The pine wood nematode: a comparison of the situation in the United States and Japan[1]

M. J. WINGFIELD AND R. A. BLANCHETTE
Department of Plant Pathology, University of Minnesota, St. Paul, MN, U.S.A. 55108

T. H. NICHOLLS
North Central Forest Experiment Station, St. Paul, MN, U.S.A. 55108

AND

K. ROBBINS
State and Private Forestry, U.S. Forest Service, St. Paul, MN, U.S.A. 55108

Received June 15, 1981[2]
Accepted October 26, 1981

WINGFIELD, M. J., R. A. BLANCHETTE, T. H. NICHOLLS, and K. ROBBINS. 1982. The pine wood nematode: a comparison of the situation in the United States and Japan. Can. J. For. Res. **12**: 71–75.

The pine wood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle, causes a wilt of pines in Japan. Severe damage to forests in Japan have been occurring for the past 30 years. Recently, the nematode has been found on conifers throughout the United States. Little is known of the biology and etiology of the pine wood nematode in North America. At present, there appears to be little threat to native coniferous forests of the United States and Canada. This is indicated by the wide host range and extensive geographic distribution of the nematode, association of the nematode on trees severely weakened by insects and diseases, and presence of the nematode in the United States since the early part of this century. Monoculture of susceptible conifers, offsite plantings and the introduction of potentially more effective vectors could, however, result in an increased damage by the nematode.

WINGFIELD, M. J., R. A. BLANCHETTE, T. H. NICHOLLS et K. ROBBINS. 1982. The pine wood nematode: a comparison of the situation in the United States and Japan. Can. J. For. Res. **12**: 71–75.

Le nématode du bois de pin, *Bursaphelenchus xylophilus* (Steiner et Buhrer) Nickle, est à l'origine d'une flétrissure des pins au Japon. Au cours des dernières 30 années, on a observé des dommages sérieux aux forêts japonaises. Récemment, ce nématode a été trouvé chez les conifères un peu partout aux États-Unis. On connaît peu la biologie et l'étiologie du nématode du bois de pin en Amérique du Nord. Pour le moment, il ne semble pas constituer une menace pour les forêts indigènes de conifères des États-Unis et du Canada. Cela découle d'observations portant sur la distribution du nématode qu'on trouve chez un grand nombre d'hôtes et sur une grande étendue géographique, son association avec les arbres fortement affaiblis par des insectes et maladies et sa présence remarquée aux États-Unis depuis le début du siècle. La monoculture d'espèces de conifères vulnérables, les plantations sur des stations inadéquates et l'introduction de vecteurs potentiellement plus efficaces pourraient cependant engendrer des dommages accrus de la part de ce nématode.

[Traduit par le journal]

Introduction

The pine wood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle, formerly *B. lignicolus* Mamiya and Kiyohara, causes a wilt of pine trees in Japan. During the last 30 years, epidemic losses have occurred on native Japanese pines (*Pinus densiflora* Sieb. et Zucc. and *P. thunbergii* Parl.). The extensive losses in stands throughout southwestern Japan have prompted the Japanese Government to allocate 35 million dollars for control procedures during 1980 (Mamiya 1980*a*). Recently, *B. xylophilus* has been found on several species of conifers throughout the United States. Concern has mounted as to the significance of the pine wood nematode in North America (Pine Wood Nematode Workshop, Columbia, MO, November 1980). This review summarizes the situation in Japan and evaluates the threat of the pine wood nematode to coniferous forests of North America.

The pine wood nematode in Japan

Bursaphelenchus xylophilus was first described by Mamiya and Kiyohara (1972), associated with extensive mortality of *P. densiflora* and *P. thunbergii* in southwestern Japan (Tokushige and Kiyohara 1969). When trees were inoculated with *B. xylophilus* in the glasshouse and field, symptoms similar to those in naturally infested trees were observed (Kiyohara and

[1]Paper No. 11 790, Scientific Journal series, Minnesota Agriculture Experiment Station, St. Paul, MN, U.S.A. 55108.
[2]Revised manuscript received October 14, 1981.

0045-5067/82/010071-05$01.00/0

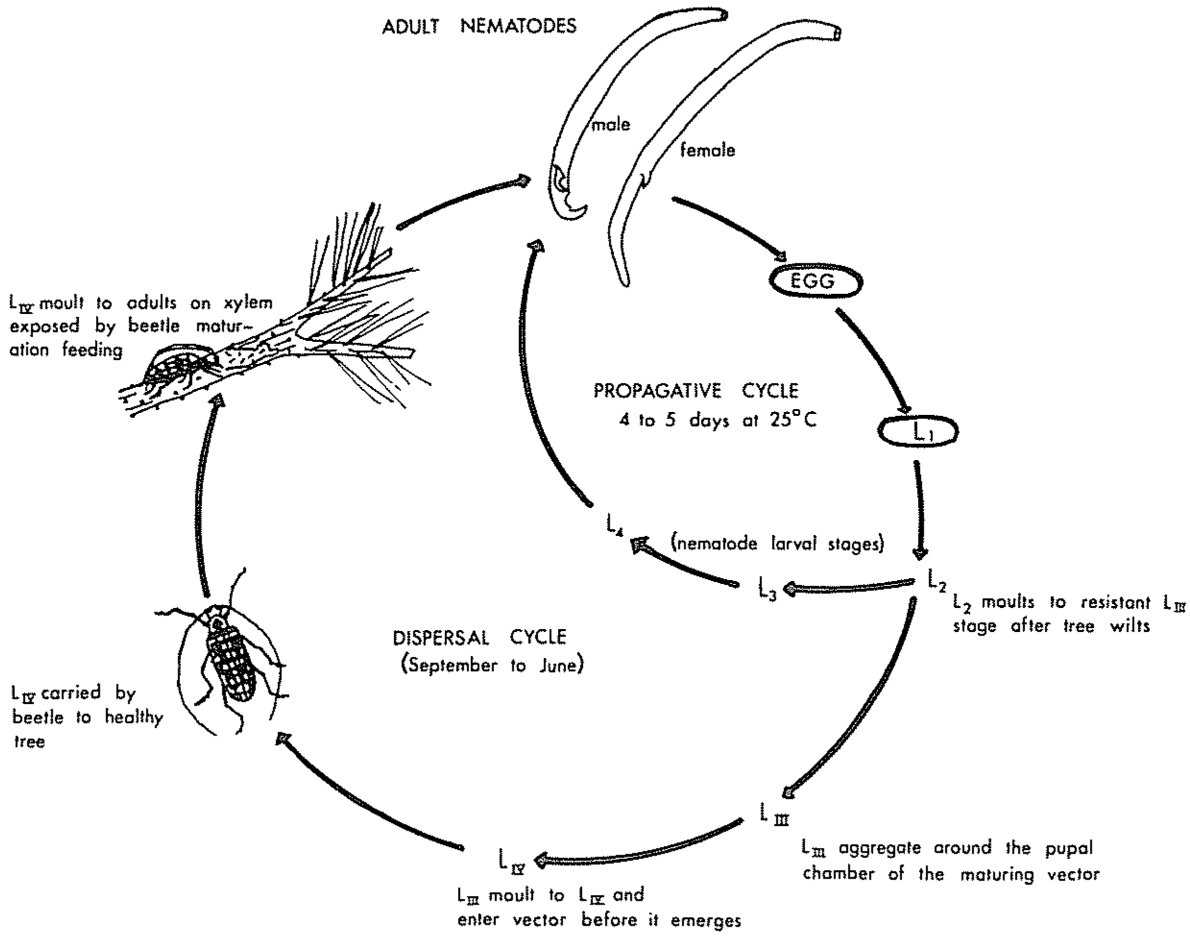

FIG. 1. The life cycle of *Bursaphelenchus xylophilus*.

Tokushige 1971; Mamiya 1972). Infested trees are conspicuous because they die soon after the first symptoms are seen. External symptoms include chlorosis, followed by browning and sudden wilt of the needles (Mamiya 1972).

The vectors for the pine wood nematode are longhorn beetles (Coleoptera: Cerambycidae) with a life cycle closely associated with that of the nematodes. *Bursaphelenchus xylophilus* has been recovered from eight species of Cerambycidae in Japan, of which *Monochamus alternatus* Hops. is considered to be the most effective vector (Mamiya and Enda 1972; Morimoto and Iwasaki 1972). The average number of nematodes carried by *M. alternatus* was 15 000 (Mamiya 1972) and the greatest number recorded from a single beetle was 230 000 (Mamiya 1976). *Bursaphelenchus xylophilus* can develop through either a dispersal or a propagative cycle (Fig. 1). Four larval stages and adult nematodes of both sexes occur in the propagative cycle which is completed in 4–5 days at 25°C (Ishibashi and Kondo 1977). The dispersal cycle includes the first two larval stages of the propagative cycle with the L_3 stage replaced by dispersal L_{III} larvae which have thicker cuticles and lipid reserves that enable them to withstand periods of adverse conditions. The L_{III} larvae are attracted to the pupal chambers of the vector. These larvae moult to the L_{IV} stage (dauerlarvae) which are resistant to moisture stress. The L_{IV} larvae enter the tracheae of the adult vector via the spiracles, shortly before the beetle emerges from the trees (Ishibashi and Kondo 1977; Kondo and Ishibashi 1978).

The vector emerges from dead trees in May or June carrying the nematode dauerlarvae. Immature beetles must feed on young shoots of healthy pines to mature. During maturation feeding, nematodes leave the beetle and moult to adults on the freshly exposed xylem (Fig. 2). The nematodes enter the resin canals of the host and feed on thin-walled epithelial cells (Mamiya and Enda 1972). The first symptoms of disease (within 2 weeks) are a decrease in oleoresin flow, and within 30 days arrest of transpiration occurs. Trees become chlorotic

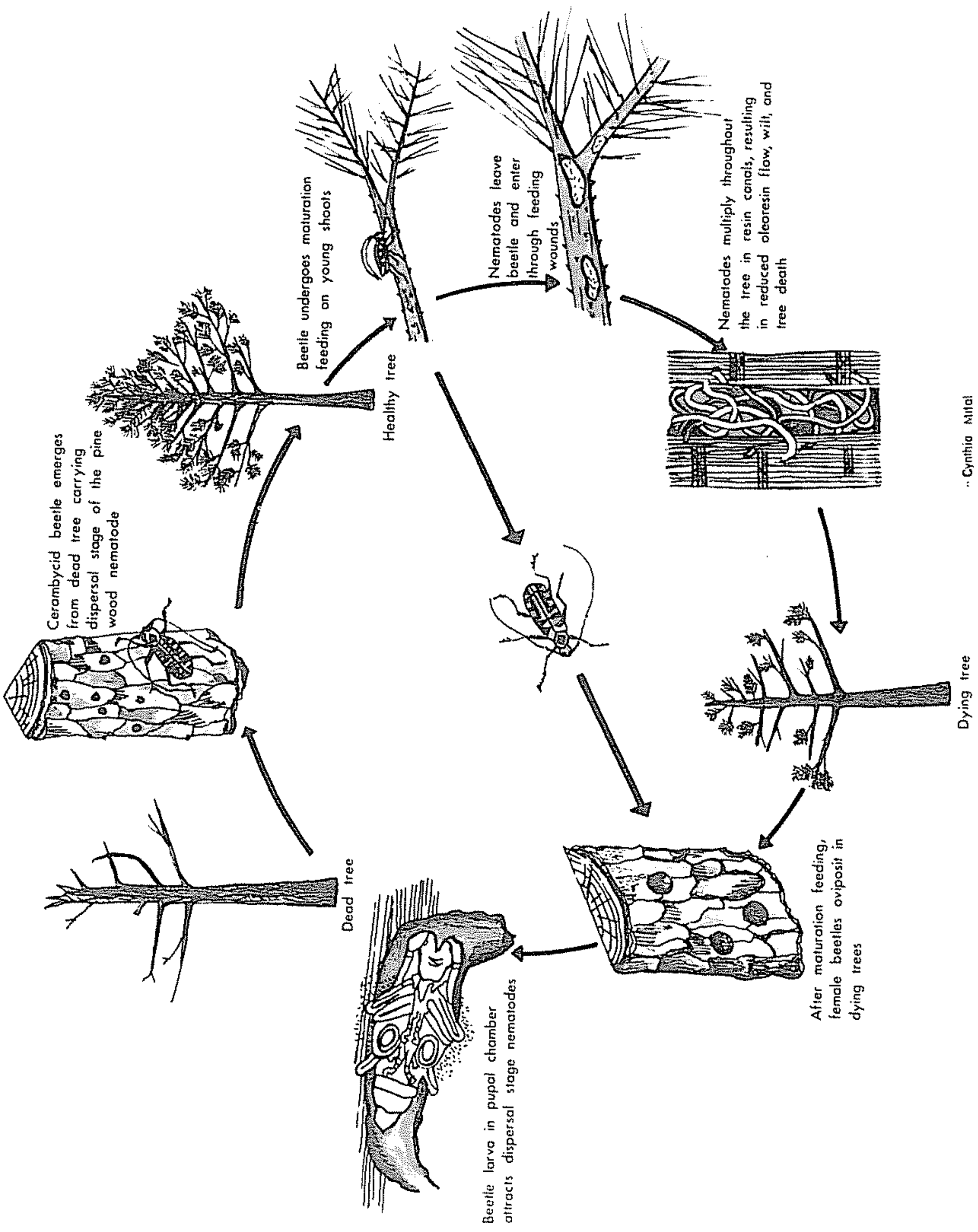

FIG. 2. The pine wilt disease cycle in Japan.

and die in approximately 3 months (Mamiya 1976). The dead and dying trees attract mature cerambycid beetles which oviposit in these trees. The beetle larvae develop within the dead trees containing nematodes and the life cycle of the nematode, closely coordinated with the beetle vector, begins once again (Fig. 2).

Preliminary inoculation studies in Japan indicate that native Japanese pines, *P. densiflora* and *P. thunbergii* are most susceptible to infestation by *B. xylophilus* whereas various exotic species such as *P. palustris* Mill., *P. taeda* L., and *P. echinata* Mill. are relatively resistant (Mamiya 1972). Bark beetle attack was originally considered responsible for the pine mortality in Japan. Nishiguchi (1970) associated bark beetle attack with climatic stress conditions. Likewise, Takashita *et al.* (1975) associated poor site conditions and water stress with the incidence of *B. xylophilus* infested trees. Although wilting has been suggested as a symptom of *B. xylophilus* infestation, Suzuki and Kiyohara (1978) have shown that these nematodes multiply only in water-stressed trees. Temperature extremes and precipitation have also been reported to affect the flight habits of the cerambycid vectors (Takashita *et al.* 1975).

The factors responsible for tree death due to infestation by *B. xylophilus* are not certain. Mamiya (1980*b*) has shown that *B. xylophilus* will destroy the epithelial cells in the resin canals, cambium, and cortex of 6-month-old *P. densiflora* and that these damaged tissues are filled with bacteria. Oku *et al.* (1980) have proposed that a toxin may be involved in the death of infested trees and that this toxin may be produced by a bacterium introduced into the trees simultaneously with *B. xylophilus*.

Studies on the biology and pathogenicity of *B. xylophilus* have been facilitated by the fact that the nematode can be maintained on fungi such as *Botrytis cinerea* Pers. ex Fr. in culture (Dozono and Yoshida 1974; Kiyohara 1976; Kiyohara and Tokushige 1971; Mamiya 1972). Kobayashi *et al.* (1974) suggest that a *Ceratocystis* sp. is transported by *M. alternatus* to healthy pine twigs and may serve as food for the nematode once *Bursaphelenchus xylophilus* has killed the twigs. This apparent interaction between fungus and nematode has received little attention by research workers.

The situation in the United States

Bursaphelenchus xylophilus was first reported in the United States (Dropkin and Foudin 1979) after being isolated from a dead Austrian pine (*P. nigra* Arnold) in Columbia, MO. Since this first report, there has been concern as to whether the forests in the United States and Canada are in jeopardy. Similarities between the biology of *B. xylophilus* in Japan and the United States are being investigated. In the United States, *B. xylophilus* has been found in 32 states on 20 pine species, Atlantic cedar (*Cedrus atlantica* Manetti), deodar cedar (*Cedrus deodara* (Roxb. Loud.), European larch (*Larix decidua* Mill.), tamarack (*Larix laricina* Du Rail K. Koch), and white spruce (*Picea glauca* Moench. Voss) but has not been reported from Canada. This wide distribution supports the hypothesis that the nematode has been present in North America for a considerable time. In fact, the timber nematode, *Aphelenchoides xylophilus* Steiner and Buhrer, isolated from *P. palustris* in Louisiana in 1931, is known to be identical with *B. xylophilus* (Nickle *et al.* 1981). *Bursaphelenchus xylophilus* has therefore been present in the United States, at least since the early part of this century, which lends support to speculation by Japanese nematologists that it originated in North America and has been introduced into Japan (Pine Wood Nematode Workshop, Columbia, MO, November 1980).

Eighteen species of pine have been tested for their susceptibility to *B. xylophilus* in Missouri. Of these all except jeffrey pine (*P. jeffreyi* Grev. and Balf) were susceptible when seedlings were inoculated with 2000 nematodes each. The five most susceptible species were jack pine (*P. banksiana* Lamb.), shortleaf pine (*P. echinata*), monterey pine (*P. radiata* D. Don.), sugar pine (*P. lambertiana* Dougl.), and scots pine (*P. sylvestris* L.). Some differences in susceptibility of pines tested in Japan and the United States are apparent. This may imply differences in pathogenicity among different isolates of the nematode (V. H. Dropkin, University of Missouri, personal communication).

Some vectors of the pine wood nematode in the United States include *Monochamus carolinensis* (Oliv.), *M. obtusus* Casey, *M. scutellatus* (Say), *M. titillator* (F), and *Arhopalus rusticus obsoletus* (Rand.) (Pine Wood Nematode Workshop, Columbia, MO, November 1980). The host range of the vector is likely to resemble the host range of the nematode. For example, *B. xylophilus* has been found on some of the same hosts as are hosts for *Monochamus scutellatus*, such as white pine (*P. strobus* L.), jack pine, red pine (*P. resinosa* Ait.), and tamarack but is likely also to occur on other tree species attacked by this beetle (Wilson 1962), such as balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* Mill. B.S.P.), and red spruce (*Picea rubens* Sarg.). It is possible that *B. xylophilus* does not have as effective a vector in the United States as *M. alternatus* proved to be in Japan. Future research should compare the numbers of nematodes carried by the beetle here and in Japan. The ease with which the nematodes are transmitted to the host should also be considered.

The presence of the pine wood nematode in the United States does not appear to be associated with a severe disease situation such as in Japan. Other than its wide distribution and the knowledge that it has been present in the United States for an appreciable time, the following facts may imply that *B. xylophilus* is no threat to local forests. (*i*) *Bursaphelenchus xylophilus* is most common on trees of low vigor that may be more susceptible to infestation or preferred by the vector. (*ii*) Branches of trees can be infested with *B. xylophilus* while the rest of the tree is seemingly free from the nematode (unpublished data by the authors). Resistance, possibly related to host vigor, may account for this phenomenon. (*iii*) Trees infested with the pine wood nematode in the north central United States are often severely weakened by various forest insects and diseases whereas vigorous trees on the same site are not infested with nematodes (unpublished data by the authors).

The pine wood nematode may indeed prove to be a threat in areas where exotic species of pine are planted (e.g., scots pine in south central United States) or native conifers planted on offsite conditions. Efforts to monitor the significance of the pine wood nematode in North America and to exclude more effective vectors from becoming established should be encouraged.

Acknowledgements

This research was funded in part by the USDA Forest Service, North Central Forest Experiment Station, St. Paul, MN, U.S.A. RWU-NC-2205. The authors thank Cynthia Mital for preparing the diagrams.

DOZONO, Y., and N. YOSHIDA. 1974. Application of the logistic curve for the population growth of pine wood nematode, *Bursaphelenchus lignicolus*, on the cultures of *Botrytis cinerea*. Nippon Rin Gakkaishi, **56**: 146–148.

DROPKIN, V. H., and A. S. FOUDIN. 1979. Report of the occurrence of *Bursaphelenchus lignicolus*-induced pine wilt disease in Missouri. Plant Dis. Rep. **63**: 904–905.

ISHIBASHI, N., and E. KONDO. 1977. Occurrence and survival of the dispersal forms of pine wood nematode, *Bursaphelenchus lignicolus* Mamiya and Kiyohara. Appl. Entomol. Zool. **12**: 293–302.

KIYOHARA, T. 1976. The decrease of pathogenicity of pine wood nematode, *Bursaphelenchus lignicolus*, induced by the extended subculturing on the fungal mat of *Botrytis cinerea*. Jpn. J. Nematol. **6**: 56–59.

KIYOHARA, T., and Y. TOKUSHIGE. 1971. Inoculation experiments of a nematode *Bursaphelenchus* sp., onto pine trees. Nippon Rin Gakkaishi, **53**: 210–218.

KOBAYASHI, T., K. SASAKI, and Y. MAMIYA. 1974. Fungi associated with *Bursaphelenchus lignicolus*, the pine wood nematode. I. Nippon Rin Gakkaishi, **56**: 136–145.

KONDO, E., and N. ISHIBASHI. 1978. Ultra-structural differences between the propagative and dispersal forms in pine wood nematode, *Bursaphelenchus lignicolus*, with reference to the survival. Appl. Entomol. Zool. **13**: 1–11.

MAMIYA, Y. 1972. Pine wood nematode, *Bursaphelenchus lignicolus* Mamiya and Kiyohara as a causal agent of pine wilting disease. Rev. Plant Prot. Res. **5**: 46–60.

——— 1976. Pine wilting disease caused by the pine wood nematode, *Bursaphelenchus lignicolus*, in Japan. JARQ, **10**: 206–211.

——— 1980*a*. Pine wilt and pine wood nematode: histopathological aspects of disease development. Workshop on the genetics of host–parasite interactions in forestry, September 1980. Wagneningen.

——— 1980*b*. Inoculation of the first year pine (*Pinus densiflora*) seedlings with *Bursaphelenchus lignicolus* and the histopathology of diseased seedlings. Nippon Rin Gakkaishi, **62**: 176–183.

MAMIYA, Y., and N. ENDA. 1972. Transmission of *Bursaphelenchus lignicolus* (nematode: *Aphelenchoididae*) by *Monochamus alternatus* (Coleoptera: Cerambycidae). Nematologica, **18**: 159–162.

MAMIYA, Y., and T. KIYOHARA. 1972. Description of *Bursaphelenchus lignicolus* n. sp. (Nematoda: Aphelenchoididae) from pine wood and histopathology of nematode infested trees. Nematologica, **18**: 120–124.

MORIMOTO, K., and A. IWASAKI. 1972. Role of *Monochamus alternatus* (Coleoptera: Cerambycidae) as a vector of *Bursaphelenchus lignicolus* (Nematoda: Aphelenchoididae). Nippon Rin Gakkaishi, **54**: 177–183.

NICKLE, W. R., A. M. GOLDEN, Y. MAMIYA, and W. P. WERGIN. 1981. On the taxonomy and morphology of the pine wood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer 1934) Nickle 1970. J. Nematol. **13**: 385–392.

NISHIGUCHI, C. 1970. Resistance of conifers to attack by secondary insects. Nippon Rin Gakkaishi, **52**: 159–168.

OKU, H., T. SHIRAISHI, S. OUCHI, S. KUROZUMI, and H. OHTA. 1980. Pine wilt toxin, the metabolite of a bacterium associated with a nematode. Naturwissenschaften, **67**: 198–199.

SUZUKI, K., and T. KIYOHARA. 1978. Influence of water stress on development of pine wilting disease caused by *Bursaphelenchus lignicolus*. Eur. J. For. Pathol. **8**: 97–107.

TAKASHITA, K., Y. HAGIHARA, and S. OGAWA. 1975. Environment analysis to pine damage in western Japan. Bull. Fukui Agric. Exp. Stn. **24**: 1–45.

TOKUSHIGE, Y., and T. KIYOHARA. 1969. *Bursaphelenchus* sp. in the wood of dead pine trees. Nippon Rin Gakkaishi, **51**: 193–195.

WILSON, L. T. 1962. White-spotted sawyer. United States, Department of Agriculture, Forest Service, Forest Pest Leaflet No. 74.