

Invitational precise

Virus-vector Longidoridae and their associated viruses in the Americas

John M. Halbrendt

The Pennsylvania State University, Fruit Research Laboratory,
P.O. Box 309, Biglerville, PA. 17307-0309, U.S.A.

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Summary. Five *Xiphinema* and one *Longidorus* species have been identified as natural vectors of nepoviruses in the Americas. *Xiphinema index* is the vector of grapevine fanleaf virus (GFLV) and was the first virus vector to be identified. Evidence suggests that the *X. index* - GFLV association probably evolved elsewhere and was imported to the Americas with grapevines. All native *Xiphinema* vectors belong to the *Xiphinema americanum*-group of nematodes and transmit tomato ringspot, tobacco ringspot, cherry rasp leaf, or peach rosette mosaic nepoviruses. *Longidorus diadecturus* is also a vector of peach rosette mosaic nepovirus. The ability of *X. index* and *L. diadecturus* to transmit associated nepoviruses is clear but controversy surrounds the *X. americanum*-group vectors and their associated nepoviruses. The controversy stems from the reappraisal of the group in 1979 which casts doubt on the identity of some vectors. The *X. americanum*-group vectors are unusual in that they have only three juvenile stages and apparently lack the high degree of specificity reported for other nematode-virus associations. Several unnatural virus-vector associations have also been reported.

Key words: nematode-virus association, *Xiphinema*, *Longidorus*, America.

The field of nematode virus-vector research began in California (USA) with the discovery by Hewitt et al. (1958) that *Xiphinema index* was the natural vector of grapevine fanleaf nepovirus (GFLV). It is generally accepted that this is an exotic pest problem in the Americas which was introduced by the importation of *X. index* infested soil with grapevine propagation material. Man has probably played an important role in the global dispersal of this nematode as it is present in almost every viticulture region of the world and since under natural conditions it is found almost exclusively with grapevine (*Vitis* sp.) and fig (*Ficus carica*) (Brown & Taylor, 1987). The nematode appears to have originated in the Middle East where it has been found in association with natural woodlands and wild grapevines (Southey, 1973; Weischer, 1975). Grapevine fanleaf virus was probably also dispersed by man and grapevine diseases similar or identical to GFLV have been

reported from many countries. The virus, which causes leaf deformity, mottling, loss of yield, and vineyard decline, is widespread in California and may cause severe economic loss where the incidence is high (Hewitt et al., 1958).

The most widespread and economically important nepovirus vectors in North and South America are members of the *Xiphinema americanum*-group of nematodes. Of the ca. 20 putative *X. americanum*-group species that have been reported from the Americas, four have been identified as being virus vectors including *X. americanum*, *X. bricolensis*, *X. californicum*, and *X. rivesi* (Robbins & Brown, 1991). *Xiphinema americanum* has been reported throughout North and South America although some reports suggest that *X. americanum* sensu stricto (s.s.) may be uncommon in South America (Allen et al., 1971; Alkemade & Loof, 1990; Luc & Doucet, 1990; Robbins & Brown, 1991). *Xiphinema*

californicum is common along the western seaboard of the Americas and is widespread throughout California, Mexico, Chile, and Peru (Lamberti et al., 1988; Alkemada & Loof, 1990; Robbins & Brown, 1991). This species has also been reported from Brazil, New York (USA) and Pennsylvania (USA) (Jaffee et al., 1987; Lamberti et al., 1987; Georgi, 1988). *Xiphinema rivesi* is found east of the Rocky Mountains and is reportedly more common than *X. americanum* in orchards of the northeastern United States and eastern Canada. It has been reported infrequently from Argentina and Peru, (Alkemada & Loof, 1990; Luc & Doucet, 1990; Robbins & Brown, 1991). *Xiphinema bricolensis* is apparently restricted to the west coast of North America and has only been reported from British Columbia and California (Ebsary et al., 1989; Cho & Robbins, 1991). The nematodes are widely distributed but most reports of nepovirus transmission come from the centers of fruit production, particularly orchards and vineyards with temperate climates.

Tomato ringspot virus (TomRSV) is by far the most widespread and economically important nepovirus in North and South America. Reported vectors for TomRSV include *X. americanum*, *X. bricolensis*, *X. californicum*, and *X. rivesi*. The virus infects many fruit crops including most stone fruits, apple, grape, raspberry, and blueberry. Tomato ringspot virus is perhaps best known as the causal agent of *Prunus* Stem Pitting disease (PSP) which occurs in peach, nectarine, and cherry. Trees affected by PSP have the general appearance of being girdled. Leaves droop, curl upwards lengthwise, and may be chlorotic. In the autumn, leaves change color and abscise earlier than comparable noninfected trees. Infected trees typically have a high fruit set but the fruit is smaller and more brightly coloured than on healthy trees. There is enlargement of the trunk at or below ground level and the bark in this region is thick and spongy. Removal of the bark reveals pits and grooves in the wood. Trees generally die within 1-2 years from the onset of symptoms. There is considerable variation in symptoms between cultivars (Mircetich & Fogle, 1976). Other stone fruits diseases caused by TomRSV include prune brown line (PBL), Stanley constriction and decline (SCAD), and yellow

bud mosaic (YBMV). Tomato ringspot virus is also the causal agent of apple union necrosis and decline (AUND). The disease is only a problem on grafted trees where the fruiting variety is resistant to TomRSV and the rootstock is tolerant (susceptible). The leaves of infected trees are small and sparse with dull pale green coloration. The terminal shoot growth is reduced, internodes are short, and trees typically set a large crop of small highly coloured fruit. There is often a noticeable swelling of the trunk above the graft union and the bark in this region is abnormally thick and spongy. Upon removal, the bark tissue appears orange and a distinct necrotic line is seen at the scion-rootstock union. The infection is not always lethal but trees are unthrifty. In severe cases, trees break off at the union (Stouffer & Powell, 1989). A number of different strains of TomRSV have been isolated and some reports suggest that the nematodes may transmit different strains with varying levels of efficiency. More research is required to confirm the transmission efficiency of different vector species for the same and different strains of TomRSV.

Cherry rasp leaf virus (CRLV) is the causal agent of cherry rasp leaf disease in western North America and is transmitted by *X. americanum*. Leaves of infected trees develop prominent enations on the underside and may be distorted. Lower spurs and branches may be killed as the virus spreads within the tree. Trees become unthrifty, produce few fruit, and may die, especially if infected while young (Nyland, 1976). Cherry rasp leaf virus is also the causal agent of flat apple disease. Shoot growth on infected trees appears bushy and foliage of affected branches is narrow and elongated. Affected fruit are about half the normal length, the stem cavity is shallow, lenticels enlarged, and the calyx basin is broad with prominent points. Normal and affected fruit may occur on the same branch (Blodgett et al., 1963; Parish, 1977).

Tobacco ringspot virus (TobRSV) is transmitted by *X. americanum* (Fulton, 1962). The virus infects a number of different crops but is only considered economically important on a few including blueberry and certain grape varieties.

Peach rosette mosaic virus (PRMV) is the causal agent of peach rosette mosaic disease which occurs in Michigan and Ontario. The virus is transmitted by *X.*

americanum and *Longidorus diadecturus*. It is unusual for a nepovirus to be transmitted by nematodes in two different genera. Infected trees develop rosettes of leaves resulting from a dramatic shortening of the internodes. In addition, trees may exhibit delayed foliation, chlorotic mottling, and distorted leaves. Typically infected trees are darker green than uninfected trees (Klos, 1976).

Common weeds may harbor latent infections of these viruses and serve as natural reservoirs. In Pennsylvania at least 23 common orchard weed species have been found naturally infected with TomRSV. Nepoviruses are seed borne in many of their weed hosts which serve as a primary means of dissemination. Viruses can be dispersed via nematode transmission, infected weed seed, vegetatively propagated weeds and dodder transmission (Powell et al., 1982; Welliver & Halbrendt, 1992). Transmission by nematodes is the only natural means of fruit tree infection. Recent studies have provided additional evidence of a lack of specificity between *X. americanum*-group nematodes and their associated nepoviruses. New virus vector associations identified were *X. bricolensis* which transmitted TomRSV and *X. californicum* and *X. rivesi* both of which transmitted CRLV and TobRSV (Brown et al., 1992).

Prior to 1979, *X. americanum* was considered to be cosmopolitan. A reappraisal of the species and subsequent critical observations have shown that many early reports probably refer to other species. The morphologic similarity and possible misidentification of species has placed in question some early reports regarding the geographic distribution and virus vector capability of dagger nematodes. Many reports of *X. americanum* in Europe for example, were subsequently referred to *X. pachtaicum* or *X. brevicolle*. More recently it has been suggested that the reports of *X. brevicolle* occurring in Europe more correctly refer to *X. taylori* (Lamberti et al., 1991). *Xiphinema rivesi* was unknown in Pennsylvania until a survey revealed that this species was more common than *X. americanum* (Lamberti & Bleve-Zacheo, 1979; Forer & Stouffer, 1982; Brown & Taylor, 1987). The geographic range of many *X. americanum*-group species overlap and it has been suggested that the number of virus vector nematodes in the Americas

may be greater than previously reported (Lamberti & Roca, 1987). Loof & Luc (1990) have suggested that a through revision of the group is necessary before any statements can be made about the number and validity of the species pertaining to it. New data and techniques are becoming available which will probably influence the future identification of species in the group. For example it has been shown that native *X. americanum*-group virus vector species in the Americas have only three juvenile stages whereas other *X. americanum*-group species, which have not been reported to vector virus, have four juvenile stages (Halbrendt & Brown, 1992).

REFERENCES

- Alkemada, J. R. M. & Loof, P. A. A. 1990. The genus *Xiphinema* Cobb, 1913 (Nematoda: Longidoridae) in Peru. *Revue de Nematologie* 13: 339-348.
- Allen, M. W., Noffsinger, W. M. & Valenzuela, A. 1971. Nematodos en huertos y vinedos de Chile. *Agricultura Tecnica* 31: 115-120.
- Blodgett, E. C., Aichele, M. D., Coyier, D. L. & Milbrath, J. A. 1963. The flatapple disease. *Plant Disease Reporter* 47: 769-771.
- Brown, D. J. F. & Taylor, C. E. 1987. Comments on the occurrence and geographical distribution of Longidorid nematodes in Europe and the Mediterranean region. *Nematologia Mediterranea* 15: 333-373.
- Brown, D. J. F., Halbrendt, J. M. & Jones, A. T. 1992. Transmission of nepoviruses by populations of four *Xiphinema americanum*-group species. *Nematologica* 38: 401-402.
- Cho, M. R. & Robbins, R. T. 1991. Morphological variation among 23 *Xiphinema americanum* populations. *Journal of Nematology* 23: 134-144.
- Ebsary, B. A., Vrain, T. C. & Graham, M. B. 1989. Two new species of *Xiphinema* (Nematoda: Longidoridae) from British Columbia vineyards. *Canadian Journal of Zoology* 67: 801-804.
- Forer, L. B. & Stouffer, R. F. 1982. *Xiphinema* spp. associated with tomato ringspot virus infection of Pennsylvania fruit crops. *Plant Disease* 66: 735-736.
- Fulton, J. P. 1962. Transmission of tobacco ringspot virus by *Xiphinema americanum*. *Phytopathology* 52: 375.
- Georgi, L. L. 1988. Morphological variation in *Xiphinema* spp. from New York orchards. *Journal of Nematology* 20: 304-308.
- Halbrendt, J. M. & Brown, D. J. F. 1992. Morphometric evidence for three juvenile stages in some species of *Xiphinema americanum* sensu lato. *Journal of Nematology* 24: 305-309.

- Hewitt, W. B., Raski, D. J. & Goheen, A. C. 1958. Nematode vector of soil-borne fanleaf virus of grapevines. *Phytopathology* 48: 586-595.
- Jaffee, B. A., Harrison, M. B., Shaffer, R. L. & Strang, M. B. 1987. Seasonal population fluctuation of *Xiphinema americanum* and *X. rivesi* in New York and Pennsylvania orchards. *Journal of Nematology* 19: 369-378.
- Klos, E. J. 1976. Rosette mosaic. In: *Virus Diseases and Noninfectious Disorders of Stone Fruits in North America*. Agriculture Handbook No 437, Agricultural Research Service, United States Department of Agriculture, pp. 135-138.
- Lamberti, F. & Bleve-Zacheo, T. 1979. Studies on *Xiphinema americanum* sensu lato with descriptions of fifteen new species (Nematoda, Longidoridae). *Nematologia Mediterranea* 75: 1-106.
- Lamberti, F., Ciancio, A., Agostinelli, A. & Coiro, M. I. 1991. Relationship between *Xiphinema brevicolle* and *Xiphinema diffusum* with redescription of *X. brevicolle* and descriptions of three new species of *Xiphinema* (Nematoda: Dorylaimida). *Nematologia Mediterranea* 19: 311-326.
- Lamberti, F. & Roca, F. 1987. Present status of nematodes as vectors of plant viruses. In: *Vistas on Nematology*. (J. A. Veech and D. W. Dicson Eds.) pp. 321-328. Hyattsville, MD, USA, The Society of Nematologists.
- Lamberti, F., Roca, F., Sharma, R. D., Pimentel, J. P., Agostinelli, A., Antonio, H. & Lordello, R. R. A. 1987. On the occurrence of species of *Xiphinema* in Brasil. *Nematologia Brasileira* 11: 286-291.
- Lamberti, F., Roca, F. & Agostinelli, A. 1988. On the identity of *Xiphinema americanum* in Chile with a key to the *Xiphinema* species occurring in Chile. *Nematologia Mediterranea* 16: 67-68.
- Loof, P.A.A. & Luc, M. 1990. A revised polytomous key for the identification of species of the genus *Xiphinema* Cobb, 1913 (Nematoda: Longidoridae) with exclusion of the *X. americanum*-group. *Systematic Parasitology* 16: 35-66.
- Luc, M. & Doucet, M. E. 1990. La familia Longidoridae Thorne, 1935 (Nemata) en Argentina. 1. Distribucion. *Revista de Ciencias Agropecuarias* 7: 19-25.
- Mircetich, S. M. & Fogle, H. W. 1976. Peach stem Pitting. In: *Virus Diseases and Noninfectious Disorders of Stone Fruits in North America*. Agriculture Handbook No.437. Agricultural Research Service, United States Department of Agriculture, pp. 77-87.
- Nyland, G. 1976. Cherry rasp leaf. In: *Virus Diseases and Noninfectious Disorders of Stone Fruits in North America*. Agriculture Handbook No.437, Agricultural Research Service, United States Department of Agriculture, pp. 219-221.
- Parish, C. L. 1977. A relationship between flat apple disease and cherry rasp leaf disease. *Phytopatology* 67: 982-984.
- Powell, C. A., Forer, L. B. & Stouffer, R. F. 1982. Reservoirs of tomato ringspot virus in fruit orchards. *Plant Disease* 66: 583-584.
- Robbins, R. T. & Brown, D. J. F. 1991. Comments on the taxonomy, occurrence, and distribution of Longidoridae (Nematoda) in North America. *Nematologica* 37: 395-419.
- Southey, J. F. 1973. Identification of *Xiphinema* species. In: *Association of Applied Biology, Nematology Group: The Longidoridae*. Rothamsted Experiment Station, pp. 37-63.
- Stouffer, R. F. & Powell, C. A. 1989. Apple union necrosis. In: *Virus and Viruslike Diseases of Pome Fruits and Simulating Noninfectious Disorders*. (P.R. Fridlung, Ed.) pp. 48-153. Cooperative Extension, College of Agriculture and Home Economics, Washington State University, Pullman, Washington.
- Weischer, B. 1975. Ecology of *Xiphinema* and *Longidorus*. In: *Nematode Vectors of Plant Viruses* (F. Lamberti, C. E. Taylor & J. W. Seinhorst. Eds.) pp. 291-301. Plenum Press, London and New York.
- Welliver, R. A. & Halbrendt, J. M. 1992. Dodder transmission of tomato ringspot virus. *Plant Disease* 76: 642.

Halbrendt J.M. Переносчики вирусов нематоды семейства Longidoridae и ассоциированные с ними вирусы в Америке.

Резюме. Пять видов рода *Xiphinema* и один вид рода *Longidorus* были зарегистрированы в Америке как естественные переносчики неповирусов. Нематода *Xiphinema index*, переносчик вируса короткоузлия винограда (GFLV), была обнаружена первой. Возможно, ассоциация *Xiphinema index* - GFLV распространена в других местах и была импортирована в Америку с культурой винограда. Все естественные переносчики из рода *Xiphinema* относятся к группе *Xiphinema americanum* и переносят неповирусы: кольцевой пятнистости томата, кольцевой пятнистости табака, скручивания листьев черешни и розеточной мозаики персика. *Longidorus diadecturus* является также переносчиком неповируса розеточной мозаики персика. Способность *X. index* и *L. diadecturus* переносить ассоциированные с ними вирусы доказана, но для нематод-переносчиков неповирусов из группы *X. americanum* она остается спорной. Сомнения связаны с правильностью определения некоторых переносчиков этой группы в 1979 году. Нематоды-переносчики вирусов из группы *X. americanum* необычны тем, что имеют только три личиночные стадии и для них, по-видимому, не характерна высокая степень специфичности, обнаруженная для других ассоциаций нематода-вирус. Сообщается также о других ассоциациях вирус-переносчик.