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Plant-Parasitic Nematodes Associated with Forest Trees in California

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As a first step in assessing the importance of plant-parasitic nematodes to California forestry, soil and root samples were taken from 32 kinds of trees in the major forested areas of California. Ninety-seven percent of the 228 samples were from conifers, and 82 percent were from trees important in the lumber industry, mainly ponderosa and Jeffrey pines, coast redwood, Douglas fir, and red fir. In the rhizosphere of these trees, 97 described and 54 undescribed, species of plant-parasitic nematodes in 46 genera were found. Species varied with climate and kind of tree. Most common overall were *Criconemella annulata, Xiphinema californicum, Gracilacus epacris, Pratylenchus macrostylus, Rhizonema sequoiae, Sphaeronema californicum, Trichodorus californicus, Tylenchorhynchus cylindricus, Filenchus vulgaris, Meloidogyne* sp., and *Ditylenchus anchilisposomus.* These nematodes were often present in large numbers and it is likely that parasitism by some species constitutes one of the stresses to California forest trees.

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INTRODUCTION

NEARLY HALF THE LAND AREA of the state of California is forested (Lane 1984). In 1977 over 100,000 people were employed in the state's lumber, wood products, and paper industries, and the value added by manufacture of industry products was over $3 billion (U.S. Dep. Commerce 1981). Plant-parasitic nematodes are known to reduce yields of all kinds of crop plants, including forest trees (Webster 1972), but those inhabiting California forests have received scant attention. A few pertinent observations can be gleaned from University of California and California Department of Food and Agriculture records (Siddiqui, Sher, and French 1973). The pinewood nematode, *Bursaphelenchus xylophilus* Steiner, has been found in isolated urban situations in Pacific Grove and Yreka, California, but has not been found in the forest, or associated with forest disease (U.S. Dep. Agric. Animal and Plant Health Insp. Serv. 1980). Effects on growth of some western forest conifer seedlings by *Xiphinema bakeri,* which occurs in California forests, and by other nematode parasites not known to occur there, have been reported (Maggenti and Viglierchio 1975; Viglierchio and Maggenti 1975; Viglierchio 1978; 1979). The survey reported here was conducted to determine which plant-parasitic nematodes occur naturally in the rhizosphere of California timber trees. We view this as an essential first step toward understanding the importance of nematodes to California forestry.

METHODS

Samples of soil and roots (228) were taken around 32 kinds of trees (table 1) from those floristic zones of California (Stebbins and Major, 1965; fig. 1) in which timber trees are found. The North Coast and Central Coast zones are similar. These climatic zones include the immediate coast, which seldom sees frost; has cool, wet winters; cool, dry but foggy summers; and is the home of the coast redwood and Douglas fir. The zones range to 1,000 m (3,300 ft) on the ridges of the Coast Range where winters are cold and ponderosa pines are found, and 2,700 m (9,000 ft) in the Trinity Alps with foxtail and western white pines.

The mountainous Cascade-Northern Sierra and Sierran zones are also similar, with mixed conifers, including ponderosa pine, incense cedar, white fir, and Douglas fir at 600 m to 2,000 m (2,000 ft to 6,600 ft) and pure stands of red fir above 2,000 m (6,600 ft). In winter, freezing temperatures are common at lower elevations, and arctic conditions prevail near the crest of the Sierra. The Inyo zone is made up of a portion of the eastern Sierra which has severe winters, is drier than the Sierran zones mentioned above, and is the home of large stands of Jeffrey and pinyon pines.

We obtained 224 of our 228 samples from the five floristic zones just described; including samples from sea level to 3,000 m (10,000 ft). Most of the samples were from Jeffrey pine, ponderosa pine, Douglas fir, coast redwood, and red fir, important timber

[1]Accepted for publication April 12, 1985.

TABLE 1. SAMPLES FROM 32 CALIFORNIA FOREST TREE SPECIES

Latin name	Common name	Number of samples
Abies concolor (Gord. & Glend.) Lindl.	White fir	9
Abies magnifica A. Murr	Red fir	24
Betula occidentalis Hook	Water birch	1
Cupressus macnabiana A. Murr.	McNab cypress	1
Cupressus macrocarpa Hartw.	Monterey cypress	2
Juniperus osteosperma (Torr.) Little	Utah juniper	2
Libocedris decurrens Torr.	Incense cedar	5
Picea sitchensis (Bong.) Carr.	Sitka spruce	1
Pinus aristata Engelm.	Bristlecone pine	1
Pinus attenuata Lemm.	Knobcone pine	2
Pinus balfourina Grev. & Balf.	Foxtail pine	2
Pinus contorta var. *murrayana* (Grev. & Balf.) Engelm.	Lodgepole pine	4
Pinus coulteri D. Don	Coulter pine	1
Pinus flexilis James	Limber pine	2
Pinus jeffreyi Grev. & Balf.	Jeffrey pine	50
Pinus lambertiana Dougl.	Sugar pine	3
Pinus monophylla Torr. & Frem.	Singleleaf pinyon pine	9
Pinus monticola Dougl.	Western white pine	1
Pinus muricata D. Don	Bishop pine	1
Pinus ponderosa Laws.	Ponderosa pine	32
Pinus radiata D. Don	Monterey pine	1
Pinus sabiniana Dougl.	Digger pine	2
Populus fremontii S. Wats.	Fremont cottonwood	1
Populus tremuloides Michx.	Quaking aspen	2
Pseudotsuga menziesii (Mirb.) Franco	Douglas fir	31
Quercus agrifolia Nee	Coast live oak	1
Quercus Kelloggi Newb.	California black oak	2
Salix lasiandra Benth.	Yellow willow	1
Salix lasiolepis Benth.	Arroyo willow	1
Salix sp.	Willow	1
Sequoia sempervirens (D. Don) Endl.	Coast redwood	31
Sequoiadendron giganteum (Lindl.) Buchholz	Giant redwood	1
Total		228

species. Each sample consisted of about 4 kg (9 lb) of soil and a handful of feeder roots taken from the 10 cm to 40 cm (4 in to 16 in) depth. An effort was made to take samples in spots where there were few or no roots of plants other than the target tree. This is feasible in many California forest locations because of the open nature of the forest.

In case of delay in the nematode extraction process, samples were stored in plastic bags at 10°C (50°F). The soil was mixed for homogeneity and nematodes were extracted from a 250 cc (1 cup) sample using Jenkins's (1964) method. The product was allowed to settle, and supernatant water was siphoned off to the 10 mL level. Nematodes in this 10 mL were killed and fixed by slow addition of 10 mL of a boiling solution of 4 percent formaldehyde and 1 percent glycerin, a modification of Robbins's (1978) method. This product was stored in 20 mL vials and numbers of each nematode species were determined by microscopic examination of aliquots. Roots were blenderized in water for 1 minute and nematodes were extracted from the product using Jenkins's (1964) method, then killed, and fixed as described above. Formaldehyde-preserved nematodes were mounted in dehydrated glycerin on 1,350 microscopic slides following Thorne's (1961) slow method.

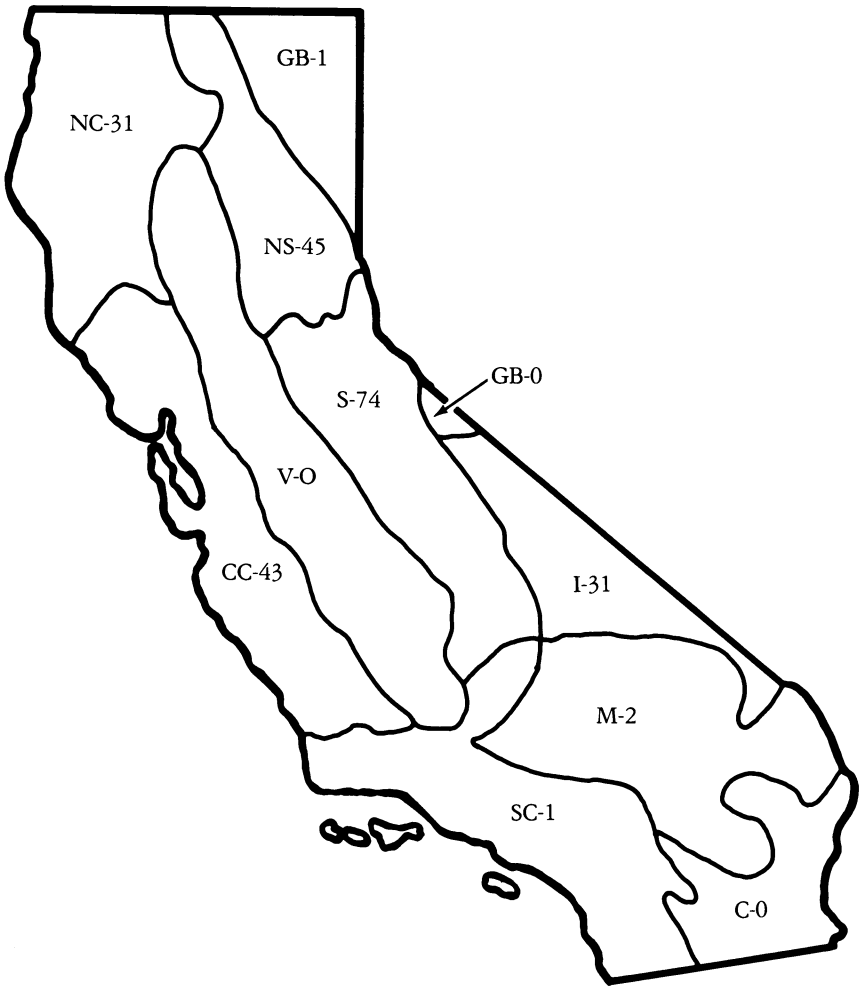

Fig. 1. Number of samples taken in each of Stebbins and Major's floristic subdivisions of California. *NC,* North Coast; *NS,* Cascade-North Sierra; *GB,* Great Basin; *CC,* Central Coast; *V,* Valley; *S,* Sierra; *I,* Inyo; *M,* Mojave; *SC,* Southern California; *C,* Colorado.

Species identifications were made using both formaldehyde-preserved and glycerin-mounted specimens because certain morphological characters are seen more easily in one or the other preservative. The specimens mounted in glycerin will be placed in the University of California Davis Nematode Collection.

RESULTS AND CONCLUSIONS

The plant-parasitic nematode species found most often was the root ectoparasite *Criconemella annulata* (table 2). It occurred in two-thirds of the Jeffrey pine samples (table 3) and with 13 other kinds of trees, often in concentrations greater than 200 per 250 cc (1 cup) of soil (table 4). *Criconemella annulata* is apparently adapted to regions with cold winters. Originally described from Montana (Taylor 1936), it has been reported on a variety of trees and shrubs from mountainous areas in California and New Mexico (Raski and Golden 1966; Raski and Riffle 1967), and in British Columbia, Alberta, and the Canadian

TABLE 2. SAMPLES CONTAINING THE 11 MOST COMMONLY FOUND PLANT-PARASITIC NEMATODES, ALL ZONES AND TREE SPECIES COMBINED

Nematode	(%)
Criconemella annulata	43
Xiphinema californica	31
Gracilacus epacris	15
Pratylenchus macrostylus	13
Rhizonema sequoiae	13
Sphaeronema californicum	13
Trichodorus californicus	11
Tylenchorhynchus cylindricus	10
Filenchus vulgaris	9
Meloidogyne sp.	9
Ditylenchus anchilisposomus	9

arctic (Wu 1965). In our study it was notably rare on coast redwood and in coastal valleys.

Xiphinema californicum was common in all zones and with nearly all tree species. This nematode has been previously identified as *X. americanum* Cobb, but all the specimens we have seen from California have the longer odontostyle and more expanded lip region of *X. californicum* (Lamberti and Bleve-Zacho 1979). Whether *X. californicum* is a species different from *X. americanum* or a race of it is debatable. No differences in host range or biology are known at present. *Xiphinema californicum* was found from sea level to 3,000 m (10,000 ft) in the Sierra, where it was present in large numbers. This apparent tolerance of a range of widely different environments seems inconsistent with the difficulties that are encountered in culturing the nematode. The culture difficulties are probably related to intolerance of rapid fluctuation in temperature and moisture (Lownsbery and Maggenti 1963) and sensitivity to low oxygen levels (Van Gundy et al. 1962), conditions more apt to obtain in culture than in nature.

Gracilacus epacris was found most frequently on the coast and on coast redwood, where it was often accompanied by *Rhizonema sequoiae, Bakernema variabile, Boleodorus thylactus,* and several species of *Basiria.* These nematodes were found in the dense mat of feeder roots that coast redwood produces in the surface layer of soil. *Gracilacus epacris* was originally described from a walnut orchard in the Central Valley of California (Allen and Jensen 1950). It has never been found in the Central Valley again, and may have been washed down there via streams originating in the Sierra, where it is fairly common. *Rhizonema sequoiae,* only recently found and described, (Cid Del Prado Vera et al. 1983) is distributed over most of the range of coast redwood, from Marin County near San Francisco to the Smith River near the Oregon border in Del Norte County. It also occurred in the Cascades-Northern Sierra and in the Sierra on ponderosa and Jeffrey pines. In past geological epochs, coast redwood grew over a much larger range than it occupies at present (Raven and Axelrod 1978). *Rhizonema sequoiae* may have parasitized coast redwood in its broader range, persisting now on trees that succeeded coast redwood. *Boleodorus thylactus* and *Basiria* spp. were rare or absent except in the coastal zones.

The *Meloidogyne* sp. often found in ponderosa and Jeffrey pine roots in the Cascade-Northern Sierra zone has perineal patterns with characteristics of both *M. arenaria* and *M. incognita.* This nematode failed to increase on either tomato or ponderosa pine in a lathhouse at Davis, California. Apparently it is a species adapted to conifers in the Sierra Nevada.

Pratylenchus macrostylus and *Sphaeronema californicum* were especially common with red fir in the Sierra and Cascade-Northern Sierra zones. *Pratylenchus macrostylus* was

TABLE 3. PERCENTAGE OF SAMPLES CONTAINING THE MOST COMMONLY FOUND PLANT-PARASITIC NEMATODES; FLORISTIC ZONES AND TREE SPECIES CONSIDERED SEPARATELY

Floristic zones				
North Coast	Central Coast	Cascade-Northern Sierra	Sierra	Inyo
Gracilacus epacris 48	*Xiphinema californicum* 44	*Criconemella annulata* 62	*Criconemella annulata* 68	*Criconemella annulata* 45
Rhizonema sequoiae 45	*Trichodorus obscurus* 26	*Meloidogyne* sp. 27	*Xiphinema californicum* 30	*Xiphinema californicum* 32
Trichodorus californicus 42	*Gracilacus epacris* 21	*Pratylenchus macrostylus* 18	*Sphaeronema californicum* 27	*Tylenchorhynchus cylindricus* 29
Bakernema variabile 29	*Trichodorus californicus* 16	*Sphaeronema californicum* 18	*Pratylenchus macrostylus* 26	*Paratylenchus alleni* 13
Boleodorus thylactus 29	*Rhizonema sequoiae* 16	*Xiphinema californicum* 18	*Ditylenchus anchilisposmus* 16	*Helicotylenchus clarkei* 10

Tree species				
Douglas fir	Coast redwood	Ponderosa pine	Jeffrey pine	Red fir
Criconemella annulata 42	*Gracilacus epacris* 65	*Criconemella annulata* 44	*Criconemella annulata* 64	*Criconemella annulata* 75
Xiphinema californicum 26	*Rhizonema sequoiae* 55	*Xiphinema californicum* 28	*Xiphinema californicum* 34	*Pratylenchus macrostylus* 42
Trichodorus californicus 26	*Boleodorus thylactus* 39	*Meloidogyne* sp. 25	*Meloidogyne* sp. 22	*Merlinius conicus* 29
Filenchus vulgaris 19	*Trichodorus californicus* 32	*Rhizonema sequoiae* 16	*Tylenchorhynchus cylindricus* 18	*Sphaeronema californicum* 25
Gracilacus epacris 19	*Xiphinema californicum* 29	*Trichodorus californicus* 13	*Sphaeronema californicum* 16	*Filenchus aquilonius* 21

described from Ontario and British Columbia (Wu 1971). We believe this is the first time it has been reported in California.

Trichodorus californicus and *T. obscurus* were the two *Trichodorus* species found most often, especially in the two coastal zones around a variety of trees.

Tylenchidae, including species of *Filenchus, Malenchus, Tylenchus, Coslenchus,* and *Miculenchus,* were widely distributed on many tree species. Feeding habits of these are not well known. Some feed on epidermal cells, root hairs, and mosses. *Ditylenchus* spp., often found in root extracts, may be mycorrhizal parasites (Riffle 1971). *Aphelenchoides* spp. were common, and probably include mycophagous species and associates of bark beetles.

TABLE 4. PLANT-PARASITIC NEMATODES FOUND IN FORESTS IN SEVEN CALIFORNIA FLORISTIC ZONES (FIG. 1), AND TREE SPECIES WITH WHICH THEY WERE ASSOCIATED, BASED ON SAMPLES FROM 228 LOCATIONS

Genus and described species	Host association	Number of detections	Floristic zones
Aphelenchoides (13)*			
A. cibolensis	White fir	1	S
Riffle	Incense cedar	1	NS
	Lodgepole pine	1	NS
	Jeffrey pine	2	NS
	Ponderosa pine	2	NS, S
	Douglas fir	1	S
A. clarus	Bristlecone pine	1	I
Thorne and Malek	Jeffrey pine	1	S
A. cyrtus	Red fir	1	S
Paesler	Jeffrey pine	6	NS, S
	Ponderosa pine	2	S, I
	Douglas fir	4	NC, S
	Coast redwood	2	NC, CC
A. saprophilus	Red fir	1	S
Franklin	Bristlecone pine	1	I
	Jeffrey pine	1	S
	Ponderosa pine	1	S
A. singhi	Bristlecone pine	1	I
Das	Jeffrey pine	1	NS
A. spinosus	McNab cypress	1	NC
Paesler	Douglas fir	1	NC
Bakernema (1)*			
B. variabile	Ponderosa pine†	1	NC
Raski and Golden	Douglas fir	1	CC
	Coast redwood†	8	NC
Basiria (5)*			
B. duplexa (Hagemeyer and Allen) Geraert	Coast redwood	1	NC
B. flandriensis Geraert	Coast redwood	1	NC
B. gracilis	Douglas fir	1	CC
(Thorne) Siddiqi	Coast redwood	3	NC, CC
B. graminophila Siddiqi	Coast redwood	1	NC
Basiroides Thorne and Malek (1)*	Coast redwood	1	NC
Boleodorus (1)*			
B. thylactus	Monterey cypress	1	CC
Thorne	Knobcone pine	1	CC
	Douglas fir	1	S
	Arroyo willow	1	SC
	Coast redwood†	12	NC, CC
Bursaphelenchus Fuchs (1)*	Jeffrey pine	1	S
Coslenchus (3)*			
C. acceptus Andrassy	McNab cypress	1	CC

(Continued on next page)

TABLE 4. CONTINUED

Genus and described species	Host association	Number of detections	Floristic zones
C. costatus (de Man) Siddiqi	Arroyo willow	1	SC
	Coast redwood	1	NC, CC
Criconema (6)			
C. crotaloides (Cobb) Schuurmans Stekhoven and Teunissen	Knobcone pine	1	CC
	Jeffrey pine	1	S
	Douglas fir	1	NC
	Coast redwood	3	NC, CC
C. longulum Gunhold	Coast redwood	1	CC
C. mutabile (Taylor) Raski and Luc	Coulter pine	1	CC
	Douglas fir	1	NS
	Coast live oak	1	CC
	Coast redwood	2	CC
C. psammophilum (Krnjaic and Loof) Raski and Luc	Douglas fir	1	CC
	Coast redwood	2	CC, NC
C. thornei (Knobloch and Bird) Raski and Luc	White fir	1	NS
	Jeffrey pine	2	NS
	Ponderosa pine	1	S
Criconemella (6)*			
C. annulata (Taylor) Luc and Raski	White fir†	7	NS, S
	Red fir†	18	NS, S
	Water birch	1	I
	Utah juniper	1	I
	Incense cedar	4	S
	Lodgepole pine	1	S
	Jeffrey pine†	32	NS, S, I
	Sugar pine	3	NS, S
	Western white pine	1	S
	Ponderosa pine	14	S, NS, CC
	Douglas fir†	13	S, NS, CC
	California black oak	1	I
	Coast redwood	1	CC
	Giant redwood	1	S
C. macrodora (Taylor) Luc and Raski	Knobcone pine	1	CC
	Ponderosa pine	1	NC
	Douglas fir	2	NC
	Coast redwood†	1	CC
C. pseudohercyniensis (DeGrisse and Koen) Luc and Raski	Willow	1	S
C. teres (Raski) Luc and Raski	Ponderosa pine	2	NS, S
	Coast redwood	3	CC
C. vernus (Raski and Golden) Luc and Raski	Yellow willow	1	I
C. xenoplax (Raski) Luc and Raski	Ponderosa pine	1	CC
	Montery pine	1	CC
	Coast redwood	1	CC
Crossonema (1)*			
C. venustum Mehta and Raski	Ponderosa pine	1	CC

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TABLE 4. CONTINUED

Genus and described species	Host association	Number of detections	Floristic zones
Deladenus (1)*			
D. durus (Cobb) Thorne	Coast redwood	1	NC
Diphthorophora de Man (1)*	Knobcone pine	1	CC
	Jeffrey pine	1	NS
	Sugar pine	1	NS
	Singleleaf pinyon pine	1	I
	Bishop pine	1	CC
	Ponderosa pine	2	NS
	Douglas fir†	4	NC, CC, S
	Coast redwood	6	NC, CC
Ditylenchus (13)*			
D. anchilisposomus (Tarjan) Fortuner	Red fir	3	S
	McNab cypress	1	CC
	Incense cedar	1	S
	Limber pine	1	S
	Jeffrey pine	5	NS, S
	Ponderosa pine	4	S
	Douglas fir	1	S
	Coast redwood	4	NC, CC
D. convallariae Sturhan and Friedman	Coast redwood	1	C
D. destructor Thorne	White fir	1	NS
D. lutonensis (Siddiqi) Fortuner	Red fir	1	S
D. myceliophagus Goodey	Red fir	1	S
	Incense cedar	1	S
	Jeffrey pine	4	NS, S
	Ponderosa pine	1	NS
	Douglas fir	1	CC
D. tenuidens Gritsenko	Coast redwood	1	CC
D. triformis Hirschmann and Sasser	Knobcone pine	1	I
	Jeffrey pine	3	S
	Douglas fir	1	CC
	Yellow willow	1	SC
Filenchus (20)*			
F. andrassyi (Szczygiel) Andrassy	Coast redwood	1	NC
F. aquilonius (Wu) comb. n.	Red fir	7	NC, NS, S
	Jeffrey pine	5	NS, S, I
	Sugar pine†	1	S
	Ponderosa pine	1	S
	Quaking aspen	1	S
	Douglas fir	1	S
F. mirus (Husain and Khan) comb. n.	Douglas fir	1	NC
	Coast redwood	1	NC
F. plattensis (Thorne & Malek) Niblack and Bernard	Red fir	2	S
	Ponderosa pine	1	S
	Douglas fir	1	NC

(Continued on next page)

TABLE 4. CONTINUED

Genus and described species	Host association	Number of detections	Floristic zones
F. quartus (Szczygiel) comb. n.	Red fir	2	S
	McNab cypress	1	CC
	Incense cedar	2	S
	Jeffrey pine	5	NS, S
	Ponderosa pine	4	NC, CC, S
	Douglas fir†	1	S
	Coast redwood	2	NC
F. thornei (Andrassy) Andrassy	Knobcone pine	1	CC
	Coast redwood	2	NC, CC
F. vulgaris (Brzeski) comb. n.	Incense cedar	2	S
	Ponderosa pine	3	S
	Quaking aspen	1	S
	Douglas fir	7	NC, CC, S
	Coast redwood	8	NC, CC
Gracilacus (4)*			
G. anceps (Cobb) Raski	Jeffrey pine	4	NS
	Douglas fir	1	S
	Arroyo willow	1	SC
G. epacris (Allen and Jensen) Raski	White fir	1	S
	Jeffrey pine	1	NS
	Sugar pine	2	NS, S
	Ponderosa pine	3	NS, S
	Douglas fir	6	NC, CC, S
	Coast redwood	21	NC, CC
G. intermedius Raski	McNab cypress†	1	CC
	Monterey cypress	1	CC
	Incense cedar	2	S
	Jeffrey pine	1	NS
	Ponderosa pine	4	CC, NS, S
	Douglas fir	1	CC
G. straelini (deConinck) Raski	Red fir	1	NS
	Ponderosa pine	1	CC
	Douglas fir	4	NC, CC
Helicotylenchus (5)*			
H. anhelicus Sher	Arroyo willow	1	SC
H. clarkei Sher	Utah juniper	1	I
	Singleleaf pinyon pine†	2	I
H. erythrinae (Zimmerman) Golden	Arroyo willow	1	SC
Hemicriconemoides (1)*			
H. californianus Pinochet and Raski	Ponderosa pine†	1	S
	Arroyo willow	1	SC
	Coast redwood	1	CC
Hemicycliophora (5)*			
H. californica Brzeski	Ponderosa pine	1	S
H. shepherdi Wu	Willow	1	S
H. vaccinium Reed and Jenkins	McNab cypress	1	CC

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TABLE 4. CONTINUED

Genus and described species	Host association	Number of detections	Floristic zones
Hexatylus Goodey (1)*	Jeffrey pine	1	NS
Hoplolaimus (1)*			
H. californicus Sher	Monterey cypress	1	CC
	Arroyo willow	1	SC
Hoplotylus s'Jacob (1)*	Douglas fir	3	NC, CC
Longidorus (1)*			
L. vineacola Sturhan and Weischer	Singleleaf pinyon pine	1	S
Malenchus (6)*			
M. acaryensis Andrassy	Knobcone pine	1	CC
Meloidogyne Chitwood (1)*	White fir	2	NS, S
	Jeffrey pine†	10	NS, S
	Ponderosa pine†	8	NS, S
	Yellow willow	1	I
Merlinius (5)*			
M. conicus (Allen) Siddiqi	White fir	1	NS
	Red fir†	7	S
	Foxtail pine†	2	S
	Jeffrey pine	6	NS, S, I
	Singleaf pinyon pine	1	I
	Ponderosa pine	2	NS, S
M. grandis (Allen) Siddiqi	Singleleaf pinyon pine	1	M
M. lineatus (Allen) Siddiqi	Jeffrey pine	1	NS
M. microdorus (Geraert) Siddiqi	Jeffrey pine	1	NS
M. nothus (Allen) Siddiqi	White fir	2	NS
	Jeffrey pine	1	NS
Miculenchus (1)*			
M. salvus Andrassy	Douglas fir	1	NC
	Coast redwood	2	NC
Nagelus (1)*			
N. leptus (Allen) Siddiqi	Willow	1	S
Neodolichodorus (1)*			
N. obtusus (Allen) Andrassy	McNab cypress	1	CC
	Digger pine	1	CC
Neopsilenchus (2)*			
N. magnidens (Thorne) Thorne and Malek	Douglas fir	2	NC, CC
	Coast redwood	4	NC, CC
Nothotylenchus (3)*			
N. acris Thorne	Sitka spruce	1	NC
	Jeffrey pine	1	S
	Coast redwood	1	NC

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TABLE 4. CONTINUED

Genus and described species	Host association	Number of detections	Floristic zones
Ottolenchus (3)*			
O. facultativus (Szczygiel) Brzeski	White fir	1	NS
	Red fir	1	S
	McNab cypress	1	CC
	Incense cedar	1	S
	Jeffrey pine	2	NS, I
	Ponderosa pine	1	NS
	Douglas fir	2	NC
	Arroyo willow	1	SC
	Coast redwood	1	CC
O. helenae (Szczygiel) Brzeski	Red fir	1	S
	Coast redwood	1	NC
Paraphelenchus Micoletzky (1)*	White fir	1	NS
	Red fir	2	S
	Incense cedar	1	S
	Jeffrey pine	6	NS, S
	Sugar pine	1	S
	Ponderosa pine	3	S
	Douglas fir	3	S
Pararotylenchus (3)*			
P. blothrotylus Baldwin and Bell	Singleleaf pinyon pine†	1	M
P. truncocephalus Baldwin and Bell	White fir	1	NS
	Jeffrey pine	1	NS
	Quaking aspen	1	S
Paratrichodorus Siddiqi (1)*	Ponderosa pine†	2	S
Paratylenchus (2)*			
P. alleni Raski	Utah juniper†	1	I
	Bristlecone pine	1	I
	Jeffrey pine	2	I
P. neoamblycephalus Geraert	Water birch†	1	I
	Ponderosa pine	1	NS
Pratylenchoides (2)*			
P. magnicauda (Thorne) Baldwin, Luc and Bell	Quaking aspen	1	S
	Yellow willow	1	S
Pratylenchus (4)*			
P. macrostylus Wu	White fir	5	NS, S
	Red fir	12	NS, S
	Incense cedar	2	S
	Jeffrey pine	4	NS, S, I
	Sugar pine	1	S
	Ponderosa pine	2	S
	Quaking aspen	1	S
	Douglas fir	1	S
	Giant redwood	1	S
P. penetrans (Cobb) Filipjev and Schuurmans Stekhoven	Ponderosa pine	1	CC
	Douglas fir	1	CC
P. sefaensis Fortuner	Jeffrey pine	2	S

(Continued on next page)

TABLE 4. CONTINUED

Genus and described species	Host association	Number of detections	Floristic zones
Pseudhalenchus (1)*			
P. minutus	Jeffrey pine	1	NC
Tarjan	Douglas fir	1	S
Rhizonema (1)*			
R. sequoiae	Jeffrey pine	2	NS
Cid del Prado Vera, Lownsbery,	Ponderosa pine†	5	NS, S
and Maggenti	Douglas fir	5	NC, CC
	Coast redwood	17	NC, CC
Rotylenchus Filipjev (2)*	Jeffrey pine	1	NS
	Ponderosa pine	1	NS
	Douglas fir	2	NS
Scutylenchus (1)*			
S. tesselatus	Jeffrey pine	1	NS
(Goodey) Siddiqi	Yellow willow	1	I
	Willow	1	S
Sphaeronema (1)*			
S. californicum	White fir	1	NS
Raski and Sher	Red fir	6	S
	Jeffrey pine†	9	NS, S
	Sugar pine	1	S
	Ponderosa pine†	7	NS, S
	Douglas fir	2	S
	Willow	1	S
	Coast redwood	1	CC
	Giant redwood	1	S
Trichodorus (7)*			
T. aequalis	Jeffrey pine†	2	I
Allen	Ponderosa pine	2	S
T. californicus	Sitka spruce	1	NC
Allen	Ponderosa pine	4	NC, S
	Douglas fir†	8	NC, CC, NS
	Yellow willow	1	SC
	Coast redwood	10	NC, CC
	Giant redwood	1	S
T. intermedius	Yellow willow	1	SC
Rodriguez M. and Bell			
T. obscurus	McNab cypress	1	CC
Allen	Monterey cypress	1	CC
	Jeffrey pine	1	NS
	Ponderosa pine	2	CC
	Digger pine	1	CC
	Douglas fir†	5	NC, CC
	Coast redwood	5	NC, CC
T. sparsus	Douglas fir	1	NC
Szczygiel	Coast redwood	1	NC
Tylenchorhynchus (1)*			
T. cylindricus	Utah juniper	1	I
Cobb	Bristlecone pine†	1	I
	Foxtail pine	1	S

(Continued on next page)

TABLE 4. CONTINUED

Genus and described species	Host association	Number of detections	Floristic zones
	Jeffrey pine	9	S, I
	Singleleaf pinyon pine†	6	S, I, M
	Ponderosa pine	1	S
	California black oak	2	I
	Yellow willow	1	SC
Tylenchus (7)*			
T. butteus Thorne and Malek	Douglas fir	1	NC
T. ditissimus Brzeski	Bristlecone pine	1	I
	Jeffrey pine	1	S
	Douglas fir	2	S
	Coast redwood	1	NC
T. maius Andrassy	Red fir	1	NS
	Jeffrey pine	2	NS, S
	Ponderosa pine	1	S
T. sandneri Wasilewska	White fir	1	NS
	Jeffrey pine	1	S
	Douglas fir	1	S
Xiphinema (2)*			
X. bakeri Williams	Ponderosa pine	2	S
	Fremont cottonwood	1	I
	Quaking aspen	1	S
	Coast redwood	1	NC
X. californicum Lamberti and Bleve-Zacheo	White fir	3	NS, S
	McNab cypress	1	CC
	Monterey cypress	2	CC
	Utah juniper	1	I
	Incense cedar	2	S
	Knobcone pine	1	CC
	Coulter pine	1	CC
	Limber pine†	1	S
	Jeffrey pine	17	NS, S, I, GB
	Singleleaf pinyon pine	3	I, M
	Western white pine	1	S
	Ponderosa pine	9	CC, NS, S
	Monterey pine	1	CC
	Digger pine	1	CC
	Quaking aspen	1	S
	Douglas fir	8	NC, CC, NS, S
	California black oak	2	I
	Yellow willow	1	SC
	Coast redwood	9	NC, CC

*Number of species (in parentheses).

†Nematode species found with that specific host at a concentration of 200 or more per 250 cc of soil.

In general, nematodes common in California agriculture (Siddiqui, Sher, and French 1973) were not found in California forests. Exceptions to this were *Xiphinema californicum* and *Tylenchorhynchus cylindricus,* which we found frequently, and *Criconemella xenoplax* and *Paratylenchus neoamblycephalus,* found very infrequently. We did not find many of the plant-parasitic nematodes reported in forests in the eastern United States, or in other parts of the world (Ruehle 1967; Kiryanova and Krall 1980). Many of these reports concerned land that had been in agricultural crops at some time, or had a climate not much different from nearby agricultural areas. With the exception of some coastal and foothill apple orchards and vineyards, California forest has never been in agriculture and has a climate greatly different from agricultural areas.

These California forest trees have been exposed to their nematode parasites for more than a million years, a time sufficient to achieve a balance allowing survival of host and parasite. This does not mean that the trees would not grow better if relieved of their burden of nematode parasites. Nematodes may be one of the agents that is weakening trees and predisposing them to attack by bark beetles. At present there is no practical way to reduce nematode populations in standing forests. We can protect nursery seedlings and avoid distributing nematodes by application of a soil fumigant before planting, and this is advisable. California foresters select seed from most vigorous trees for propagation in nurseries. They may be selecting indirectly for nematode tolerance by this process. Common occurrence of the virus vector *Xiphinema californicum* in all zones is of interest. Virus diseases are not known to be important in conifers, but Fulton (1969) has transmitted tobacco ringspot virus to roots of *Cupressus arizonica.*

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