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Combating Nematode Vectors of Plant Viruses

Several nematode-borne viruses, including grapevine fanleaf, cherry leaf roll, and tobacco rattle, are found throughout the world. Others, such as tomato black ring, raspberry ringspot, arabis mosaic, strawberry latent ringspot, and pea early browning, are confined largely to Europe. Still others, including peach rosette mosaic, tobacco ringspot, and tomato ringspot, are seen only in North America. Generally, viruses and vectors follow the same geographic pattern. Virus distribution may be limited by environmental factors unfavorable to reproduction of the vector, as with some American viruses transmitted by *Xiphinema americanum*.

The two major groups of nematode-vectored viruses are nepoviruses, with isometric particles, and tobraviruses, with straight tubular particles. Six species of *Xiphinema* Cobb and five of *Longidorus* (Micoletzky) Filipjev (Nematoda, Longidoridae) are implicated in transmission of the 15 known nepoviruses, and five species of *Trichodorus* Cobb and seven of *Paratrichodorus* Siddiqi (Nematoda, Trichodoridae) transmit the two known tobraviruses (Table 1). An additional three viruses have been transmitted by nematodes under experimental conditions. Tobraviruses infect only herbaceous crops, whereas nepoviruses infect woody as well as herbaceous plants.

How Viruses Are Disseminated and Transmitted to Plants

Nematode-borne viruses may be disseminated over long distances by infected propagating plant material, which may also have live vectors on the roots. Introduction of a virus in an uninfected area can be prevented by importing healthy plant material, preferably officially certified, and by enforcing an efficient quarantine survey to ensure careful inspection of root systems and adherent soil particles.

Although longidorid and trichodorid nematodes usually do not withstand desiccation, some might survive in moist soil around roots or in containers and on agricultural machinery. When nematode vectors are suspected, dipping the roots of planting stock in a water emulsion or suspension of systemic nematicide is advisable.

Nematodes that come in contact with a suitable host when conditions are optimal for reproduction can cause major infestations within a few months. *Paratrichodorus* and *Trichodorus* species have a relatively short life cycle (18–45 days) and affect a wide range of hosts, including numerous weeds. Reproduction cycles of *Longidorus* and *Xiphinema* species are

Table 1. Nematode-vectored viruses and species implicated in transmission

Virus	Vector
	Nepoviruses
Arabis mosaic	
Type strain	*Xiphinema diversicaudatum, X. coxi*
Hop strain	*X. diversicaudatum*
Grapevine fanleaf	*X. index, X. italiae*
Cherry leaf roll	*X. coxi, X. diversicaudatum, X. vuittenezi*
Cherry rasp leaf	*X. americanum*
Peach rosette mosaic	*X. americanum*
Strawberry latent ringspot	*X. diversicaudatum, X. coxi*
Tobacco ringspot	*X. americanum, X. coxi*
Tomato ringspot	*X. americanum*
Artichoke Italian latent	*Longidorus apulus*
Cacao necrosis	Unknown
Grapevine chrome mosaic	Unknown (*X. vuittenezi?*)
Myrabolan latent ringspot	Unknown
Tomato black ring	
English strain	*L. attenuatus*
Scottish strain	*L. elongatus*
Mulberry ringspot	*L. martini*
Raspberry ringspot	
English strain	*L. macrosoma, L. elongatus*
Scottish strain	*L. elongatus*
Cherry strain	*L. macrosoma, X. diversicaudatum*
	Tobraviruses
Pea early browning	
English isolates	*Paratrichodorus anemones, Trichodorus primitivus, T. viruliferus*
Dutch isolates	*P. pachydermus, P. teres*
Tobacco rattle	
European isolates	*P. anemones, P. nanus, P. pachydermus, P. teres, T. cylindricus, T. minor, T. primitivus, T. similis, T. viruliferus*
American isolates	*P. allius, P. christiei, P. porosus*
	Other viruses
Brome mosaic	*X. diversicaudatum, L. macrosoma*
Carnation ringspot	*X. diversicaudatum, L. elongatus*
Prunus necrotic ringspot	*L. macrosoma*

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much longer, eg, *X. index* may actively reproduce in 2–4 months at 20–22 C.

Multiplication of the population in the soil increases the chances of nematodes contacting a virus source, acquiring the virus, and inoculating healthy plants. A nematode can become viruliferous with a single brief feed on an infected plant. The longer the nematode feeds on a virus source or on healthy plants after acquiring the virus, the more efficient the transmission (15).

Some plant-nematode-virus interactions are essential to efficient transmission. *X. diversicaudatum*, for example, is a very efficient vector of the arabis mosaic virus, whereas *L. elongatus* and *L. macrosoma* are inefficient vectors of their respective strains of the raspberry ringspot virus (17). Trichodorids have less developed vector specificity than longidorids and thus much greater transmission efficiency. Persistence of a virus within the nematode also influences transmission and dissemination. Viruses may persist for several months in *Xiphinema* and trichodorid species without further access to a source, whereas raspberry ringspot and tomato black ring persist in *L. elongatus* for only about 8 weeks (15).

In nematode vectors, virus particles are adsorbed to the cuticular lining of the anterior portion of the alimentary tract—on the inner surface of the guiding sheath and on the odontostyle of *Longidorus* species, in the esophageal lumen of *Xiphinema* species, and on the pharynx and esophagus of the trichodorids (15).

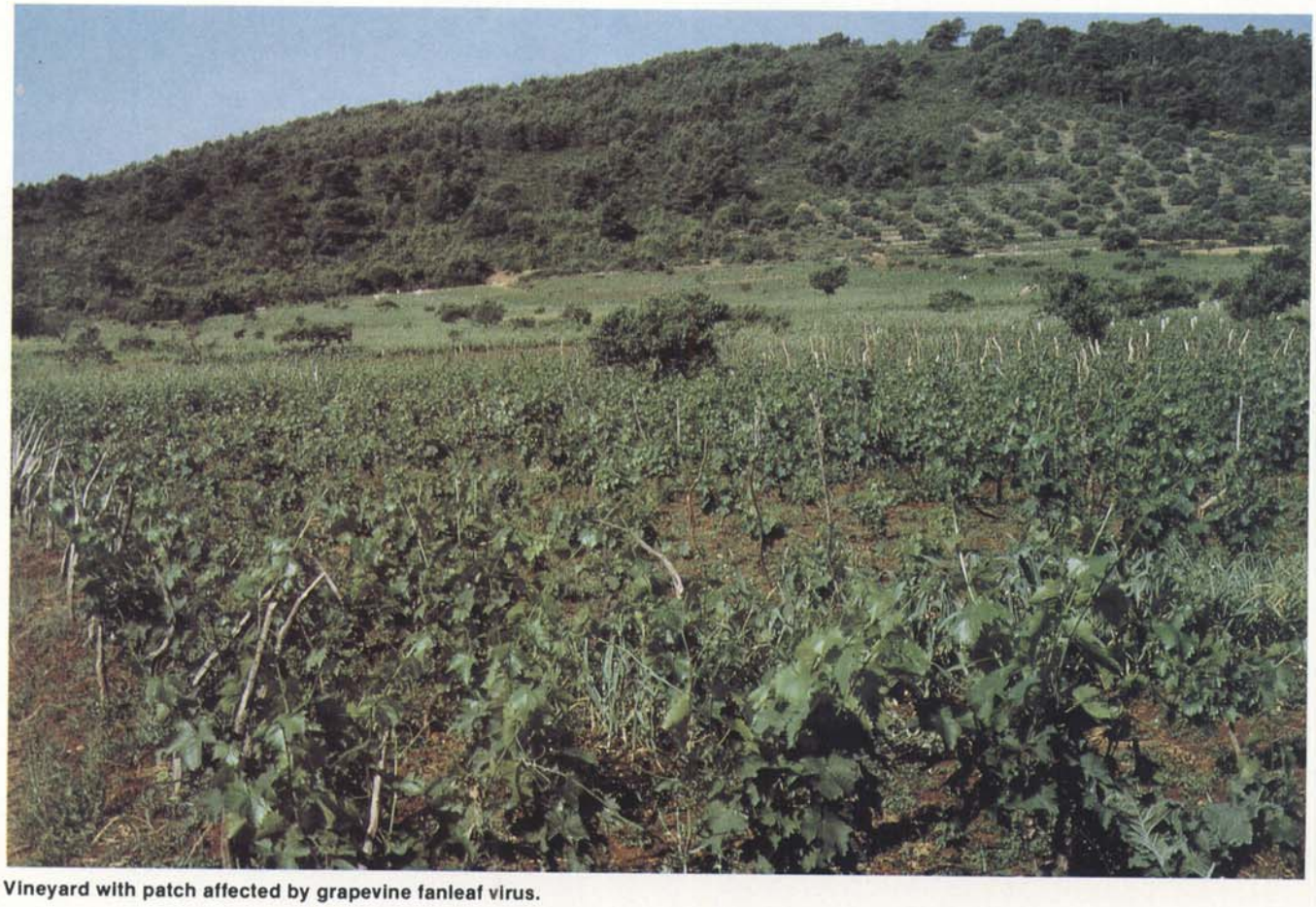
A nematode vector does not necessarily become viruliferous when feeding on a host infected by the virus it normally transmits. Evidence exists that only the particles free in the cytoplasm are adsorbed at the retention site and that virions contained in membranous tubules pass into the intestine. Specific adsorption at retention sites involves surface interaction determined by charge densities (16). Virus particles are released by changes in the pH or ionic condition occurring during salivation (16). Viruses do not persist through a molt, since all cuticular linings are shed and do not pass through eggs (15).

Factors Complicating Control

Nematodes are the main agents for spreading nepoviruses and tobraviruses over short distances but, because of limited mobility, are not very efficient; spread by nematode vectors only seldom exceeds 1–1.5 m a year. Many nematode-borne viruses are also seedborne, however, and several weed species are hosts for both viruses and nematode vectors (16). Although not significant for vegetatively propagated plants, infected seeds constitute a reservoir for vectors in which viruses persist only a short time.

Economical and practical rotations to control nematode-vectored viruses are difficult to adopt because the range of hosts is wide and seed and pollen transmit many of the viruses. The vector of grapevine virus, *X. index*, does not thrive on weeds; because root fragments from previous crops remain in the soil as virus reservoirs for over 3 years, short-range rotation is almost impossible. In France, a 7-year interval is advised between removing nematode-infected grapevines and planting new ones, with cereal or alfalfa grown during the interval. In Italy, rotation has not controlled tobacco rattle virus in soil infested by *T. viruliferus*, even at population densities below detection level. Soil fumigation followed by 2 years of complete fallow, on the other hand, controls arabis mosaic virus in hop fields infested by *X. diversicaudatum* (4).

One of the most attractive practices for disease control in modern agriculture is



Vineyard with patch affected by grapevine fanleaf virus.

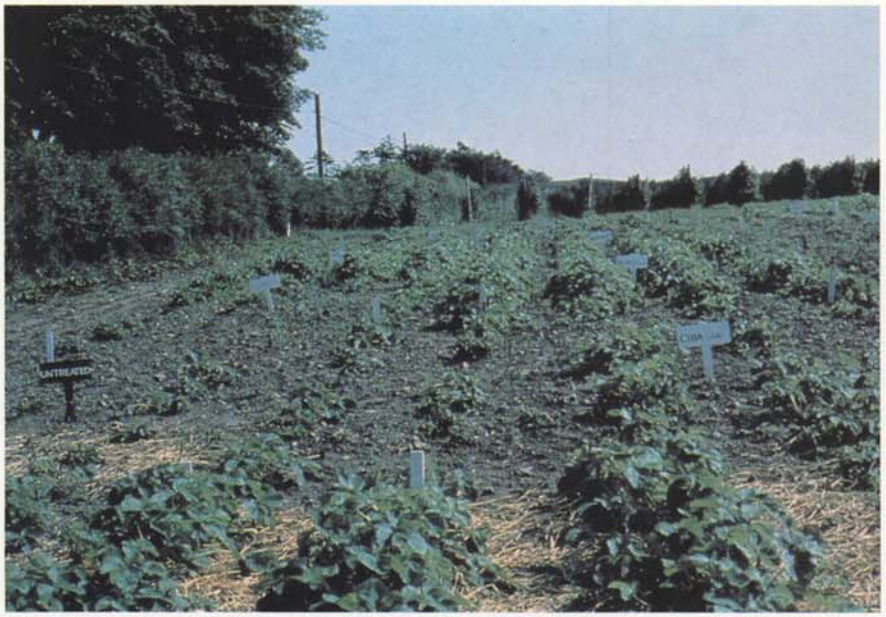
growing resistant cultivars. Cultivars must be resistant to the virus, however, since resistance to the nematode vectors provides very little protection. A single stylet probe in an attempt to feed is sufficient to inoculate virus particles into host cells; this occurs with raspberry ringspot virus on raspberry, which is not a suitable host for the nematode vector, *L. elongatus* (4). Red raspberry (*Rubus idaeus*) is resistant to several nepoviruses, and 38 of 300 pea cultivars tested in the Netherlands showed varying degrees of resistance to the tobravirus pea early browning.

Nematicides: Most Practical

Although the best way to control virus diseases is to use virus-free plant material, the most practical method of preventing spread of nematode-vectored viruses is to apply nematicides. Because of the epidemiologic features of nematode-borne viruses, the vector must be almost eradicated.

A number of interacting abiotic and biotic factors affect efficiency of nematode control. All nematode vectors of plant viruses are ectoparasitic and therefore are readily exposed to chemicals in the soil. Laboratory tests have shown that *X. italiae* is less sensitive to 1,2-dibromo-3-chloropropane (DBCP) than *L. euonymus* (5), but no data are available on the comparative susceptibility of various nematode genera and species to nematicides. Application of 1,200–2,000 L/ha of fumigants containing 1,3-dichloropropene (DD) (14) eradicated *Meloidogyne incognita* to a depth of 2 m in the field. Laboratory tests indicate that a 100% kill of second-stage larvae of *M. incognita* would require a 3-day exposure to 2.5 μg of DD per gram of dry soil (2). The same dosage should be sufficient to control 99.9% of all stages of *X. index* (11). Larvae of *X. index* seem to be less sensitive than adults to methyl bromide; 27-hour exposure to 600 ppm is required to kill larvae, compared with 43-hour exposure for adults (19). Total kill of all stages of *X. index* was achieved with 530, 350, and 50 ppm of methyl bromide and exposure times of 24 hours, 3 days, and 21 days, respectively (1). Temperature affects toxicity of nematicides; for a 95% kill of soil-living stages of plant-parasitic nematodes, 35, 81, and 290 ppm of ethylene dibromide in the soil water phase were necessary at 25, 15, and 5 C, respectively (11).

Nonfumigant nematicides, such as aldicarb and oxamyl, seem to have nematostatic rather than nematicidal action. At certain doses, these agents temporarily affect nematode behavior by delaying egg hatching, reducing motility, or preventing feeding and therefore are effective only on crops with a short period of susceptibility to a virus. Some chemicals are systemically translocated in plants but do not protect a crop against virus infection, since to be intoxicated the nematode must first feed on the roots. In the case of oxamyl, the nematicidal substance is exuded from the roots.



Strawberry latent ringspot virus transmitted by *Xiphinema diversicaudatum*: (left) untreated plants and (right) plants treated with a nematicide.

Raspberry ringspot virus transmitted by *Longidorus elongatus*: (foreground) untreated plants and (background) plants treated with a nematicide.

Importance of Nematicide's Movement and Persistence

Efficiency of control is greatly influenced by the movement and persistence of the nematicide in the soil. The toxicant must reach the nematode, which should be exposed long enough to absorb a lethal dose. Nonfumigant nematicides, such as the organophosphates and oxime carbamates, move through the soil in water. Therefore, their distribution pattern can be improved by appropriate irrigations or their persistence can be greatly reduced by abundant rain that moves them into deeper layers of soil. Generally, the organophosphates, such as fenamiphos, are most effective at temperatures above 25 C and the carbamates, such as aldicarb and oxamyl, at temperatures below 20 C.

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Fumigants, on the other hand, move through the soil primarily in the gaseous phase, when diffusion is at least 1,000 times faster than in the water phase. High soil moisture greatly limits the movement of a fumigant like DD, where 1% of the total concentration is dispersed in the air phase, 10–20% is dissolved in the water phase, and 80–90% is adsorbed to the soil (9). Pore spaces are blocked in saturated soil, severely restricting diffusion. Soils with small pores impede fumigant and moisture movement the most. Usually, the deeper the soil, the smaller the pores.

Clay soils are the most difficult to treat because pores are small and cracking occurs during drought. Fumigants tend to diffuse upward, especially when the deep soil layers are compacted or water-saturated, and are not retained in clay or other coarse soils long enough to be effective. An estimated 5–10% of DD applied at a depth of 0.3 m under normal conditions in agricultural soils is lost to the atmosphere (11).

A nematicide must be thoroughly diffused to control nematode vectors of plant viruses. Viruliferous *X. index* have been found as deep as 2 m in old vineyards in southern Italy and 3.6 m in California. The largest populations, however, are generally located at depths between 0.3 and 0.6–0.8 m.

High doses of DD completely killed plant parasitic nematodes to a depth of 2 m in California. McKenry (10) suggests that lethal doses are possible to a depth of 0.75–1.5 m when the rate of application is selected on the basis of soil structure, moisture, and temperature—the factors affecting diffusion of the fumigant in the soil. Applying split doses at different depths improves downward diffusion (13). However, DD penetrated 1.2 m of soil with a moisture content of 7.7% but only 0.46 m of soil with a moisture content of 23% (11). Methyl bromide moves first by mass flow and therefore disperses faster in the soil, especially downward; injection to 0.75–0.8 m was lethal to nematodes to a depth of 2.44 m (3).

Soil structure, moisture, and temperature also affect persistence of a fumigant. DD disappears at a rate of 2–3.5% daily in sandy soils at 15–20 C and at a rate of about 25% in clay soils (18). In southern Italy, DD injected in August in sandy soil with a moisture content of 0.8% and a temperature of 25–30 C persisted for 18 days at a depth of 0.25 cm (6). When the same field was treated in January when soil temperature was 5–8 C and water content was close to saturation, DD was detected up to 92 days after injection. In a sandy clay soil, the fumigant persisted for 122 days after application in August with soil moisture at 4% and for 152 days after application in January to saturated soil. Soil adsorption and biodegradation also affect chemical persistence.

Preparing the Soil and Timing the Application

Although success or failure of treatment generally depends on choosing the nematicide that best suits the local situation, preparation of the soil and timing and method of application are also important. Soil should be cultivated deeply to break up layers that prevent vertical diffusion, residues of the previous crop should be removed, and soil clods that may be protecting nematodes should be broken. Compacting or slightly wetting the soil surface after treatment helps restrict upward movement of the fumigant into the atmosphere.

In temperate climates, nematicides with long persistence should be applied in the autumn, when soil temperature is still high enough to allow uniform distribution of the chemical and before the rainy season. Conditions are optimal in subtropical regions at the end of winter or beginning of spring, before the dry season. The temperature limits for fumigant application generally range between 5 and 25 C (11). Application rates are usually selected according to the crop (annual or perennial) and soil structure and depth. Soils with high clay or organic matter content require larger doses. DD control of grapevine fanleaf virus in France was more efficient at a rate of 1,000 L/ha in shallow soils than at a rate of 1,500 L/ha in deep soils (7).

Very high rates of chemicals are generally used, since the aim of treatment is to eradicate nematodes; rates of DD up to 2,500 L/ha have been used in California (13). Such treatments are very expensive, and the economics should be evaluated for each case and local situation.

In Scotland, DD applied at a rate of 200–400 L/ha almost completely controlled tobacco rattle virus in a potato crop, reducing the population of trichodorid nematodes to less than 1% of the initial density (8). Virus infection in the same field was greatly reduced the second year after treatment but was unaffected the third year. In California, grapevine fanleaf virus and the vector *X. index* were controlled for 4 years in vineyards treated at replanting with 2,500 L/ha of DD (13). In France, good control for up to 16 years was obtained with DD in doses of 1,000 L/ha (7). In Germany, the cost of treatment in vineyards is estimated as paid for by the fourth cropping year.

Failures and Drawbacks

In England, on the other hand, arabis mosaic virus in heavy soils of hop fields was poorly controlled by preplanting fumigation with various chemicals, even though the vector population was reduced by more than 95% (12). In addition, DD applied at the rate of 500–1,000 L/ha to vineyard soil in southern Italy had very little effect on the nematode populations and did not increase grape yields during the first 4 years after treatment.

Treatment failure is not related only to improper use of a chemical or unsuitable conditions. Some side effects of nematicides on plants suppress or reduce the benefits of nematode control. When time between treatment and planting is insufficient, phytotoxicity may occur. High doses may increase chemical persistence by killing the agents that biodegrade the chemical and by altering the nitrification balance of the soil, or by

reducing the population of endomycorrhizae.

Finally, nematode populations, including vectors, often increase rapidly after soil fumigation. This may be due to the absence of competitors or natural enemies or to as yet unknown factors. Speed and intensity of recolonization depend on various environmental factors, including the host and the structure and temperature of the soil.

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