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An Overview of the Pine Wood Nematode Ban in North America

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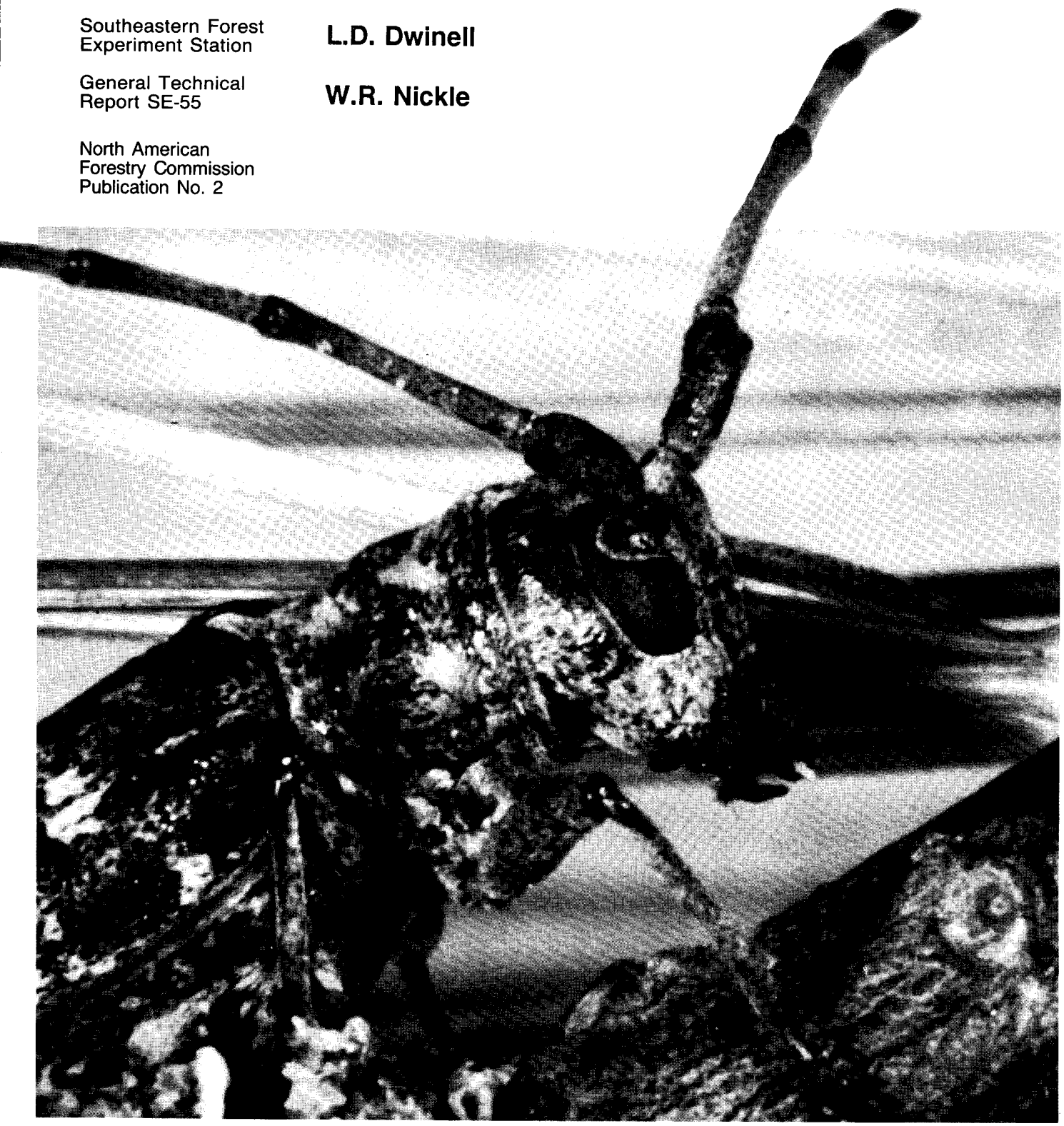

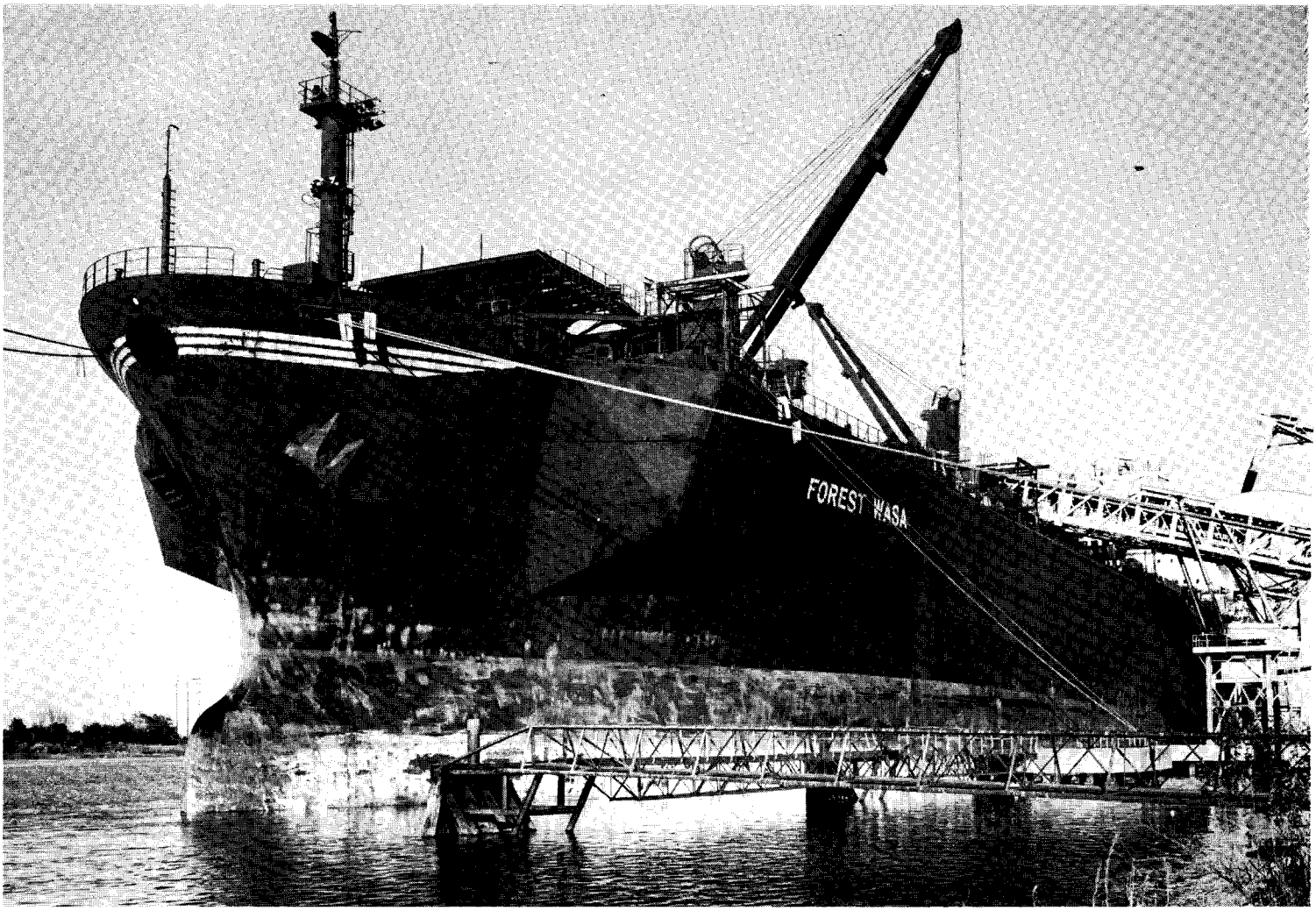

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An Overview of the Pine Wood Nematode Ban in North America

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ABSTRACT

The history, ecology, and biology of the *Bursaphelenchus-Monochamus* complex in North America are reviewed. The pine wood nematode (*B. xylophilus*) is a secondary associate of native conifers and the most common mode of transmission is during oviposition of the *Monochamus* vector. The pine wood nematode is a primary pathogen of exotic pines, however. Primary and secondary transmission of *B. xylophilus* are described. Since the nematode is seldom a primary pathogen in North America, distribution there cannot be equated with the distribution of the pine wilt disease. Recent research on the incidence, control, and risks of the pine wood nematode and its vectors in exported softwood products is reviewed.

Keywords: *Bursaphelenchus xylophilus*, *Bursaphelenchus mucronatus*, *Pinus*, embargo, softwood products, *Monochamus*, pine wilt disease.

Embargo

Recent events have focused new attention on the status of the pine wood nematode, *Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle (= *B. lignicolus* Mamiya & Kiyohara), in North America. In 1984, pine chips headed for Finland from the United States (fig. 1) and Canada were found to be infested by pine wood nematodes (Rautapaa 1986). Since this nematode was considered to be the causal agent of pine wilt disease (Mamiya 1983, 1984), Finland in 1985 banned importation of conifer chips and timber cut from softwood trees grown in areas of the world in which the pine wood nematode occurs (Rautapaa 1986). The other Scandinavian countries followed suit. In July 1985, the European Plant Protection Organization (EPPO) recommended that Europe as a whole ban softwood products except kiln-dried lumber from countries known to have *B. xylophilus* (Smith 1985).

These events resulted in a rapid exchange of information between the countries concerned. Fact-finding teams from Finland, Norway, and Sweden visited the United States and Canada. The ban has been costly to the forest industries in North America. Understandably, however, the importing countries are concerned about the health of their forests and do not want to experience a pine wilt disease epidemic such as has occurred in Japan (Mamiya 1983, 1984). They must evaluate the magnitude of the problem in Japan, the problem on Scotch pine in the Midwestern United States, and the possible threat to the forests of Nordic and other European countries. Recent discussions with European scientists and government officials suggest that the current status of the pine wilt disease in North America is not fully understood there. For example, the opinion has been expressed that some exported pine chips are from trees killed by a pine wilt epidemic in North America. One of the main arguments put forth by Rautapaa (1986) of Finland was that "the nematode has caused significant economic damage to pines in USA and in Japan." EPPO (1986) stated that the pine wood nematode is associated with tree dieback in Canada. In fact, pine wood nematodes are seldom, if ever, the primary cause of mortality of conifers in the forests of North America.

New Perspectives on Past Research

Research on a pest such as the pine wood nematode is a dynamic process. Each new discovery provides fresh insight, which sometimes changes one's perceptions of the pest and the disease it causes, and requires a critical reevaluation of the previous literature. Scientists in a network that actively exchanges information frequently recognize the subtle changes in direction before the scientific community at large. Unfortunately, the significance of such discoveries is not always fully appreciated.

This report examines some new observations on the pine wilt disease complex. It places the current status of the pine wood nematode and the pine wilt disease in North America into perspective. "Perspectives," as Van Gundy (1986) noted, "are the way we see and interpret things based on our own experience and individual philosophies."

Initial Reaction to Rediscovery of Pine Wood Nematode in North America

The pine wood nematode (as *B. lignicolus*) was first reported from North America in 1979. It was found on dead Austrian (*Pinus nigra* Arnold) and Scotch (*P. sylvestris* L.) pines in Missouri (Dropkin and Foudin 1979), and was thought to have been introduced from Japan. The initial reaction by the scientific community, reflected in the literature of the time, was "We've been invaded!" (Holdeman 1980). In 1981 *B. lignicolus*, the Japanese nematode, was synonymized with *B. xylophilus* (Nickle and others 1981), a species known to occur in North America. Earlier, Nickle (1970) had transferred *Aphelenchoides xylophilus* Steiner & Buhrer to *Bursaphelenchus*. *Aphelenchoides xylophilus* had been found in association with fungi in downed timber (Steiner and Buhrer 1934). Although the pine wood nematode has been known to be in North America for at least 60 years and is probably a native species, research in the United States has continued to emphasize pathogenesis. In a thorough evaluation of the problem, Holdeman (1980) concluded that the pine wood nematode was not a threat to conifers in California. Some landmarks in the history of research on the pine wood nematode are outlined in table 1.

Relationship of *Bursaphelenchus* With *Monochamus*

Most of the 49 described species of *Bursaphelenchus* have a phoretic relationship with insects, especially bark beetles and wood borers, and all are mycophagous (Massey 1974; Rühm 1956). The pine wood nematode and other closely related species of *Bursaphelenchus* are vectored principally by cerambycid longhorn beetles (also referred to as sawyers) in the genus *Monochamus*. These beetles are saprophytic wood borers in the larval stage (Hellrigl 1971; Linit 1987; Webb 1909).

In Japan, China, and Taiwan, *M. alternatus* Hope is the primary vector of *B. xylophilus* (Mamiya 1987; Mamiya and Enda 1972). *Monochamus nitens* Bates & *M. saltuarius* Gebler are also considered to be vectors in Japan (Kobayashi and others 1984). *Bursaphelenchus mucronatus* Mamiya & Enda, a species similar to *B. xylophilus*, may be the aboriginal inhabitant of *M. alternatus* in Japan (Mamiya 1983; Mamiya and Enda 1979).

In the United States, dauerlarvae of *B. xylophilus* have been recovered from adult beetles of *M. carolinensis* Oliver, *M. scutellatus* Say, *M. titillator* Fabricus, *M. mutator* LeConte, *M. scutellatus oregonensis* (LeConte), and *M. notatus* Drury (Holdeman 1980; Linit and others 1983; Nickle and others 1980; Tarjan and others 1980; Wingfield and Blanchette 1983. A possible strain of *B. xylophilus* in which the adult females have mucronate tails similar to those of *B. mucronatus* is phoretic on *M. marmorator* and *M. scutellatus* (Wingfield and Blanchette 1983).

In Canada, 14 potential insect vectors of the pine wood nematode are known to be present (Garland 1985). These include six species of longhorn beetles: *M. carolinensis*, *M. marmorator*, *M. mutator*, *M. obtusus* Casey, *M. scutellatus*, and *M. titillator*. *Bursaphelenchus xylophilus* was first reported in Canada in 1983 (Knowles and others 1983).

Research in Mexico on longhorn beetles has been limited. *Monochamus notatus* has been reported on *Pinus* spp. and *Abies* spp. in Mexico State, and *M. rubigineus* Bates (= *M. clamator rubigineus* (Bates) Linsley & Chemsak) have been found on *P. patula* in Hidalgo State (Samaro 1987). Reportedly, *M. clamator rubigineus* has a range from southeastern Arizona to Honduras, and the host plants include *P. leiophylla* Schiede & Deppe and *P. ponderosa* Dougl. ex Laws. (Linsley and Chemsak 1984). Samano (1987), however, believes that several other species of *Monochamus*, including known vectors of the pine wood nematode, occur in Mexico. Although *B. xylophilus* has not been reported in Mexico, its existence there is highly probable.

The biologies of the Asian, North American, and Euro-Siberian *Monochamus* species are similar. Species differ in geographical distributions, host plants, oviposition site preferences (location on trunk, etc), numbers of instars, and length of life cycle (Hellrigl 1971; Kobayashi and others 1984; Linit 1987; Linsley and Chemsak 1984; Webb 1909).

The adult sawyers are attracted to recently dead or dying trees and freshly felled timber (including logs) for breeding. The cause of the conifer's mortality is not particularly significant. In the United States, for example, sawyers breed in pines killed by other insects such as the southern pine beetle (*Dendroctonus frontalis* Zimm.) (Coulson and others 1976; Dwinell 1988) or the engraver beetle (*Ips calligraphus* Germ.) (Miller 1984), by root rot and drought (Dwinell

Table 1.—Some landmarks in the history of pine wood nematode research

Year	Event	Reference
1909	Biology of *Monochamus titillator* described	Webb 1909
1929	*Aphelenchoides xylophilus* found in association with fungi in timber	Steiner and Buhrer 1934
1969	*Bursaphelenchus* sp. found in wood of dead pine trees in Japan	Tokushige and Kiyohara 1969
1970	*Aphelenchoides xylophilus* transferred to *Bursaphelenchus*	Nickle 1970
1971	Pathogenicity of *Bursaphelenchus* sp. demonstrated by inoculating 25-year-old *Pinus densiflora*	Kiyohara and Tokushige 1971
1972	Pine wood nematode described as *B. lignicolus*	Mamiya and Kiyohara 1972
	Transmission of *B. lignicolus* by *Monochamus alternatus* reported (maturation feeding)	Mamiya and Enda 1972
1979	*Bursaphelenchus mucronatus* is described	Mamiya and Enda 1979
	Pine wilt disease reportedly found in the United States	Dropkin and Foudin 1979
1981	*Bursaphelenchus lignicolus* placed as a synonym of *B. xylophilus*	Nickle and others 1981
1983	Transmission of *B. xylophilus* during oviposition of *Monochamus* vectors reported	Wingfield 1983
	Bursaphelenchus xylophilus found in Canada	Knowles and others 1983
1984	*Bursaphelenchus xylophilus* intercepted in pine wood chips imported into Finland from the United States and Canada	Rautapaa 1986

1987b; Highley and others 1982), by dwarf mistletoe (*Arceuthobium americanum* Nutt.) (Burnes and others 1985), or by flooding (Esser and others 1983). Sawyers also attack fire-damaged, blown-down, or lightning-struck trees (Hellrigl 1971; Webb 1909). An exception is *M. marmorator* Kilby, which attacks standing green balsam fir (*Abies balsamae* (L.) Mill.) and hastens the death of trees weakened from other causes (Craighead 1950).

The bark must still be on the tree or log for beetles to oviposit and for the insect larvae to develop (Craighead 1950; Hellrigl 1971; Webb 1909). The female gnaws an irregular hole through the bark (oviposition pit) and inserts from one to six eggs. Nematodes can be transmitted at this time. The larva feeds from 1 to 2 months on the cambial-fiber layer, consuming all cambial and soft bark tissues. 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 in the sapwood just beneath the outer bark. After pupation, the adult emerges by gnawing through the bark. In the more northern parts of the ranges, 2 years are required to complete the life cycle (Hellrigl 1971; Linit 1987; Webb 1909).

Ecologically, the life cycles of the cerambycid vector and the pine wood nematode are well integrated. The nematodes have distinct life cycles for propagation and dispersal. The propagative nematode may feed on the epithelial cells of the resin ducts (phytophagous) or on the fungi that invade the wood (mycophagous). The dispersal cycle takes place during times of stress, such as when the wood becomes dry after tree death or in the late fall. The nonfeeding third larval dispersal stage is adapted to surviving unfavorable conditions (Mamiya 1983, 1984; Wingfield 1987; Wingfield and others 1984).

In the presence of the callow adult (pupa) of the vector (fig. 2), the third larval dispersal stage moults to the fourth larval stage, which is referred to as the "transmission stage" or "dauerlarva." Up to as many as 100,000 dauerlarvae may enter the callow adult of the insect through the thoracic spiracles and are held in a quiescent state only in the tracheae. Dauerlarvae are adapted to being carried by the insect vector to a new habitat (Linit 1987; Mamiya 1983, 1984; Wingfield and others 1984). However, not all sawyers become infested by *B. xylophilus*. For example, Kinn (1987) found that 31.4 percent of the

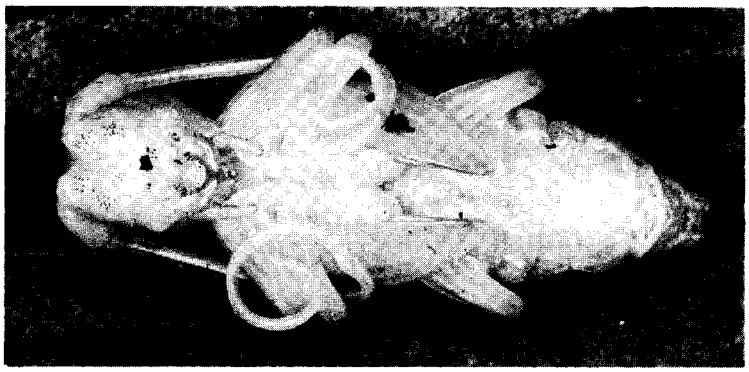

Figure 2.—The pupa (callow adult) of the pine sawyer may become infested with the dauerlarvae of *Bursaphelenchus* sp. Shown here is a pupa of *Monochamus titillator*, the southern pine sawyer.

M. titillator and 50 percent of the *M. carolinensis* recovered from barrier traps carried dauerlarvae of the pine wood nematode.

Upon emergence, the adult beetle moves to a suitable live host to feed on the bark of young branches (Kobayashi and others 1984; Linit 1987; Mamiya 1983, 1984) (fig. 3). Nematode dauerlarvae emigrate from the spiracles and enter the tree through wounds caused by maturation feeding (Mamiya and Enda 1972). This mode of transmission is termed "primary"

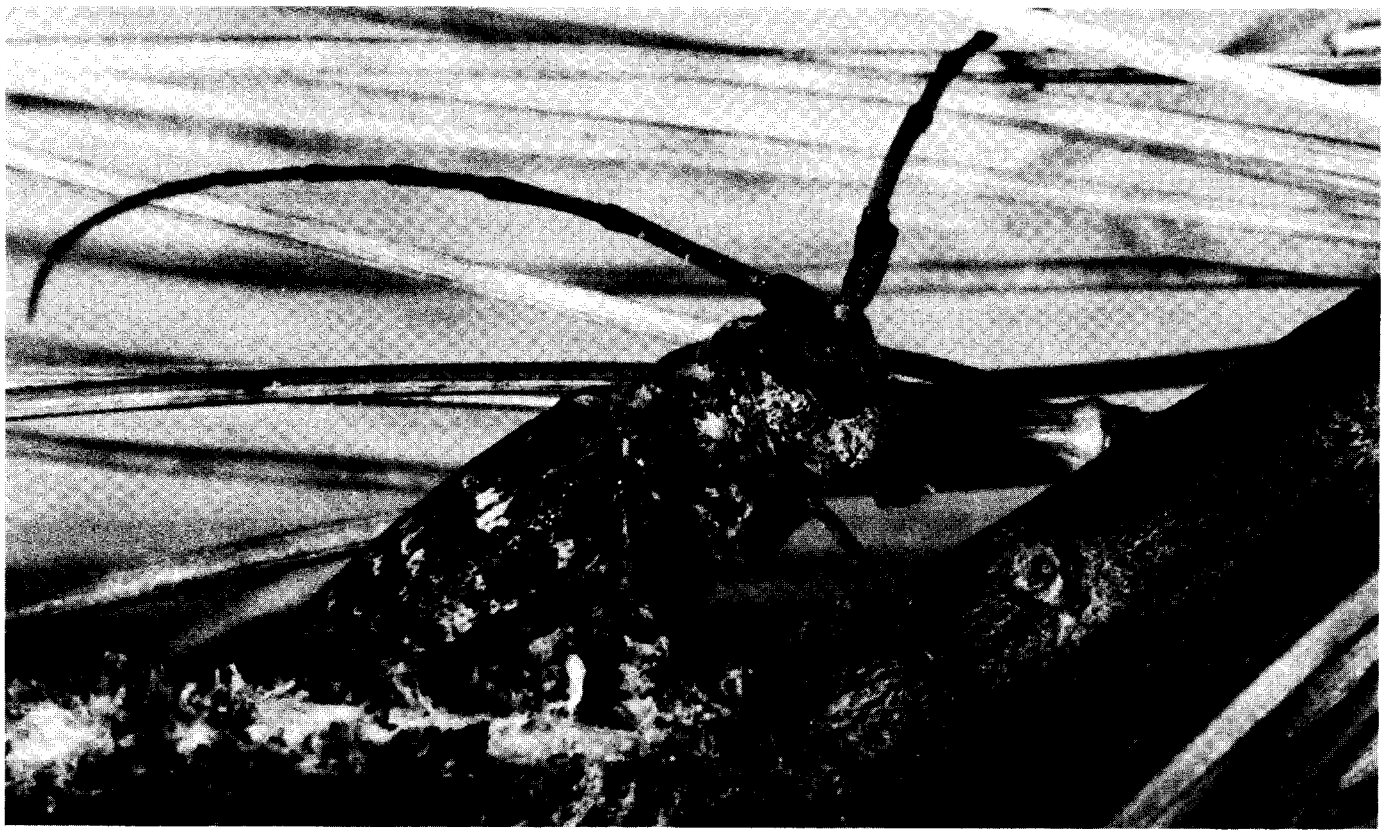

Figure 3.—Primary transmission occurs during maturation and subsistence feeding of pine sawyers on shoots of susceptible species of pine.

because primary infection of an apparently healthy tree occurs (Linit 1987). Once within the stressed tree, the nematode reproduces rapidly and the infected tree shows symptoms of decline and wilt (Kobayashi and others 1984; Linit 1987; Mamiya and Enda 1972). If these events occur, the nematode is functioning as a primary pathogen and the resultant disease is known as pine wilt.

Pathogenicity of *B. xylophilus* to North American Pines

Much of the information about pathogenicity of the pine wood nematode in North America is based on seedling pathogenicity tests. Misinterpretation of test results may have contributed to the impression that the pine wilt disease is epidemic in North America. Pathogenicity on inoculated pine seedlings does not imply pathogenicity on established trees (Bedker 1987; Wingfield 1987; Wingfield and others 1984). Bedker (1987) cites numerous studies which suggest that seedling mortality in tests does not indicate that *B. xylophilus* can kill trees in the field. Also, many scientists in North America have conducted unsuccessful field pathogenicity tests with the pine wood nematode. Because the results were negative, they often were not published. For example, slash pine (*P. elliottii* Engelm. *elliottii*) seedlings can be killed by *B. xylophilus* in greenhouse inoculations (Dwinell 1985; Luzzi and Tarjan 1982), but Dwinell's bole inoculations in 1986 on 10-year-old slash pines (up to 10^5 nematodes/bole) during the worst drought on record in Georgia resulted in no disease development and these results were not published. As Wingfield and others (1984) noted, "Inoculation of seedlings in the greenhouse only provides clues to what may be happening in the forest". The inferences that can be made from greenhouse seedling inoculations are generally limited to the conditions under which the studies were conducted.

Based on field pathogenicity tests in which the inoculation procedure approached the natural infection process and satisfied Koch's postulates, only Scotch (Bedker and Blanchette 1984), slash (Luzzi and others 1984), Japanese red (*P. densiflora* Sieb. & Zuc.), and Japanese black (*P. thunbergii* Parl.) (Mamiya and Enda 1979) pines currently should be considered suscepts of the pine wood nematode. That is, susceptibility to the pine wilt disease in nature has been satisfactorily demonstrated only on these four pines. Because of high inoculum density and an inoculation procedure that did not fully mimic maturation feeding by pine sawyers, the study reported by Bedker and Blanchette (1988) for Scotch pine is not definitive. In a similar study, shoot inoculations with pine wood nematodes resulted in dieback but not in tree mortality (Bedker and others 1987). Luzzi and others (1984) demonstrated pathogenicity on 10-year-old field-grown slash pines in Florida when the nematodes were transmitted to the host by *M. titillator* Fabricus. Luzzi and Tarjan (1982), however, reported that no infection occurred when branches of 10-year-old slash pines were artificially inoculated with up to 25,000 *B. xylophilus*. Of the four pine species with proven susceptibility, only slash pine is native to North America. However, mortality of slash pine trees due to the pine wilt disease is extremely rare. Until proved otherwise by field pathogenicity tests that mimic the natural infection process, conifers native to North America should be considered to be immune or highly resistant to the disease. The classification of conifers as "resistant" or "susceptible" to *B. xylophilus*, based on greenhouse seedling tests or field inoculation procedures that do not simulate the natural infection process, is artificial.

Implications of Secondary Transmission

The pine wood nematode is transmitted to dead or dying pines during oviposition. Secondary transmission, first reported by Wingfield in 1983, occurs when *B. xylophilus* enters the tree through oviposition wounds. This mode of transmission has been confirmed (Luzzi and others 1984; Wingfield and Blanchette 1983) and is now considered the most common means of transgenerational transfer of species of *Bursaphelenchus*. The realization that *Bursaphelenchus* is transmitted during oviposition essentially redefined the status of the pine wood nematode in North America (Wingfield and others 1984). This revelation requires that the previous literature on the nematode be critically reevaluated taking secondary transmission into consideration. For example, if oviposition pits are noted on dead or dying pines, and the nematode is isolated, it cannot be automatically inferred that the tree succumbed to the pine wilt disease. Numerous studies since 1983 have demonstrated that the nematode is a secondary associate of the tree in these cases and does not contribute to tree mortality (Bedker 1987; Burnes and others 1985; Dwinell 1987b; Wingfield and Blanchette 1983; Wingfield and others 1982). Although Wingfield presented his hypothesis on transmission during oviposition in 1982, major review articles published as late as 1985 (except Wingfield and

others 1984) do not refer to secondary transmission. In the development of a hypothesis on the distribution of the pine wilt disease with respect to temperature, Rutherford and Webster (1987) did not fully consider secondary transmission. The EPPO (1986) publication that defines *B. xylophilus* as a quarantine organism does not mention secondary transmission.

The *Monochamus-Bursaphelenchus* Complex Outside North America

In assessing the risk of the pine wood nematode in exported softwood products, it is also necessary to look briefly at the *Monochamus-Bursaphelenchus* complex in Europe. Unfortunately, critical information is lacking on possible associations of species of *Bursaphelenchus* with the European species of *Monochamus* (for example, *M. sartor* F., *M. sutor* L., and *M. galloprovincialis* Oliv.). *Bursaphelenchus sutoricus* Devdariani (Devdariani 1974) and *B. kolymensis* Korentchenko (Korentchenko 1980) have been described and are phoretic in *M. sutor*, a species of *Monochamus* found in northern Scandinavia, Finland, and throughout central Europe (Hellrigl 1971). The range of *B. sutoricus* and *B. kolymensis* in relation to *M. sutor* has not been determined. The biology and pathogenic potential of *B. sutoricus* and *B. kolymnensis* have not been studied. *B. mucronatus* has been found from *M. sutor* in Sweden and this *Bursaphelenchus-Monochamus* complex is currently being studied by Swedish scientists (Magnusson and others 1988).

De Guiran and others (1986) noted that, "the taxonomic situation of *B. xylophilus* and related species is rather puzzling." In 1979, Mamiya and Enda described *B. mucronatus* from wood of Japanese red pine in Japan. This new nematode is similar morphologically to *B. xylophilus* but has a distinct mucro at the tail terminus in females and larvae (fig. 4). Mamiya (1986) reported that crosses of the Japanese isolates of *B. xylophilus* and *B. mucronatus* do not produce fertile offspring. The validity of *B. mucronatus* was questioned by Baujard (1980), who synonymized it with *B. xylophilus*. This change, however, has not been accepted. *Bursaphelenchus mucronatus* have also been taken from Scotch pine in Norway (McNamara and others 1988). Schauer-Blume (1987) found a nematode similar to *B. mucronatus* (=*B. fraudulentus* (Ruhm 1956)) in dying or dead oak (*Quercus*), cherry (*Prunus*), and beech (*Fagus*) trees in West Germany.

Wingfield and others (1983) isolated from balsam fir nematodes whose adult females had mucronate tails similar to those of *B. mucronatus*. The nematode with the mucronate tail mated with *B. xylophilus* from pine but not with *B. mucronatus* from Japan.

The Two Forms of *Bursaphelenchus* Isolates From North America

Currently, North American isolates of *B. xylophilus* are referred to by some as one of two forms: "R" (round tail) and "M" (mucronate tail). The "R" form is considered the causal agent of the pine wilt disease.

Wingfield and Blanchette (1983) report that the "M" form of *B. xylophilus* is phoretic in *M. marmorator* and *M. scutellatus*. Balsam fir is the exclusive host of *M. marmorator* (Craighead 1950; USDA FS 1985), whereas *M. scutellatus* is found on many conifers including species of *Pinus*, *Abies*, *Larix*, and *Picea* (Linsley and Chemsak 1985). The "M" form of *B. xylophilus* from balsam fir may therefore not be restricted to balsam fir (Wingfield and Blanchette 1983). In Canada, for example, the "M" form has been reported from balsam fir, black spruce (*Picea mariana* (Mill.) B.S.P.), eastern white pine (*Pinus strobus* L.), red pine (*P. resinosa* Ait.), and jack pine (*P. banksiana* Lamb.). The "R" form has been isolated from red and jack pines (Canadian Forestry Service 1985). Both forms were found in single trees. The distribution of the "M" and "R" forms is probably due to preference of the nematode and host preferences of species of *Monochamus*. It is currently our opinion that the "M" form of *B. xylophilus* is part of a *B. mucronatus* complex and is not a true strain of the pine wood nematode.

Baujard and others (1979) reported the presence of *B. xylophilus* in France. The French strain has the mucronate female tail of *B. mucronatus* but can hybridize with both *B. xylophilus* and *B. mucronatus* (De Guiran and Boulbria 1986). Enzyme electrophoresis has shown phenotypic differences among *B. xylophilus*, *B. mucronatus*, and the French strain. The French strain may be intermediate between *B. xylophilus* and *B. mucronatus* (De Guiran and others 1985). On the basis of this research in France, Rutherford and Webster (1987) concluded that pine wilt disease is present in Europe.

Many gaps in our knowledge of the taxonomy of *Bursaphelenchus* cloud an international perspective of the problem. For example, no information is available on what insects (i.e., *Monochamus* spp.) are associated with the French strain. However, the "R" form of the nematode is the culprit and its distribution is of primary concern.

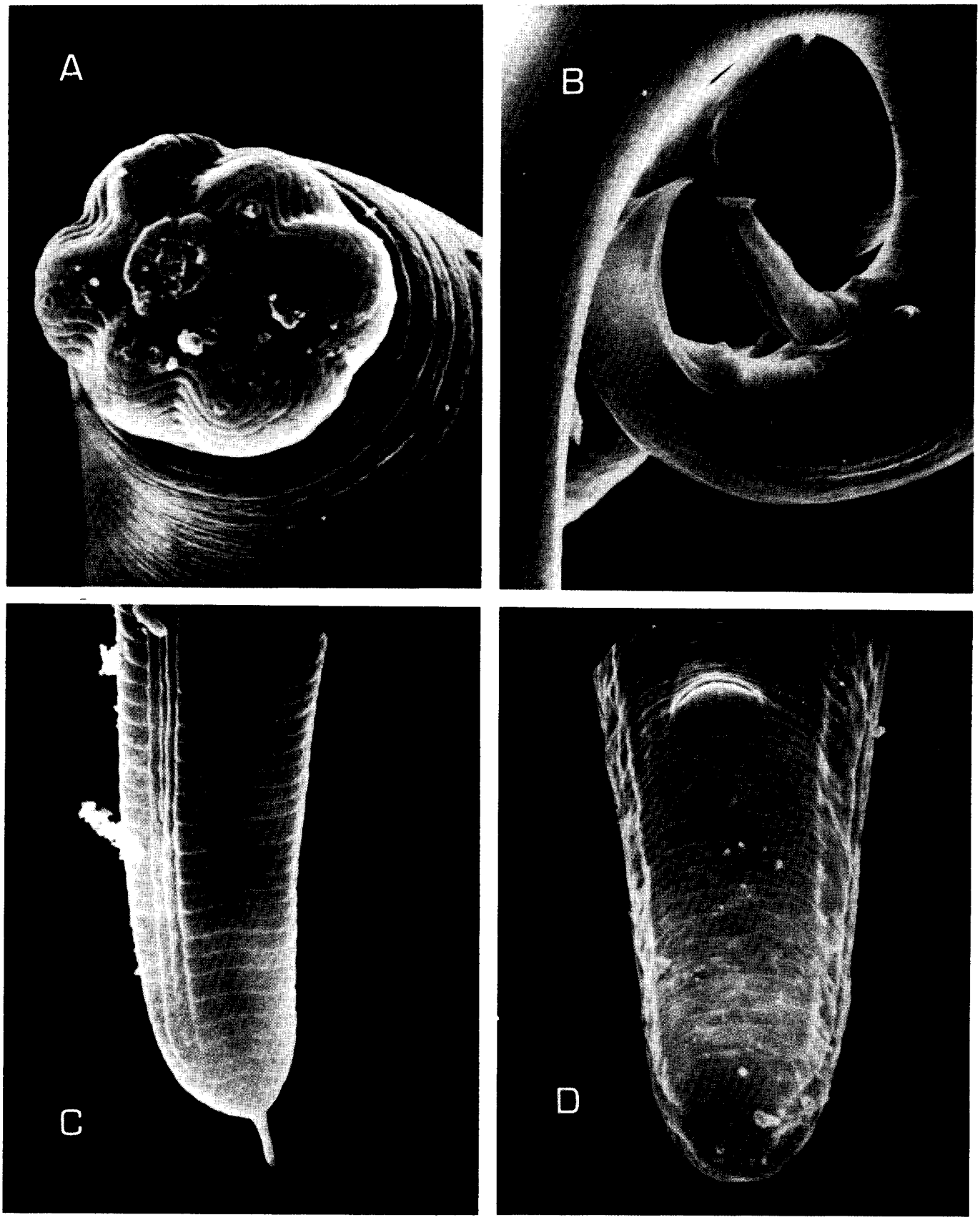

Figure 4.—Scanning electron microscope pictures. *A.* Front end, female lip region of *B. xylophilus*. *B.* Male, tail of *B. xylophilus* showing typical spicule, caudal alae, and papillae. *C.* Female tail end, *B. mucronatus* showing distinctive mucron at tip of tail. *D.* Female tail end, *B. xylophilus* showing rounded tail tip.

Bursaphelenchus xylophilus Not Synonymous With Pine Wilt Disease

The literature shows a marked tendency to treat *B. xylophilus* and the pine wilt disease as the same entity. They are not! Although the pine wood nematode is the causal agent of the pine wilt disease, it normally exists in nature independent of the disease. Thus, the distribution of *B. xylophilus* cannot be equated with the distribution of pine wilt disease in North America. Because of secondary transmission, *B. xylophilus* can be expected to be found throughout North America wherever recently killed or dying conifers are colonized by species of *Monochamus*. Also, in Canada and the Northern United States one would expect to find both the so-called R and M forms (Canadian Forestry Service 1985; Wingfield and Blanchette 1983; Wingfield and others 1983). The so-called M form has not been reported from the southern pines.

From 1979 to 1982, Robbins (1982) compiled reports of the pine wood nematode from across the United States. She emphasized "that these reports deal with trees from which pine wood nematodes have been extracted and not with reports of pine wilt disease." These data have frequently been used erroneously to infer that the pine wilt disease is widespread in the United States and involves several conifer species.

In North America, the pine wilt disease appears to be limited primarily to stressed exotic pines—namely, Scotch, Austrian, Japanese red, and Japanese black pines. Of these four pines only Scotch pine has been demonstrated to be a possible suscept in North America by field pathogenicity tests (Bedker and Blanchette 1988). Scotch pines have been planted extensively in North America as ornamentals, windbreaks, and Christmas trees. Losses normally follow summers with above-average temperatures and drought conditions (Malek and Appleby 1984). It is not clear from available data what percentage of the Scotch pines that have died since 1979 have actually succumbed to the pine wilt disease. For example, Malek and Appleby (1984) noted that cerambycid beetles often began ovipositing in dying trees before the onset of foliar symptoms. It is possible that many of the Scotch pines were dying for reasons other than pine wilt (i.e., root rot (Horner and others 1987; Highley and others 1982)) and that the pine wood nematode had been transmitted during oviposition. Further field studies are needed to show the full significance of the pine wood nematode in the mortality of Scotch pine. We feel the whole situation with Scotch and other exotic pines needs to be reevaluated.

Mamiya (1984) states that in Japan high temperatures and dry growing seasons greatly favor the intensification and spread of pine wilt. The heaviest annual loss in volume and number of pine trees was recorded in 1978 in Japan and was attributed to an unusually hot and dry summer. Takeshita and others (1975) demonstrated that low summer precipitation (less than 30 mm during 40 days of the summer season) and high temperatures (more than 55 days with a mean daily temperature above 25 °C throughout the season) were highly responsible for the incidence of severe damage. Dwinell (1986), furthermore, reported the optimum temperature for the reproduction of the pine wood nematode in wood chips was about 35 °C. The Nordic countries seldom have this degree of heat and drought.

Scientists are concerned that changing forest management practices could result in the increased incidence of diseases such as pine wilt. The pine wood nematode may have been responsible for the mortality of slash and sand (*P. clausa* (Chapm. ex Engelm.) Vasey ex Sarg.) pines in seed orchards in Florida in the early 1980's (Blakeslee and others 1987). Pathogenicity was not demonstrated, however. The pine wood nematode was associated with dying Virginia pines (*P. virginiana* Mill.) in a progeny test in Georgia and in a seed orchard in Alabama, but was probably a secondary invader of these dying pines (Dwinell and Barrows-Broaddus 1983). In a study of mortality of sand pine in a seed orchard in central Georgia, it was concluded that *B. xylophilus* was a secondary associate and did not contribute to tree mortality (Dwinell 1987b). Except for a few isolated cases, there is no evidence that pine wilt disease is a problem on southern pines.

The spread and development of the pine wilt disease to epidemic proportions in Japan suggests that the pine wood nematode was introduced into Japan. Since *B. xylophilus* is widespread in North America, it has been speculated that it originated in North America (Mamiya 1983, 1987). This hypothesis is not supported by experimental data and is currently being questioned. It has been suggested that both *M. alternatus* and *B. xylophilus* came to Japan from China and that the sawyers were free of native parasites and therefore more vigorous and the populations built up to very large numbers (up to 60,000/hectare). Whatever its origin, the nematode probably entered Japan in some form of raw softwood product (i.e., unbarked logs). The only documented case of transfer of pine wilt occurred in Okinawa when infested logs were brought in from Japan to build a pier, and vector beetles emerged and spread the nematode to nearby stands of luchu pines (*P. luchuensis* Mayr.) (Mamiya 1983).

Monochamus in Exported Wood

For 200 years, massive quantities of North American raw softwood products, including dunnage, logs, poles, wood chips, lumber, and other products, have been shipped to Europe and other countries. During these 200 years, the quantity and quality of these exported products have increased significantly. Over the last 12 years, Canada and the United States have shipped nearly 5 million tons of softwood chips representing $160 million f.o.b. to Scandinavia. It would be naive to believe that some wood products did not harbor pine wood nematodes and the vector longhorn beetles at one time or another. The problem of pests in wood and wood products is not of recent occurrence, only our perception of it.

Numerous reports exist of the interception of longhorn beetles from pine wood pallets and crates (dunnage). According to Holdeman (1980), live specimens of *M. notatus*, a species native to the Northeastern United States, emerged from pallets in California that had originated in West Virginia. He also found records of a *Monochamus* species being recovered from dunnage aboard Japanese cargo ships docked in San Francisco Bay. From 1985 to 1987, longhorn beetles have been found associated with dunnage for commodities (manhole covers, granite, marble or tiles) imported into the United States from China, Spain, and Italy (USDA-APHIS 1985-87). Longhorn beetles have been intercepted at New Zealand ports on many occasions (New Zealand Research Institute 1984).

The Scandinavian embargo includes timber cut from softwood trees. Canada reports that its graded lumber is free of pine wood nematode-infested longhorn beetles (Hopper 1987). This aspect of the problem has not been investigated in the United States, but there is no reason to believe that air-dried lumber represents a problem. The efficient logging management practices, quality controls, and inspection and grading rules utilized in the United States should preclude contamination by *Monochamus* spp.

The rationale for the embargo on kiln-dried lumber by some countries is not consistent with the available scientific knowledge on the organism. Commercial kiln drying of lumber is effective in killing all stages of insects in wood, including *Monochamus* spp. (Ostaff and Cech 1978). Dwinell [In press] has found that *B. xylophilus* is eradicated from sawed lumber by kiln drying. Nematode mortality was attributed to high wood temperature (60 °C), not to moisture loss from the wood. One hour at 71 °C in a kiln was sufficient to eliminate nematodes from 2 by 4's sawed from *B. xylophilus*-infested southern pine logs.

Infestation of Pine Chips: Risks and Management

The infestation of pine chips is what precipitated the bans by the Nordic countries. Dwinell (1986) has studied the ecology of the pine wood nematode in southern pine chip piles and determined that the optimum temperature for the reproduction of *B. xylophilus* in pine chips was 35° C. Mamiya (1983) reports that the nematodes will not reproduce at over 33° C on a mesophilic fungus in culture. In wood chips, the nematode reproduces on mesophilic and thermo-tolerant fungi that invade the wood.

Dwinell (1987a) also studied the incidence of the pine wood nematode in southern pine chip piles from (1) input onto the chip pile, (2) output from chip pile to ship, and (3) discharge of chips in Sweden. *Bursaphelenchus xylophilus* was found in chips being delivered to the terminal. Samples taken when the ships were being loaded revealed that the population of the nematode either declined or remained unchanged in the piled chips. Discharge samples indicated, however, that the nematode population increased significantly during the trans-Atlantic voyage. Distribution of nematodes in the holds could be related to the temperature of chips during transit. Maximum population levels occurred when the temperature was around 35 °C.

Because of the deterioration of pulpwood chips in outdoor storage, wood chip piles are very complex ecosystems. The development of micro-organisms in the chip piles is governed mainly by temperature. The interior of a pile of fresh wood chips rapidly rises to 60 °C. Within a few days, the living sapwood cells die and there is a 50-percent loss in monoterpenes (Bergman 1985). After 3 days, piled fresh chips of southern pine no longer attract adult pine sawyers (Cade 1987). Furthermore, the basic biological requirements of pine sawyers (Hellrigl 1971; Webb 1909) cannot be met by wood chips. The risk of the nematode being vectored from wood chips appears to be extremely remote.

After assessing the life history of the pine wood nematode and its complex association with longhorned beetles of the genus *Monochamus*, North American authorities agreed that the risk associated with importing wood chips and lumber into Scandinavia is virtually nonexistent. Scientists from the Nordic countries, however, suggested there was a risk due to chance transmission of the nematode to the Scandinavian forests through casual visits of insects to wood chip piles awaiting processing or the migration of the nematode through the soil into adjacent forest trees (Magnusson 1986).

In North America, nematodes have been found in association with several insects, other than species of *Monochamus* emerging from nematode-infested wood (Linit and others 1983; Wingfield and Blanchette 1983). For example, Linit and others (1983) found 3 out of a total of 40 adult pales weevils (*Hylobius pales* Herbat) from Scotch pine had a mean of 10 *B. xylophilus* per adult weevil. Other studies, in Florida on slash pine (Luzzi and Tarjan 1982) and in Minnesota on Austrian pine (Wingfield and Blanchette 1983), examined 143 adult pales weevils without finding pine wood nematodes in any of them. *Monochamus* spp. are considered to be the only efficient vectors of the pine wood nematode (Kobayashi and others 1984; Linit 1987; Mamiya 1983, 1984; Wingfield and Blanchette 1983).

In comparison with other nematodes, *B. xylophilus* is unusual because it is a parasite of aboveground parts of trees, is carried by an insect, and does not enter the soil (Wingfield and others 1984). The suggestion of possible soil transmission is based on a study by Kiyohara and Tokushige (1971). Whether they demonstrated soil transmission is debatable. In an experiment that lacked comparable controls, Kiyohara and Tokushige (1971) dug out the stem base and root system of five pines, attached a nematode-infested disk to the root system, and covered it with soil. The trees subsequently died. It is quite possible, however, that the roots were wounded by excavating them. In a greenhouse study, Halik and Bergdahl (1987) mixed pine wood nematode-infested wood chips into the soil around wounded roots of 5-year-old eastern white pine seedlings. Seven of 12 seedlings treated with infested chips wilted. Unfortunately, they did not use unwounded root controls. Because of the probability of nematode-infested wood being adjacent to a wounded root, neither of these studies demonstrates soil transmission. Mamiya and Shoji (1988) concluded that disease transmission through soil is negligible. They reported that pine wood nematodes added to soil died within 48 hours. In an unpublished study, I (Dwinell) mulched seedlings with *B. xylophilus*-infested chips for 12 months. The nematode was not transmitted to Scotch pine roots through the soil. I also surveyed the soil immediately below and around chip piles contaminated with pine wood nematodes and failed to extract any. Research to date suggests that the risk of soil transmission is minimal.

To further minimize these risks, Davis and others (1987) tried shipboard fumigation to kill nematodes. In 1986, a shipment of wood chips to Sweden was experimentally fumigated with phosphine (PH_3). The fumigation treatment was quite successful in eliminating nematodes from wood chips. Intransit fumigation was envisioned as a short-term solution to the problem that would allow trade to continue until further research and evaluation of the problem had been accomplished. The exporters cannot afford to close down their terminals indefinitely.

In conclusion, it has become increasingly evident since 1983 that the pine wood nematode is mainly a secondary associate of conifers native to North America and that the most common mode of transmission is during oviposition of the *Monochamus* vector. Whether *B. xylophilus* is a primary pathogen of stressed exotic pines is still open to question. In light of our current knowledge about the biology of the pine wood nematode, European and other countries might want to reconsider their ban on U.S. and Canadian softwood forest products.

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Mention of tradenames and companies is solely to identify experimental materials and does not constitute endorsement by the U.S. Department of Agriculture, nor does it imply approval of a product to the exclusion of others that may also be suitable.

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