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Nematode–Vector Relationships in the Pine Wilt Disease System[1]

M. J. LINIT[2]

Abstract: Pinewood nematode, *Bursaphelenchus xylophilus,* is the causal agent of pine wilt disease in North America and Japan. Dispersal stage dauer larvae are transported to new host trees on the body surface and within the tracheal system of several beetle species. Worldwide, 21 species of Cerambycidae, 1 genus of Buprestidae, and 2 species of Curculionidae are known to carry pinewood nematode dauer larvae upon emerging from nematode-infested trees. Five species of cerambycids in the genus *Monochamus* are known to transmit dauer larvae to new host trees, four North American species and one Japanese species. Primary transmission to healthy trees occurs through beetle feeding wounds on young branches. Secondary transmission to stressed trees or recently cut logs occurs through *Monochamus* oviposition sites.
Key words: Bursaphelenchus xylophilus, Cerambycidae, insect vector, *Monochamus alternatus, Monochamus carolinensis, Monochamus scutellatus, Monochamus titillator,* pine sawyer, pine wilt disease, pinewood nematode, transmission.

Pinewood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer, 1934) Nickle, 1970, is associated with dead and dying conifers, particularly pines, and recently cut conifer logs throughout North America and Japan. The nematode is the causal agent of pine wilt disease (34) but is also associated with trees stressed or killed by other mortality factors, both biotic and abiotic (57). The nematode population builds rapidly within a susceptible host tree feeding on epithelial cells of resin canals (33) and fungi introduced by secondary insects. These insects provide the nematode with transportation to new host trees. The association between the nematode and its insect vector is essential, for without the benefit of insect transport the nematode population is stranded within a rapidly degrading resource. The ability of the nematode to locate and contact an insect vector within the dying tree or log is necessary for the continued survival of the nematode population. As such, this association is an essential component in the population dynamics of *B. xylophilus* and the epidemiology of pine wilt disease.

Numerous insect species colonize weakened and dying pine trees (6,13). Insects associated with dying pines in the United States and Japan have been examined for the presence of *B. xylophilus.* These include families of Coleoptera (Cerambycidae, Curculionidae, Scolytidae, Buprestidae, Elateridae), Hymenoptera (Siricidae), Homoptera (Cercopidae), and Isoptera (Rhinotermitidae) (2,24,25,29,56). *B. xylophilus* is associated with several species of beetles but no insects from other orders. Garland (11) compiled a worldwide list of insect associates of *B. xylophilus* that included 21 species of Cerambycidae, 1 genus of Buprestidae, and 2 species of Curculionidae (Table 1). The associations between *B. xylophilus* and beetles in the genus *Monochamus* are the most significant, based upon the mean number of nematodes carried per beetle and the frequency of the nematode–beetle association (25,29,56). Nine species of *Monochamus* have been reported to carry *B. xylophilus.* Of these, five species have been demonstrated to transmit the nematode to new host trees or logs. Aspects of beetle biology and the association between *B. xylophilus* and its insect vectors are discussed as they relate to the transmission of this pathogen.

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[2] Department of Entomology, University of Missouri–Columbia, Columbia, MO 65211.
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TABLE 1. Insect species known to carry *Bursaphelenchus xylophilus* dauer larvae, with notes on insect range, host trees, and documentation of transmission. Adapted from Garland (11).

Family, species	Range†	Hosts‡	Transmission§	Ref. no.
Cerambycidae				
Acaloptera fraudatrix Bates	Japan	n.d.	n.d.	25,34
Acanthocinus griseus F.	Japan	n.d.	n.d.	25,36
Amniscus sexguttatus (Say)	N.A.	Pi, Pc	n.d.	29,56
Arhopalus rusticus L.	Japan	n.d.	n.d.	35,36
Arhopalus rusticus obsoletus (Randall)	N.A.	Pi	n.d.	29
Asemum striatum (L.)	N.A.	Pi, Pc	n.d.	29
Corymbia succedanea Lewis	Japan	n.d.	n.d.	25,35,36
Monochamus alternatus Hope	Japan	Pi, Pc, A, L	yes (48)	25,35,36,48
Monochamus carolinensis (Olivier)	N.A.	Pi	yes (26,27,31,56)	9,12,24,26, 27,29,31,56
Monochamus marmorator Kirby	N.A.	A, Pc	n.d.	56
Monochamus mutator LeConte	N.A.	Pi	yes (56)	56
Monochamus obtusus Casey	N.A.	Pi, Ps, A	n.d.	14
Monochamus scutellatus (Say)	N.A.	Pi, A, Pc, L	yes (56)	14,56
Monochamus titillator (Fabricius)	N.A.	Pi, Pc, A	yes (30,54)	4,9,24,30,37,54
Monochamus nitens Bates	Japan	n.d.	n.d.	25
Monochamus saltuarius Gebler	Japan	Pi	n.d.	25
Neacanthocinus obsoletus (Olivier)	N.A.	Pi, A	n.d.	4,24
Neacanthocinus pusillus (Kirby)	N.A.	Pi, A, Pc	n.d.	56
Spondylis buprestoides L.	Japan	Pi	n.d.	25,34,35
Uraecha bimaculata Thomson	Japan	Pi	n.d.	25,34
Xylotrechus saggitatus (Germar)	N.A.	Pi	n.d.	56
Buprestidae				
Chysobothris spp.	N.A.	Pi	n.d.	29,56
Cucurlionidae				
Hylobius pales (Herbst)	N.A.	Pi	n.d.	29
Pissodes approximatus Hopkins	N.A.	Pi, Pc	n.d.	29

† Range: N.A. = North America.
‡ Hosts: Pi = *Pinus,* Pc = *Picea,* A = *Abies,* L = *Larix,* Ps = *Pseudotsuga,* n.d. = not documented.
§ Transmission: n.d. = not documented; yes = transmission documented, see reference(s) indicated.

BIOLOGY OF *MONOCHAMUS*

The genus *Monochamus* includes several important wood-boring species that breed in conifers, especially *Pinus, Picea, Abies,* and *Pseudotsuga.* The genus contains a number of North American species, but the exact number and status of each is uncertain (10). Dillon and Dillon (5) listed 11 North American species, while Arnett (1) recently listed 8. Studies on the life histories and biology of several species have been published: *M. alternatus* (25,58), *M. carolinensis* (2,43,44,51,52), *M. titillator* (2,53), *M. scutellatus* (45), and *M. notatus* (40).

Species within the genus differ somewhat with respect to voltinism, developmental rates, and oviposition behavior; however, all share aspects of a common life cycle (10,50). Adult beetles are attracted to stressed trees and recently cut logs for mating and oviposition. Ikeda et al. (21,22) demonstrated that *M. alternatus* is attracted to mixtures of monoterpene hydrocarbons and ethanol released from dying host material. No sexual pheromones have been identified for *Monochamus,* and the volatile tree components appear to serve as a mechanism for bringing adults of both sexes together. Mating and oviposition occur on the dying host tree or log, usually during darkness hours (42,52).

Eggs are deposited beneath the bark through slit-like or pit-like niches (52,56, 58). The number of eggs deposited per oviposition site varies within the genus. A single egg is most common for *M. carolinensis* (52) and *M. alternatus* (33,58). *M. titillator* deposits multiple eggs per site with as many as nine eggs recorded (2,53). The larvae, called sawyers because of the sound they produce during gallery construction, feed initially on the inner bark, cambium, and outer sapwood. This creates surface galleries that are filled with coarse, fibrous shavings and frass. Later instars bore into the woody tissue forming a characteristic U-shaped gallery which terminates a few millimeters short of the cambial layer. *M. alternatus* (58) and *M. scutellatus* (45) develop through four larval instars prior to pupation. Instar development is variable in *M. carolinensis* reared on artificial diet with 3–8 instars observed prior to pupation (43). The number of instars is dependent upon the temperature at which the larvae are reared but is independent of the sex of the individual. Pupation occurs in the terminal end of the gallery in a chamber formed when the larva packs the gallery with shredded wood from gallery construction. The adult emerges by chewing a round hole through the remaining wood and bark. Emergence occurs within a few days of eclosion (43,45,58).

Newly emerged adults fly to healthy host trees and feed on the bark of young twigs. This feeding is necessary for maturation of the reproductive system (56,58). Adults feed for the duration of their lives and move between dying trees and recently cut logs for mating and oviposition and healthy trees for feeding.

Nematode–Beetle Association

Nematode attraction to the beetle: B. xylophilus juveniles aggregate in the xylem tissue surrounding the pupal cell of *Monochamus* vectors and molt to nonfeeding dauer larvae (33,34). Dauer larvae enter the pupal cell following beetle eclosion and climb onto the newly formed callow adult beetle. It appears that nematode attraction to the pupal cell is chemically mediated. Miyazaki et al. (in 58) reported that insect-produced fatty acids, such as linoleic acid, deposited on the walls of the pupal cell act as aggregation stimulants for *B. xylophilus*. They also found that dauer larvae are attracted by gases (CO_2) released during beetle respiration. No work on nematode attraction to North American vectors has been reported.

Within-beetle nematode distribution: Dauer larvae inhabit the tracheal system throughout the body of the adult life stage of *Monochamus* spp. (7,16,20,25,29,34,56). The majority of dauer larvae reside in the tracheae (Fig. 1) arising from the metathoracic spiracles and are distributed to a lesser extent within tracheae located in the abdomen, appendages, and the head. Some dauer larvae remain on the exterior body surface of the beetle (25). Dauer larvae have never been reported within the hemocoel of the adult insect nor within the respiratory system of the immature stages of the beetle. Carbon dioxide exits through the metathoracic spiracle during cerambycid respiration (3); thus dauer larvae may concentrate in tracheae of this body segment in response to the CO_2 gradient.

Within-beetle nematode density: Insect vectors of *B. xylophilus* have been collected extensively in North America and Japan. Only insect species within the genus *Monochamus* carry a high mean number of *B. xylophilus* dauer larvae per adult beetle. Linit et al. (29) reported that seven species of beetles carried *B. xylophilus* dauer larvae in Missouri; however, only *M. carolinensis* averaged more than 300 dauer larvae per adult. Similar results have been reported by investigators in Illinois (31,32), Minnesota and Wisconsin (56), and Virginia (4). Dauer larvae have been recovered from adults of eight species of cerambycids in Japan. The greatest number and highest frequency occurred in *M. alternatus*; the other cerambycids carried dauer larvae less commonly (33). Kobayashi et al. (25) summarized numerous reports on the mean number of *B. xylophilus* dauer larvae collected from recently emerged *M. alternatus* adults from various prefectures in Japan between 1974 and 1978. Mean nematode loads per beetle varied among collection years within prefectures and among prefectures within years. Mean values varied among the 18 reports from a minimum of 170 to a maximum of 19,500 dauer larvae per beetle. Similar values have been reported for

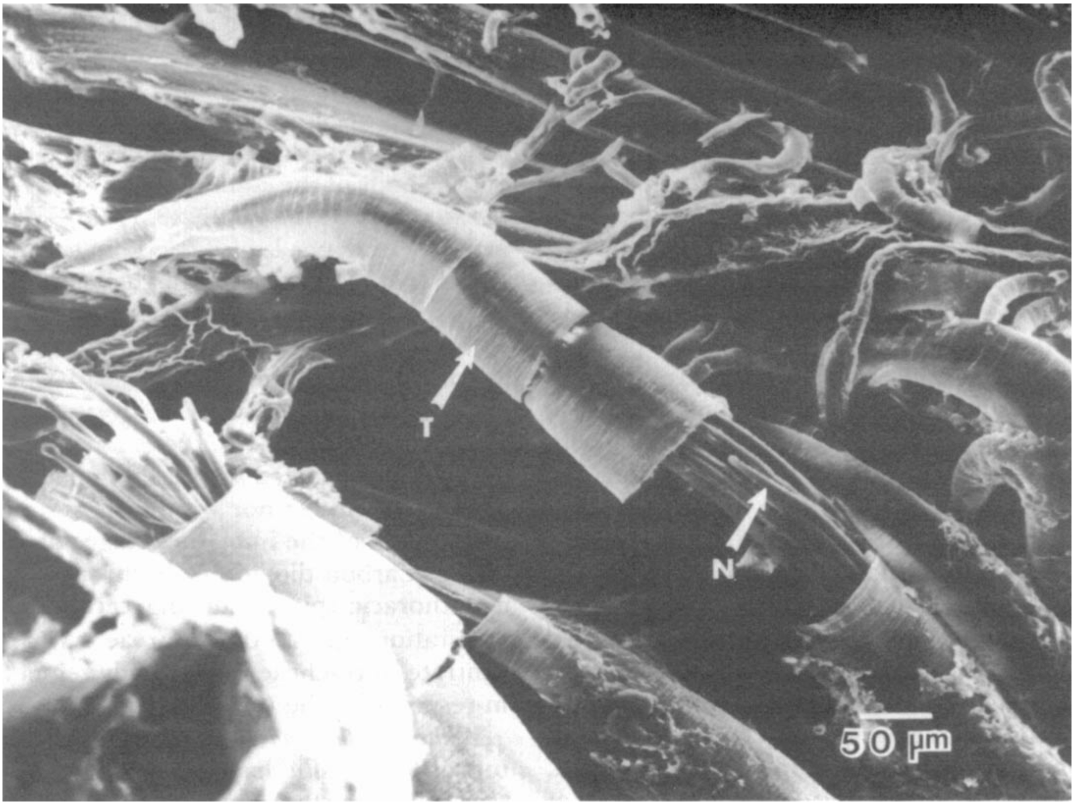

FIG. 1. Metathoracic trachea (T) of *Monochamus carolinensis* containing pinewood nematode dauer larvae (N).

North American species of *Monochamus* (29,31,32,56). The percentage of *M. alternatus* containing nematodes varied from 27 to 95. Beetle populations with the highest proportion of nematode-carrying beetles tended to have the highest mean nematode density per beetle. The highest nematode density reported for an individual adult *M. alternatus* was 289,000.

Variation in nematode density among beetles within a population is high, suggesting a contagious distribution of dauer larvae among the emerging beetle population. Whereas most beetles carry a low number of dauer larvae upon emergence from a nematode-infested tree, a few beetles carry a high nematode load. Kobayashi et al. (25) reported that more than 90% of the total number of dauer larvae extracted from a population of *M. alternatus* were obtained from only 20% of the insects, those having more than 1,000 nematodes per beetle. Hosoda et al. (19) reported a similar pattern.

Within-beetle nematode density is not related to the sex of the beetle in any of the *Monochamus* species that have been studied (19,29,47,56); however, relationships between nematode density and certain morphological qualities and seasonal patterns of emergence have been documented. Several investigators (20,29,47) have found a positive correlation between the weight of newly emerged *Monochamus* adults and the number of dauer larvae that they carry. Hosoda (15), however, found no correlation between beetle body length and nematode density. Japanese investigators have reported higher nematode densities in beetles that emerge early in the season compared with those that emerge later (25). Iwasaki and Morimoto (23) found the highest nematode density in *M. alternatus* adults collected in early June. Nematode density fell to near zero in beetles collected in early July. Takizawa (47) found nematode density highest during *M. alternatus* peak emergence in the spring. Similar studies on North American species have not been conducted.

NEMATODE TRANSMISSION

Insect transmission of *B. xylophilus* can occur in two ways (Fig. 2). Primary transmission occurs when nematodes enter a healthy tree through feeding wounds made by *Monochamus* vectors. Should this occur on a susceptible tree species, the tree may die as a consequence of nematode infection. Secondary transmission occurs when nematodes enter a dying tree or recently cut log through *Monochamus* oviposition sites. Although this form of nematode transmission does not contribute to the death of the host tree, it does serve to maintain a reservoir of nematodes to be dispersed by *Monochamus* beetles developing within the tree or log. Individual trees killed as a result of primary transmission of nematodes will likely be inoculated again during beetle oviposition. Secondary transmission of *B. xylophilus* to recently cut logs targeted for export as chipwood has recently stimulated embargo activity by several Scandinavian nations.

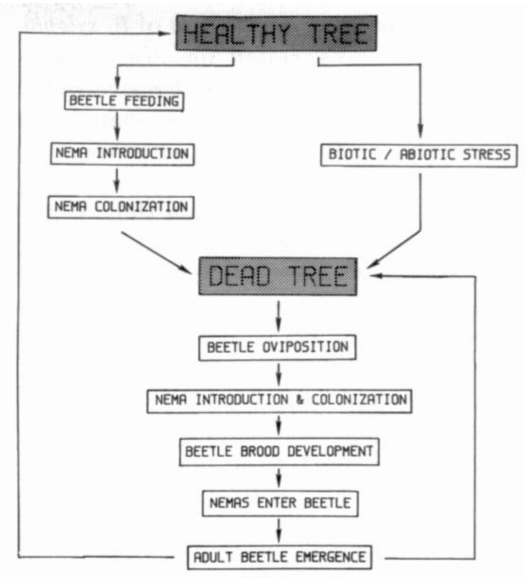

FIG. 2. Conceptual model of pinewood nematode transmission pathways. Primary transmission occurs when dauer larvae enter a healthy tree through *Monochamus* feeding wounds. Secondary transmission occurs on stressed trees or logs during *Monochamus* oviposition.

Nematode exit from beetles: The number of dauer larvae carried by beetles decreases with time following emergence of the adult beetle from the tree in which it developed. Dauer larvae exit the beetle through the spiracles, move toward the tip of the beetle's abdomen, then travel down the setae on the terminal abdominal sclerites and drop off (25,33). The drop-off rate has generally been reported to be low during week 1 following adult beetle emergence, reaching a maximum during the next 2 weeks, then declining and remaining low for the duration of the beetle's adult life stage. Enda (8) reported that 25% of all dauer larvae leave the body of *M. alternatus* within 10 days after beetle emergence, 87% by day 20 and 94% by day 30. Nakane (41) reported that drop-off begins immediately upon beetle emergence but is slow during week 1, maximized during week 2, then reduced beyond that time. Hosoda and Kobayashi (18) found the earliest dauer larval exit 3–5 days after beetle emergence, with the majority of nematode exit occurring after day 10. In another study (17), nematode exit peaked during week 3 then declined through week 5 and was somewhat consistent, but low, through week 10. Recently, Togashi (48) reported the majority of nematode exit occurred 10–40 days after *M. alternatus* emergence. Some Japanese workers concluded that the exit rate is so discontinuous that generalization may not be realistic (25). Linit et al. (28) followed nematode exit from *M. carolinensis* on a weekly basis and found a 12% (approximate) reduction in nematode density for each of the first 3 weeks following adult beetle emergence. Dauer larval exit from *Monochamus* is difficult to characterize because of a lack of standardized experimental procedures employed by researchers and poor comprehension of the processes mediating this behavior.

Primary transmission: Much research has been devoted to transmission of *B. xylophilus* dauer larvae through *Monochamus* feeding wounds on healthy trees because of the extent of host tree mortality associated with this pathway. Primary transmission is an essential component in the epidemiology of pine wilt disease in Japan (33,34) and certain parts of North America (30). The occurrence of primary transmission to pine seedlings and excised pine twigs has been documented by many investigators (7,26, 38,39,47,56). Review of this literature, largely in Japanese, is not covered here. This discussion is limited to primary transmission of dauer larvae to mature, field-grown trees. This pathway has been documented for *M. alternatus* on Japanese black pine (*Pinus thunbergii*) in Japan (7), *M. titillator* on slash pine (*P. ellioti*) in Florida (30), and *M. carolinensis* on Scots pine (*P. sylvestris*) in Missouri (27).

Enda (7) caged nematode-infested *M. alternatus* on 3–5-year-old branches of healthy 9-year-old (n = 10) and 20-year-old (n = 10) Japanese black pines for 30 days. All trees wilted, and *B. xylophilus* was recovered from each. Luzzi et al. (30) caged pairs of 3-week-old, nematode-carrying *M. titillator* on one lateral branch terminal on each of seven healthy 10-year-old slash pines. Individual branches contained 22–107 nematodes after 1 week of exposure to the beetles. Foliage on four of the trees wilted about 4 weeks later, followed by browning of the needles about 9 weeks after beetle feeding. No wilt symptoms were observed on the remaining three trees.

Linit (27) caged individual nematode-infested *M. carolinensis* adults on branches of nematode-free Scots pines for 24 hours. Nematodes were recovered from nearly 50% of the caged twigs, but nematode density was low. The percentage of twigs to which nematodes were successfully transmitted was dependent upon the age of the caged beetle. Transmission occurred on only 18% of the twigs fed upon by 1-week-old beetles, whereas nematodes were recovered from over 50% of the twigs fed upon by 2–3-week-old beetles. There was no difference in frequency of successful transmission between male and female beetles. Individual twigs contained up to 600 nematodes (unpubl.). Mean density was 27 nematodes per twig fed upon by female beetles and 8 for twigs fed upon by males. There was little difference in the number of nematodes recovered from twigs fed upon by beetles of different ages, with the exception that 1-week-old beetles were relatively poor transmitters. No correlations were found between the number of nematodes recovered per twig and either the number of nematodes carried per beetle or the amount of feeding on the twig. Togashi (48) found that the number of nematodes transmitted by *M. alternatus* to excised Japanese black pine twigs was highest for twigs fed upon by beetles with the highest nematode density.

Shibata (46) used a simulation model to estimate the seasonal fluctuation in *B. xylophilus* transmission by *M. alternatus* in a Japanese pine stand. He determined that dauer larvae began to invade trees about 10 June, peaked about 25 June, then gradually declined. The invasion period lasted about 65 days and peaked 2 weeks after adult beetle abundance was at its highest level.

The ability of a beetle to transmit dauer larvae to new hosts may be influenced by the number of nematodes that it carries. The longevity of *M. alternatus* adults is inversely related to the initial number of nematodes that it carries (49). Therefore, beetles carrying a high number of nematodes would be expected to possess a lower reproductive potential than the longer lived individuals in the same population that carry fewer nematodes. Togashi (48) suggested that nematode density divides the beetle population into three functionally different subpopulations. Beetles carrying numerous nematodes can successfully inoculate new host trees that become food for the next generation of beetles. Those carrying few nematodes do not inoculate new host trees with enough dauer larvae to overcome the host, but they do comprise the majority of the reproductive effort of the beetle population. The third group, carrying moderate nematode numbers, is characterized as being intermediate.

Secondary transmission: Transmission of *B. xylophilus* dauer larvae through *Monochamus* oviposition sites has received less research attention than the primary pathway. This is somewhat of an historical artifact, since Japanese investigators and researchers in the central United States have been faced with extensive tree mortality and therefore concentrated their attention on transmission to healthy trees. Wingfield (55), working in Minnesota where there is little nematode-associated mortality, was the first to report transmission of dauer larvae through insect oviposition scars. Nematode-free bolts of Austrian (*P. nigra*), jack (*P. banksiana*), and red (*P. resinosa*) pines were placed in a pine stand for 4 weeks. Bolts with cerambycid oviposition scars and larval development contained *B. xylophilus*, while the remaining bolts were nematode free. In another study (56), pairs of adult *M. carolinensis* and *M. scutellatus* from Austrian pine in Minnesota and *M. mutator* from red pine in Wisconsin were caged with nematode-free Austrian pine bolts. *B. xylophilus* was recovered from wood surrounding oviposition sites of all three *Monochamus* species. Luzzi et al. (30) documented secondary transmission in Florida slash pine. Pairs of *M. titillator* adults were placed in cages with nematode-free bolts. Nematodes were extracted from the wood underlying beetle oviposition scars in all seven replicates.

Future Directions

Research over the past 15 years has helped define the nematode–vector association and the role of insect vectors in the pine wilt disease system. Many questions remain unanswered, and new questions continue to arise in response to recent advances in our understanding of this complex system. A short list of relevant questions relating to the association between the pinewood nematode and its insect vectors follows.

How many *Monochamus* species vector *B. xylophilus* dauer larvae through either the primary or secondary pathways? What are the relative efficiencies of these species? Are any non-*Monochamus* species important vectors? Are vector differences important in explaining observed differences in pine wilt severity across geographical areas?

What mechanisms mediate dauer larval movement onto and into *Monochamus* vectors? Are these mechanisms the same for all vector species? What mechanisms mediate dauer larval exit from insect vectors? Are host plant volatiles important, or is drop-off a random process?

What interaction does environment have with the effectiveness of nematode transmission? Do temperature and humidity affect transmission efficiency?

What are the evolutionary implications of primary and secondary transmission occurring within a single disease complex?

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