., and Mitchell, M.J., 1986, Purification and properties of lucerne Australian symptomless virus, a new virus infecting lucerne in Australia, *Ann. Appl. Biol.* **109:**307–315.
100. Roberts, I.M., and Brown, D.J.F., 1980, Detection of six nepoviruses in their nematode vectors by immunosorbent electron microscopy, *Ann. Appl. Biol.* **96:**187–192.
101. Robertson, W.M., 1987, Possible mechanisms of virus retention in virus vector nematodes, *Ann. Rpt. Scott, Crop Res. Inst. 1986*:127.
102. Robertson, W.M., and Henry, C.E., 1986a, A possible role of carbohydrates in the retention of nematode-transmitted viruses, *Ann. Rpt. Scott. Crop Res. Inst. 1985*:113.
103. Robertson, W.M., and Henry, C.E., 1986b, An association of carbohydrates with particles of arabis mosaic virus retained within *Xiphinema diversicaudatum, Ann. Appl. Biol.* **109:**299–305.
104. Robertson, W.M., and Wyss, U., 1983, Feeding processes of virus-transmitting nematodes, in Harris, K.F., (ed): Current Topics in Vector Research, New York, Springer-Verlag, pp. 271–295.
105. Robinson, D.J., and Clark, J., 1987, Genome sequence homology among

strains of raspberry
1986:172–173.
106. Robinson, D.J., and
genome parts of tol
separate viruses, *J.* (
107. Robinson, D.J., and I
band virus is a new
66:2003–2009.
108. Robinson, D.J., Harr
1987, Two anomalou:
in nature, *J. Gen. Vi*
109. Roca, F., Martelli, G
Longidorus attenuati
ship with artichoke I
110. Rudel, M., 1985, G
combinations, *Phyto*
111. Russo, M., Gallitelli
broad bean yellow b:
105:223–230.
112. Salazar, L.F., and
CMI/AAB Descriptic
gical Institute/Associ
113. Salomao, T.A., 1973
II Congr. Internaz. S
114. Sauer, M.R., 1968,
14:457–458.
115. Savino, V., Gallitelli
newly recognized vi
253.
116. Savino, V., Cherif, C
of grapevine fanleaf
117. Savino, V., Quacqua
1977, Il virus dell'ac
cazione e caratterizz
118. Sequeira, L., 1978, I
Rev. Phytopathol. **1(**
119. Smith, S.H., and Tr
virus-infected peache
120. Stace-Smith, R., 198
Viruses, No. 309, As
121. Stace-Smith, R., and
Descriptions of Plar
stitute/Association o
122. Stace-Smith, R., and
Harris, K.F. (ed): *Cr*
Verlag, pp. 131–166.
123. Tarjan, A.C., 1969,
(Nematoda:Longidor
124. Taylor, C.E., 1971,

strains of raspberry ringspot nepovirus, *Ann. Rpt. Scott. Crop Res. Inst. 1986*:172–173.
106. Robinson, D.J., and Harrison, B.D., 1985a, Unequal variation in the two genome parts of tobraviruses with evidence for the existence of three separate viruses, *J. Gen. Virol.* **66**:171–176.
107. Robinson, D.J., and Harrison, B.D., 1985b, Evidence that broad bean yellow band virus is a new serotype of pea-early browning virus, *J. Gen. Virol.* **66**:2003–2009.
108. Robinson, D.J., Hamilton, W.D.O., Harrison, B.D., and Baulcombe, D.C., 1987, Two anomalous tobravirus isolates. Evidence for RNA recombination in nature, *J. Gen. Virol.* **68**:2551–2561.
109. Roca, F., Martelli, G.P., Lamberti, F., and Rana, G.L., 1975, Distribution of *Longidorus attenuatus* Hooper in Apulian artichoke fields and its relationship with artichoke Italian latent virus, *Nematol. Medit.* **3**:91–101.
110. Rudel, M., 1985, Grapevine damage induced by particular virus–vector combinations, *Phytopatholo. Medit.* **24**:183–185.
111. Russo, M., Gallitelli, D., Vovlas, C., and Savino, V., 1984, Properties of broad bean yellow band virus, a possible new tobravirus, *Ann. Appl. Biol.* **105**:223–230.
112. Salazar, L.F., and Harrison, B.D., 1979, Potato black ringspot virus, CMI/AAB Descriptions of Plant Viruses, No. 206, Commonwealth Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
113. Salomao, T.A., 1973, Soil transmission of artichoke yellow band virus, *Atti II Congr. Internaz. Studi Carciofo, Bari 1973*:831–854.
114. Sauer, M.R., 1968, Nematodes in an irrigated vineyard, *Nematologica,* **14**:457–458.
115. Savino, V., Gallitelli, D., and Barba, M., 1983, Olive latent ringspot virus, a newly recognized virus infecting olive in Italy, *Ann. Appl. Biol.* **1203**:243–253.
116. Savino, V., Cherif, C., and Martelli, G.P., 1985, A natural serological variant of grapevine fanleaf virus, *Phytopathol. Medit.* **24**:29–34.
117. Savino, V., Quacquarelli, A., Gallitelli, D., Piazzolla, P., and Martelli, G.P., 1977, Il virus dell'accartocciamento fogliare del ciliegio nel noce. I. Identificazione e caratterizzazione, *Phytopathol. Medit.* **16**:96–102.
118. Sequeira, L., 1978, Lectins and their role in host-pathogen specificity, *Ann. Rev. Phytopathol.* **16**:453–481.
119. Smith, S.H., and Traylor, J.A., 1969, Stem pitting of yellow bud mosaic virus-infected peaches, *Pl. Dis. Rep.* **53**:666–667.
120. Stace-Smith, R., 1985, Tobacco ringspot virus, AAB Descriptions of Plant Viruses, No. 309, Association of Applied Biologists, Warwick, England.
121. Stace-Smith, R., and Hansen, A.J., 1976, Cherry rasp-leaf virus, CMI/AAB Descriptions of Plant Viruses, No. 159, Commonwealth Mycological Institute/Association of Applied Biologists, Kew, Surrey, England.
122. Stace-Smith, R., and Ramsdell, D.C., 1987, Nepoviruses of the Americas, in Harris, K.F. (ed): *Current Topics in Vector Research,* New York, Springer-Verlag, pp. 131–166.
123. Tarjan, A.C., 1969, Variation within the *Xiphinema americanum* group (Nematoda:Longidoridae), *Nematologica* **15**:241–252.
124. Taylor, C.E., 1971, Nematodes as vectors of plant viruses, in Zuckerman,

B.M., Mai, W.F., and Rhode, R.A. (eds): Plant Parasitic Nematodes/ Volume II, New York, Academic Press, pp. 185–211.
125. Taylor, C.E., 1978, Plant-parasitic Dorylaimida: Biology and virus transmission, in Southey, J.F. (ed): Plant Nematology, London, HMSO, pp. 232–243.
126. Taylor, C.E., 1980, Nematodes, in Harris, K.F., and Maramorosch, K. (ed): Vectors of Plant Pathogens, New York, Academic Press, pp. 375–416.
127. Taylor, C.E., and Brown, D.J.F., 1981, Nematode-virus interactions, in Zuckerman, B.M., Rhode, R.A. (ed): Plant Parasitic Nematodes Volume III, Academic Press, New York, pp. 281–301.
128. Taylor, C.E., and Cadman, C.H., 1969, Nematode vectors, in Maramorosch, K. (ed): Viruses, Vectors and Vegetation, New York, Interscience, pp. 55–94.
129. Taylor, C.E., and Robertson, W.M., 1969, The location of raspberry ringspot and tomato black ring viruses in the nematode vector *Longidorus elongatus* (de Man), *Ann. Appl. Biol.* **64:**43–48.
130. Taylor C.E., and Robertson, M.W., 1970a, Sites of virus retention in the alimentary tract of the nematode vectors *Xiphinema diversicaudatum* (Micol.) and *X. index* (Thorne et Allen), *Ann. Appl. Biol.* **66:**373–380.
131. Taylor, C.E., and Robertson, W.M., 1970b, The location of tobacco rattle virus in the nematode vector *Trichodorus pachydermus* Seinhorst, *J. Gen. Virol.* **6:**179–182.
132. Taylor, C.E., and Robertson, W.M., 1975, Acquisition, retention and transmission of viruses by nematodes, in Lamberti, F., Taylor C.E., and Seinhorst, J.W. (eds): Nematode Vectors of Plant Viruses, New York, New York, pp. 253–276.
133. Taylor, C.E., and Robertson, M.W., 1977, Virus vector relationships and mechanics of transmission, *Proc. Am. Phytopathol. Soc.* **4:**20–29.
134. Taylor, C.E., Thomas, P.R., and Converse, R.H., 1966, An outbreak of arabis mosaic virus and *Xiphinema diversicaudatum* (Micolestsky) in Scotland, *Pl. Pathol.* **15:**170–174.
135. Topham, P.B., and Alphey, T.J.W., 1985, Faunistic analysis of Longidorid nematodes in Europe, *J. Biogeogr.* **12:**165–174.
136. Trudgill, D.L., and Brown, D.J.F., 1978a, Frequency of transmission of some nematode-borne viruses, in Scott, P.R., and Bainbridge, A. (eds): Plant Disease Epidemiology Oxford, Blackwell, pp. 281–289.
137. Trudgill, D.L., and Brown, D.J.F., 1978b, Ingestion, retention and transmission of two strains of raspberry ringspot virus by *Longidorus macrosoma, J. Nematol.* **10:**85–89.
138. Trudgill, D.L., Brown, D.J.F., and Robertson, W.M., 1981, A comparison of the four British vector species of *Longidorus* and *Xiphinema, Ann. Appl. Biol.* **99:**63–70.
139. Trudgill, D.L., Brown, D.J.F., and McNamara, D.G., 1983, Methods and criteria for assessing the transmission of plant viruses by longidorid nematodes, *Revue Nematol.* **6:**133–141.
140. van Hoof, H.A., 1962, *Trichodorus pachydermus* and *T. teres,* vectors of the early browning virus of peas. *Tijdschr. Plantenziekten* **68:**391.
141. van Hoof, H.A., 1968, Transmission of tobacco rattle virus by *Trichodorus* species, *Nematologica* **14:**20–24.

142. Vrain, T.C., and Yo
of the Okanagan vall
143. Yagita, H., and Kon
by *Longidorus marti*
144. Zhigang, Xu, Polst
soybean mosaic, soi
soybean in the Peopl

142. Vrain, T.C., and Yorston, J.M., 1987, Plant parasitic nematodes in orchards of the Okanagan valley of British Columbia, Canada, *P. Disease* **71**:85–86.
143. Yagita, H., and Komuro, Y., 1972, Transmissiom of mulberry ringspot virus by *Longidorus martini* Merny, *Ann. Phytopathol. Soc. Japan* **38**:275–283.
144. Zhigang, Xu, Polston, J., and Goodman, R.M., 1986, Identification of soybean mosaic, southern bean mosaic and tobacco ringspot viruses from soybean in the People's Republic of China, *Ann. Appl. Biol.* **108**:51–57.