Community Structure of Plant-parasitic Nematodes Related to Soil Types in Illinois and Indiana Soybean Fields[1]

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Abstract: Comparisons of plant parasitic nematode populations using a resemblance equation and community ordination showed that community structure tends to be similar on dark-colored, highly productive soybean soils throughout Indiana and Illinois. On lighter-colored soils community structures differed somewhat from those of darker soils and from each other.
Key Words: Ecology, Dendrogram, Similarity indices, Community ordination, *Helicotylenchus pseudorobustus*, *Pratylenchus* spp., *Paratylenchus projectus*, *Tylenchorhynchus acutus*; *Tylenchorhynchus martini*, *Xiphinema americanum*.

Objective mathematical methods are utilized herein to summarize community structure of nematode associations and to classify such associations ecologically. The study is part of an 11-year investigation of plant parasitic nematodes in soybean soils of Illinois and Indiana, and interpretations of the quantitative classifications are based largely on information previously reported (2, 3, 4, 5, 6).

MATERIALS AND METHODS

FIELD METHODS: Established soybean-breeding blocks maintained under federal-state cooperative projects in Indiana and Illinois were sampled, and the plant parasitic nematode species recovered, identified, and counted. All blocks were rotated according to recommended practices to corn, wheat, oats, and forage, but only nematodes from blocks in soybeans were a part of the present analyses. The sampling was carried out for 11 years (1957–1967) in Illinois and for 3 years (1965–1967) in Indiana at the 14 sites shown in Fig. 1. Methods for sampling the 1-hectare blocks for nematodes once each year, between mid-July and mid-August, and for processing by standardized techniques were the same as those given previously (2, 4). Each sample consisted of 20 ea. 25-cm cores taken with a 2.5 cm diameter sampling probe at intervals of 15 m on a rectangular grid pattern. The nematodes were extracted from a 473 cc (one U. S. pint) subsample by a uniform method of washing through screens and resuspending the residues in Baermann funnels. The nematodes in two aliquots from each subsample were counted at 40× magnification on a compound microscope in a counting chamber designed so that specimens in question could be also examined at 100× magnification. Tests of reproducibility of sampling results and of consistency of laboratory methods have been described elsewhere (2, 4, 5).

ANALYTIC PROCEDURES: Indices of similarity (1-z) were obtained by the resemblance equation of Preston (8) for all possible pairs of locations using values calculated

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for x and y to enter Preston's (9) z-Table (range of 0.00 to 1.00 for z). The values for x and y were calculated according to the formulae:

$$x = F_1/(F_1 + F_2 - F_{1+2}) \quad (1)$$
$$y = F_2/(F_1 + F_2 - F_{1+2}) \quad (2)$$

where F_1 = the number of species in Area 1, F_2 = the number of species in Area 2, and F_{1+2} = the number of species common to both areas.

To construct the dendrogram, a generalized formula (7) was used to calculate the index of similarity (I) between a single site (B) and two or more grouped sites (A_1, A_2, . . .A_m). The formula is as follows:

$$I(A_1, A_2, \ldots A_m; B) = \frac{I(A_1B) + I(A_2B) + \ldots I(A_mB)}{m} \quad (3)$$

The index of similarity between one group of sites (A_1, A_2, . . .A_m) and a second group of sites (B_1, B_2, ...B_n) is determined (7) from the following formula:

$$\frac{1}{mn} \sum_{i=1}^{m} \sum_{j=1}^{n} I(A_iB_j) \quad (4)$$

Calculations for the three-dimensional community ordination technique (1) were by means of the ORDCOM computer program written by Dr. R. L. Giese, Department of Entomology, Purdue University. In this technique sites are compared on the basis of their dissimilarities in nematode population structure. Coefficients of similarity-dissimilarity were figured using data for total density for each species at each site, with no data for frequency included in the calculation, as is customary in such ordinations. This was done because only three years of data were available for the Indiana sites. Data for the same three years were used for Illinois. Intersite distances were then calculated from the matrix of coefficients and plotted in a 3-dimensional ordination.

FIG. 1. Location of rotation and breeding blocks in Illinois (**1**, DeKalb; **2**, Pontiac; **3**, Girard; **4**, Edgewood; **5**, Eldorado; **6**, Miller City; **7**, Urbana; **8**, Trenton) and Indiana (**9**, Knox; **10**, Bluffton; **11**, Lafayette; **12**, Greenfield; **13**, Worthington; **14**, Evansville) from which soil samples were collected.

RESULTS AND DISCUSSION

SPECIES RECOVERED: The parasitic nematode species found throughout the soybean-growing areas of the two states were remarkably similar. *Helicotylenchus pseudorobustus* (Steiner) Golden was found at every site in at least one sampling. It was present in excess of 300 per 473 cc soil at least one year in all sites except Edgewood and Trenton. Species of the genus *Pratylenchus* were as common as *H. pseudorobustus* in fields of both states. Typically, several species of *Pratylenchus* occurred together including *P. hexincisus* Taylor and Jenkins, *P. scribneri* Steiner, *P. penetrans* Cobb, *P. neglectus* Rensch, and *P. crenatus* Loof. One additional species, designated as '*Pratylenchus*

6', was found in large numbers at Knox. This undescribed species is similar in appearance to *P. neglectus*, but is distinct and was treated separately in the analyses. DeKalb and Edgewood were the only sites in which the counts of *Pratylenchus* species were always very low, never reaching 100 per 473 cc of soil. *P. scribneri* was the most common species encountered. Large numbers of *P. penetrans* and others also were encountered in some fields.

Paratylenchus projectus Jenkins was widespread throughout the two-state area. It was the only species of *Paratylenchus* commonly encountered in these rotated fields. This species was not recovered at Knox or Worthington, and was recovered in very small numbers only from Eldorado and Miller City. More than 500 per 473 cc soil were found at Evansville, Lafayette, Bluffton, Trenton, Urbana, and Edgewood.

Tylenchorhynchus acutus Allen and *T. martini* Fielding were found in both states. *T. acutus* was the more common, appearing occasionally at most of the Illinois sites, although in only two of the Indiana locations. It was present at some time at Eldorado, Urbana, Miller City, and Trenton in numbers over 200 per 473 cc of soil. In one year at Trenton more than 1,000 per 473 cc soil were recovered. *T. martini* was recovered in numbers over 100 per 473 cc soil only at Greenfield and Urbana. It was found in much lower numbers at a few other locations. Occasionally small numbers of other species of *Tylenchorhynchus* were recovered also. One of these, an undescribed species, designated as '*Tylenchorhynchus* 10', was present in sufficient numbers to be considered in the analyses.

Xiphinema americanum Cobb was found at all locations, although at half of these, less than 50 per 473 cc soil were found. Pontiac, Eldorado, Urbana, Lafayette, and Greenfield all had this species present at greater than 100 per 473 cc soil. The highest populations of *X. americanum* were at Lafayette.

COMPARISONS USING DENDROGRAM OF SIMILARITY INDICES FROM RESEMBLANCE EQUATION: Species buildup for the 14 sites is summarized in Table 1. A given species was not considered to increase at a given site, unless it was found to be present in at least one year in numbers exceeding an arbitrary level based on previous experience of the authors (Table 1). A higher critical level was set for species commonly present in large numbers, and lower ones for species not ordinarily found in high numbers in these cultivated soils.

The similarity values calculated for all pairs of locations are presented in Table 2 in the form of an area matrix and are the values used to construct the dendrogram, Fig. 2. According to Preston, a similarity value of 1.00 (or 100%) indicates that the two faunae are identical. Where the value is greater than .73, the values are samples of a larger unit; and where values are less than .73 (but greater than zero), there has been isolation of the two faunae of varying degrees.

Reasons for taxonomic resemblance of areas, or lack of it are not easy to deduce from data that are readily available. Extensive information regarding each sampling and sampling site should be considered. Some of the soil and climate characteristics of the 14 sites are listed in Table 3. It is reasonable to assume that for soil-inhabiting organisms soil factors might be very important in determining build-up of the organisms. Previous data indicate that the nature of the soil is a primary factor in determining presence or absence of a particular species of nematode (6, 10). The influence of soil in a given area, however, results from a combina-

TABLE 1. Summary of buildup of eight nematode species at 14 study sites in Illinois and Indiana soybean fields.

Study Site	Code Number	*Helicotylenchus pseudorobustus*[a]	*Paratylenchus projectus*[b]	*Pratylenchus complex*[c]	*Pratylenchus-6*[c]	*Tylenchorhynchus acutus*[c]	*Tylenchorhynchus martini*[c]	*Tylenchorhynchus-10*[c]	*Xiphinema americanum*[d]
DeKalb	(1)	X	X						
Pontiac	(2)	X	X	X					X
Girard	(3)	X	X	X					
Edgewood	(4)		X						
Eldorado	(5)	X		X		X		X	X
Miller City	(6)	X		X		X			
Urbana	(7)	X	X	X		X	X		X
Trenton	(8)		X	X		X			
Knox	(9)	X		X					X
Bluffton	(10)	X	X	X	X				
Lafayette	(11)	X	X	X					X
Greenfield	(12)	X	X	X			X		X
Worthington	(13)	X		X					
Evansville	(14)	X	X	X					

[a] An "X" denotes 300 or more nematodes/473 cc soil in at least one sample collected during the study period.
[b] X denotes 150/473 cc soil in at least one sample.
[c] X denotes 100/473 cc soil in at least one sample.
[d] X denotes 50/473 cc soil in at least one sample.

tion of many complex factors, including the types of the major and associated soils, the texture and permeability of the subsoil, organic matter, and available moisture. In the present study a different field in the general area discussed was sampled each year of the study. Considerable variation may occur within the same field as well as between fields. Some generalizations can be made, however, which provide a satisfactory explanation of the groupings obtained on the dendrogram (Fig. 2).

Pontiac and Lafayette, which unite at the 100% level, both have dark colored silty clay loams. These areas also are at about the same latitude and might be expected to share similar patterns of rainfall and moisture. Urbana and Greenfield, which joined just below 90% both have highly productive silty clay loams, with Greenfield in an area of a Brookston-Crosby complex with some areas of poor drainage. These four highly productive areas join at the level of 85%. Knox joins these four locations at a level just above 80%. Initially the position of Knox appears somewhat puzzling. Knox is in an area of fine sandy loam soil with a fairly high water table. The fields studied are located in an old lake bed near the Kankakee drainage ditch. Flooding occurs occasionally, especially in the spring. The soil is fairly heterogeneous. Moisture conditions were highly variable during the years of sampling. Further sampling in selected areas of this very interesting site should provide valuable additional data.

Girard and Evansville, which unite at 100% are widely separated geographically,

TABLE 2. Matrix of similarity indices for all 14 study sites in Illinois and Indiana soybean fields (Preston's measure of similarity = 1-z).

Study Site	Code Nos. ↓ →	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
DeKalb	(1)	—	.73	.82	.73	.26	.33	.63	.30	.33	.73	.73	.67	.40	.82
Pontiac	(2)		—	.85	.55	.59	.50	.82	.68	.85	.68	1.00	.88	.73	.85
Girard	(3)			—	.63	.44	.58	.73	.50	.58	.85	.85	.79	.82	1.00
Edgewood	(4)				—	0.0	0.0	.45	.55	0.0	.55	.55	.50	0.0	.63
Eldorado	(5)					—	.79	.65	.59	.79	.36	.59	.50	.67	.44
Miller City	(6)						—	.73	.50	.58	.50	.50	.44	.82	.58
Urbana	(7)							—	.82	.73	.53	.82	.89	.63	.73
Trenton	(8)								—	.50	.40	.68	.59	.30	.50
Knox	(9)									—	.50	.85	.79	.82	.58
Bluffton	(10)										—	.68	.59	.73	.85
Lafayette	(11)											—	.88	.73	.85
Greenfield	(12)												—	.67	.79
Worthington	(13)													—	.82
Evansville	(14)														—

but do have somewhat similar soil types. Girard has a slowly permeable light-colored silt loam and the Evansville soil is primarily a highly productive brownish gray Montgomery and Zipp silty clay loam with a level terrain. Bluffton, in an area of dark grayish-brown Blount silt loam, joins the Girard and Evansville sites at 85%. DeKalb, with a permeable dark colored silt loam joins the latter three sites just above Preston's "phenon" line at 73%.

The next three sites which group above the 73% "phenon" line are all sites with chiefly alluvial soils. Miller City is situated along the Mississippi River, and has the distinction of being the farthest south, with a milder climate and less severe winters than the rest. Worthington has a productive soil which is frequently flooded, and the nematode species found there are those which have been shown to develop best with high soil moisture (6). It should also be noted that during the years of sampling, the Worthington soil had a *p*H value of 7.8, the highest of the Indiana sites. Eldorado with a bottomland silty clay loam joins the other two at about the 73% level.

Trenton and Edgewood stand apart from each other, and from the rest of the sites. Both sites have light-colored soil. Edgewood, in particular, is distinct from all the rest in being an upland light-colored soil with a very tight subsoil.

COMPARISONS USING COMMUNITY ORDINATION: The 14 sites were compared on the basis of their dissimilarities in nematode population structure utilizing a three-dimensional community ordination technique (1) incorporating data for density of each species under consideration. The plots for the distances between sites on three axes are shown in Fig. 3. A photograph of the ordination model (Fig. 4) shows the relationships in three-dimensions.

The bulk of the sites are clustered in the right portion of the XY plane and in the upper part of the XZ and YZ planes. This clustering was due to the relative importance of *H. pseudorobustus*, the dominant species at all of these sites. The separation of Knox (Site-9) on the Y-axis reflects the fact that in one year, extraordinarily high counts of *H. pseudorobustus* were found at this site.

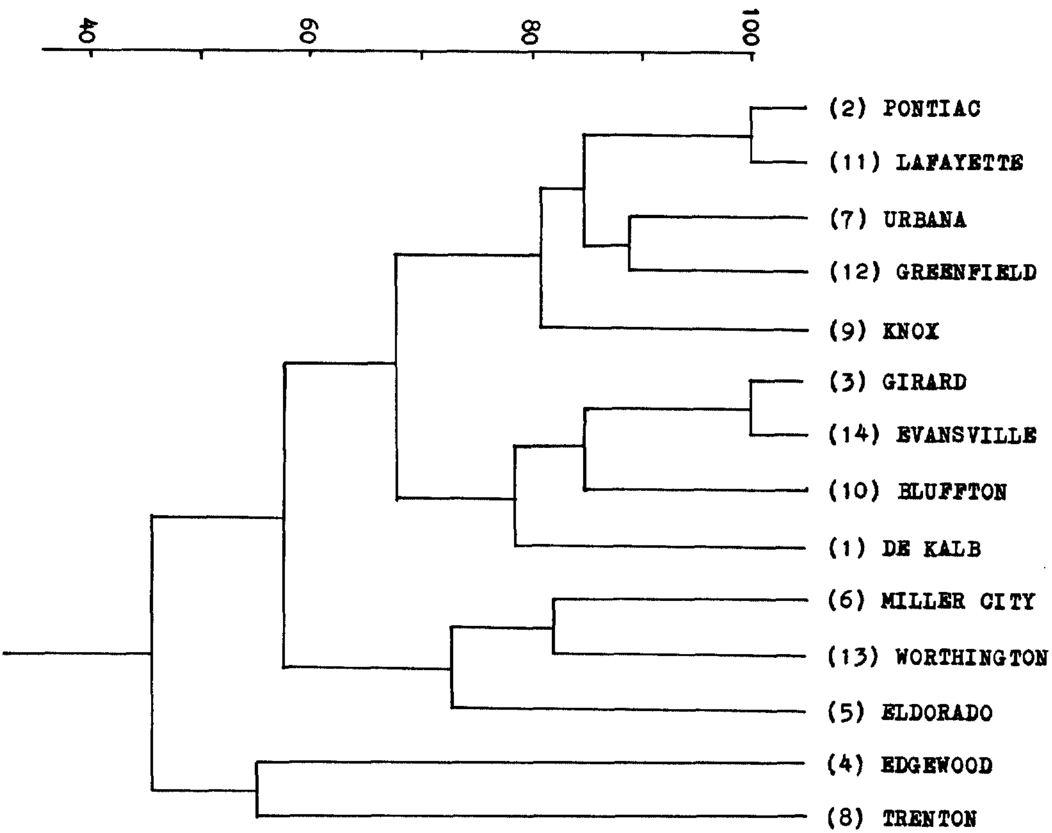

FIG. 2. Dendrogram of locations based on Preston's (8,9) similarity indices.

Edgewood and Lafayette, Sites 4 and 11, in the left portion of the XY plane, were dominated by *P. projectus*. In previous work with these two species on diverse soil types, it was shown that *H. pseudorobustus* built up only in heavy soils, whereas *P. projectus* did well only in light-colored soils where drier conditions prevailed (6). The fact that Lafayette (Site-11) had high counts of both *H. pseudorobustus* and *P. projectus*, plus the highest counts of *X. americanum*, resulted in its central position in the ordination. Edgewood (Site-4) stands far from the other sites, reflecting the fact that *P. projectus* was the only species to build up. Bluffton (Site-10) stands apart because the dominant species was the *Pratylenchus* species not found at the other sites, and because a very high number of this species was present in one of the three years. The Bluffton site had several other species in common with other sites. This explains the difference between its location in the ordination and in the dendrogram (Fig. 2), where density was not a factor in calculating similarity indices except in establishing the criteria for recording presence or absence of buildup. Trenton (Site-8) was dissimilar to the other sites because of the dominance of *T. acutus*. Buildups of *P. projectus*, the usual *Pratylenchus* species, and *X. americanum* explain its central position in the XY plane.

TABLE 3. Soil and climatic characteristics of 14 sampling sites in Illinois and Indiana soybean fields.

Site Name and Code		Latitude	Characteristics of major soil types	Average frost-free period (days)	Average annual temperature (°F) Max.	Min.	Average annual precipitation (inches)	Average soybean yield with good management (Bu/acre)
DeKalb	(1)	41° 48′	Sidell, Catlin, Flanagan, Drummer. Permeable dark colored silt loams.	152	59	37	35	46
Pontiac	(2)	40° 57′	Mixed dark and moderate to dark silt loams.	173	62	42	34	42
Urbana	(7)	40° 7′	Sidell, Catlin, Flanagan, Drummer. Permeable dark colored silt loams.	181	62	42	37	46
Girard	(3)	39° 22′	Hasmer, Stoy, Wier slowly permeable light colored silt loams.	180	65	43	38	43
Trenton	(8)	38° 29′	Light colored soils, moderate to poorly drained, including Hasmer, Stoy, Wier soils.	187	66	46	40	47
Edgewood	(4)	39° 2′	Gray prairie silt loam with clay subsoil.	180	66	47	40	38
Eldorado	(5)	37° 45′	Bottomland silty clay loam.	191	70	46	42	48
Miller City	(6)	37° 9′	Bottomland fine sandy loam.	213	67	51	45	43
Knox	(9)	41° 17′	Maumee fine sandy loam. Deep, neutral, dark brownish gray. Formed from sands in swales. High water table.	147	61	38	35	41
Bluffton	(10)	40° 44′	Blount silt loam. Deep, dark grayish brown. Formed from fine textured glacial till on level to undulating areas.	157	62	40	38	43
Lafayette	(11)	40° 26′	Chalmers silty clay loam. Deep, dark grayish brown to nearly black on low flats.	163	63	40	37	50
Greenfield	(12)	39° 45′	Brookston-Crosby complex-silty clay loam and silt loam. Deep, very dark grayish brown to brownish gray. Gentle slopes.	171	63	42	39	40
Worthington	(13)	39° 7′	Genesee silt loam. Deep, dark grayish brown bottomland. Frequently flooded.	174	65	43	42	49
Evansville	(14)	38° 0′	Montgomery and Zipp silty clay loams. Deep, grayish brown to dark brownish gray. Nearly level.	192	69	48	43	49

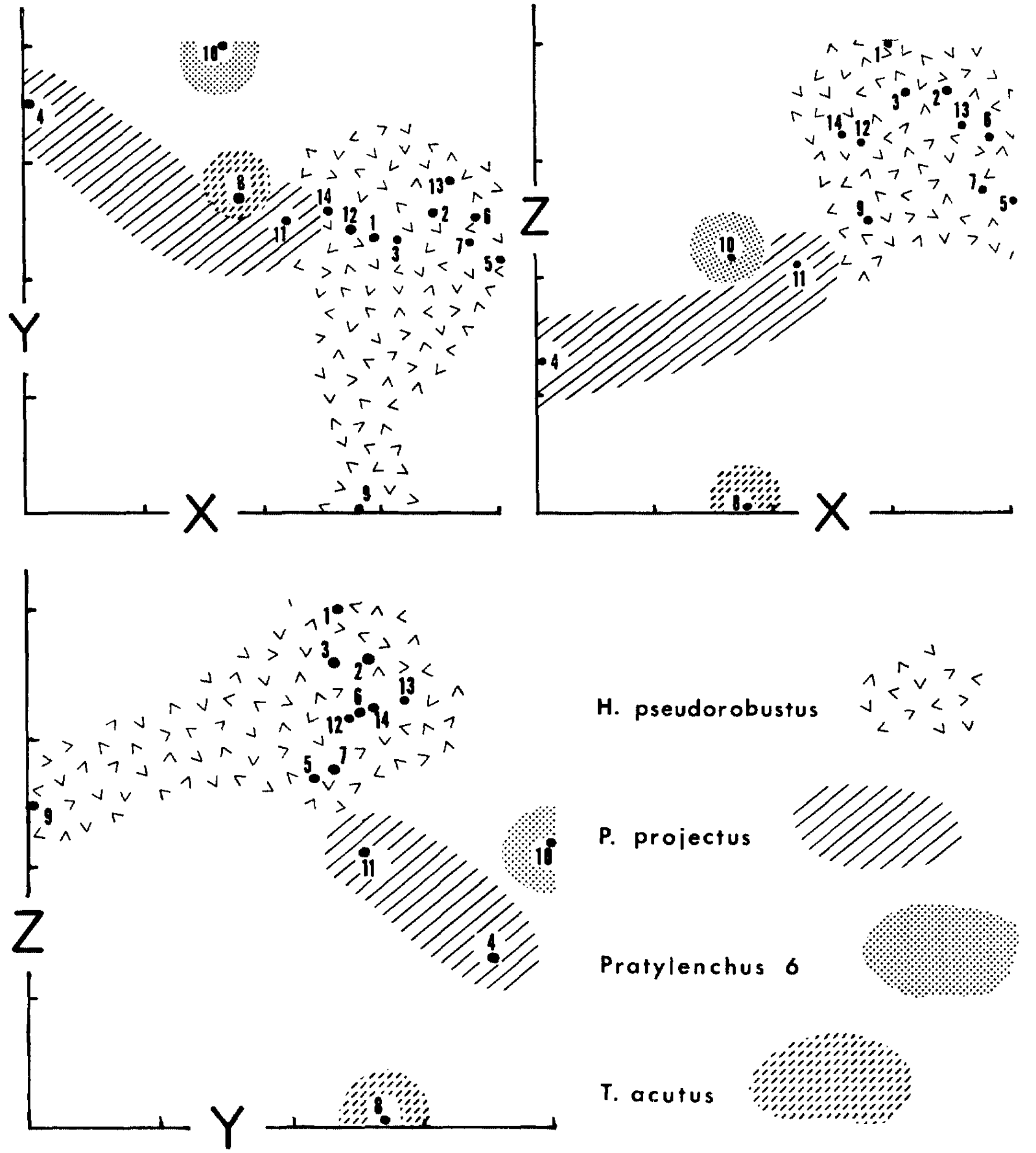

FIG. 3. X-y, x–z, and y–z ordination of total density of nematode species at each location. Species in highest density for each site are represented by designated symbol.

CONCLUSIONS

It should be possible to associate the relationships revealed by the ordination and the dendrogram with gradients in climatic or other environmental characteristics of the sites. The quantifiable characteristics of Table 3 cannot be clearly correlated with the locations of the sites along any of the axes

FIG. 4. Three-dimensional model of ordination. Numbered spheres represent the 14 sites.

of Fig. 3. Based on dominant species recovered, it is likely that the X-axis is related to the total available moisture. If additional counts had been taken over a longer period of years, calculations of similarity coefficients could have included species frequency and volume occupied by each species, as well as density. Sampling over a longer period would tend to minimize the importance of an occasionally high count, such as those of Knox and Bluffton, which affected the ordination so drastically. It is possible that such calculations, following a longer sampling period, might result in a separation of the sites in ways that could be correlated with discrete characteristics of the environment. It is also possible that the nematode population structure in a given site results from a combination of a number of factors, with the total effect difficult to measure or quantify in the usual manner. In fact, the groupings on the dendrogram, in particular, seem quite reasonable when the total soil picture is evaluated in terms of major types of surface soils, nature of the predominant subsoils, and availability of moisture from all sources. The same can be said of the groupings resulting from the ordination, taking into consideration the exceptions noted above.

In general it might be concluded that in soybean fields maintained according to recommended practices, as were these test plot fields, the community structure of the plant parasitic nematodes tends to be similar on the dark-colored, highly productive soils throughout the two-state region. On lighter soils the community structures differ somewhat from the darker soils and from each other, possibly reflecting the more diverse nature of the lighter soils. As more knowledge becomes available concerning pathogenicity of these widely occurring species, information of the kind reported here will have predictive value in deciding where and when a given species is likely to become a problem, and where prospective control measures, such as resistant varieties, should be tested in the field. Quantitative techniques such as those utilized herein show promise as valuable tools in classifying nematode communities on an ecological basis.

LITERATURE CITED

1. BRAY, J. R., AND J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325–349.
2. FERRIS, V. R., AND R. L. BERNARD. 1958. Plant parasitic nematodes associated with soybeans in Illinois. Plant Dis. Rep. 42: 798–801.
3. FERRIS, V. R., AND R. L. BERNARD. 1961. Seasonal variations of nematode populations in soybean field soil. Plant Dis. Rep. 45: 789–793.
4. FERRIS, V. R., AND R. L. BERNARD. 1967. Population dynamics of nematodes in fields planted to soybeans and crops grown in rotation with soybeans. I. The genus *Pratylenchus* (Nemata: Tylenchida). J. Econ. Entomol. 60:405–410.
5. FERRIS, V. R., AND R. L. BERNARD. 1971. Crop rotation effects on population densities

of ectoparasitic nematodes. J. Nematol. 3: 119–122.
6. Ferris, V. R., and R. L. Bernard. 1971. Effect of soil type on population densities of nematodes in soybean rotation fields. J. Nematol. 3:123–128.
7. Mountford, M. D. 1962. An index of similarity and its application to classificatory problems. p. 43–50 *In:* P. W. Murphy (ed.) Progress in soil zoology. Butterworths, London.
8. Preston, F. W. 1962. The canonical distribution of commonness and rarity: Part 1. Ecology 43:185–215.
9. Preston, F. W. 1962. The canonical distribution of commonness and rarity: Part 2. Ecology 43:410–432.
10. Winslow, R. D. 1964. Soil nematode population studies. I. The migratory root Tylenchida and other nematodes of the Rothamsted and Woburn six-course rotations. Pedobiologia 4:65–76.