Is the Pine Wood Nematode an Important Pathogen in the United States?

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ABSTRACT—The pine wood nematode, Bursaphelenchus xylophilus, *causes a serious disease of native pines in Japan. The nematode was recently identified as a pathogen in the United States, and pathologists have speculated that it may threaten forests here. Its ability to kill native North American pines growing in forests has not been established, but evidence suggests that it kills exotic pines (Scotch pine,* Pinus sylvestris, *and Japanese black pine,* P. thunbergii*) in this country. Insect vectors transmit the nematode to cut timber and dying trees during vector oviposition. Thus the nematode can be present in dying trees without being the primary cause of death. Transmission during oviposition may explain its recent association with stressed trees in the United States.*

Nematodes are microscopic worms which are not generally considered to be important pathogens of forest trees except in nursery seedbeds. Most pathogenic nematodes on forest trees are found in the soil and cause slow declines rather than rapid tree death. Recent discovery of the pine wood nematode in the United States, however, has prompted pathologists to change their attitude, for this pest has been causing epidemic losses in forests of Japan.

The pine wood nematode was first described by Mamiya and Kiyohara (1972) as *Bursaphelenchus lignicolus*. It was associated with heavy losses of native Japanese pines (*Pinus densiflora* and *P. thunbergii*) originally thought to be killed by bark beetles. Two million cubic meters of wood have been lost since 1978; and during 1981 alone, $30 million was spent to control the disease (Oku 1982).

In comparison to other nematodes, the pine wood nematode is unusual because it is a pathogen of aboveground parts of trees, is carried by an insect, and does not enter the soil. Other related nematodes carried by insects to aboveground parts of trees feed on fungi in insect galleries and do not kill trees. One exception is *Rhadinaphelenchus cocophilus*, which causes red ring, a serious disease of coconut. This nematode is carried by palm weevils and is transmitted to coconut palms when the weevils oviposit.

Disease Cycle

The pine wood nematode *(fig. 1A)* is carried by cerambycid beetles (Coleoptera:Cerambycidae), insects that are best known as wood borers in their larval stage. These beetles oviposit through the bark of dead and dying trees, leaving eggs in the bark-wood interface. Larvae penetrate the wood and feed on sugars in the wood cells. The result is a serious loss of wood volume and quality. Beetle larvae are inactive during the winter and pupate and emerge in spring. After emergence *(fig. 1B)*, the adult beetles feed (maturation feeding) on the phloem of young pine branches.

Ecologically, the life cycles of cerambycid beetles and that of the pine wood nematode are well integrated. The nematodes have two cycles of reproduction *(fig. 2)*. The propagative cycle begins in the spring and continues throughout the growing season. Under optimum environmental conditions, growth of nematodes from eggs to reproductive maturity is completed in five days. During this period the nematodes develop very rapidly in newly infected trees and also on fungi in dying or recently killed trees. In addition to the propagative cycle, nematodes may also develop through a dispersal phase. This phase takes place during times of stress such as when the wood becomes dry after tree death or in late fall. Here, as the nematodes moult from the second larval stage to the third larval dispersal stage, they contain high levels of lipids and are extremely resistant to adverse environmental conditions such as freezing and dessication.

At the end of winter, nematodes moult from the dispersal stage to the fourth larval stage and are called transmission or dauer larvae. Dauer larvae develop in response to the presence of maturing cerambycid beetle pupae. Dauer larvae enter the spiracles of the beetles and are carried from the dead trees with emerging beetles in spring (Ishibashi and Kondo 1977).

In Japan, beetles carrying nematodes emerge from trees in May and June (Mamiya and Enda 1972) and begin maturation feeding. Dauer larvae leave the tracheae through the spiracles and enter feeding wounds made by the insect. The nematodes moult to the adult stage, mate, and reproduce rapidly in the resin canals of the host. Within 30 days, Japanese pines exhibit decreased transpiration and oleoresin flow. Trees become chlorotic and die within three months (Mamiya 1972). Cerambycid beetles carrying the nematodes are attracted to dying trees and oviposit in them. Therefore, cerambycid larvae develop in trees containing millions of nematodes that later colonize the adult insects before their emergence as adults. The beetles thus transmit a pathogenic nematode to healthy trees. As the trees die ..ey provide wood essential for beetle development.

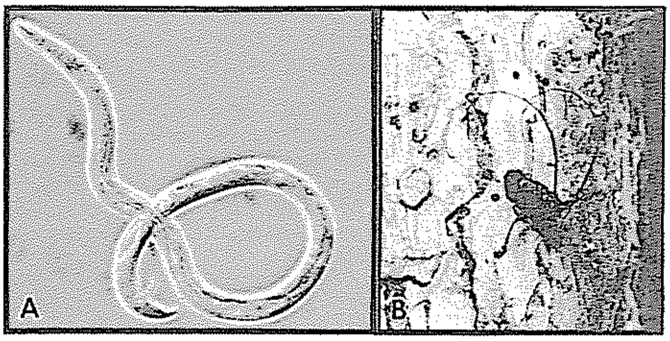

Figure 1A.—Adult male pine wood nematode. B.—Cerambycid beetle **(Monochamus carolinensis)** ***emerging from dead pine log.***

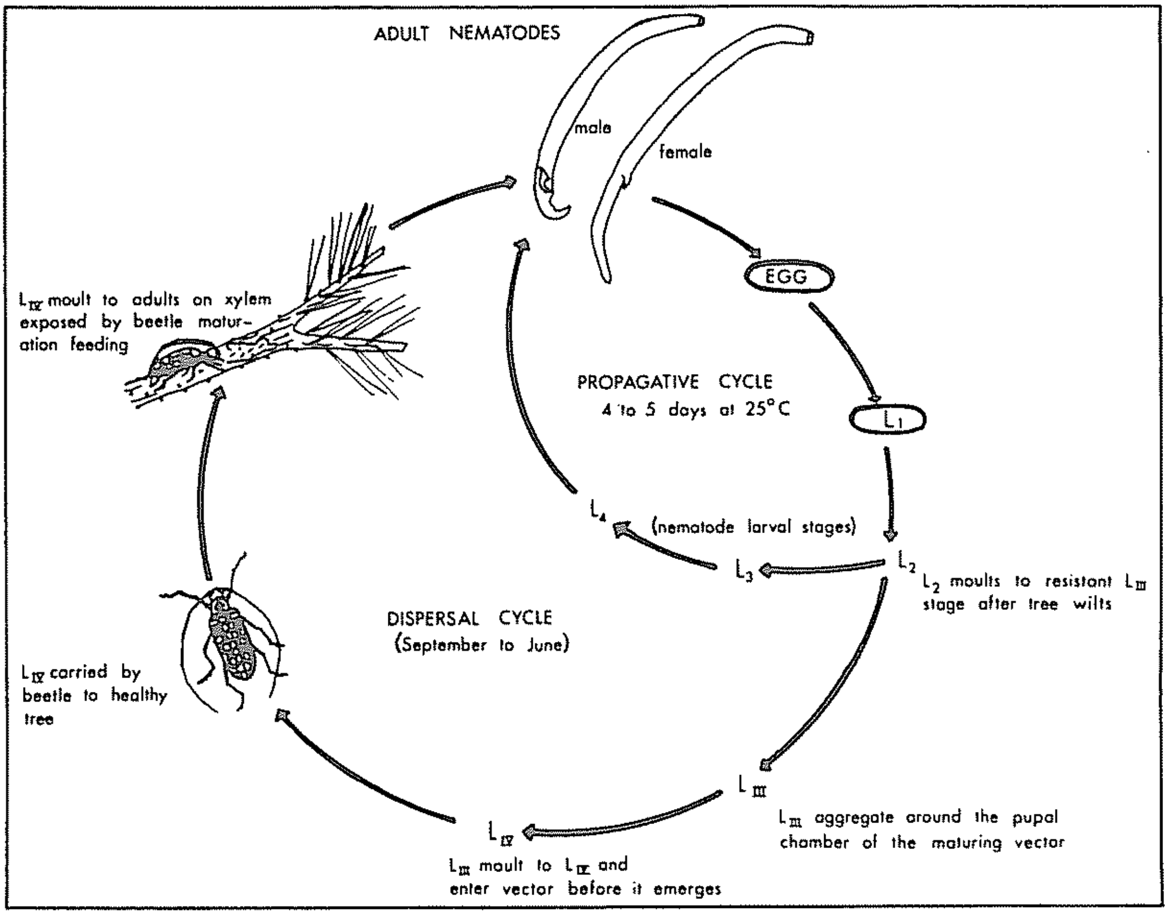

Figure 2. Life cycles of the pine wood nematode. In the propagative cycle, L_2 to L_4, development usually is rapid. Larvae develop through the dispersal cycle (L_2, L_{III}, L_{IV}) during late fall, when temperatures drop.

Occurrence and Pathogenicity in the United States

In 1979, the pine wood nematode was found in a dying Austrian pine *(P. nigra)* in Columbia, Missouri (Dropkin and Foudin 1979). Knowledge of the disease associated with the nematode in Japan led to speculation concerning the potential threat to United States forests (Dropkin et al. 1981, Wingfield et al. 1982a).

Soon after the nematode was found, it was realized that it was identical to *Aphelenchiodes xylophilus*, collected from dead pine wood in 1929. The name *B. lignicolus* was therefore changed to *B. xylophilus* (Nickle et al. 1981). The nematode has thus been present in this country for a considerable time. The apparent absence of an epidemic such as that in Japan has led to speculation that it is native to the United States.

Since the discovery in Missouri, researchers have found the nematode widely distributed on many pines and other conifers (Robbins 1982). In view of the infestation in Japan, is severe damage likely to occur in North America? The first step in answering this question is to determine whether the nematode is a primary pathogen and able to kill trees. Inoculation in the greenhouse showed that it can kill seedlings of native American pines (Kiyohara and Tokushige 1971, Dropkin and Foudin 1979). It was subsequently found to be pathogenic on seedlings of conifers such as larch (*Larix* spp.) and balsam fir *(Abies balsamea)*.

Inoculations of seedlings in the greenhouse only provide clues to what may be happening in the forest. To prove that the nematode is killing trees, it is necessary to inoculate trees in a forest as was done in Japan. During the summer of 1981, we inoculated large numbers of jack pine *(P. banksiana)*, red pine *(P. resinosa)*, and Austrian pine in Minnesota and Wisconsin forests with *B. xylophilus* isolates that killed pine seedlings in greenhouse tests. Nematodes were inoculated into wounded branches in tree crowns during late spring, the time when cerambycid beetles started emerging. Trees were each inoculated with up to 40,000 nematodes, similar numbers to those used in successful field inoculations in Japan (Mamiya 1972). These inoculations did not result in any apparent damage to the trees.

The nematode has been reported most commonly from Scotch pine in the United States and this pine may be more sensitive to infestation than the others. However, this pine is most commonly grown as an ornamental or in Christmas tree plantations, and one would therefore expect that dying trees would be more obvious and tested for the causal agent more often than forest trees have been. In recent research a small number of Scotch pines died after inoculation in the field (Malek 1982). In greenhouse inoculations Scotch pines have also been more sensitive than other pines (Dropkin et al. 1981). Jack pine has been reported to be among the most sensitive species in greenhouse tests (Dropkin et al. 1981), but we have not been able to infect this species in the forest.

Careful inoculations in United States forests are clearly needed before pathologists and foresters are able to com-

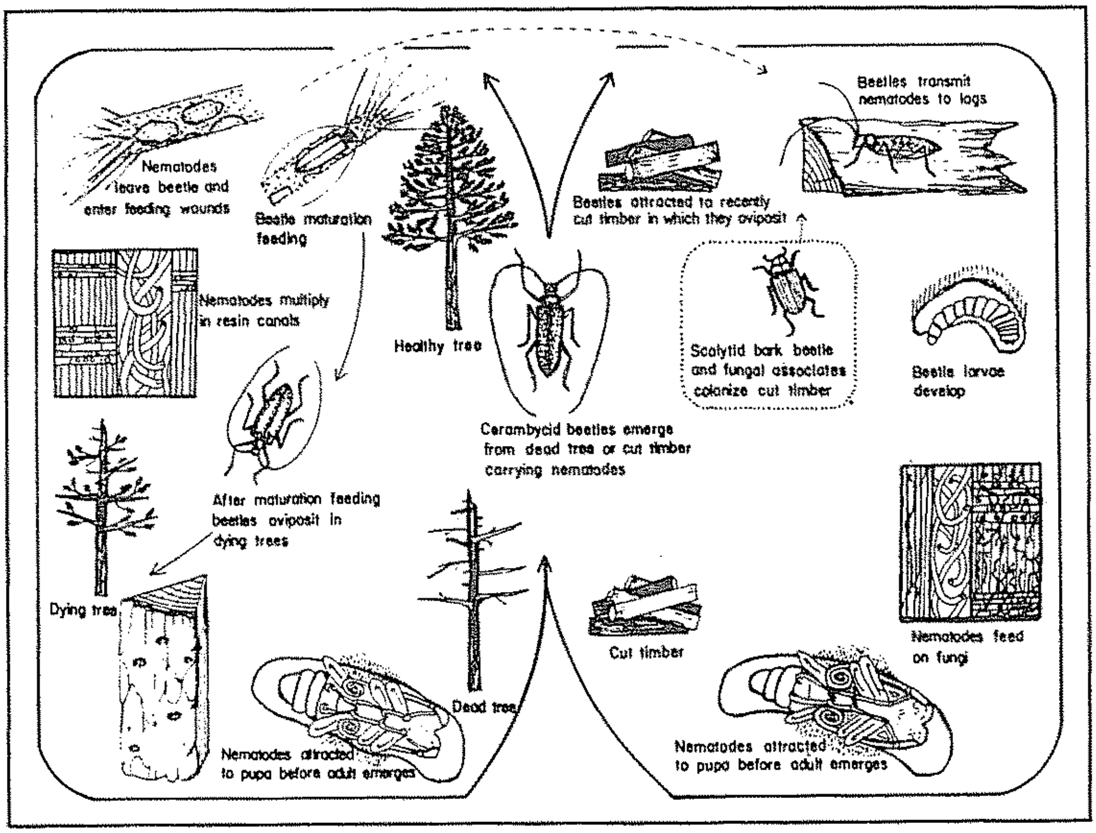

Figure 3. Possible interactions between the pine wood nematode, cerambycids, and scolytids. Left side of figure depicts nematode-associated disease cycle as described in Japan. A similar cycle may occur in the United States. Right side of the figure illustrates a disease cycle in dead or dying trees. Nematodes are transmitted to cut timber or dying trees either before or after maturation feeding on healthy trees. They feed on fungi transmitted to the same wood by scolytid bark beetles. Once in the cut timber or dying trees, they develop in association with the cerambycids as in the cycle on the left side of the figure.

ment on the potential pathogenicity of the pine wood nematode to all conifer species in this country.

Association with Stressed Trees

If the nematode is not necessarily the primary cause of tree death in the United States, why is it so common in dead and dying trees? In all areas examined, we have found that dying trees infested with *B. xylophilus* are affected by some other factor able to kill trees independently. For example, tops of eastern white pine *(P. strobus)* killed by blister rust *(Cronartium ribicola)* were found to be infested with the nematode (Wingfield et al. 1982b).

These observations have led us to hypothesize that the nematode can be transmitted when the beetle vectors oviposit in dying trees and cut timber. We were aware that the nematodes were transmitted during maturation feeding in Japan but speculated that it was possible for beetles to transmit nematodes during egg laying. To test the hypothesis we first attempted to ascertain that *B. xylophilus* could be transmitted to cut timber. The tests involved felling healthy, nematode-free trees and allowing cerambycid beetles to oviposit in the logs. After four months, pine wood nematodes were found in the previously uninfested wood (Wingfield 1982). This was circumstantial evidence that *B. xylophilus* can be transmitted during cerambycid beetle oviposition. More detailed laboratory observations confirmed the observation (Wingfield and Blanchette 1983). The presence of nematodes in trees killed by insects, pathogenic fungi, or factors such as lightning strikes is thus most likely due to transmission during beetle oviposition in dying trees.

Suggestions that North America cerambycids may not be as effective vectors as is *Monochamus alternatus* in Japan (Wingfield et al. 1982a) are worth considering. However, preliminary tests indicate that cerambycids in the United States carry comparable numbers of nematodes and can transmit them to seedlings of susceptible tree species. Thus, if American native pines are resistant to pine wood nematode infestation, it is unlikely that a more effective vector would provide the difference between the situation in the United States and Japan.

Survival of Nematodes in Dead Trees

B. xylophilus belongs to a group of nematodes that commonly feed on fungi. Cerambycid beetles oviposit in dying trees at approximately the same time that the trees are infested by bark beetles and their fungal associates. Therefore, nematodes transmitted to dying trees during cerambycid beetle oviposition are able to enter and feed on blue stain fungi, including *Ceratocystis* spp., associated with bark beetles in dying trees. The transmission of the nematode to cut timber and dying trees and its survival on fungi in the dead wood represent an alternative life cycle to that described in Japan, where the nematode infests healthy trees *(fig 3)*. This cycle provides an ecologically efficient means for the nematode to perpetuate itself in the absence of susceptible trees. It also explains the frequency with which it is found in trees dying of other causes. All possible causes should be considered before tree death is attributed to nematode infestation alone.

The common occurrence of the nematode in dead pines in the United States and its adaption to survive in cut timber increase the possibility of its being introduced into new areas. Such spread could easily occur if packing cases or dunnage contain infested wood.

If Scotch pine is as sensitive as preliminary investigations indicate, it is crucial that the nematode not be introduced into areas where this pine is native. A serious effort should be made to see that packing cases and dunnage leaving the United States and Japan do not contain wood infested with cerambycid beetles or pine wood nematodes. An attempt should also be made to alert quarantine officers in other countries of the need to inspect wood for this potentially important pathogen.

The View at Present

What then is the significance of *B. xylophilus* as a pathogen on trees in this country? Research suggests that Scotch pine seedlings are susceptible in greenhouse tests, and preliminary evidence shows that this may also apply in the field. Scotch pine is an important ornamental species in some areas and is a popular Christmas tree species. The nematode may be a significant problem in these cases.

All indications are that our native pines and other conifers are resistant. This inference is supported by evidence that the nematode is probably native to the United States, but careful field inoculations will be needed to clarify the question. ■

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