Annu. Rev Phytopathol. 1997. 35:153–66

THE PINEWOOD NEMATODE: Regulation and Mitigation

L. David Dwinell
USDA Forest Service, Southern Research Station, Athens, Georgia 30602;
e-mail: ldavidd@negia.net

KEY WORDS: *Bursaphelenchus*, **eradication, exotic pests, temperature, transmission**

ABSTRACT

In North America, the native pinewood nematode (PWN), ***Bursaphelenchus xylophilus***, kills exotic pines. When inadvertently introduced to Japan and other Asian countries, PWN became a destructive pest of pines. The PWN has been intercepted in pine shipments from North America to Europe, where there is concern that it may also kill pines and other conifers. To protect their forests from the PWN and other pests, the European Union and other countries now regulate the import of all coniferous chips, sawn wood, and logs. Several species of ***Bursaphebnchus*** have a phoretic relationship with *Monochamus* spp., which carry them to recently felled logs and dead or dying conifers, particularly pines. As a result, species of *Monochamus*, ***Bursaphelenchus,*** or both may be found in chips, unseasoned lumber, and logs. During the past decade, procedures to disinfest transported unprocessed wood have been investigated. These mitigation measures include prevention, host selection, and treatment by fumigation, irradiation, chemical dips, and elevated temperatures.

INTRODUCTION

Pests that cause tree disease are not confined within geopolitical boundaries. Exotic pests have destroyed the economic and aesthetic value of many of the world's most versatile and important trees. Countries in North America and around the world have suffered the consequences from the introduction of pests into highly susceptible host populations. Tree diseases introduced into North America include chestnut blight, Dutch elm disease, and beech bark disease.

0066-4286/97/0901-0153$08.00

The gypsy moth, ***Lymantria dispar,*** and balsam woolly adelgid, ***Adelgespiceae, are*** among the exotic insects causing irreparable damage to forested ecosystems in the United States. Other examples include the introduction of the European woodwasp, ***Sirex noctilio,*** into New Zealand, and pine bark beetles, ***Ips grandicollis,*** into Australia. The pinewood nematode (PWN), ***Bursaphelenchus xylophilus***, was introduced into Japan where it has caused major losses in pine timber.

Within the past few years, many countries have developed comprehensive regulations to eliminate significant pest risks associated with importing wood chips, unseasoned lumber, and logs. When the PWN was intercepted in wood chip shipments to Finland from North America, many countries, especially members of the European community, immediately banned the import of coniferous wood grown in areas where the PWN was known. However, the trading blocks-the European Union (EU) and North America-have not reached consensus on the risk to the forests of Europe from the PWN and its insect vectors in transported wood (27, 28). The issue of exotic pests, such as the PWN, takes on an emotional dimension and is rapidly politicized, making resolution hard to reach.

BAN

Interceptions

In 1984, the Finnish Plant Quarantine Service discovered that pine chips imported from Canada and the United States were infested with the PWN (51). Again, in the early 1990s, Finnish inspectors intercepted the PWN in unseasoned lumber (60, 61) and packing-case wood (58) imported from Canada. In 199 1, the European Union conducted a PWN survey of lumber shipments from North America to seven member states (27). In France, inspectors found the PWN in 1 of 163 planks shipped from Canada to Le Hâvre and ***B. mucronatus*** in 2 of 80 boards shipped to St. Malo. Some 99% of the unseasoned lumber parcels sampled were free of the PWN (27).

The PWN's insect vectors, ***Monochamus*** spp., have been found in pallets, crates, and dunnage (25). Holdeman (33), for example, found records of ***Monochamus*** spp. recovery from pallets aboard Japanese cargo ships docked in San Francisco Bay. At ports in the United States, species of ***Monochamus*** have been discovered in crates or dunnage for commodities (manhole covers, granite, marble, or tiles) from China, Spain, and Italy (25). These insects have also been intercepted at ports in New Zealand on many occasions (48); in 1988, ***Monochamus sutor,*** a species found widely in continental Europe, was captured in England (29).

Response

When Finnish inspectors intercepted the PWN in imported pine chips, the import of conifer chips and timber cut from softwood trees grown in areas of the world where the PWN occurs was immediately banned (51). Sweden and Norway imposed similar import restrictions; the Norwegian restriction included kiln dried lumber (2, 25). South Korea also established restrictions on importing certain types of pinewood (2). In July 1985, the European Plant Protection Organization (EPPO) placed the PWN on the Al list of quarantine pests and recommended that Europe as a whole ban softwood products, except kiln-dried lumber from countries known to have *B. xylophilus* (53). By 1989, the EU had emerged as the most visible regulatory agency in Europe, even though its regulations apply only to member countries. Non-EU member countries follow the recommendations of EPPO. Also, EPPO treats the EU as one country (DG McNamara, personal communication). Overlapping responsibilities for import regulations in Europe have caused some confusion in North America.

The interceptions of the PWN in pine chips and unseasoned lumber has led to the publication of several pest risk assessments. For example, the potential of the PWN to become established in Sweden (44), Finland (59), and Russia (38) has been explored. In 1993, the EU invited international authorities on the PWN to meet in Brussels, Belgium, to explore the risk of transmission of the PWN and its vectors to the forests of Europe (28). These risk assessments concluded that the PWN in transported coniferous wood was a potential threat to their respective forests and, therefore, should be regulated.

Impact

The embargoes have had an economic impact on North American softwood export trade. However, because environmental, business, regulatory, and supply issues also affect wood exports, the complete economic impact is unknown. From 1972 through 1989, Canada and the United States shipped almost 5 million tons of softwood chips, representing $160 million f.o.b., to Scandinavia (25). One company claimed a $20 million loss in potential sales of southern pine chips to European markets as a direct result of the embargoes (2). The last shipment of pine chips to Europe from the United States was on the M/V ***Florani*** in 1986 (7, 40). For the last decade, the Scandinavian countries have purchased pine chips from Chile and other countries outside North America.

The expansion of the ban to include unseasoned coniferous lumber was of great concern to North American wood exporters. Annually, approximately 5 million m^3 of sawn timber are exported from North America to the European Union (27). In Canada alone, CAN$3 billion in exports of forest products were jeopardized (56). The forest industry in the United States could potentially lose more than $100 million annually in green lumber exports to Europe (CM Hicks, personal communication).

NEMATODE

Taxonomy

The PWN (as ***B. lignicolus)*** was first reported from North America in 1979. It was found on dead Austrian *(Pinus* ***nigra)*** and Scotch *(P.* ***sylvestris)*** pines in Missouri (8). The initial reaction by the scientific community was, "We've been invaded!" (33). In 1981, ***B. lignicolus*** was synonymized with ***B. xylophilus*** (50), a species native to North America. Nickle (49) had already transferred ***Aphelenchoides xylophilus*** to ***Bursaphelenchus. Aphelenchoides xylophilus*** had been found in association with bluestain and other fungi in logs of longleaf pine *(P.* ***palustris)*** and in the bole of a bark beetle-killed shortleaf pine (*P.* ***echinata) (55).***

Wingfield & Blanchette (69) reported that the tails of the female ***B. xylophilus*** extracted from two-species of ***Monochamus*** emerging from balsam fir ***(Abies balsamea)*** logs were mucronate, unlike the rounded tails of female ***B. xylophilus.*** Morphologically, these nematodes were similar to ***B. mucronatus*** described in Japan in 1979 (47). Because ***B. mucronatus*** is common in Europe and Asia, the risk of introducing ***B. xylophilus*** has generated considerable interest in the taxonomic relationship among species of ***Bursaphelenchus*** vectored by ***Monochamus.*** Basically, in North America, two forms of ***B. xylophilus,*** "r" and "m", and ***B. mucronatus*** apparently exist. Webster et al (67) grouped these morphological forms and species into the pinewood nematode species complex (PWNSC), and several different molecular techniques have been used to learn more about speciation within the PWNSC (4, 31, 57). However, worldwide, ***B. xylophilus,*** sensu Nickle et al (50), is the only form ("r") or species in the PWNSC associated with tree mortality and is considered the causal agent of pine wilt.

Distribution

Indigenous to North America, the PWN, *B.* ***xylophilus,*** has been reported from the United States (8, 55, 70), Canada (5, 6, 37), and Mexico (14). The "m" form of ***B. xylophilus*** has been reported from ***A.*** *balsamae* in Minnesota (69) and from several conifer species across Canada (6). ***Bursaphelenchus xylophilus is*** an introduced pest in Japan (36, 45, 46), the People's Republic of China (72), Taiwan (63), and South Korea (73). Molecular and chromosomal data support the hypothesis that the PWN was introduced into Japan from the United States (4, 57). A Canadian isolate (C2), initially designated as ***B. xylophilus*** "m" form, has been identified by molecular techniques as ***B. mucronatus*** (4, 31).

Bursaphelenchus mucronatus has also been found in many Asian and European countries (36, 39, 45, 46, 52, 62).

Pathogenicity

Defining the pathogenicity of ***B. xylophilus*** and related species has been difficult. Much of the information on the pathogenicity of the PWN is based on seedling pathogenicity tests. Pathogenicity of inoculated conifer seedlings does not imply pathogenicity on established trees (1, 25, 36, 70). Bedker (1), for example, cites numerous studies suggesting that seedling mortality in tests does not indicate that the PWN can kill trees in nature. Misinterpretation of test results may have contributed to the impression that pine wilt disease is epidemic in North America.

Hosts

In nature, ***B. xylophilus*** is a pathogen of pines. In Japan, it causes extensive mortality of Japanese red pine (*P. densiflora*) and Japanese black pine (***P. thunbergii***) (36, 45, 46). Suscepts of the PWN in China and Korea are *P. densiflora* and *P.* ***thunbergii*** (72, 73). In Taiwan, the suscepts are *P. lucheusis* and *P.* ***thunbergii (63).***

In North America, the PWN is rarely, if ever, a primary pathogen of native pines. The pine wilt disease appears to be confined largely to stressed exotic pines, especially *P. sylvestris*, in the eastern United States (2, 25, 33, 70).

VECTORS

Insects

In North America and Japan, the PWN has been found in association with several insect species emerging from PWN-infested wood (25, 36, 69). However, beetles in the genus ***Monochamus are*** currently considered to be the only significant vectors of ***B. xylophilus*** (25, 28, 36).

Phoresy

Most of the 49 described species of ***Bursaphelenchus*** have a phoretic relationship with insects, especially bark beetles and woodborers. Furthermore, most species of ***Bursaphelenchus,*** including ***B. xylophilus,*** are mycophagous. The PWN and other closely related species of ***Bursaphelenchus*** (i.e. ***B. mucronatus) are*** vectored principally by cerambycid longhorn beetles (sawyers) in the genus ***Monochamus.*** These beetles are saprophytic woodborers in the larval stage (41, 66).

In North America, dauerlarvae of ***B. xylophilus*** have been recovered from adult beetles of most species of ***Monochamus*** (25, 56). Elsewhere in the Northern Hemisphere, ***B. mucronatus*** appears to be the most common species of

Bursaphelenchus associated with ***Monochamus*** (36, 47, 52, 62). The biologies of the Asian, North American, and Euro-Siberian ***Monochamus*** species are similar. Species differ in geographical distribution, host plants, oviposition site preferences, number of instars, and length of life cycle (32, 41, 42).

Adult sawyers are attracted to recently dead or dying trees and freshly felled timber (including logs) for breeding (32, 42, 66). The cause of the conifer's mortality is not significant (12, 32, 66, 70). Sawyers oviposit and the larvae develop only in trees or in logs with bark (32, 66). The female gnaws an irregular hole through the bark (oviposition pit) and inserts her eggs. The ***Monochamus*** larva feeds from 1 to 2 months on the cambial-fiber layer. The entire bark is loosened from the wood and the space is packed with excelsior and frass. Later, the larva bores into the sapwood, forming an oval entrance hole. The tunnel is usually u-shaped, and the pupal cell is located in the sapwood just beneath the outer bark.

The dauerlarvae of the PWN invade the callow ***Monochamus*** adult through the thoracic spiracles and are held in a quiescent state only in the tracheae (36, 41, 45, 46, 70). After pupation, the adult emerges by gnawing through the sapwood and exits the log. The sawyer life cycle is normally one year in southern areas and either 1 or 2 years in northern areas (32, 41, 42, 66).

TRANSMISSION

Primary

Upon emergence, the adult beetles move to a suitable host to feed on the bark of young branches. Female beetles reach sexual maturation about 14 to 20 days after emergence. Nematode dauerlarvae emigrate from the spiracles and enter the tree through wounds caused by the beetle feeding. This mode of transmission is termed "primary" because primary infection of a susceptible host occurs. Once inside a susceptible host, the nematode molts to adults, migrates throughout the tree, feeds on the parenchyma cells of the ray canals, and reproduces (45). Such PWN-infected trees exhibit wilt symptoms and die rapidly. If these events occur, the nematode is a primary pathogen and the resulting disease is pine wilt (25, 36, 45, 46, 70).

Secondary

Secondary transmission, first reported by Wingfield in 1983 (68), occurs when ***B. xylophilus*** enters the tree through oviposition wounds caused by the *Monochamus* vectors. This mode of transmission, also confirmed for ***B. mucronatus (52)*** and ***B. cocophilus*** (30), is now considered the most common means of transgenerational transfer of species of ***Bursaphelenchus.*** However, secondary transmission has not been reported in Japan. The realization that ***Bursaphelenchus*** is transmitted during oviposition essentially redefined the status of the PWN in North America (25, 68, 70). If oviposition pits are noted on a dead or dying pine and the PWN is isolated, one cannot automatically infer that the tree succumbed to the pine wilt disease. Numerous studies since 1983 have demonstrated that the nematode is a secondary invader or associate of the tree in these cases and does not contribute to tree mortality (1, 10, 25, 70). As a result of secondary transmission, species of ***Bursuphelenchus*** may be found in logs, unseasoned lumber, and chips (13, 25).

Historically, ***B.*** *xylophilus* and pine wilt disease have often been treated as the same entity. They are not! Although the PWN is the causal agent of pine wilt disease, it normally exists in nature independent of the disease. Thus, the distribution of the PWN cannot be equated with the distribution of pine wilt disease in North America. Because of secondary transmission, the PWN will be found throughout North America wherever recently killed or dying conifers are colonized by species of ***Monochamus.*** Worldwide, species of ***Bursaphelenchus are*** codistributed with their ***Monochamus*** hosts (25, 67).

MITIGATION

To ensure global transport of wood fiber without causing environmental harm or ecological disaster, the wood must be free of pests. Mitigation procedures investigated over the last decade include prevention, host selection, and treatment by fumigation, irradiation, chemical dips, and elevated temperature. The type of wood product exported-chips, green lumber, or logs-determines treatment(s) used.

Prevention

Prevention is the best approach to controlling ***Bursaphelenchus*** and ***Monochamus.*** Logs should not be exposed during the July-to-September egg-laying period of ***Monochamus.*** If bark is immediately peeled from felled green trees, damage by sawyers is prevented (32, 66). A mill certification program (no bark, no grub holes) is strongly supported by the United States and Canada. Based on the biology of ***Monochamus,*** this program assumes that if no grub (entrance) holes are visible, no insects in the sawn wood will emerge and transmit the PWN. Furthermore, the European ***Monochamus,*** which requires bark for oviposition, will be unable to breed in bark-free wood, eliminating contamination by the PWN.

Host Selection

The regulations of the European Union and European Plant Protection Organization apply to all coniferous wood. However, not all conifers host the PWN and its *Monochamus* vectors. Pines are the primary hosts of these organisms. Numerous conifer species, including white fir *(A. concolor)*, eastern hemlock (*Tsuga canadensis*), western hemlock (*T. heterophylla*), western redcedar *(Thuju plicata)*, Douglas fir *(Pseudotsugu menziezii)*, and redwood *(Sequoia sempervirens)*, are rarely, if ever, colonized by *Monochamus* in their natural range (LD Dwinell, unpublished information). In surveys for the PWN in Canada from 1985 to 1990, it was reported that the PWN was occasionally recovered from five species of pine, balsam fir, and white spruce *(Piceu glauca)*, but not from several other conifer species (5).

In 1993, mills were surveyed in Oregon and California for the PWN in unseasoned lumber (15). The PWN was not found in any samples of Douglas fir, redwood, or white fir. In Canada, a survey of eastern hemlock and western redcedar green lumber at several mills revealed no PWN (43, 71).

Chips

Woodchips from several southern pine species infested with the PWN were treated in transit using phosphine fumigation (7, 40). All five holds of a wood chip carrier were treated with aluminum phosphide at a rate of 4 gPH_3/m^3. Pinewood nematode mortality was attributed to elevated temperature, accumulation of carbon dioxide, and phosphine concentration. This successful in-transit fumigation awaits broader application.

The PWN can be killed in pine chips by irradiation. Scientists in the southern United States treated PWN-infested pine samples in a cesium-137 irradiator; 9 kGy was the lethal dosage (26). Subsequently, Canadian scientists reported that 7 kGy (cobalt 60 gammacell 220 irradiator) will eliminate the PWN in aqueous solution (54). These data support the contention that a higher dosage is necessary to eliminate the PWN in vivo than in vitro. Because pine chips are low in value, scientists concluded that the cost of 9 kGy irradiation was too high (26).

PWN can be exterminated in southern pine chips by immersion in a 0.15% solution of sodium N-methyldithiocarbamate (35). However, metam-sodium, which is efficacious as a dip (35) or fumigant (LD Dwinell, unpublished data), is currently considered impractical for decontaminating large volumes of pine chips.

Temperature markedly affects the population dynamics of the PWN in piled softwood chips. Ecologically, a shift from mesophilic to thermotolerant and thermophilic organisms occurs in piled chips because heat is generated during the decomposition process (3). In piled southern pine chips, the PWN primarily inhabits fresh chips and chips on the outer shell of the pile. The nematode does not inhabit chips in the interior of the pile where oxidative processes cause spontaneous heating to 60°C (9, 11).

The population dynamics of the PWN in southern pine chips during transoceanic transport is affected by temperature. The temperature in the bottom of the holds of ships during transit from Georgia to Sweden averaged 35°C (11, 40). The highest PWN population levels occurred when the temperature was around 35°C (11). In a study on the ecology of the PWN, Dwinell (9) found that the PWN reproduces quite well in pine chips at 35°C. However, few PWN were recovered in the middle of the holds, where the temperature averaged 48°C. The bottom of the ship holds can serve as an incubator for the nematode during the 17–19-day voyages.

The population densities of the PWN in pine chips rapidly declines at temperatures above 45°C. Dry heat ranging from 120–135°C must be applied for 8-10 min to kill all nematodes present in chips (34). However, lower temperatures, for example, two min at 55°C, were lethal when the chips were immersed in hot water. In a study on time-temperature requirements for decontaminating pine chips by dry heat, pine core temperatures averaged 63°C, and no nematodes were extracted after 45-, 35-, 30-, and 25-min exposures to 70, 80, 90, and 100°C, respectively (17). Nematodes were not extracted from chips dipped in hot water after 60 s for 60, 70, and 80°C and 15 s for 90°C. Moreover, nematodes were not extracted from chips exposed to live steam (100°C) for 60 s or longer. These data indicate that wet heat is more effective than dry heat for decontaminating pine chips (9, 17, 34). Mortality of PWN in wood is primarily a function of heat source, wood moisture, time, and temperature (20).

Using radio waves to decontaminate pine chips, Dwinell & Carr (22) determined that mortality of the PWN in pine chips exposed to radio frequency waves (27.1 MHZ) was a function of temperature. In a subsequent study (23), radio waves and steam, alone or in combination, were evaluated as decontaminators of PWN-infested chips. Radio waves and live steam effectively eradicated the PWN in pine chips when the wood temperature exceeded 57°C. High temperatures (81–95°C) can be reached in less time by combining steam and radio waves, suggesting that the relationship between the two heat sources may be synergistic.

Lumber

Two basic approaches when using elevated temperature to decontaminate unseasoned lumber are pasteurization and sterilization. Pasteurizing sawn wood does not significantly reduce the wood moisture content (13, 20, 24, 64). Sterilization of unseasoned lumber may or may not involve wood moisture loss.

Heat-treating (pasteurizing) dimension southern pine lumber to a target core-wood temperature of 55–60°C was sufficient to eradicate the PWN (13, 24). In a Canadian study (54), pasteurizing unseasoned coniferous lumber at an operational temperature of 59°C for 30 min resulted in total mortality for the

PWN. Scientists in a trilateral study involving Canada, the United States, and the European Union concluded that heat-treating unseasoned lumber to a corewood temperature of 56°C for 30 min eradicates the PWN and its pine sawyer vectors (27). It is necessary to calibrate the heat-treatment facility to determine when the required pasteurization temperature is reached for various sizes of lumber, species, densities, and schedules (13, 20, 54, 64). The European Union now requires heat-treating coniferous wood to a core temperature of 56°C for 30 min before importation,

Drying coniferous wood at conventional kiln schedules is essentially a wood sterilization process (64). Much higher time-temperature schedules are required to dry sawn wood to commercial standards than to eradicate pests-a fact confirmed in numerous studies (13, 16). With a 82°C final temperature common to most conventional kiln schedules (64), commercial kilns effectively kill all organisms in wood. South Korea now allows the import of kiln-dried pine lumber.

The success of a radio-frequency/vacuum kiln in eradicating the PWN in unseasoned pine lumber was a function of wood moisture and temperature (21). The greatest efficiency, in terms of nematode eradication, occurs when the wood is heated to a temperature greater than 56°C before drying.

Logs

There is a paucity of critical information on mitigation procedures for eradicating the PWN and its vectors in conifer logs. Neither liquid nor the powder formulations of sodium borate were effective in controlling the PWN or pine sawyers (16). Methyl bromide fumigation of eastern white pine (*P. strobus*), slash pine (*P. elliottii* var. *elliottii*), and loblolly pine (*P. taeda*) logs was effective in eliminating PWN from the fumigated logs, and no sawyers emerged (16). Because methyl bromide has been classed as a ozone-depleting substance, the production and import of methyl bromide will be banned in the United States after January 1, 2001. Therefore, fumigation with methyl bromide is not a viable long-term option.

Heat-treating Virginia pine (I! *virginiana)* naturally infested logs effectively controlled wood borers (*Monochamus* spp.), nematodes, and wood-colonizing fungi. A corewood temperature of 53°C for 30 min killed the wood borers, and 60°C for 30 min eliminated the nematodes and fungi. These results suggest that temperature schedules that eradicate mesophilic organisms in logs are similar to those in wood chips and unseasoned lumber. The possible contamination of heat-treated logs by the PWN and its insect vectors should be investigated. Heat-treating fresh eastern white pine and Virginia pine (*P. virginiana*) logs did not reduce their susceptibility to attack by pine sawyers or colonization by PWN (19).

SUMMARY

The PWN has been intercepted in Europe in unprocessed wood imported from North America. As a result of these interceptions and the pine wilt disease in Japan and other Asian countries, the European Union and other countries regulate the import of all coniferous chips, sawn wood, and logs to protect their forests from the PWN and other exotic pests. The United States has also implemented regulations designed to hinder the introduction of exotic pests (65).

Control measures that require a thorough knowledge of the life histories of the target pest and the wood management system used begin in the forest. Efficient logging management practices, quality control, and inspections can minimize or eliminate pest problems. Unfortunately, countries do not agree on the risk of the PWN in coniferous chips, unseasoned lumber, and debarked logs, and some require treatment of all coniferous wood-a questionable requirement. Mitigation procedures, such as heat-treatments, are insurance against perceived failures in the wood management system.

Procedures designed to disinfest transported coniferous wood include irradiation, fumigation with phosphine or methyl bromide, and chemical dips. In-transit fumigation with phosphine does not require a major capital investment and may be the best short-term solution for eradicating the PWN in pine chips. The use of elevated temperatures to eradicate the PWN and its *Monochamus* vectors in coniferous wood shows the most promise. Heating coniferous wood to a core temperature of 56°C for 30 min will eradicate the PWN and its insect vectors.

Literature Cited

1. Bedker PJ. 1987. Assessing pathogenicity of the pine wood nematode. See Ref. 68a, pp. 14-12
2. Bergdahl DR. 1988. Impact of pinewood nematode in North America: present and future. *J. Nematol.* 20:260–65
3. Bergman 0. 1985. Deterioration and protection of pulpwood chips in outdoor storage. *Rep. 170, Swed. Vniv. Agric. Sci., Uppsala*
4. Bolla RI, Bochert M. 1993. Pinewood nematode species complex: interbreeding potential and chromosome number. *J. Nematol.* 25:227–38
5. Bowers WW, Hudak J, Raske, AG, eds. 1992. Host and vector surveys for the pinewood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle (Nematoda: Aphelenchoididae) in Canada. *Inf. Rep.* N-X-285, *For: Can., Nfld. Labrador Reg.* 51 pp.
6. Can. For. Serv. 1985. *Forest Insect and Disease Conditions in Canada in 1985*, pp. 47-50. Ottawa, Canada
7 Davis R, Leesch JG, Simonaitis RA, Dwinell LD. 1987. The "Florani" experiment. In-transit fumigation of woodchips to control the pinewood nematode. *Int. For. Prod. Transp. Assoc. J.* 4:8–9
8 Dropkin V, Foudin AS. 1979. Report of the occurrence of *Bursaphelenchus lignicolus*-induced pine wilt disease in

Missouri. *Plant Dis. Rep.* 65: 1022-27

9. Dwinell LD. 1986. Ecology of pinewood nematode in southern pine chips. *Res. Pap. SE-258. USDA For. Serv.* Southeast, For. Exp. Stn., Asheville, NC. 14 pp.
10. Dwinell LD. 1987. Role of *Bursaphelenchus xylophilus* in the mortality of sand pine in a seed orchard in central Georgia. *J. Nematol.* 4:520 (Abstr.)
11. Dwinell LD. 1987. Pine wood nematode in southern pine chips exported from Georgia. See Ref. 68a, pp. 50-57
12. Dwinell LD. 1988. Distribution of the pine wood nematode in southern beetle-killed loblolly pine colonized by pine sawyers. *Phytopathology* 78:1555 (Abstr.)
13. Dwinell LD. 1990. Heat-treating and drying southern pine lumber infested with pinewood nematodes. *For. Prod. J.* 40:53-56
14. Dwinell LD. 1993. First report of the pine wood nematode (*Bursaphelenchus xylophilus*) in Mexico. *Plant Dis.* 69:440
15. Dwinell LD. 1993. Incidence of the oine wood nematode in green coniferous sawn wood in Oregon and California. *Res. Note SE-367. USDA For. Serv.,* Southeast. For. Exp. Stn., Asheville, NC. 4 pp.
16. Dwinell LD. 1994. Evaluation of sodium borate for the control of nematodes and wood-borers in pine logs. *Proc. Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct.,* pp. 95-l. Kissammee, FL
17. Dwinell LD. 1994. Using heat to decontaminate pine chips infested with the pinewood nematode. *Proc. Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct.,* pp. 96-1,2. Kissammee, FL
18. Dwinell LD. 1995. Using heat to decontaminate unbarked Virginia pine logs. *Proc. Annu. Meet. For. Prod. Soc.,* Portland, OR
19. Dwinell LD. 1995. The colonization of heat-treated pine logs by *Bursaphelenchus xylophilus* and its *Monochamus* vectors. *J. Nematol.* 27:498 (Abstr.)
20. Dwinell LD. 1996. Using heat to decontaminate softwood chips, lumber, and logs. *Proc. Importing Wood Prod.: Pest Risks to Domestic Ind.,* pp. 91-100. Portland, OR
21. Dwinell LD, Avramidis S, Clark JE. 1993. Evaluation of a radio-frequency/vacuum dryer for the eradication of the pinewood nematode in green sawn wood. *For. Prod. J.* 44: 19-24
22. Dwinell LD, Carr WW. 1991. Using radio waves to eradicate *Bursaphelenchus xylophilus* in southern pine chips. *J. Nematol.* 23:527 (Abstr.)
23. Dwinell LD, Carr WW. 1995. Radio waves and steam, alone or in combination, for the eradication of *Bursaphelenchus xylophilus* in southern pine chips. *Proc. Annu. Res. Conf. Methyl Bromide Altern. Emiss. Reduct.,* pp. 81-1,3. San Diego, CA
24. Dwinell LD, Chung Y, Lee D, Yi C. 1995. Heat-treating loblolly pine lumber to eradicate *Bursaphelenchus xylophilus:* verification tests. *Proc. Annu. Int. Res. Conf. Methyl Bromide Altern. Emiss. Reduct.,* pp. 80-1,3. San Diego, CA
25. Dwinell LD, Nickle WR. 1989. An overview of the pine wood nematode ban in North America. *Gen. Tech. Rep. SE-55. USDA For. Serv.* Southeast. For. Exp. Stn., Asheville. NC. 13 pp.
26. Eichholz 'GG, Bogdanov AA, Dwinell LD. 1991. Radiation sensitivity of pine wood nematodes in woodchips. *Appl. Radiat. Isot.* 42: 177-79
27. EOLAS, Irish Science and Technology Agency. 199 1. *The development of treatment schedules to ensure eradication in timber of the pinewood nematode (Bursaphelenchus xylophilus and its insect vectors.* Final Rep., EOLAS. Glasnevin. Dublin
28. Evans H, Hart-Tree M, Kubicek QB. 1993. Risk of transmission of pinewood nematode, its vectors and pine wilt to EC forests. *Rep. EC/Canada/USA Tech. Team.* 25 pp.
29. Gibbons N. 1988. *Monochamus sutor* (L.) (Col., Cerambycidae) a foreign longhorn beetle found in Suffolk. *Trans. Suffolk Nat. Soc.* 24:39
30. Griffith R. 1987. Red ring disease of coconut palm. *Plunt Dis.* 77:193-96
31. Harmey JH, Harmey MA. 1993. Detection and identification of *Bursaphelenchus* species with DNA fingerprinting and polymerase chain reaction. *J. Nematol.* 25:406-15
32. Hellrigl KG. 1971. Die Bionomie der europaischen Monochamusarten (Coleopt., Cerabycid) und ihre Bedeutung fur die Forst- und Holzwirtschaft. Bolzano, Italy: Cent. Entomol. Alp. For. Cons. Naz. Richerche, Publ. 154: 367-509
33. Holdeman QL. 1980. *The pinewood nematode (Bursaphelenchus lignicolus* Mamiya and Kiyohara 19972) *and the associated pine wilt disease of Japan.* Rep. prepared for Dep. Food Agric., Agric. Comm. Calif., Sacramento. 45 pp.
34. Kinn DN. 1986. Heat-treating wood chips: a possible solution to pinewood nematode contamination. *Tappi* 69:97-98

35. Kinn DN, Springer EL. 1985. Using sodium N-methyldithiocarbamate to exterminate the pine wood nematode in wood chips. *Tappi J.* 70:88
36. Kishi Y. 1995. ***The Pine Wood Nematode and the Japanese Pine Sawyer.*** Tokyo, Jpn: Thomas. 301 pp.
37. Knowles K, Beaublen Y, Wingfield MJ, Baker FA, French DW. 1883. The pinewood nematode new in Canada. ***For. Chron.*** 59:40
38. Kulinich OA, Kolossova NV. 1995. The potential of the pinewood nematode *Bursaphelenchus xylophilus* to become established in countries of the former USSR. ***Russ. J. Nematol.*** 3:35–48
39. Kulinich OA, Kruglic L, Eroshenko AS, Kolossova NV. 1994. Occurrence and distribution of the nematode ***Bursaphelenchus mucronutus*** in the Russian Far East. ***Russ. J. Nematol. 2:*** 113-1 9
40. Leesch JG, Davis R, Simonaitis RA, Dwinell LD. 1989. In-transit shipboard fumigation of pine woodchips to control *Bursaphelenchus xylophilus.* ***EPPO Bull.*** 19:173–81
41. Linit MJ. 1987. The insect component of pine wilt disease in the United States. See Ref. 68a, pp. 66-73
42. Linsley EG, Chemsak JA. 1984. ***The Cerambycidae of North America,*** Part ***7, No.*** 1: ***Taxonomy und Classification of the Subfamily Laminae, Tribes Parmeineni through Acanthoderini.*** Berkeley: Univ. Calif. Press. 258 pp.
43. Magasi LP, Harrison KJ, Hurley JE. 1990. Survey of eastern hemlock for insects and pinewood nematode in New Brunswick and Nova Scotia. ***Tech. Note 240, For. Can., Marit. Reg.,*** Fredericton, NB. 4 pp.
44. Magnusson C. 1986. Potential for establishment of ***Bursaphelenchus xylophilus*** and the pine wilt disease under Nordic conditions. ***EPPO*** Bull. 16:465–71
45. Mamiya Y. 1983. Pathology of the pine wilt disease caused by ***Bursaphelenchus xylophilus. Annu. Rev. Phytopathol.*** 21:201–20
46. Mamiya Y. 1984. The pine wood nematode. In ***Plant and Insect Nematodes,*** ed. WR Nickle, pp. 589–626. New York: Marcel Dekker
47. Mamiya Y, Enda N. 1979. ***Bursaphelenchus mucronatus*** n. sp. (Nematoda: Aphelenchoididae) from pine wood and its biology and pathogenicity to pine trees. *Nematologica* 25:353–61
48. NZ For. Res. Inst. 1984. ***Entomology und Forest Health,*** pp. 23-26. Rotorua, NZ: For. Res. Inst.
49. Nickle WR. 1970. A taxonomic review of the genera of the Aphelenchoidea (Fuchs, 1937) Thorne, 1949. (Nematoda: Tylenchida). ***J. Nematol.*** 2:375–92
50. Nickle WR, Golden AM, Mamiya Y, Wergin WP. 1981. On the taxonomy and morphology of the pine wood nematode, ***Bursaphelenchus xylophilus*** (Steiner & Buhrer, 1934). *J.* Nematol. 13:385–92
51. Rautapaa J. 1986. Experiences with ***Bursaphelenchus*** in Finland. Conf. Pest and Disease Problems in European forests. ***EPPO Bull.*** 16:453–56
52. ***Schroeder*** M, Magnusson C. 1992. Transmission of ***Bursaphelenchus mucronatus*** (Nematoda) to branches and bolts of ***Pinus sylvestris*** and ***Piceu abies*** by the cerambycid beetle ***Monochamus sutor. Scand. J. For. Res. 7:*** 107-12
53. Smith IM. 1985. Pests and disease problems in European forests. *FAO Plant Prot.* Bull. 33: 159-64
54. Smith RS, ed. 1991. The use of heat treatment in the eradication of the pinewood nematode and its insect vectors in softwood lumber. ***Rep. Task Force Pasteurization Softwood Lumber:*** Forintek Can. Corp., Vancouver, BC, Canada. 72 pp.
55. Steiner G, Buhrer EM. 1934. ***Aphelenchoides xylophilus*** n. sp., a nematode associated with bluestain and other fungi in timber. ***J. Agric. Res.*** 48:949–5 1
56. Sutherland JR, Webster JM. 1993. Nematode pests of forest trees. In ***Plant Parasitic Nematodes in Temperate Agriculture,*** ed. K Evans, DL Trudgill, JM Webster, pp. 351–80. Wallingford, UK: CAB Int. 648 pp.
57. Tares S, Abad P, Bruguier N, de Guiran G. 1991. Identification and evidence for relationships among geographical isolates of *Bursaphelenchus* spp. (Pinewood nematode) using homologous DNA probes. ***Heredity 68: 157-64***
58. Tomminen J. 1991. Pinewood nematode, ***Bursaphelenchus xylophilus,*** found in packing case wood. *Silva Fenn.* ***25:109-*** 11
59. Tommenin J. 1993. ***An assessment of the pinewood nematode and related species in wood products und their potential risk to Finnish forests.*** Rep. 18, pp. l-53. Univ. Helsinki, Finland
60. Tommenin J, Lahtinen JH. 1990. Interception of the pinewood nematode, ***Bursaphelenchus xylophilus,*** in green lumber imported to Finland from Canada. *Nematologica* 36:397 (Abstr.)
61. Tomminen J, Nuorteva M. 1992. Pinewood nematode, ***Bursaphelenchus xylophilus,*** in commercial sawn wood

and its control by kiln-heating. *Scand. J. For. Res.* 7: 113-20

62. Tomminen J, Nuorteva M, Pulkkinen M, Vakeva J. 1989. Occurrence of the nematode *Bursaphelenchus mucronatus* Mamiya & Enda 1979 (Nematoda: Aphelenchoididae) in Finland. *Silva Fenn.* 23:271–77

63. Tzean SS, Tang JS. 1985. The occurrence of the pine wood nematode, *Bursaphelenchus xylophilus*, in Taiwan. *Proc. ROC Symp. Electron Microsc., 6th*, pp. 38-39

64. US Dep. Agric., Animal Plant Health Serv. 1995. Importation of logs, lumber, and other manufactured wood articles. Final rule. *Fed. Regist.* 60:27665–82

65. US Dep. Agric., For. Serv. 1991. Dry *Kiln Operator's Manual.* Agric. Handb. No. 188, For. Prod. Lab., Madison, WI. 274 pp.

66. Webb JL. 1909. The southern pine sawyer, US *Dep. Agric. Bur. Entomol. Bull. 58.*56 pp.

67. Webster JM, Anderson RV Baillie DL, Beckenbach K, Curran J, Rutherford TA. 1990. DNA probes for differentiating isolates of the pinewood nematode species complex. *Rev. Nematol.* 13:255–63

68. Wingfield MJ. 1983. Pine wood nematode transmitted to cut timber and girdled trees, *Plant Dis.* 67:35–37

68a. Wingfield MJ, ed. 1987. *Pathogenicity of Pine Wood Nematode.* St. Paul, MN: APS Press. 122 pp.

69. Wingfield MJ, Blanchette RA. 1983. The pine-wood nematode, *Bursaphelenchus xylophilus,* in Minnesota and Wisconsin: insect associates and transmission studies. *Can. J. For. Res.* 13:1068–76

70. Wingfield MJ, Blanchette RA, Nicholls TH. 1984. Is the pine wood nematode an important pathogen in the United States? *J. For.* 82:232–35

71 Wood CS, Van Sickle GA. 1991. Forest insect and disease conditions, British Columbia and Yukon 1990. *Inf. Rep. BC*-X-326. *For. Can., Pacific & Yukon Reg.,* Victoria, BC. 34 pp.

72 Yang B, Qouli W. 1989. Distribution of the pinewood nematode in China and susceptibility of some Chinese and exotic pines to the nematode. *Can. J. For. Res.* 19:1527–30

73. Yi C, Park J, Chang K. 1989. Occurrence of pine wood nematode. *Bursaphelenchus xylophilus* (Steiner et. Buhrer) Nickle, and its vector, *Monochamus alternatus* Hope, in Korea. In *Proc. IUFRO Reg. Workshop For. Insect Pests and Tree Dis. NE Asia,* Tsukuba, Jpn., pp. 183–93. For. Prod. Res. Inst.