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Relative Susceptibility of Four Pine Species to Infection by Pinewood Nematode[1]

M. J. LINIT[2] AND H. TAMURA[3]

Abstract: Mature trees of eastern white, jack, Scotch, and shortleaf pines were inoculated with 25,000–34,000 pinewood nematodes, *Bursaphelenchus xylophilus,* isolated from infected Scotch pines in Missouri. Equal numbers of trees of each species inoculated with distilled water served as controls. Nine of fifteen Scotch pines died within 4 months of nematode infection or during the winter and early spring following infection. A single eastern white and shortleaf pine died. No jack pines died. A single Scotch pine control died, apparently the result of natural nematode infection. No other controls died. Mean oleoresin flow did not differ among nematode-inoculated jack and shortleaf pines and their respective controls. Oleoresin flow in nematode-inoculated eastern white and Scotch pines was significantly lower than in their controls. Oleoresin flow was temporarily reduced in mortality-resistant eastern white and Scotch pines following nematode infection. Thus a sublethal impact of nematode infection on mortality-resistant host trees was documented.
Key words: Bursaphelenchus xylophilus, Monochamus carolinensis, mortality, oleoresin, pinewood nematode, *Pinus banksiana, Pinus echinata, Pinus strobus, Pinus sylvestris,* resistance.

The pinewood nematode *Bursaphelenchus xylophilus* (Steiner and Buhrer, 1934) Nickle, 1970 is the causal agent of pine wilt disease in Japan and the United States (9,15). *B. xylophilus* hosts include several genera of conifers; the most common hosts are pines. Scotch pine, *Pinus sylvestris* L., has the highest incidence of nematode-associated wilt of any species in the United States, with 134 of 365 reports of the nematode citing this pine species (18). Scotch pine plantations in Boone County, Missouri, suffer high mortality while adjacent plantations of other pine species are nearly disease free. The frequency of nematode-associated Scotch pine mortality may be the result of a feeding preference by an insect vector of the nematode, *Monochamus carolinensis* (Coleoptera: Cerambycidae) (10); the susceptibility of this pine species to invasion by the nematode (9,12,18); or a combination of both.

Walsh and Linit (25) studied the feeding preference of newly emerged adult *M. carolinensis* on four pine species. Beetles fed on all species tested, but preferred Scotch pine over jack (*P. banksiana* Lamb), shortleaf (*P. echinata* (Mill.)), and eastern white (*P. strobus* L.) pines.

Previous inoculation studies have utilized pine seedlings maintained under controlled conditions (2,3,9,11,16). Seedlings may not accurately reflect susceptibility in mature trees. Additionally, seedlings maintained under controlled conditions are not subject to environmental variability and stress, which may predispose trees to nematode-induced wilt (22).

The objectives of this study were to determine the relative susceptibility of four pine species to pinewood nematode infection under field conditions and to document changes in host tree oleoresin flow following nematode infection.

MATERIALS AND METHODS

Study trees, all approximately 20 years old, were selected from plantations of eastern white pine, jack pine, Scotch pine, and shortleaf pine at the Ashland Wildlife Research Area (AWRA), Boone County, Missouri. Three of the plantations were located within 200 m of each other. The white pines were located ca. 1,000 m from the others.

Study trees were tested for *B. xylophilus* infection before inoculation. Two xylem samples were removed with a brace and 1.25-cm bit from the bole of each potential study tree between 1 and 2 m above ground

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[1] Contribution from the Missouri Agricultural Experiment Station. Journal Series No. 10080.
[2] Department of Entomology, University of Missouri–Columbia, Columbia, MO 65211.
[3] Forestry and Forest Products Research Institute, Kansai Branch, Momoyama, Fushimi, Kyoto 612, Japan.
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level. Nematodes were collected from the samples using a modified Baermann technique (20). Only nematode-free trees with no obvious insect or pathogen associations were used. Five trees of each species were inoculated with 25,000 *B. xylophilus* in 2 ml distilled, sterilized water during July 1982, and 10 trees of each species (except white pine) were inoculated with 34,000 *B. xylophilus* in 2 ml distilled, sterilized water during June 1983. Only four white pines were inoculated in 1983 because of their limited availability at the AWRA. Inoculations were made through a 1.3-cm-d hole drilled ca. 6 cm into the trunk ca. 1.5 m above ground level. Nematodes were obtained from a laboratory colony of *B. xylophilus* isolated from naturally infected Scotch pines at the AWRA and reared on *Botrytis cinerea* Pers. grown on potato-dextrose agar. Equal numbers of trees treated with 2 ml distilled, sterilized water served as controls. Drill holes were plugged with sterile styrofoam and sealed with petroleum jelly following inoculations.

Trees were observed 1, 2, 3, 4, 12, 13, 14, 15, and 16 months postinoculation. Thus, trees inoculated in 1982 were observed through November and then from July through November 1983, and the 1983 trees were observed through October and then from June through October 1984. Each month, oleoresin flow was measured on all trees using the technique developed by Oda (17) and used by Mamiya (14) and Kobayashi (8). A 13-mm-d section of bark and phloem was removed from the trunk of each tree. All samples were taken between 1 and 2 m above ground level. The exact location of each sample was influenced by physical irregularities such as branch whorls and the location of previous sample sites. An effort was made to distribute the samples to minimize physical damage to the tree. Oleoresin exudation was evaluated after 1 hour using the following classification: 1 = no resin, sapwood discolored and dry; 2 = no droplets or tiny droplets of resin, sapwood moist; 3 = small aggregates of resin on sapwood; 4 = abundant resin accumulating at bottom of wound; 5 = abundant resin overflowing wound. Oda considered categories 4 and 5 as representative of normal oleoresin flow, whereas the remainder represent abnormal flow. Changes in foliage coloration and attack and colonization by *M. carolinensis* were noted during monthly oleoresin measurements.

Trees were checked for the presence of *B. xylophilus* 3 or 4 months and 16 months after inoculation. Samples of xylem tissue were collected within 1 m of the inoculation site. Nematodes were collected using a modified Baermann technique.

Tree mortality, *B. xylophilus* recovery, and *M. carolinensis* activity were used to assess relative susceptibility of the four pine species. Oleoresin flow data were analyzed as a split-plot design with main plots consisting of tree species, and inoculation treatment, and subplots consisting of months postinoculation. The least significant difference procedure was used to separate means and *t*-tests were used to compare oleoresin flow between inoculation treatments by month for each pine species. All statistical differences are reported at $P = 0.05$.

Results

Relative susceptibility: Pine species differed greatly in their response to *B. xylophilus* inoculation (Table 1). Jack pine was resistant: no trees died, no insect activity was noted, and no *B. xylophilus* were recovered. A single shortleaf pine died during the winter following nematode inoculation. Symptoms of infection were first noted 12 months after inoculation when foliage was a reddish color. The tree was under attack by *Ips* spp. bark beetles (Scolytidae: Coleoptera) but was never colonized by *M. carolinensis. B. xylophilus* was not recovered from this tree at the 3-month sample but was recovered 16 months after inoculation. The foliage of one white pine began to fade 4 months after inoculation (Table 2). *B. xylophilus* was not recovered at the 3-month or 16-month sample, and no insect colonization was noted during the course of the study. *B. xylophilus* was re-

TABLE 1. Total number of trees of each pine species tested in 1982 and 1983, number that died, and number from which *Bursaphelenchus xylophilus* was recovered.

Pine species	Distilled water + nematodes: Trees tested	Trees died	Trees from which nematodes recovered	Distilled water only: Trees tested	Trees died	Trees from which nematodes recovered
Jack	15	0	0	15	0	0
Scotch	15	9	5	15	1	1
Shortleaf	15	1	1	15	0	0
Eastern white	9	1	1*	9	0	0

* *B. xylophilus* recovered from an apparently healthy tree, not from the tree that died.

covered from another nematode-inoculated white pine 16 months after inoculation, but no foliage changes or insect attack occurred. This tree remained healthy 1 year after the study was concluded.

Scotch pine was very susceptible to nematode infection. Three of five trees in the 1982 test and six of ten in the 1983 test died following treatment. Foliage remained green on these trees for 1 month after inoculation (Table 2). Foliage faded to yellow-green or red on six trees 2 months after inoculation and on two more by month 3. The final tree did not begin to fade until month 4. *B. xylophilus* was recovered from six of the trees (nos. 1, 3 in 1982; 3, 4, 6, 8 in 1983) during the 3- or 4-month sample but from only a single tree (no. 4) at the 16-month sample. No nematodes were recovered from tree no. 5 at 3 months, but they were recovered at 10 months; no nematodes were found in either sample from trees 7 and 10. *B. xylophilus* was recovered from two apparently healthy Scotch pines in the 3- or 4-month sample but not at month 16, and these trees appeared to be vigorous at the conclusion of the study.

Seven trees were colonized by *M. carolinensis*. The timing of *M. carolinensis* attack was variable, but most attacks occurred while tree foliage was green or yellow-green. Two trees (nos. 5, 10) were never attacked by *M. carolinensis* but were colonized by *Ips* spp. These trees faded slowly and were probably not attractive as oviposition hosts until after the *M. carolinensis* adult activity ceased in the fall.

TABLE 2. Monthly oleoresin flow, foliage coloration, and *Monochamus carolinensis* activity of each nematode-inoculated tree which died following treatment through 4 months after inoculation.

Pine species	Inoculation date	Tree number	Month 1 OR*	Month 1 FC†	Month 1 MC‡	Month 2 OR	Month 2 FC	Month 2 MC	Month 3 OR	Month 3 FC	Month 3 MC	Month 4 OR	Month 4 FC	Month 4 MC
Scotch	1982	1	1	g	n	2	r	n	1	r	n	1	r	o
		3	1	g	n	1	r	n	1	r	o	1	r	l
		5	1	g	n	2	y	n	2	y	n	1	y	n
	1983	3	3	g	n	2	g	o	1	r	l	1	r	l
		4	1	g	n	2	g	o	1	y	o	1	y	l
		6	1	g	n	1	y	o	1	r	l	1	r	l
		7	5	g	n	1	y	o	1	y	o	1	r	l
		8	5	g	n	1	y	o	1	r	l	1	r	l
		10	1	g	n	1	g	n	3	g	n	2	y	n
Shortleaf	1983	4	2	g	n	1	g	n	2	g	n	1	g	n
White	1983	4	2	g	n	1	g	n	1	g	n	1	y	n

* Oleoresin flow: 1 = no resin flow to 5 = abundant resin flow.
† Foliage coloration: g = green, y = yellow-green, r = red.
‡ *Monochamus carolinensis* activity: o = oviposition, l = larval stages, n = none.

TABLE 3. Analysis of variance of oleoresin flow.

Source of variation	df	SS	F	$P > F$
Species	3	86.79	11.65	0.0041
Treatment	1	155.65	62.66	0.0001
Species × treatment	3	195.81	26.28	0.0003
Error a	7	17.39		
Month	8	167.80	4.75	0.0001
Month × species	24	30.58	0.29	0.9994
Month × treatment	8	9.36	0.26	0.9749
Month × species × treatment	24	43.27	0.41	0.9915
Error b	64	282.79		
Residual	828	857.80		

TABLE 4. Mean oleoresin flow for all combinations of pine species and treatments. Oleoresin flow for each species–treatment combination is pooled for all months.

Pine species	Treatment*	n	Mean†
Scotch	Water	135	3.93 a
Shortleaf	Nematodes	135	3.54 ab
Shortleaf	Water	135	3.44 b
Eastern white	Water	81	3.43 b
Jack	Water	135	3.21 b
Jack	Nematodes	135	3.09 b
Eastern white	Nematodes	81	2.04 c
Scotch	Nematodes	135	1.80 c

* Water = 2 ml distilled water. Nematodes = nematodes plus distilled water.

† Means followed by the same letter are not significantly different according to a test of least significant difference, $P \leq 0.05$.

Only one tree in the control treatment was found to be infected by *B. xylophilus.* A single Scotch pine in the 1982 test died during the second year of observation. A change in foliage coloration was noted during month 14, and insect colonization and *B. xylophilus* recovery were noted 16 months after inoculation.

Oleoresin flow: Mean oleoresin flow did not differ significantly among the 1982 and 1983 tests, and the tests for the two years were treated as a block effect. There was a significant interaction between tree species and inoculation treatment, indicating that tree species were not consistent in their mean oleoresin flow response to the inoculation treatments (Table 3). Oleoresin flow also differed among months postinoculation. This variable did not interact significantly with any others, indicating that the tree species–inoculation treatment interaction was consistent for all months.

Shortleaf and jack pine oleoresin flow did not differ between inoculation treatments (Table 4). Nematode-inoculated eastern white and Scotch pines, however, had significantly lower oleoresin flow than their respective water-treated counterparts.

Reduction in oleoresin flow in inoculated Scotch and eastern white pines was observed early. Mean Scotch pine oleoresin flow was significantly lower in the nematode-inoculated trees 1 month after inoculation and for the duration of the study (Fig. 1A). All nematode-inoculated Scotch pines that died had abnormally low oleoresin flow by month 2, most as quickly as month 1 (Table 2).

Eastern white pine oleoresin flow was significantly lower in the nematode-inoculated trees 1 and 3 months after inoculation during year 1 and months 12–15 of year 2 (Fig. 1B). No difference was noted during month 4, probably because of a low autumn oleoresin flow in the control trees. Oleoresin flow in the nematode-inoculated group increased steadily throughout year 2 of the study until it approached the value of the control group during month 16. White pine appeared to be a resistant species on the basis of tree mortality measurements. Only one nematode-inoculated tree died during the study, so the observed reduction in oleoresin flow represents a sublethal effect of pinewood nematode inoculation. The reduction in oleoresin flow appeared to be temporary, and a return to normal oleoresin flow might be expected during the third growing season postinoculation. The reason for high oleoresin flow in the nematode-inoculated group during month 2 is unknown.

There were no significant differences in oleoresin flow between inoculation treatments for either jack or shortleaf pines during any month of the study (Fig. 1C, D).

Evidence of a sublethal impact on oleo-

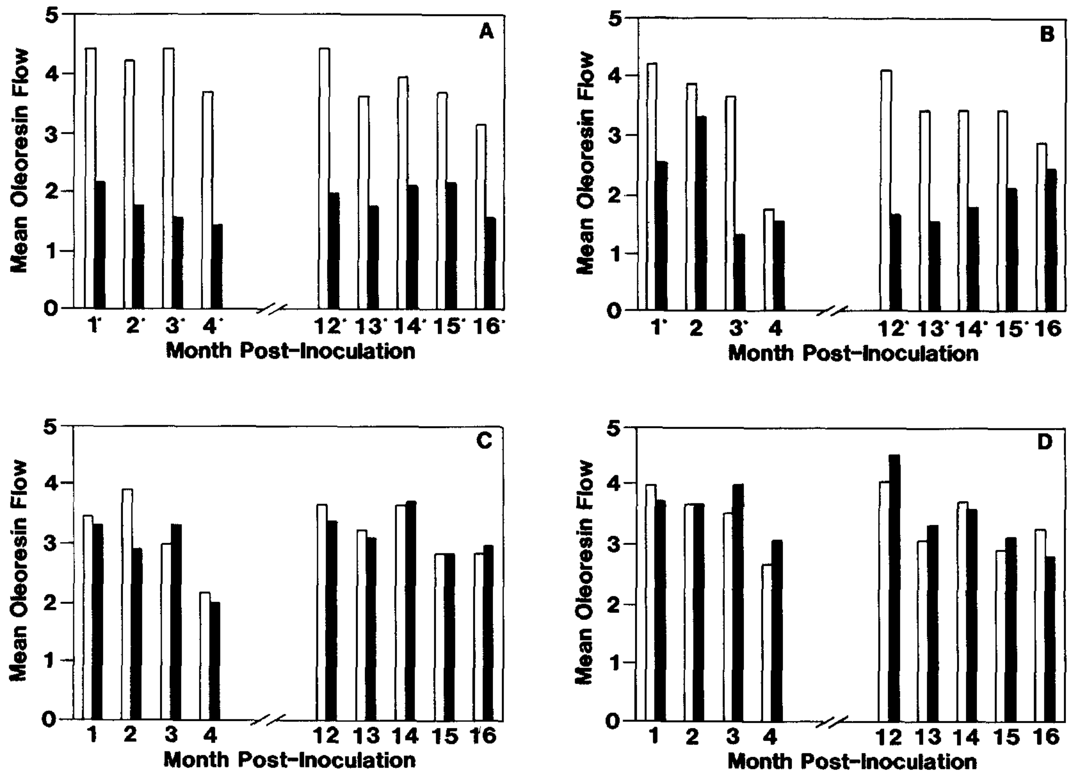

FIG. 1. Monthly mean oleoresin flow for water-treated (□) and nematode-inoculated (■) Scotch (A), eastern white (B), jack (C), and shortleaf (D) pines. Each bar is the mean of 15 trees in A, C, and D and nine trees in B. Mean oleoresin flow was significantly different ($P \leq 0.05$) between treatments during months indicated by an asterisk.

resin flow in nematode-inoculated white pines prompted a search for evidence of a similar response in the Scotch pines that survived the inoculation treatments. Mean oleoresin flow of trees in the two inoculation treatments was compared, for each month of the study. For these tests, however, all Scotch pines that died during the study, nine nematode-inoculated and one control, were deleted from the analysis. Among surviving trees, oleoresin flow was significantly lower for the nematode-inoculated group through month 12 of the study (Fig. 2). Again, the sublethal impact on oleoresin flow was temporary and lasted about 1 year postinoculation.

DISCUSSION

Relative susceptibility of four pine species to *B. xylophilus* infection as measured by tree mortality in our study confirms the previous work of some researchers and contradicts others. Direct comparisons between this study and previous inoculation studies in the United States (2,3,9,11,16) are difficult because of differences in study protocols. Inoculum levels have varied from as low as 500 (11,16) to as high as 200,000 (9) nematodes per tree. Variation in pathogenicity among *B. xylophilus* isolates from different geographic areas, as well as different host tree species and genera, has been reported by several others (1,13,26). Dropkin et al. (2) inoculated pine species with *B. xylophilus* from Missouri and Japan; Dwinell (3) used isolates from Alabama, Georgia, and South Carolina; Luzzi and Tarjan (11) tested a Florida isolate; and Myers (16) worked with *B. xylophilus* isolated in New Jersey. Finally, these workers utilized trees of seedling age grown in individual pots or plastic flats maintained in greenhouses or screenhouses. Dwinell (3) recently cited the need for field studies to further define the relative susceptibilities of pine species.

Scotch pine ranks as the most susceptible species in our study. Sixty percent of the nematode-inoculated Scotch pines died within 4 months of infection or during the winter and early spring following infection. *B. xylophilus* was recovered from all but two of the dead Scotch pines. Disease symptoms in these trees were identical with those of killed trees from which nematodes were recovered. Currently, no statistically sound method of nematode recovery from infected trees exists, and the method used in this study was not intensive. We feel that lack of nematode recovery is a reflection of the poor state of nematode sampling rather than a truly negative nematode sample. A single Scotch pine in the control group died, apparently the result of natural infection during year 2 of the study. Eastern white pine and shortleaf pine had a low rank of susceptibility, whereas jack pine was resistant to nematode infection under our study conditions. Scotch pine has been reported susceptible by other researchers (2,9,16); however, Dropkin et al. (2) reported higher mortality in shortleaf and jack pine seedlings than in Scotch pines in the same test. Eastern white pine was reported as highly susceptible by Myers (16) and moderately susceptible by Dwinell (3). Our results confirm field observations of widespread nematode-associated mortality in Scotch pines (12,18,25). The present study, as well as others by one of the authors, suggests that such mortality results from a nematode-susceptible host tree and a feeding preference (25) for that host by an insect vector of the nematode, *M. carolinensis.*

The impact of *B. xylophilus* infection on host trees was found to involve sublethal effects. Oleoresin flow was temporarily reduced in mortality-resistant Scotch pines and eastern white pines following nematode inoculation. All oleoresin samples were taken within 1 m of the inoculation site; therefore, the extent of oleoresin flow reduction in other portions of the host tree is unknown. The phenomenon of oleoresin flow reduction is well documented in trees that ultimately died following nematode inoculation (8,13,14). However, we have found a similar response in trees that survived infection.

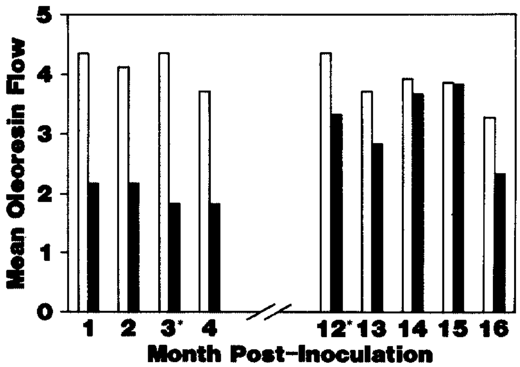

FIG. 2. Monthly mean oleoresin flow for water-treated (□, n = 14) and nematode-inoculated (■, n = 6) Scotch pines that survived. Mean oleoresin flow was significantly different ($P \leq 0.05$) between treatments during months indicated by an asterisk.

A recovery phenomenon in nematode-inoculated seedlings and trees has been reported by other researchers (4,19,21–23). These trees did not die; however, oleoresin flow temporarily decreased or individual branches died. Sasaki et al. (19), Sugawa (21), and Suzuki and Kiyohara (22) observed a recovery phenomenon in susceptible species. Tamura and Dropkin (23) observed this phenomenon cytologically and physiologically in resistant species. One study (24) found unusually heavy oleoresin exudation close to nematode inoculation sites on stems of 6-year-old white pines during the early stage of infection. Formation of traumatic resin canals and defense wells in these trees was also observed. Futai and Furuno (4) reported the same formations in white pines of the same age. High oleoresin flow in nematode-inoculated white pines during month 2 of the present study may be explained by the abnormal oleoresin exudation reported by these investigators.

Oleoresin flow is the principal defense mechanism of pine trees under bark-beetle attack (5). Hodges et al. (6,7) demonstrated a strong relationship between physical properties of host tree oleoresin flow, such as total oleoresin flow, and success of attacks by the southern pine beetle, *Dendroctonus frontalis* Zimmerman. Therefore, sublethal pinewood nematode infection may temporarily increase the susceptibility of host trees to invasion by subcortical insects, such as bark beetles and wood borers.

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