Distribution of Selected Plant Parasitic Nematodes Relative to Vegetation and Edaphic Factors[1]

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Abstract: The occurrence of selected plant-parasitic nematodes in the hemlock-hardwood-white pine, boreal forest, tundra, and oak-hickory associations in some northern states was compared. *Helicotylenchus platyurus* and *Xiphinema americanum* were not found in the boreal forest and tundra, and occurred infrequently in the hemlock-hardwood-white pine areas. They were found frequently, however, in the oak-hickory forest of Iowa. It is questioned that vegetational differences among the areas account directly for the major differences in nematode occurrence. Presence and absence of nematodes and their numbers in the oak-hickory association were clustered by similarity coefficients by sites and correlated with soil pH, percentage organic matter, percentage sand-silt-clay, and field capacity. Of the soil factors measured, pH gave the strongest correlations with nematode numbers. *Xiphinema chambersi* was found only in soils with a pH between 4.5 and 6.4 while the largest numbers of *H. platyurus, H. pseudorobustus,* and *X. americanum* occurred in soil above pH 6.0. *Key Words*: forests, soil texture.

Although considerable knowledge has been accumulated regarding interrelations between trees with associated biota and abiotic factors, information concerning nematodes in woodlands is fragmentary. Since ecological data about nematodes are often contradictory, we can only speculate on the functional role of nematodes in woodland ecosystems.

Ruehle (6) collated reports of plant-parasitic nematodes associated with forest trees and Winslow (14) presented a comprehensive discussion of saprobes and plant-parasitic nematodes found in non-agricultural soil. There are few publications, however, devoted entirely to ecology of plant-parasitic nematodes in woodlands. Johnson et al. (4) and Yuen (15) found that certain nematode taxa were associated with vegetational dominants in deciduous woodlands, but recognized that other factors may be important in determining the composition of nematode communities.

Numerous species of plant-parasitic nematodes have been found in the deciduous forests of Iowa, but data on geographical and ecological factors that might provide insight to their distribution and habitat relationships were recorded only recently. Similar data were collected from different vegetational associations in other states and the results reported herein reflect not only differences in distribution of selected plant-parasitic nematodes, but also some contrasting edaphic factors that might be important in governing nematode distribution and population size.

MATERIALS AND METHODS

Samples were collected from four

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northeastern and three midwestern states. In the northeastern U.S., New York samples were taken from the foothills of the Adirondack Mountains north of Utica to the Flowed Land, and from the tundra of Mt. Algonquin; Vermont samples were taken from the Middlebury area, and from Mt. Horrid to Mt. Abraham; New Hampshire samples were from the slopes of Mt. Madison; and Maine samples were from the lower areas in western Maine. In all northeastern states, samples were also taken enroute to the specified areas. In the Midwest, samples were collected from the northern forests of Wisconsin and Minnesota, and from the deciduous woodlands of Iowa. Each sample represents one site.

Individual 1-liter soil samples were collected from the top 15-cm at each site. Soil was collected from where the fibrous roots emanated from the main roots and close enough to the trunk to insure identification of the roots with a specific tree. While we are reasonably certain that a sample included roots of a specified tree, we can be less certain that spreading roots of adjacent tree species or dormant roots were not included. Samples were processed individually for nematodes by a centrifugal-flotation method (3) within 2-3 days of collection in the Midwest and 10-20 days in the Northeast. During the Northeast collection trip, eight soil samples with a known nematode composition were transported from Iowa during the entire trip and stored under the same conditions as the newly collected samples. These eight samples were processed upon return to Iowa; only minor changes in numbers of the plant-parasitic nematodes occurred indicating that transportation and storage conditions were suitable. Determinations were made on all samples for soil pH using a 2:1 water-soil ratio, organic matter (7), texture, and field capacity (12). Because of the contrasting distribution patterns obtained, data concerning *Helicotylenchus platyurus* Perry and *Xiphinema americanum* Cobb are emphasized. Species of *Criconema* and *Criconemoides* were common in all areas samples, but their occurrence and distribution patterns were not similar to those reported here (2). Data on the *Criconematinae* are being reported more extensively elsewhere.

A cluster analysis based on similarity coefficients of occurrence and numbers of nematodes with site, was made only for the Iowa collections using the same equation that was used in Iowa prairies studies (8, 10, 11). A computer-drawn dendograph was programmed after McCammon and Wenninger (5). Data from other states were not analyzed in this manner because of the infrequency and small numbers of recovery of the nematodes reported herein.

RESULTS

Soil factors and numbers of three nematode species per sample in each major vegetational area are summarized in Tables 1 and 2, respectively. Data from the vegetational zones of the northeastern states are combined because

TABLE 1. Average values for edaphic factors of soil samples collected from different plant associations, 1969-1972. (Ranges given in parentheses).

Plant associations and locations	No. samples	pH avg	Organic matter (avg %)	Sand (avg %)	Silt (avg %)	Clay (avg %)	Field capacity (%)
Hemlock-Hardwood, Boreal Forest, and Tundra of N.Y., Vt., N. Hamp., and Maine	267	4.0 (2.8-6.9)	7.7[ab] (1.8-14)	66[a] (4-93)[b]	24[a] (3-51)[b]	10[a] (1-27)	98 (6-324)
Hemlock-Hardwood-White Pine Forest of Minn. and Wis.	53	4.9 (3.6-7.0)	7.9[c] (2.0-15.0)	76[c] (49-96)	20[c] (3-45)	4[c] (1-9)	26 (7-98)
Oak-Hickory association of Iowa	172	6.1 (4.4-7.8)	6.0 (0.8-15)	34 (1-92)	52 (4-81)	13 (0-29)	26 (6-44)

[a]86 samples; the remaining samples were 100% duff and are not included.

[b]61 samples < 15% organic matter; remaining 25 samples > 15% organic matter, but recorded as 15%.

[c]13 samples were 100% duff and are not included.

of soil similarity and the recovery of few nematodes. The areas sampled outside of Iowa, and especially those in the Northeast, contained mostly shallow soils and were underlain with bedrock, resulting in little vertical profile. Sixty-eight percent of the samples from the northeastern states consisted entirely of duff; 23 percent were mineral; and the remaining were a mixture of mineral soil and duff. Samples from Minnesota and Wisconsin contained a high percentage of duff but little duff occurred in the Iowa samples.

Xiphinema americanum and *Helicotylenchus platyurus* were found in 9

TABLE 2. Numbers of selected nematodes associated with tree species in different vegetational formations in the northern Midwest and Northeast U.S., 1969-1972.

Vegetational type	Primary associated plant	No. samples collected	*X. americanum* times found		*X. chambersi* times found		*H. platyurus* times found	
Hemlock-Hardwood, Boreal Forest, and Tundra of N. Y., Vt., N. Hamp., and Maine	*Abies balsamea* (L.) Mill.	34	0	(0)[1]	0	(0)[1]	0	(0)[1]
	Picea rubens Sarg.	28	0	(0)	0	(0)	0	(0)
	Pinus strobus L.	11	3	(10)	0	(0)	1	(50)
	Tsuga canadensis (L.) Carr	24	0	(0)	0	(0)	0	(0)
	Acer saccharum Marsh.	30	0	(0)	0	(0)	0	(0)
	Acer pensylvanicum L.	6	0	(0)	0	(0)	0	(0)
	Acer rubrum L.	8	0	(0)	0	(0)	0	(0)
	Betula papyrifera Marsh. var. *cordifolia* (Reg.) Fern.	17	0	(0)	0	(0)	0	(0)
	Betula alleghaniensis Brit.	32	0	(0)	0	(0)	0	(0)
	Betula papyrifera Marsh.	15	1	(40)	0	(0)	1	(30)
	Fagus grandifolia Ehrh.	24	0	(0)	0	(0)	2	(31)
	Populus tremuloides Michx.	7	2	(12)	0	(0)	1	(20)
	grass	7	0	(0)	0	(0)	0	(0)
	moss	6	0	(0)	0	(0)	0	(0)
	Misc. trees sampled 1-4 times	18	3	(7)	0	(0)	2	(24)
	Total	267	9	(17)	0	(0)	7	(31)
Hemlock-Hardwood-White Pine Forest of Minn. and Wis.	*Pinus resinosa* Ait.	7	1	(7)[1]	0	(0)	0	(0)[1]
	Pinus strobus	6	2	(9)	0	(0)	1	(1)
	Tsuga canadensis	5	2	(7)	0	(0)	0	(0)
	Betula papyrifera	10	3	(6)	0	(0)	1	(1)
	Misc. trees sampled 1-4 times	25	5	(3)	0	(0)	1	(5)
	Total	53	13	(6)	0	(0)	3	(2)
Oak-Hickory association of Iowa	*Pinus strobus*	10	5	(40)	0	(0)	2	(25)
	Pinus resinosa	5	1	(10)	0	(0)	3	(10)
	Carya ovata (Mill.) K. Koch	9	2	(55)	1	(33)	5	(44)
	Celtis occidentalis L.	7	6	(17)	0	(0)	5	(68)
	Juglans nigra L.	5	2	(10)	0	(0)	3	(37)
	Ostrya virginiana (Mill.) Koch	7	4	(50)	3	(10)	3	(23)
	Parthenocissus sp.	10	7	(29)	3	(17)	7	(70)
	Quercus alba L.	10	1	(20)	4	(18)	6	(25)
	Quercus macrocarpa Michx.	10	5	(94)	2	(30)	6	(128)
	Tilia americana L.	12	7	(33)	0	(0)	9	(57)
	moss	13	5	(16)	1	(10)	7	(29)
	Misc. trees sampled 1-4 times	74	34	(38)	15	(13)	42	(49)
	Total	172	79	(34)	29	(19)	98	(47)

[1]Average number of nematodes per 100 cc of soil in samples in which the species occurred.

(3.4%) and 7 (2.6%) sites, respectively, of the 267 samples obtained in the northeastern states (Table 2). They were found mostly in samples containing some mineral soil collected in the valleys or on the lowest mountain slopes of the hemlock-hardwood formation, and never in soils consisting entirely of duff. By contrast, *X. americanum* and *H. platyurus* occurred in 79 (46%) and 98 (57%) of the samples, respectively, from the Oak-Hickory association of Iowa. Besides the *Criconematinae*, few other plant-parasitic nematodes were found in forested areas of the northeastern states, Minnesota, or Wisconsin.

Since *H. platyurus, X. americanum,* and to a lesser degree *H. pseudorobustus* (Steiner) Golden, and *X. chambersi* Thorne, were the principal plant-parasitic nematodes, exclusive of the *Criconematinae*, in Iowa woodlands, a cluster analysis by site was made with these species. The dendograph is too long to be presented here. Because of the greater vegetational heterogeneity in Iowa compared with other areas sampled, soil was collected from around more plant species with fewer samples being obtained from any one plant taxon (Table 2). There was little nematode clustering with any one plant species in Iowa, but there was clustering of nematodes with plant communities that occupy similar habitats. The largest populations, > 140/100 cc soil, of *H. platyurus* occurred around *Carya ovata, C. tomentosa* Nutt., *Celtis occidentalis, Ostrya virginiana, Quercus macrocarpa, Rhus glabra* L., *R. typhina* Torner, and *Tilia americana*, all occurring on moist (but well-drained) slopes. Only moderate numbers were found in soil under bottomland trees such as *Acer negundo, Juglans nigra,* and *Ulmus americana*. The associations for *X. americanum* were restricted to fewer tree species. The largest populations occurred around *Acer nigrum, A. saccharum, Betula papyrifera, O. virginiana, Q. macrocarpa, R. typhina,* and *T. americana. X. americanum* was not commonly found in bottomland sites. *Xiphinema chambersi* was found only in small populations, <30/100 cc soil, and these occurred in moist, well-drained sites. It was associated frequently with *H. platyurus*, but not *X. americanum*. In only one instance were the three nematodes found in the same sample and numbers of each were less than 20/100 cc soil.

The most contrasting soil factors in samples between the northeastern states and those from Iowa were pH, percentage organic matter, and field capacity, the latter being mostly a reflection of the amount of organic matter. Soil samples from the northeastern states contained mostly duff and the pH was usually between 3.0 and 4.5, with 88% of the samples being under pH 5.0. In the northeastern vegetational formations, *H. platyurus* and *X. americanum* were never found where the soil pH was below 4.3, either in organic or mineral soils, and they were found in soils with higher average pH values than the average of all samples taken from the area (Table 3). For example, the lowester pH of soil containing *X. americanum* was 4.3 which was above the average soil pH of 4.0 (Table 1). The average pH of soils

TABLE 3. Average pH and pH limits of soil containing *Helicotylenchus platyurus* or *Xiphinema americanum* in different vegetational areas.

Plant associations and locations	*H. platyurus*			*X. americanum*		
	Times found	pH avg	pH range	Times found	pH avg	pH range
Hemlock-Hardwood, Boreal Forest, and Tundra of N.Y., Vt., N. Hamp., and Maine	7	5.2	4.3-6.5	9	5.2	4.3-6.7
Hemlock-Hardwood-White Pine Forest of Minn. and Wis.	3	4.7	4.0-5.6	13	5.0	4.2-7.0
Oak-Hickory association of Iowa	98	6.3	4.5-7.4	79	6.4	4.6-7.7

containing *X. americanum* was 5.2. Thus, *X. americanum* occurred in soils in the upper pH range of the northeastern region, although numbers were few in all instances. Similar comparisons hold for *H. platyurus* (Tables 1, 3). A slightly greater occurrence of these nematodes in the hemlock-hardwood-white pine forests of Minnesota and Wisconsin coincided with the presence of more mineral soil and a higher pH. The sites that clustered in the oak-hickory deciduous forest of Iowa were examined for possible affinities in the edaphic factors measured that might give some insight in the predictability of nematode occurrence. Scatter diagrams were constructed using the edaphic factors measured and nematode numbers. Meaningful correlations occurred only with nematode numbers and pH. These are presented graphically in Fig. 1. Even though a fairly even distribution of samples was obtained having a pH between 4.5 and 7.4 (Fig. 1-E), only *X. chambersi* was most abundant in the lower pH ranges (Figs. 1-A to D), and this was not found in soils with a pH above 6.4. *Helicotylenchus pseudorobustus* and *X. americanum* were not common in the lower pH range.

DISCUSSION

Results of this study indicate that *Helicotylenchus platyurus* and *Xiphinema americanum* are rare inhabitants of the hemlock-hardwood forests of New York, New Hampshire, Vermont, and Maine. They were not found in the boreal forest or tundra in those states. They were common, however, in the oak-hickory deciduous formation in Iowa. While vegetational differences might seem to be important as causal differences in distribution of these nematodes, there are indications that this is not so. In view of the heterogeneity of plant communities sampled in Iowa, it is probable that the widespread occurrence of *H. platyurus* and *X. americanum* reflects a rather extensive host range for these nematodes. In addition, up to 240 *X. americanum*/100 cc soil were associated with white birch, *B. papyrifera*, in Iowa, but it was rarely associated with this plant species in the Northeast (Table 2), although the tree is more common in the latter area.

Of the soil factors measured, those which varied most widely between the northeastern states and Iowa were pH, percentage organic

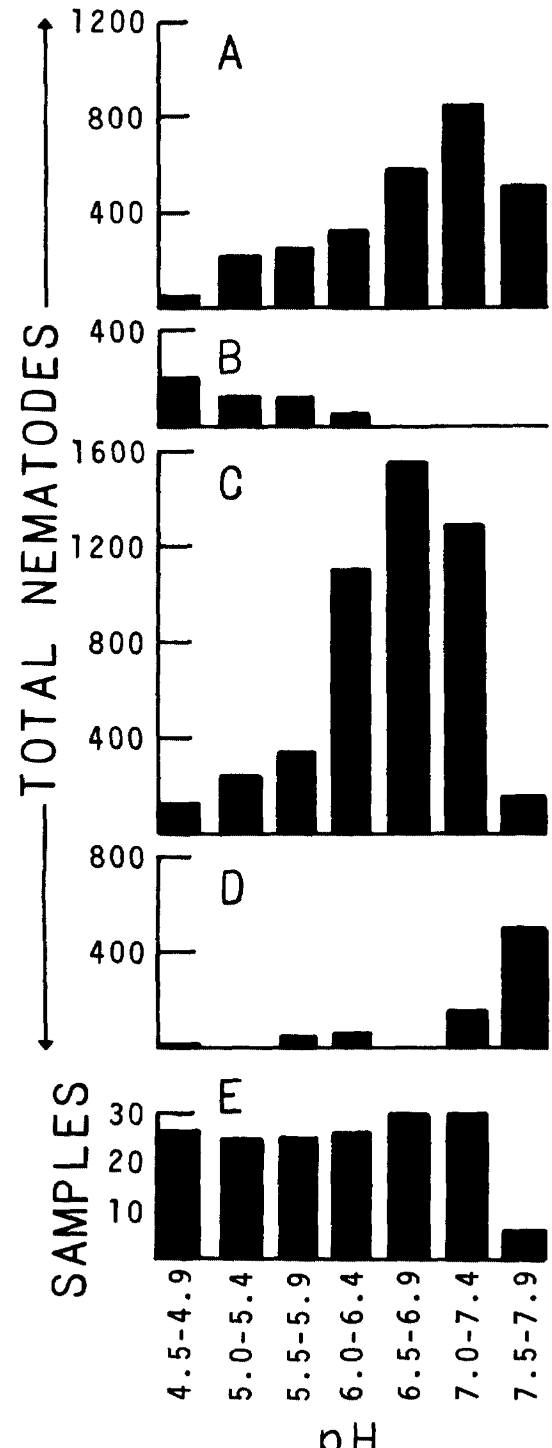

FIG. 1-(A to D). Numbers of four nematodes in Iowa soil samples at different pH levels. A) *Xiphinema americanum*, B) *X. chambersi*, C) *Helicotylenchus platyurus*, D) *H. pseudorobustus*, E) Sample distribution at different pH levels.

matter, and field capacity. The duff soils of the Northeast are well aerated and in spite of the high field capacity of these soils, aeration probably is not a factor in limiting nematode occurrence. Members of *Criconema* and *Criconemoides* were common in all areas studied (2), including the highly organic soils, indicating that the habitats are favorable for some plant-parasitic nematodes. Conceivably, either differences in pH or percentage organic matter could be partially responsible for differences in distribution and populations of *H. platyurus* and *X. americanum*, but the interrelations between these factors and possibly others makes analysis difficult. There were correlations, however, between nematode numbers and pH (Fig. 1) in Iowa, but not with percentage of sand-silt-clay, percentage organic matter, or field capacity. While correlations do not prove causation, soil pH might be used as a tool to predict where the nematodes are apt to occur. Nevertheless, nematode behavior responses to pH are being examined, however, with increasing numbers of correlations of pH and nematodes phenomena occurring (1, 9, 13). With the demonstrated importance of pH and the interrelated factors in biological systems, it would be surprising if nematodes are an exception with responses to similar ionic and related changes, directly or indirectly.

Only 53 samples were collected from the hemlock-hardwood-white pine association of northern Minnesota and Wisconsin, but the few occurrences and small populations of *H. platyurus* and *X. americanum* were more similar to results from the Northeast than from Iowa. This is not surprising since the forests and soils of northern Minnesota and Wisconsin are more closely related to those areas sampled in northeastern states than they are to those in adjacent Iowa.

Although *Helicotylenchus platyurus* and *Xiphinema americanum* occurred most abundantly in well-drained soils, the former is the more mesic species as moderate numbers were found in bottomlands, a site uncommon for *X. americanum*. This agrees in general with interpretations of data from Tippecanoe County, Indiana (4) where *H. platyurus* was frequently dominant, but not restricted to, swamp forest communities.

This preliminary report indicates that patterns of nematode distribution are different in different major vegetational areas. This is what one should expect since the habitats vary and similar phenomena have been commonly found with other organisms. The reasons for these differences are not known, but indications are that factors other than host are of major importance.

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