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Pinewood Nematode: A Threat

In February 1979, a portion of the trunk of an Austrian pine (*Pinus nigra*) arrived in Einar Palm's diagnostic clinic at the University of Missouri, Columbia. The previous summer, with no warning, the 39-year-old tree suddenly died; the needles lost their green color and became reddish brown but were retained. Seiji Ouchi, a plant pathologist from Japan who happened to be visiting the clinic that day, suggested that a nematode, *Bursaphelenchus xylophilus*, might be involved. Much to the surprise of clinic personnel, the log contained a huge population of a nematode identified as this species by V. H. Dropkin and confirmed by Y. Mamiya, the scientist who had originally described the species in Japan. And so the fun began. After notice of the find was published (3), interest in the disease grew rapidly, and it has now been reported from about half the states in the United States (Fig. 1).

Nematodes are known to be associated with insects in two diseases of trees: red ring of coconut and sudden wilt of pines. In both examples, nematodes travel from diseased to healthy trees during the life cycle of an insect—transmitted by a weevil among coconuts and by a wood-boring beetle among pines. In both diseases, the parasites gain entry through wounds made by the insects, increase to enormous populations, invade the entire plant, and survive in dead trees. The vector insect oviposits in the infected tree, and the emerging adult carries the nematodes when it flies to a healthy tree.

The occurrence of *B. xylophilus* in the United States has been documented in 18 species of pine in 28 states and in one species of larch in one state (Table 1). Most of these finds have been assembled by foresters, county agents, and other observers rather than by systematic surveys. The nematode identifications have usually been confirmed by experienced nematologists in Beltsville, Maryland, or in the various states. We suspect that the disease occurs throughout the United States. Although Japan is now experiencing a major epidemic in forests of *P. thunbergii* and *P. densiflora* (Fig. 2), the disease occurs sporadically elsewhere. Nematode-induced pine wilt is also known in France (1).

The disease was first recorded in Kyushu, Japan, during the second decade of this century. It spread rapidly through Kyushu and Shikoku and into Honshu. During 1948, 1,280,000 m^3 of pine wood were killed. Strenuous efforts to destroy wilted trees reduced annual losses to 400,000 m^3, but the disease persisted, and in 1975 the loss rose to 1,000,000 m^3 (8). Current losses are high. All pines in some localities in the prefecture of Ibaraki, Honshu, have died. The pine forests of the United States have not suffered large losses from this disease until now.

Biology of the Disease

In Japan, affected trees appear healthy during early summer. The first symptom is reduced flow of oleoresin from wounds, and within 2 weeks of nematode inoculation, oleoresin flow ceases. Transpiration diminishes, then halts 20–30 days after inoculation. The needles turn yellow, then brown 30–50 days after the first symptom, and the tree dies during late August to October (8). No detailed description of symptom development in U.S. pines has been published.

Populations of *B. xylophilus* rapidly build to high levels in all parts of inoculated trees, including roots, trunks, branches, and leaves. This nematode develops along two pathways: the propagative and the dispersal (5,7). During rapid reproduction (propagative pathway) there are four larval stages—L_1, L_2, L_3, and L_4—plus adults of both sexes. When reproduction diminishes, development switches to the dispersal pathway. The L_1 and L_2 are the same as in the propagative cycle, but a different form of the third stage appears—the dispersal, L_{III}. The cuticle of this larva is thicker than that of the propagative L_3, and lipid droplets accumulate within the intestine, which also undergoes degenerative changes.

The L_{III} survives starvation well, gradually utilizing its lipid stores. It molts to a fourth stage, the L_{IV} (known as the

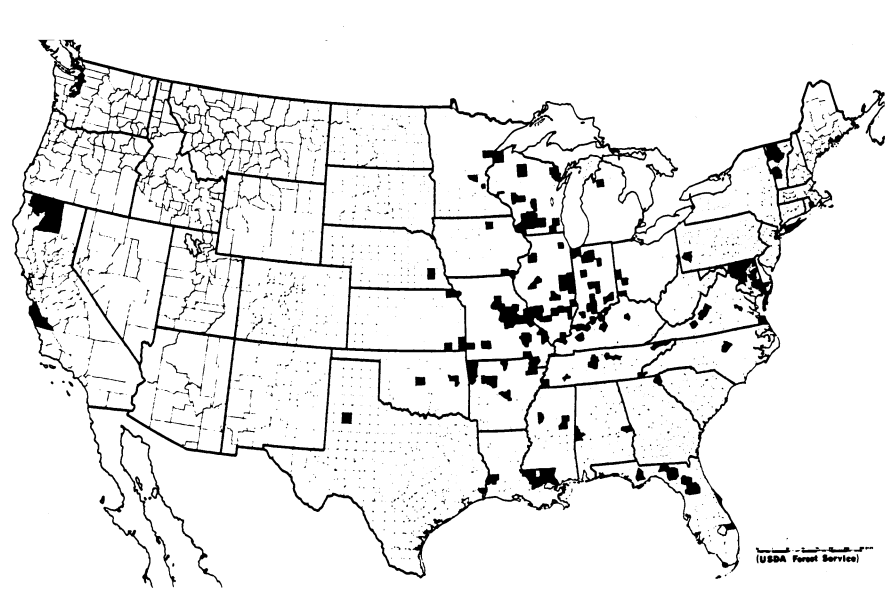

Fig. 1. Distribution of the pinewood nematode in the United States, 1980.

This research was supported by funds provided in part by the U.S. Department of Agriculture Forest Service, R U W FS-NC2205.

Experiment Station Journal Series No. 8793.

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Dauerlarva), which differs from the corresponding L_4. Dauerlarvae are adapted for transport by insect vectors and survive moisture stress. The cuticle structure undergoes further modification, lipid is partly replaced by glycogen, and the stylet, esophagus, and esophageal glands disappear. In Japan, L_{III}'s in infected pines migrate to the pupal chambers of the vectors, *Monochamus alternatus* (Coleoptera: Cerambycidae). Here they molt to Dauerlarvae that penetrate the spiracles of newly molted adult beetles still in the pupal chambers.

In Japan, *M. alternatus* emerges from dead trees in May or June carrying Dauerlarvae in its trachea. Young adults fly to the tops of healthy pines and feed on the bark of succulent stems (Fig. 3). During this maturation feeding, the Dauerlarvae leave the beetles, enter the wood of healthy trees through the feeding scars, and soon molt into adults. The nematodes penetrate resin canals to feed on epithelial cells of the lining and build to enormous populations in host trees. During this time, adult beetles mature and mate. Cerambycids are secondary invaders and prefer to oviposit in stressed or weakened pines, including trees whose oleoresin secretion has stopped because of *B. xylophilus*. The adult female beetle chews through the bark and deposits an egg into the oviposition site. The early instars forage beneath the bark. The third instar penetrates into the xylem, molts to a fourth instar, and passes the winter in that stage. The fourth instar pupates in early spring and emerges from the tree as an adult. Table 2 shows the coordinated life cycles of *B. xylophilus* and *M. alternatus*.

Eight species of Cerambycid beetles have been found to carry *B. xylophilus* in Japan: *M. alternatus* Hops., *M. nitens* Bates, *Acalolepta fraudatrix* Bates, *Acanthocinus griseus* Fabricius, *Arhopalus rusticus* Linne, *Corymbia succedanea* Lewis, *Spondylis buprestoides* Linne, and *Uraecha bimaculata* Thomson (10). *M. alternatus* is the principal vector. From 75 to 100% of specimens collected from infected dead trees had an average of 15,000 Dauerlarvae each (maximum, 230,000). The nematodes were most numerous in metathoracic tracheae but occurred under the elytra as well.

Fig. 2. Japanese red pine (*Pinus densiflora*) in Japan killed by the pinewood nematode. (Courtesy Y. Mamiya)

Fig. 3. An adult Cerambycid beetle (*Monochamus alternatus*) feeding on the smaller branches of a healthy pine. At this time, the nematodes leave the beetle's trachea through the spiracles and enter the wounds caused by the insect's feeding. (Courtesy Y. Mamiya)

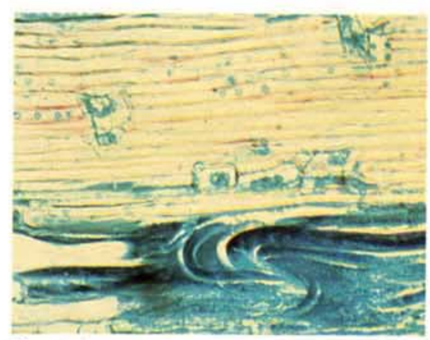

Fig. 4. Longitudinal section of first-year seedling of *Pinus densiflora* 27 days after inoculation with pinewood nematodes, showing masses of bacteria and nematodes occupying the axial resin canal. (Courtesy Y. Mamiya [9])

The search for vectors in the United States has just begun. Dauerlarvae of *B. xylophilus* have been found in *M. carolinensis* (Oliv.), *M. titillator* (F.), *M. scutellatus* (Say), *M. obtusus* Casey, and *Arhopalus rusticus obsoletus* (Rand.). The numbers of nematodes per beetle appear to be lower than those reported from Japan.

Epithelial cells of resin canals in infected pines are destroyed by the feeding of *B. xylophilus*. Mamiya (9) inoculated 5-month-old seedlings of *P. densiflora* with about 60 nematodes inserted into the hypocotyl on a piece of filter paper. By the sixth day post inoculation, nematodes had invaded resin canals, cambial tissues, and cortex, destroying parenchyma cells in all three. Masses of bacteria occupied the cavities resulting from the nematodes' activities (Fig. 4).

The pinewood nematode in culture reproduces well on several fungi, including *Botrytis cinerea*, *Ceratocystis* spp., *Fusarium* spp., *Pestalotia* spp., *Rhizosphaera* spp., and probably others (6). Female nematodes cultured on *B. cinerea* produced an average of 79 eggs during their adult life span of 15 days at 25 C. The life cycle took 4.5 days, and the net reproductive rate per generation was 42.3 (11).

The sudden wilting and loss of leaf coloration is a puzzling aspect of this disease. Is cell destruction in itself sufficient to cause these symptoms, or is there reason to suspect the action of a toxin? Oku and associates are investigating the existence of a toxin in affected trees (12). Their evidence suggests that a bacterium introduced together with *B. xylophilus* into pines produces a toxin. Cultures of bacteria contained a wilt-inducing component only when grown on media that included pine leaf homogenate. R. Bolla at the University of Missouri, St. Louis, has extracted a wilt-inducing toxin from diseased wood. No toxin is present in healthy pine extracts (R. Bolla, *personal communication*). In our laboratory, we are isolating bacteria from infested wood and inoculating aseptic pine seedlings with *B. xylophilus* from aseptic cultures grown on a standard medium for cultivation of *Caenorhabditis elegans* nematodes (technique of Bolla). We believe that nematodes without bacteria induce the same symptoms as those occurring naturally.

Table 1. Distribution of *Bursaphelenchus xylophilus* in the United States, December 1980[a]

Species	No. of counties	No. of states	States
Pinus sylvestris	82	17	Arkansas, Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Minnesota, Missouri, New York, Ohio, Oklahoma, Tennessee, Vermont, Virginia, West Virginia, Wisconsin
P. taeda	21	10	Alabama, Arkansas, Florida, Louisiana, Maryland, Mississippi, North Carolina, Tennessee, Texas, Virginia
P. nigra	18	10	Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Minnesota, Missouri, Tennessee, Wisconsin
P. resinosa	18	7	Illinois, Indiana, Iowa, Ohio, Tennessee, Vermont, Wisconsin
P. thunbergii	14	6	Arkansas, Maryland, Missouri, Nebraska, Oklahoma, Virginia
P. elliottii	12	2	Florida, Louisiana
P. strobus	12	11	Illinois, Iowa, Kentucky, Maryland, Michigan, Minnesota, Missouri, Nebraska, North Carolina, Tennessee, Virginia
P. virginiana	7	5	Illinois, Indiana, Maryland, South Carolina, Virginia
P. mugo	4	4	Illinois, Indiana, Missouri, Virginia
P. banksiana	4	3	Illinois, Indiana, Wisconsin
P. ponderosa	4	2	California, Missouri
P. echinata	3	3	Arkansas, Indiana, Kentucky
P. palustris	3	2	Florida, Louisiana
P. radiata	2	1	California
P. clausa	2	1	Florida
P. contorta var. *murrayana*	1	1	California
P. cembra	1	1	Pennsylvania
P. densiflora	1	1	Virginia
Larix laricina	3	1	Vermont

[a]Compiled by K. Robbins.

Table 2. Life cycles of *Bursaphelenchus xylophilus* and *Monochamus alternatus* and development of pine wilt in Japan[a]

Season	*M. alternatus*	*B. xylophilus*
Spring	Adult beetle carrying nematodes, bacteria, and fungi flies to healthy tree.	Nematodes carrying bacteria enter tree during beetle's feeding.
Summer	Beetle oviposits in dying tree.	Nematodes multiply in resin canals, and tree dies. As dead tree dries, resistant stages of nematodes appear in the population.
Fall and winter	Larvae burrow under bark, then move to deeper tissues.	Nematodes feed on tree-colonizing fungi.
Spring	Insect pupates and molts to adult, which chews its way to tree surface and flies to healthy tree.	Nematode Dauerlarvae invade thoracic spiracles of newly molted adult beetle.

[a]Adapted from Figure 5 of Mamiya (8).

Comparison of Japanese and U.S. *B. xylophilus*

Most of what we know about the biology of *B. xylophilus* has been learned in Japan, and determining whether this knowledge also applies to U.S. populations of pinewood nematodes is important. E. Kondo mated females of a Missouri population with males of a Japanese population. They reproduced as well as either parent population (*unpublished*).

Another test of similarity of populations is to compare their pathogenicity in various pine species. In November 1979, forest pathologists from the continental United States assembled in Columbia, Missouri, for a 1-day workshop. They asked us to conduct susceptibility tests on 19 species of pine seedlings, which they supplied. We inoculated these with *B. xylophilus* from Ashland, Missouri, and compared results with those of a similar but more extensive test in Japan (4). In both cases, nematodes were cultured on *B. cinerea.* The Japanese inoculated 5- to 11-year-old trees of 30 *Pinus* species with 2,000 nematodes applied to a wad of cotton fastened over a small area of the stem from which the bark had been removed. The cotton was held in place with Parafilm. Our inoculations of 1,000, 2,000, and 20,000 nematodes obtained from cultures of *B. cinerea* or extracted from diseased wood were made on 3- to 4-year-old seedlings in the same way and the cotton was held in place with latex bandage tape.

Table 3 compares the results of the Japanese tests (4) with ours. The species are ranked in order of decreasing susceptibility to the Missouri population of nematodes. In the U.S. study, trees inoculated with 1,000 nematodes did not all show the same symptoms. Jeffrey, lodgepole, red, eastern white, longleaf, and an unknown species from the West survived this dose, but 14–75% of the seedlings in the other 13 species succumbed. Seedlings of 10 species were inoculated with 2,000 larvae; no Jeffrey pine seedlings died, but 25–100% of the seedlings in the remaining nine species died. Inoculation with 20,000 nematodes killed all of the seedlings in 10 species, half of the seedlings in eight species, and none of the Jeffrey pine seedlings.

Differences between the U.S. and Japanese studies are apparent. Jack (*P. banksiana*) and Monterey (*P. radiata*) pines were highly susceptible in our test but resistant and moderately resistant, respectively, in Japan. Loblolly (*P. taeda*) was more resistant and southwestern white (*P. strobiformis*) more susceptible in the Japanese test. Although tests were conducted under different conditions and the seedlings in Japan were older, the results suggest that the population of *B. xylophilus* in Missouri differs from that in Japan. We believe that differences in susceptibility may also occur in populations of this nematode from different regions of the United States.

The Japanese authors found that oleoresin flow was reduced in most, but not all, of the inoculated trees while they still appeared healthy. Species in which healthy-appearing inoculated trees retained their capacity to exude oleoresin after inoculation were *P. strobus, P. sylvestris, P. tabulaeformis, P. elliottii, P. rigida,* and *P. banksiana*. The Japanese authors also found certain trees of *P. strobus* and *P. taeda* that appeared resistant after inoculation with 2,000 *B. xylophilus* but succumbed after two more inoculations with the same number of nematodes. Their results suggest that selection for resistant individuals within several species of pine would be useful.

Field Studies

Twenty miles south of the University of Missouri campus at Columbia is a plantation of 20-year-old Scotch pine in the Ashland Wildlife Area. The stand contains about 2,000 trees and is heavily infected with *B. xylophilus* (Fig. 5). The area provides an excellent opportunity for the study of the insect vector(s) of the nematode. In addition to the Ashland area, we have located three Christmas tree plantations in Missouri in which significant numbers of Scotch pine infected with *B. xylophilus* have died this year.

Last spring, intensive trapping of insects emerging from trees known to be infected with *B. xylophilus* was undertaken. The captured live insects were identified, and each species was checked to determine the percentage of individuals carrying the nematode and the density of nematodes carried per individual insect. Once identified, candidate vectors were placed on healthy seedlings to determine if they transmit the nematodes to healthy hosts.

When the insect vector(s) has been determined, the Scotch pine plantations in Missouri will be used to study the biology and population dynamics of that species. This information will be useful in developing and implementing control measures aimed at the vector.

Table 3. Comparison of inoculations of pines with *Bursaphelenchus xylophilus* in the United States and Japan

	Dead in U.S. test[a]		Dead in Japanese test[b]	
Pines	%	No.	%	No.
Shortleaf (*P. echinata*)	80	5	...	...
Jack (*P. banksiana*)	75	4	0	14
Monterey (*P. radiata*)	73	15	33	3
Sugar (*P. lambertiana*)	64	11	...	...
Scotch (*P. sylvestris*)	60	5	43	14
Limber (*P. flexilis*)	50	2	...	...
Slash (*P. elliottii*)	50	2	33	9
Virginia (*P. virginiana*)	50	12	...	...
Western white (*P. monticola*)	42	12	29	7
Ponderosa (*P. ponderosa*)	33	9	50	14
Austrian (*P. nigra*)	33	3	43	14
Red (*P. resinosa*)	30	10	21	14
Loblolly (*P. taeda*)	25	4	7	14
Southwestern white (*P. strobiformis*)	21	14	60	15
Lodgepole (*P. contorta*)	17	6	14	14
Longleaf (*P. palustris*)	0[c]	3	...	...
Eastern white (*P. strobus*)	0[c]	5	3	29
Jeffrey (*P. jeffreyi*)	0[d]	10	...	...

[a] Test terminated 7–9 weeks after inoculation of 3- to 4-year-old seedlings with 1,000 or 2,000 *B. xylophilus*.
[b] Test terminated 10 months after inoculation of 5- to 11-year-old seedlings with 2,000 *B. xylophilus* (4).
[c] Seedlings inoculated with 20,000 *B. xylophilus* died.
[d] Seedlings inoculated with 20,000 *B. xylophilus* survived.

Speculations

This disease is an example of a complex interaction among pines,

Fig. 5. Brown trees in a plantation of 20-year-old Scotch pine at the Ashland Wildlife Area in Missouri were killed by pinewood nematodes.

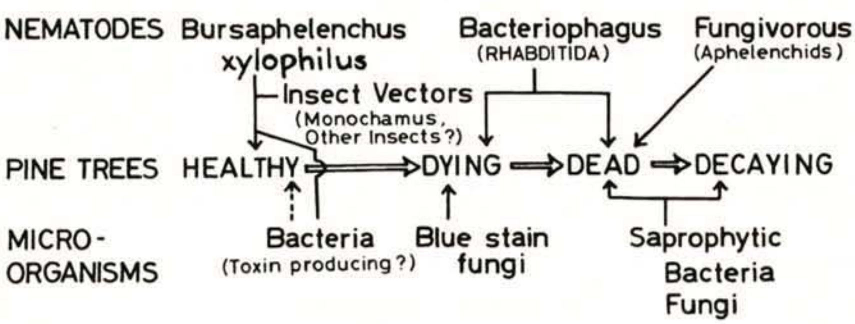

Fig. 6. Probable succession of organisms in pine trees killed by pinewood nematodes.

Cerambycid beetles, nematodes, and perhaps other organisms. Figure 6 depicts the probable succession of organisms inhabiting pine trees from the onset of pine wilt to the beginning of decay. Signals must be operating at several points in the life cycle of the nematode to permit passage from one stage to the next: the switch in development from propagative to dispersal L_{III} and L_{IV} stages, attraction to pupal chambers, entry into thoracic spiracles of the adult vector, and movement from the insect to the tree during feeding.

This kind of complex association is well known among parasitic nematodes. For example, human filariasis is caused by nematodes inhabiting lymphatic tissues. Larvae (microfilariae) are released to the blood circulation in synchrony with feeding habits of vector mosquitoes. Microfilariae appear during the night in areas with night-biting species and during the day in areas with day-biting species. After developing within the insect, the nematodes move to the proboscis, migrate to the skin surface of the host, and penetrate while the mosquito is feeding. Associations of nematodes and bacteria are also known. For example, a fatal disease of sheep results from a toxin produced when *Corynebacterium rathayi* is carried by *Anguina agrostis*, a nematode that induces galls of ryegrass (2).

Pine wilt is apparently endemic in the United States and not epidemic, as in Japan. The wide geographic distribution of the nematode and its occurrence in many species of pines and one species of larch indicate that the disease has been present here for a long time. The earliest record (1929) was published in 1934 (13). Perhaps sections of pine from the early history of the country preserved in museums would show that *B. xylophilus* has been present for hundreds of years. *P. sylvestris*, an introduced species, is by far the most commonly reported host (Table 1) and is probably a preferred host of the insect vectors. The epidemic in Japan may be related to the introduction of the nematode from abroad. In addition, the disruption of forests during World War II and the shift from utilization of wood to petroleum for energy contributed to the rapid increase of vector beetle populations.

We saw more cases of pine wilt in the summer of 1980 than in 1979, the first summer of survey. The number of trees with *B. xylophilus* in several locations (a local golf course, a University of Missouri horticulture farm, a Christmas tree plantation) was severalfold greater than in the same locations the previous summer. We speculate that the severe winters of 1977–78 and 1978–79 depressed the overwintering populations of Cerambycid beetles. January 1978 and 1979 were 5–8 degrees (C) colder than normal, but in 1980 the mean temperature was almost exactly normal. Temperatures of February 1978 and 1979 were closer to normal but lower than that of February 1980. Another possible effect of weather may be that the severe drought of 1980 increased the susceptibility of pines to the wilt, especially in infections with low numbers of nematodes. As data accumulate over the years, we should be able to determine the influence of weather on the occurrence of the disease.

Symptom development in U.S. infections and the results of our host susceptibility tests suggest that genetic components of each member of the association of *B. xylophilus*, Cerambycid beetles, and pines may be different in the United States and Japan. Reports from Illinois and California indicate that wilt may occur in parts of trees without affecting the whole tree. Further, there are certain differences in host range. Our Missouri population apparently affects *P. taeda* more frequently than the Japanese population does. We do not know whether this indicates differences in insects or nematodes or both. The report of infected larch in forests of Vermont strengthens our contention that *B. xylophilus* in the United States differs from the same species in Japan. Since the two populations can successfully breed with each other, they belong to the same species. We have noted morphological variations in nematodes from various localities in the United States and believe that more than one species may be involved in this disease. In addition, differences in climate between Japan and the United States may influence symptoms. It would be useful to compare symptoms on the same pine clones inoculated with *B. xylophilus* from the same population but grown in various parts of our country.

Both *B. xylophilus* and *Rhadinaphelenchus cocophilus* belong to a group of nematodes that has undergone extensive evolution in insect tunnels in wood. Nematodes of this group feed on fungi inhabiting the insect frass. It seems likely that species with the ability to invade trees and to build large populations in wood have evolved more than once. We believe that more extensive surveys of wood in dying trees are warranted to delineate the role of nematodes in tree diseases.

Genetic resistance offers excellent

opportunities for control of pine wilt. Both the Japanese data (12) and our results indicate that individual trees within a host species are not all equally susceptible to the infection. A large-scale search for resistant varieties should therefore be made in Scotch pine as well as in other species. This might be done both by inoculation with nematodes and by testing response to toxins extracted from infected wood. Jeffrey pine is especially interesting with respect to the nature of resistance.

In conclusion, the discovery of *B. xylophilus* as an important agent of death of pines gives us an additional means of unraveling the intricacies of forest ecology. The practical importance of pine wilt may be minor now in some U.S. forests, but the experience in Japan shows that a potential for important damage exists. Further, the potential for losses in Christmas tree plantations seems great. Plant nematologists and entomologists therefore have a clear obligation to examine this intricate association in detail. Attempts to formulate control tactics can begin once more is known about the biology of all the organisms in this association and about their relationships with each other and with the host tree.

Added in galley: Pine wilt disease has now (August 1981) been reported on 21 species of pine, 2 of cedar, 2 of larch, and 2 of spruce in 33 states.

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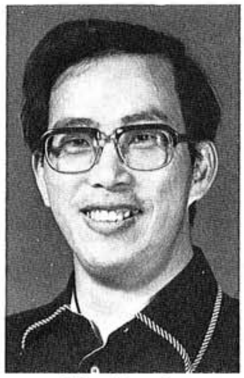

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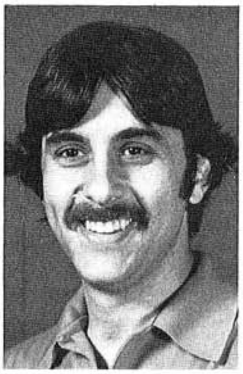

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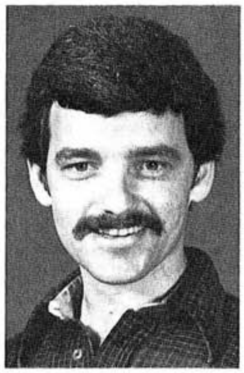

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