Nematode Community Structure of Forest Woodlots: III. Ordinations of Taxonomic Groups and Biomass[1]

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Abstract: Nematode communities of 18 Indiana mixed hardwood stands were comprised of an average of 23% tylenchid species, 31% dorylaimid species, and 46% species of six other orders. Based on total numbers of individuals present the stands averaged 42% tylenchids, 20% dorylaimids, and 38% individuals of other orders. Ordination of the sites using data only for tylenchid species gave an even distribution of sites, indicating little effect of site disturbances on tylenchid populations. By contrast an ordination using data for dorylaimid species showed a high degree of dissimilarity between reference sites indicating that disturbances at some sites had drastically affected the dorylaimid fauna. An ordination utilizing biomass of all species present was very similar to the ordination based on data for dorylaimid species only. *Key Words:* Indiana hardwood stands; Tylenchida; Dorylaimida; Rhabditida; Teratocephalida; Araeolaimida; Monhysterida; Chromadorida; Enoplida.

Within recent years interest has increased in the study of nematode faunas of natural habitats (8,9,14,16,17,18) because such knowledge is an essential step in the evaluation of the role of nematodes in the soil (5,18). Several techniques have been suggested for analysis of nematode faunas, including Yeates' (18) technique for indicating relative diversity and relative abundance of species; and the clustering techniques used by the present authors and by Schmitt and Norton (6,8,9,14).

Previous papers of this series (8,9) demonstrated by two different clustering techniques that nematode communities in mixed hardwood stands can be related to forest types, successional stages of the tree communities, and to major soil characteristics. Of the techniques used, community ordination gave the most information regarding the relationships. It was thought that a more meaningful interpretation of intersite relationships might be made if additional information regarding the taxonomic structure of the nematode communities were obtained, and if further ordinations were performed in which taxonomically related groups of nematodes were analyzed separately. Moreover, in view of an increasing emphasis on a consideration of biomass in decomposer processes (4,13,17), an additional ordination utilizing total biomass of each species in the community would provide information on relative species importance when biomass is a major consideration in an ecological study.

MATERIALS AND METHODS

Analysis of taxonomic structure and biomass: Details of the study area of 18 Indiana mixed hardwood stands of varying plant composition, soils, physiography, and past management practices has been given (9). Site characteristics are summarized in Table 1. Methods for sampling each site three times during each of 2 yr, for processing, identifying, and counting specimens, as well as a list of all species recovered, have been given elsewhere (8,9). In the present study, a Fortran IV computer program was written to sum the total numbers of species and individuals belonging to the Tylenchida, the Dorylaimida, and to a third group comprising the six remaining orders represented (Rhabditida, Teratocephalida, Araeolaimida, Monhysterida, Chromadorida, and Enoplida). A second computer program was

Received for publication 27 January 1974.

[1]Portion of a Ph.D. dissertation submitted by the senior author to Purdue University. Journal Paper No. 5386, Purdue University Agricultural Experiment Station, W. Lafayette, Indiana 47907. This study was supported in part by National Science Foundation Grant GZ-416.

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written to calculate the volume and fresh weight of each species (based on the adult) using Andrássy's (1) method, and to calculate the total volume and weight of individuals of each species at each site.

Ordinations: Community ordination (3), a technique utilizing quantitative data on density, frequency, and dominance, whereby sites are arrayed in a multidimensional order, was discussed previously (6,8). Separate ordinations based on species density and frequency were calculated for the orders Tylenchida, Dorylaimida, and the group comprised of species of the six orders named above. Another ordination was performed which utilized the total biomass of each species (in all orders) present at the sites in developing the similarity-dissimilarity matrix. All ordinations were calculated utilizing the computer program ORDCOM written by R. L. Giese of the Purdue Entomology Department.

RESULTS AND DISCUSSION

Taxonomic structure based on species composition: For the 18 sites, the average composition included 23% tylenchid species, 31% dorylaimid species, and 46% species belonging to the six other orders. The percentage of tylenchid species was highest at site R, Wabash River, where they comprised 31% of the total species. Sites I, Livestock, and P, Black Locust, also had a higher than average percentage of tylenchid species with 30% and 28% respectively. Tylenchid species were the smallest percent (19%) of the total species at sites L, Higley Woods, and M, Bramer 26.

The highest percent value for the dorylaimid species (36%) occurred at the following four sites: A, Stewart Hillside; C, Stewart Stream; M, Bramer 26; and O, Bramer 550. Dorylaimid species represented the smallest percent of the total at sites P (21%), I (23%), and R (24%) where tylenchid species attained their highest percent of the total species.

Species in the group comprised of the remaining six orders attained their highest percent of the total at site P (52%) and E, Leitner North, (51%). Their lowest value was 31% of the total at sites H, McCormick East, and Q, Open Oaks.

A comparison of the genera and the number of species within a given genus found in forest soils of central Germany by Bassus (2) and those found in the woodlots in Indiana show a remarkable similarity. The almost nonexistent

TABLE 1. Characteristics of 18 Tippecanoe County, Indiana, forest woodlot sites. All of the sites except C and G are as described by MacLean (11).

Site						
Code	Name	Hectares	Management	Dominant tree species	Soil type	Soil drainage rank[a]
A	Stewart Hillside	16.30	Natural	Sugar Maple	Russell silt loam	2
B	Stewart Beech	16.30	Natural	Beech-Sugar Maple	Miami silt loam	2
C	Stewart Stream	16.30	Natural	Beech-Sugar Maple	Miami silt loam	2
D	Leitner South	2.88	Cut-grazed	Mixed	Brookston silty clay loam	5
E	Leitner North	2.88	Cut	Sugar Maple	Fincastle silt loam	3
F	McCormick West	11.39	Cut	Mixed	Brookston silty clay loam	5
G	McCormick Ditch	11.39	Cut	Mixed	Brookston silty clay loam	5
H	McCormick East	11.39	Cut	Sugar Maple	Miami silt loam	2
I	Livestock	4.27	Grazed[b]	Mixed	Brookston silt loam	5
J	Workman	1.40	Grazed	Sugar Maple	Brookston silt loam	5
K	Cason	2.57	Grazed	Beech-Sugar Maple	Cope silt loam	4
L	Higley	3.04	Cut	Sugar Maple	Fincastle silt loam	3
M	Bramer 26	3.20	Natural	Oak-Maple	Fincastle silt loam	3
N	Starrett	1.57	Cut	Mixed	Cope silt loam	4
O	Bramer 550	4.18	Cut-grazed	Mixed	Fincastle silt loam	3
P	Black Locust	3.21	Cut	Black Locust	Russell silt loam	2
Q	Open Oaks	3.42	Grazed[b,c]	White Oak	Fox loam	1
R	Wabash River	1.67	Flooded[b]	Silver Maple-Cottonwood	Genessee silty clay loam	2

[a]Based on Indiana Soil Profile Ranking. Ranges from excessively-drained (1) to very poorly-drained (5).
[b]Recent (within 1-4 yr of this study).
[c]Data available for 1968 only.

dorylaimid fauna in the German forest is an outstanding difference. Yuen (19) also observed that dorylaimid genera, which were a constant feature of a regenerated English woodland, were not listed by Bassus (2). She suggested that the differences may indicate more heterogeneity between similar, but geographically isolated, habitats than previously realized (12).

Taxonomic structure based on numbers of individuals of each species: The nematode community structure at the 18 sites based on total individuals counted (mean number, 1.8 million m^{-2}) averaged 42% tylenchids, 20% dorylaimids, and 38% for the other six orders.

The tylenchids reached their highest value at site P, Black Locust, where they accounted for 56% of the nematode population and their lowest value at site F, McCormick West, where they were only 29% of the total population. The dorylaimids reached their highest proportion at site L, Higley Woods, where they were 35% of the total population. The lowest values for dorylaimids were at site I, Livestock, and P, Black Locust, at 4% and 5% respectively. Counts of individuals belonging to the other orders were highest at site F, McCormick West, where they were 54% of the population and lowest at site M, Bramer 26, where they accounted for 23% of the total population.

Ordination of members of the order Tylenchida: The results of the ordination based on the members of the order Tylenchida are presented in Fig. 1. Although the distribution of the sites in the ordination is the result of the combined influence of 35 tylenchid species, the large numbers of *Tylenchus* spp. 1 and 5, *Tylenchorhynchus silvaticus,* and *Helicotylenchus platyurus* at the sites exerted the greatest influence in determining the position of each site in the ordination. The

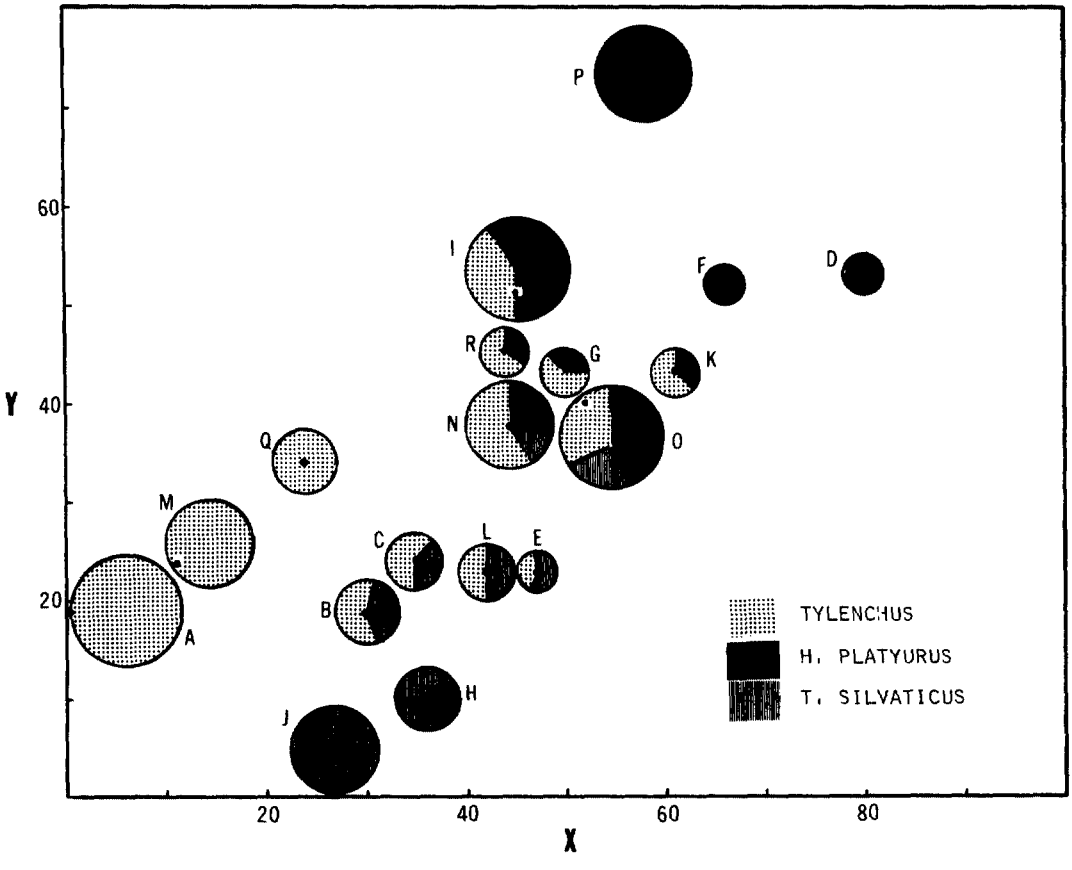

FIG. 1. Ordination of the nematode order Tylenchida at 18 forest sites in Tippecanoe County, Indiana. X-Y plane. Circle size depicts relative numbers of *Tylenchus* spp. 1 and 5, *Helicotylenchus platyurus,* and *Tylenchorhynchus silvaticus* which were dominant throughout the sites.

relationships among the sites can be largely explained by these four species that represent 62% of the total number of tylenchids.

Site A, Stewart Hillside, the low X-axis reference site, was where *Tylenchus* spp. 1 and 5 reached their highest numbers. Site D, Leitner South, was the most dissimilar to site A and thus became the high X-axis reference site. Site D was one of the sites that was very poor in tylenchid species. *H. platyurus* was the dominant tylenchid species at site D. Sites with high numbers of *Tylenchorhynchus silvaticus* are near the low end of the X-axis (showing a closer relationship to sites dominated by *Tylenchus* sp. 1 and 5), and sites dominated by *H. platyurus* are near site D on the high end of the X-axis.

The distribution of the sites along the X-axis shows a gradient from well-drained sites with sugar maple, white oak, and hickory at the low end toward sites that are very poorly-drained and have a mixture of hydromesophytic tree species. Site P, Black Locust, was the only site which showed exception to this gradient, but site P has shown a closer relationship to the poorly-drained, hydro-mesophytic sites in all ordinations (8).

The distribution of the sites on the Y-axis can be explained largely by the relationship between *Tylenchorhynchus silvaticus* and *H. platyurus*. Site J, Workman Woods, the low Y-axis reference site, was where *T. silvaticus* reached its highest numbers. Site P, Black Locust, the high Y-axis reference site, is where

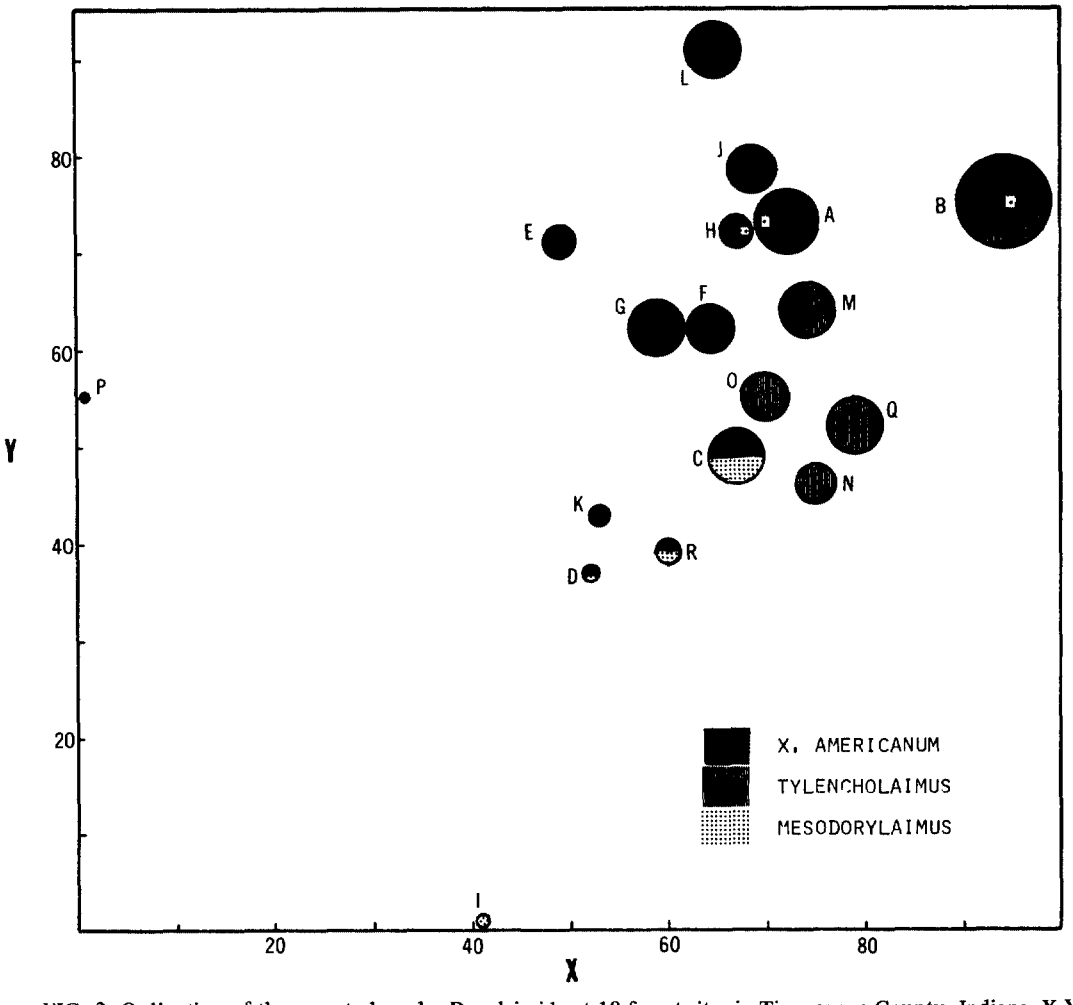

FIG. 2. Ordination of the nematode order Dorylaimida at 18 forest sites in Tippecanoe County, Indiana. X-Y plane. Circle size depicts relative numbers of *Xiphinema americanum, Tylencholaimus* sp. 1, and *Mesodorylaimus* sp. 4 which were dominant throughout the sites.

H. platyurus attained its highest numbers. If we consider site P to be more characteristic of the poorly-drained sites with hydro-mesophytic tree species, then the gradient here is from that type community at the high end of the Y-axis toward sites that are imperfectly-drained but with higher percentages of sugar maple and white oak.

There appear to be three distinct tylenchid communities represented in this ordination. The first is where *Tylenchus* spp. 1 and 5 are the dominants, and they are found at the well-drained sites that have higher percentages of oak and hickory. The second is where *Tylenchorhynchus silvaticus* is the major dominant, and *Tylenchus* sp. 1 and 5 are also present in fairly large numbers. This community, dominated by *T. silvaticus,* is found at the imperfectly-drained, disturbed sites where sugar maple is the dominant tree species, but white ash and red elm are also well represented. The third tylenchid community is dominated by *Helicotylenchus platyurus* with *Tylenchus* spp. 1 and 5 present. The *H. platyurus* community is found associated with the poorly-drained, disturbed sites that have a mixture of hydro-mesophytic tree species. White or black ash are two of the common tree species at these poorly-drained sites, and Yuen (19) also found the distribution of two species of *Helicotylenchus* to coincide with the distribution of the ash in a reclaimed woodland.

Sites N and O, almost centrally located in the ordination, are representative of areas where the three tylenchid communities overlap. Although *Tylenchus* spp. 1 and 5 are the major dominants at site N, *T. silvaticus* and *H. platyurus* are also well represented. *H. platyurus* is the major dominant at site O, but again the other three species are well represented.

These two sites occur on poorly-drained soils that are representative of the"first step down" toward very poorly drained soils (15). They both have a mixture of tree species and are representatives of the transitional forest

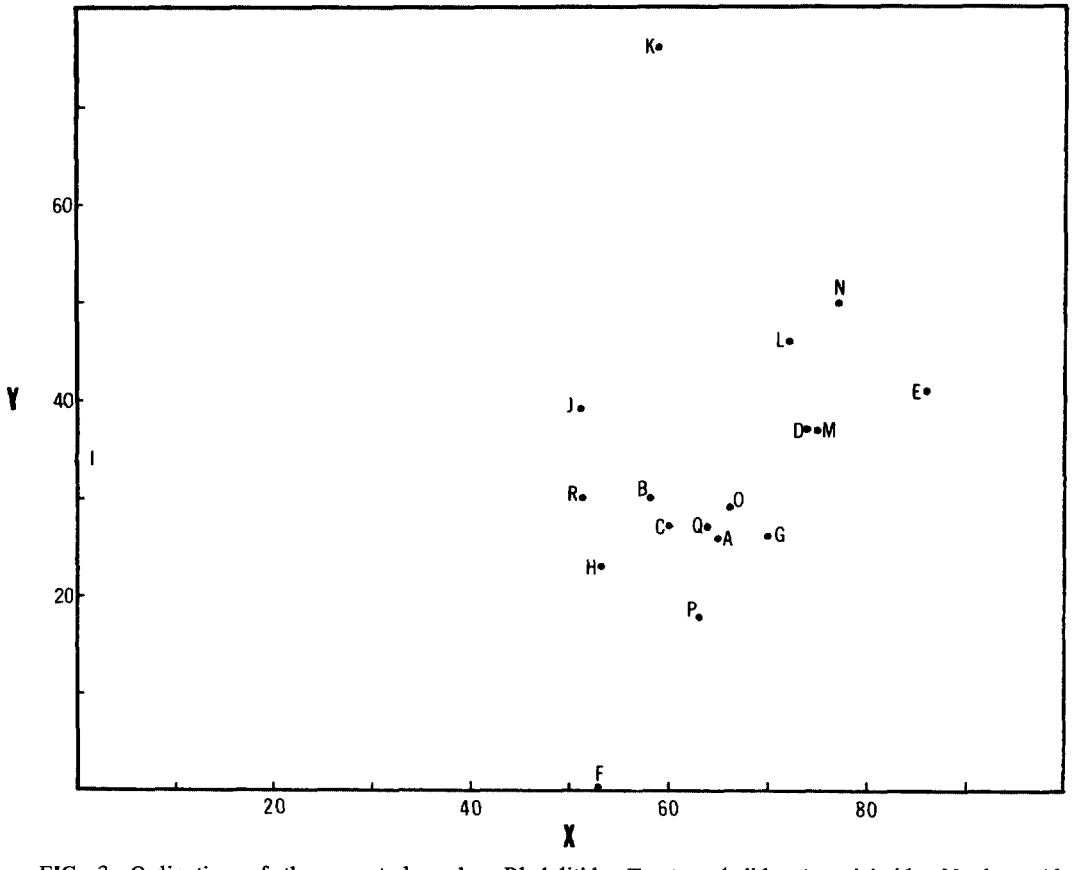

FIG. 3. Ordination of the nematode orders Rhabditida, Teratocephalida, Araeolaimida, Monhysterida, Chromadorida, and Enoplida at 18 forest sites in Tippecanoe County, Indiana. X-Y plane.

community (7). Site N is in a later stage of transition than O, as indicated by the presence of more of the climax species such as beech, sugar maple, basswood, and hickory. Site O is still in an earlier stage as indicated by the presence of such hydro-mesophytic species as swamp white oak, red elm, and cottonwood.

Ordination of the members of the order Dorylaimida: The results of the ordination based on the Dorylaimida are presented in Fig. 2. Again, the ordination includes 60 dorylaimid species, but can best be explained by the dominant species found at the different sites. These four species (*Aporcelaimellus obscurus, Mesodorylaimus* sp. 4, *Tylencholaimus* sp. 1, and *Xiphimena americanum*) represent 33% of dorylaimids in this ordination.

Site P, Black Locust, was the most dissimilar with regard to dorylaimid fauna and thus the low X-axis reference site. *Xiphinema americanum* was the dominant dorylaimid species at site P, which was also characterized by having the fewest number of dorylaimids. Site B, Stewart Beech, was the high X-axis reference site and contained the largest number of dorylaimids. *Xiphinema americanum* and *Tylencholaimus* sp. 1 were the dominant dorylaimid species at site B.

The poor dorylaimid fauna at site P and its selection as the low X-axis reference site resulted in a grouping of most sites toward the high end of the axis. Sites poor in dorylaimid fauna are at the low end of this group whereas sites with larger numbers of dorylaimids are at the high end. Sites with *Tylencholaimus* sp. 1 as the dominant dorylaimid species are nearest site B at the high end of the X-axis.

Site I, Livestock, the low Y-axis reference site, also had a very poor dorylaimid fauna. *Aporcelaimellus obscurus* and *Mesodorylaimus*

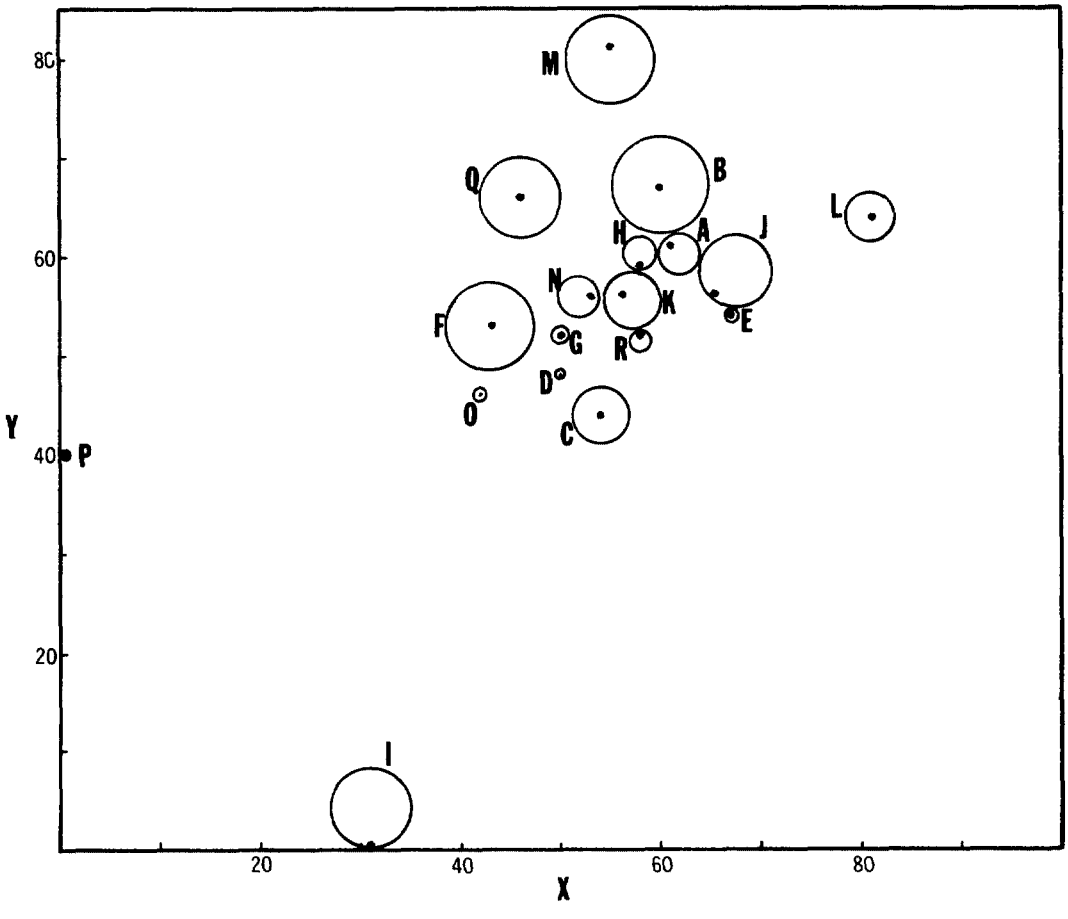

FIG. 4. Ordination based on species biomass at 18 forest sites in Tippecanoe County, Indiana. X-Y plane. Circle size represents total nematode biomass.

sp. 4 were the dominant species there. Site L, Higley Woods, the high Y-axis reference site, was where *X. americanum* reached its highest numbers. The other sites are spread out more on the Y-axis than they were on the X-axis, but they still fall toward the high end.

The disturbed, poorly-drained sites D and K, and the periodically flooded site R, on the Wabash River, show the most similarity to site I. The relationship of sites in the X-Y plane is similar to that for the other ordinations (8) with regard to tree species and soil types. This was unexpected inasmuch as the dorylaimids comprised only 20% of the average total nematode population. But the most striking feature of this ordination is the length of the two axes, indicating the high degree of dissimilarity between the reference sites. This is the greatest dissimilarity found in any of the ordinations and when compared to the ordination based on tylenchid nematodes, indicates that the disturbances at sites I (heavily grazed) and P (cut over) have had a much more drastic effect on the dorylaimid fauna than on the tylenchid fauna. Most tylenchid species have maintained themselves at these two sites even though *Helicotylenchus platyurus* is the major dominant, but the dorylaimids have become a very small percentage of the nematode population (5% at site P and 4% at site I), in contrast to an average of about 20% at the other sites. The findings that tylenchid nematodes are a major portion of the total population in disturbed areas, whereas dorylaimids constitute only a very small portion of the total population, are similar to findings for cultivated fields (J. M. and V. R. Ferris, *unpublished*) and in a disturbed grassland by Yuen (19).

Ordination of members of the remaining orders: An ordination based on the 66 species of the remaining six orders was performed. The results are depicted in Fig. 3. The location of the sites can be explained somewhat by the dominant species at each site. Members of the order Rhabditida were the most numerous of the species in this group and probably exerted the greatest influence on the ordination.

Site I, Livestock, the low X-axis reference site, was very dissimilar to all other sites, as evidenced by the clustering of the other sites at the high end of the axis. The large number of *Mesodiplogaster* sp. 1 at site I (8) were undoubtedly responsible for this degree of dissimilarity. Site E, Leitner North, the high X-axis site, was characterized by having three codominant species, *Mesorhabditis* sp. 1, *Rhabditis* sp. 5, and *Eucephalobus oxyuroides*, although they all occurred in relatively low numbers.

Site F, McCormick West, the low Y-axis reference site, was where *Rhabditis* sp. 5 attained its highest numbers and was the dominant species. Site K, Cason Woods, was the high Y-axis reference site. *Rhabditis* sp. 7 was the dominant species and was present in large numbers. This resulted in most sites grouping in the lower portion of the Y-axis toward site F.

The general cluster of sites is in the lower right portion of the X-Y plane indicating the high degree of dissimilarity between the other sites and sites I and K. Attempts to correlate the position of the sites in this ordination with known physical or floristic factors proved fruitless. The many species represented in these diverse orders do not respond similarly to the same environmental factors. These species also represent a large number of bacterial feeders that fluctuate radically in numbers depending on available food material. The large number of *Mesodiplogaster* sp. 1 at site I in the spring of 1968 when cattle were being grazed and their subsequent drastic decrease in numbers (8) after the cattle were removed is a good example. Many other species are predators on nematodes or other small soil organisms.

Ordination based on biomass: Results of the ordination utilizing total biomass for each species at each site is presented in Fig. 4. The most striking feature of this ordination is its similarity to the dorylaimid ordination (Fig. 2). The low reference sites on the X and Y axes are the same, and site L has moved from the high Y-axis reference site to the high X-axis reference site. Site M is the new high reference site on the Y axis. The main cluster of sites is at the high end of the X-Y plane and is similar to that for the dorylaimid ordination but somewhat tighter. The use of the biomass of each species in this ordination was expected to show an increase in the importance of some of the larger dorylaimids and larger members of the other orders, but the high degree of similarity between the dorylaimid ordination and the biomass ordination was not expected.

The distribution of the sites along the X-axis appears to be due mainly to the importance of *X. americanum*. Site P at the low end is poor in dorylaimid fauna in general and also in numbers of *X. americanum*. Site L at the high X-axis

point is where *X. americanum* reached its highest numbers. Site I, the low Y-axis reference site, has a relatively high total biomass, but this is probably the result of the high numbers of *Mesodiplogaster* sp. 1 since it appears to have little in common with most of the other sites.

Site B, Stewart Beech, in the upper portion of the X-Y plane had the highest total biomass at 2,126 mg m^{-2}. This is not too surprising since site B also had the most nematodes and the largest number of dorylaimids. Site P, Black Locust, the site with the smallest total biomass value at 1,038 mg m^{-2}, had high numbers of *Helicotylenchus platyurus,* but it was very poor in dorylaimid fauna. The average total biomass for the 18 sites was 1,729 mg m^{-2}.

These figures for total live biomass are within the range of those obtained by Overgaard-Nielson (12). Andrássy (1) considers the figures of Overgaard-Nielson to be high since the latter treated the nematodes as a cylinder of equal diam at either end. Although Andrássy's formula takes this into consideration, the total nematode biomass obtained in the present study was also probably high since we based calculations on counts of both adults and juveniles.

CONCLUSIONS

At most of these forest sites the tylenchid nematodes outnumbered the dorylaimid fauna in individuals, although more dorylaimid species were present. The dorylaimid fauna was very poor at the highly disturbed sites I and P where tylenchid nematodes occurred in high numbers. The percentage of the total nematode community comprised of individuals belonging to the rest of the orders combined was fairly consistent at most sites.

The ordinations of the separate orders of nematodes depict the compositional differences of the communities at the sites. Although the tylenchid ordination reflects differences in community structure, the fairly even distribution of the sites in the X-Y plane indicates relationships in which no one site or a few sites are highly dissimilar to all other sites. However, the distribution of the sites in the X-Y plane of the dorylaimid ordination shows a high degree of dissimilarity between the highly disturbed sites I and P and the remaining sites. This indicates that dorylaimids are very sensitive to site disturbance. The ordination utilizing total biomass of all species showed a remarkable degree of similarity to the ordination of the dorylaimid nematodes indicating the influence of this group, which includes many of the larger nematode species.

A few generalizations are possible using the terminology of modern ecological theory with respect to r- and K- selection (10). It would appear that the dorylaimid species are the "K strategists" of the nematodes in forest habitats. Although we know little about the life histories of most dorylaimid species, they appear to be adapted to specialized habitats of undisturbed areas, they tend to be large, and many have relatively long life spans with few offspring per individual (*unpublished,* our laboratory). By contrast, many of the species (such as rhabditids) used in the ordination of Fig. 3, must be considered extreme "r strategists," which tend to build up rapidly under a variety of environmental conditions, exploiting temporary situations. The tylenchids as a group are neither extreme "K strategists" nor extreme "r strategists." Many tylenchid species seem able to compete well in stable habitats and also to retain the ability to utilize disturbed areas, as indicated by the distribution of sites in the ordination. The fact that the dorylaimid nematodes as a group are much more sensitive to disturbances in the forest habitats than are tylenchid nematodes, makes the dorylaimids more valuable as indicators of ecological change.

LITERATURE CITED

1. ANDRÁSSY, I. 1956. Die Rauminhalts-und Gewichtsbestimmung der Fadenwürmer (Nematoden). Acta Zool. 2(1-3):1-15.
2. BASSUS, W. 1962. Untersuchungen über die Nematoden-fauna mitteldeutscher Waldböden. Wiss. Z. Humboldt-Univ., Berl., Math.-Nat. Reihe 11:145-177.
3. BEALS, E. 1960. Forest bird communities in the Apostle Islands of Wisconsin. Wilson Bull. 72:156-181.
4. FERRIS, J. M. 1972. Terrestrial decomposition processes: Population and energy dynamics of selected invertebrates. Eastern Deciduous Forest Biome Memo Report No. 72 - 166.
5. FERRIS, V. R. 1972. The importance of discoveries in nematology to human welfare. BioScience 22:237-239.
6. FERRIS, V. R., J. M. FERRIS, R. L. BERNARD, and A. H. PROBST. 1971. Community structure of plant-parasitic nematodes related to soil types in Illinois and Indiana soybean fields. J. Nematol. 3:399-408.
7. FRIESNER, R. C., and C. M. EK. 1944. Correlation of microclimatic factors with species distribution in Shenk's Woods, Howard

County, Indiana. Butler Univ. Bot. Studies 6:87-101.

8. JOHNSON, S. R., J. M. FERRIS, and V. R. FERRIS. 1973. Nematode community structure in forest woodlots. II. Ordination of nematode communities. J. Nematol. 5:95-107.

9. JOHNSON, S. R., V. R. FERRIS, and J. M. FERRIS. 1972. Nematode community structure of forest woodlots. I. Relationships based on similarity coefficients of nematode species. J. Nematol. 4:175-183.

10. MAC ARTHUR, R. H. 1972. Geographical ecology. Patterns in the distribution of species. Harper and Row, New York. 269 p.

11. MAC LEAN, D. B. 1969. Ordinations of forest insect and plant communities in West Central Indiana. Unpublished Ph.D. Thesis. Purdue University, Lafayette, Indiana. 333 p.

12. OVERGAARD-NIELSON, C. 1949. Studies on the soil microfauna II. The soil inhabiting nematodes. Nat. Jutlandica 2:1-132.

13. REICHLE, D. E. (ed.) 1970. Analysis of temperate forest ecosystems. Springer-Verlag, New York. 304 p.

14. SCHMITT, D. P., and D. C. NORTON. 1972. Relationships of plant parasitic nematodes to sites in native Iowa prairies. J. Nematol. 4:200-206.

15. ULRICH, H. P., T. E. BARNES, B. A. KRANTZ, J. K. ABLEITER, and O. C. ROGERS. 1959. Soil survey of Tippecanoe County, Indiana. U.S. Dep. Agric., Soil Conserv. Serv. Series 1940, No. 22. 115 p.

16. WASILEWSKA, L. 1970. Nematodes of the sand dunes in the Kampinos Forest. I. Species structure. Ekol. Pol. 18:429-443.

17. WASILEWSKA, L. 1971. Nematodes of the dunes in the Kampinos Forest. II. Community structure based on numbers of individuals, state of biomass and respiratory metabolism. Ekol. Pol. 19:651-688.

18. YEATES, G. W. 1970. The diversity of soil nematode faunas. Pedobiologia 10:104-107.

19. YUEN, P. H. 1966. The nematode fauna of regenerated woodland and grassland of Broadbalk Wilderness. Nematologica 12:195-214.