

Age Structure and Community Diversity of Nematodes Associated with Maize in Iowa Sandy Soils¹

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Abstract: Age structure of nematode populations around maize growing in sandy soils in Iowa was studied at soil depths of 0–15 and 15–30 cm for 2 years. Numbers of *Longidorus breviannulatus* were generally greater at 0–15 cm than at 15–30 cm deep until mid-to-late season. The decline in numbers of females as the season progressed indicates that fecundity slowed and is evidence of only one generation per year. Peak populations of *Pratylenchus scribneri* and *Xiphinema americanum* occurred in late August or early September. Adults of *Hoplolaimus galeatus* were few in the roots but common in the soil, indicating that fertilization occurred mostly in the soil. Numbers of *P. scribneri* were generally greater at the lower depth, especially late in the season. Community diversity (*H'*) was less when nematode biomass was used instead of numbers. Numbers of *H. galeatus* did not decline over the winter. Numbers of *L. breviannulatus*, *P. scribneri*, and *X. americanum* declined significantly over the winter, but not between spring cultivation and planting.

Key words: age structure, biomass, *Hoplolaimus galeatus*, *Longidorus breviannulatus*, maize, *Paratrichodorus minor*, *Pratylenchus scribneri*, *Quinisulcius acutus*, *Xiphinema americanum*.

Knowledge of nematode temporal population patterns is essential to understanding nematode biology, measuring pathogenicity, determining control measures, studying multispecies communities, measuring age structure, and in relating nematodes to resources and environments. Life tables of migratory plant-parasitic nematodes in the field are difficult to construct because overlapping generations are common; survivorship curves, or numbers of births and deaths, are usually unknown; and reproduction, at least in temperate zones, is restricted to a few months. In the absence of discrete cohorts, monitoring age structures may give an understanding of 1) the number of generations per year, 2) variations in growth patterns, and 3) their relation to environments. The objectives of this research were to 1) monitor age structures of plant-parasitic nematode populations associated with maize in sandy soils in north-central Iowa, 2) measure diversity and nematode productivity of the plant-parasitic nematode communities, and 3) measure the effects of overwintering and spring plowing on nematode populations.

MATERIALS AND METHODS

Plant-parasitic nematodes were monitored in Butler County, Iowa, in 1983–84. The area used was a field of dryland maize divided into 10 sampling units of four 9.1-m rows spaced 76 cm apart. The 1984 test was superimposed on that of 1983. Cultivar A619Ht × A632Ht was planted at 54,000 seeds/ha on 28 April 1983 and on 7 May 1984. The soil was a loamy sand (82% sand, 12% silt, 6% clay, pH 6.1, 1.5% organic matter). Plots were kept weed free with conventional herbicides (Dual and Bladex) as used by the farmer. There was no fall plowing in 1983, but the land was disked and chisel plowed in early May 1984.

Samples were taken eight times in 1983 at 0, 20, 34, 46, 67, 85, 118, and 138 days after planting (DAP) and nine times in 1984 at -31, 0, 22, 35, 49, 70, 84, 120, and 134 DAP. At each sampling, 10 cores (2.5 cm d) were collected in the row at 0–15 and 15–30 cm depths. Except for *Longidorus breviannulatus* Norton and Hoffmann, nematodes were extracted from soil by centrifugal-flotation (6) and from roots by a shaker method (2). Ten percent of the nematodes in each sample were counted by taking a 10% aliquot after processing and counting the numbers with a Hawksley slide. *Longidorus breviannulatus* was extracted by sieving through 1190- μ m-pore and 150- μ m-pore sieves (16 and 100 mesh),

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TABLE 1. Seasonal total active nematode fresh-weight biomass associated with maize at two soil depths in Butler County, Iowa, in 1983 and 1984.

	Biomass ($\mu\text{g}/100 \text{ cm}^3 \text{ soil}$)			
	0-15 cm		15-30 cm	
	1983	1984†	1983	1984†
<i>Hoplolaimus galeatus</i>	1,104	692	749	490
<i>Longidorus breviannulatus</i>	178	286	91	172
<i>Xiphinema americanum</i>	177	141	80	150
<i>Paratrichodorus minor</i>	21	19	23	16
<i>Pratylenchus scribneri</i>	8	29	13	57
<i>Quinisulcius acutus</i>	2	6	4	6
LSD ($P = 0.01$)	88	69	56	72

† Excluding -31 DAP.

and total numbers were counted. Recovery efficiencies were measured by infesting 100 cm³ sandy soil with a known number of nematodes and allowing the system to stabilize for 2 days after which the soil was processed by the methods described. There were three replications for each nematode species. Recovery efficiency was 81% for *Hoplolaimus galeatus* (Cobb) Thorne, 47% for *Longidorus breviannulatus*, 63% for *Paratrichodorus minor* (Colbran) Siddiqi, 33% for *Pratylenchus scribneri* Steiner, 49% for *Quinisulcius acutus* (Allen) Siddiqi, and 88% for *Xiphinema americanum* Cobb. Different nematode stages for each species were determined by measuring 25-30 individuals from a mixture of all stages and by observing gonadal development. These results were used as standards. Biomass measurements were made by Andrassy's (1) method. Fresh-weight nematode biomass measures give an index of the nematode population potentially capable of feeding daily on the roots for the period covered. Diversity (H') and evenness (J') were measured by the equations $H' = -\sum_{pi} \log_{pi}$ and $J' = H'/H'_{\text{max}}$, respectively (13). Overwintering was monitored by comparing numbers of nematodes at the last sampling in 1983 with the first sampling in 1984 (-31 DAP) which was after frost disappearance but before spring plowing. Effects of spring cultivation were estimated by comparing numbers at -31 DAP and 0 DAP in 1984.

Data were analyzed by ANOVA using

Fisher's LSD for paired comparisons. Regression analyses and correlation coefficients were used for seasonal biomass changes.

RESULTS

Nematode biomass productivity: The seasonal biomass of *H. galeatus* was greater than for all other species in the soil (Table 1). Biomass of *L. breviannulatus* and *X. americanum* was also significantly greater than that of *P. minor*, *P. scribneri*, and *Q. acutus*. There were no significant differences in species biomass in the roots in 1983, but *P. scribneri* seasonal biomass was greater than that of *H. galeatus* at both depths in 1984 (Table 2). Although there were significant increases in total nematode biomass in the soil over the season, the statistical model accounted for little of the variation in the data; thus, the data are not considered meaningful. Nematode biomass increased significantly in the roots at both depths in both years (Fig. 1). Populations declined in the roots at the last sampling.

General population trends: Few *Q. acutus* were found and are not considered here. Age structure of the nematodes are depicted in Figures 2-6. As expected, juveniles dominated populations at most samplings. In both years, numbers of *L. breviannulatus* were generally greater at all stages and fluctuated more at the upper than at the lower depth until 85 DAP (Fig. 2). From about 34-85 DAP, numbers of

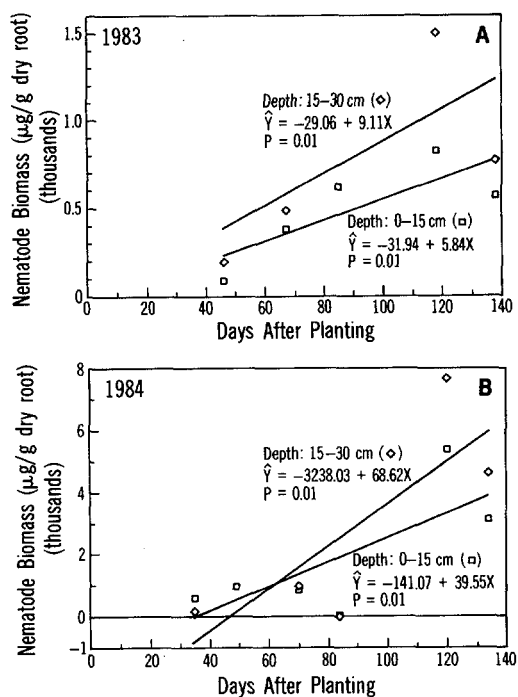


FIG. 1. Total nematode biomass in maize roots from two soil depths in 1983 and 1984, Butler County, Iowa.

females at the upper depth were more stable in 1983 than in 1984. Except for the lower depth in 1983, numbers at all stages generally declined markedly after 85 DAP. Females generally peaked early or at mid-season. Females were the most numerous stage early in the season in 1984 but not in 1983.

In contrast with *L. breviannulatus*, peaks in numbers of *X. americanum*, especially females, usually occurred about 120 DAP (Fig. 3). Numbers were greater at the upper than at the lower depth, except late in 1984.

Females of *H. galeatus* in the soil usually outnumbered individuals in any juvenile stage after 35 DAP (Fig. 4), but there were few females per gram dry root (Fig. 5). Numbers of females in the soil were generally more constant than numbers of juveniles throughout the season at each level (Fig. 4). Males were few in the roots, being recovered in 3.6% of 220 root samples, compared with recovery in 57.1% of 340 soil samples. Based on numbers of females, there is no evidence of discrete generations.

There were too few *P. scribneri* in the soil to observe population trends. Numbers of *P. scribneri* in the roots were generally greater at the lower than at the upper depth, especially late in the season (Fig. 6). Although total juveniles nearly always outnumbered females, the ratios of females to any juvenile stage varied considerably.

Individuals of *P. minor* were too few to obtain a good separation of developmental stages. The maximum number obtained was 47/100 cm³ soil. The population pattern was consistent, however, in that all peaks occurred during the first half of the season and few nematodes were recovered after 60–70 DAP.

Fecundity: There were no sharp peaks in observable fecundity of the nematodes. The majorities of gravid females, however, were seen at different times with different nematodes. Gravid females of *X. americanum* were seen later in the season (85–118 DAP) than *L. breviannulatus* (34–70 DAP). Few gravid *X. americanum* females were seen at the lower depth. No gravid *H. galeatus* were seen in the soil before 35 DAP, and most occurred between 49 and 84 DAP.

TABLE 2. Seasonal total active nematode fresh weight extracted from maize roots at two soil depths in Butler County, Iowa, in 1983 and 1984.

	Biomass (µg/g dry root)			
	0–15 cm		15–30 cm	
	1983	1984	1983	1984
<i>Hoplolaimus galeatus</i>	1,474	2,267	2,118	1,561
<i>Pratylenchus scribneri</i>	1,016	8,700	1,872	12,772
LSD ($P = 0.01$)	NS	2,811	NS	4,319

LONGIDORUS BREVIANNULATUS (Days After Planting)

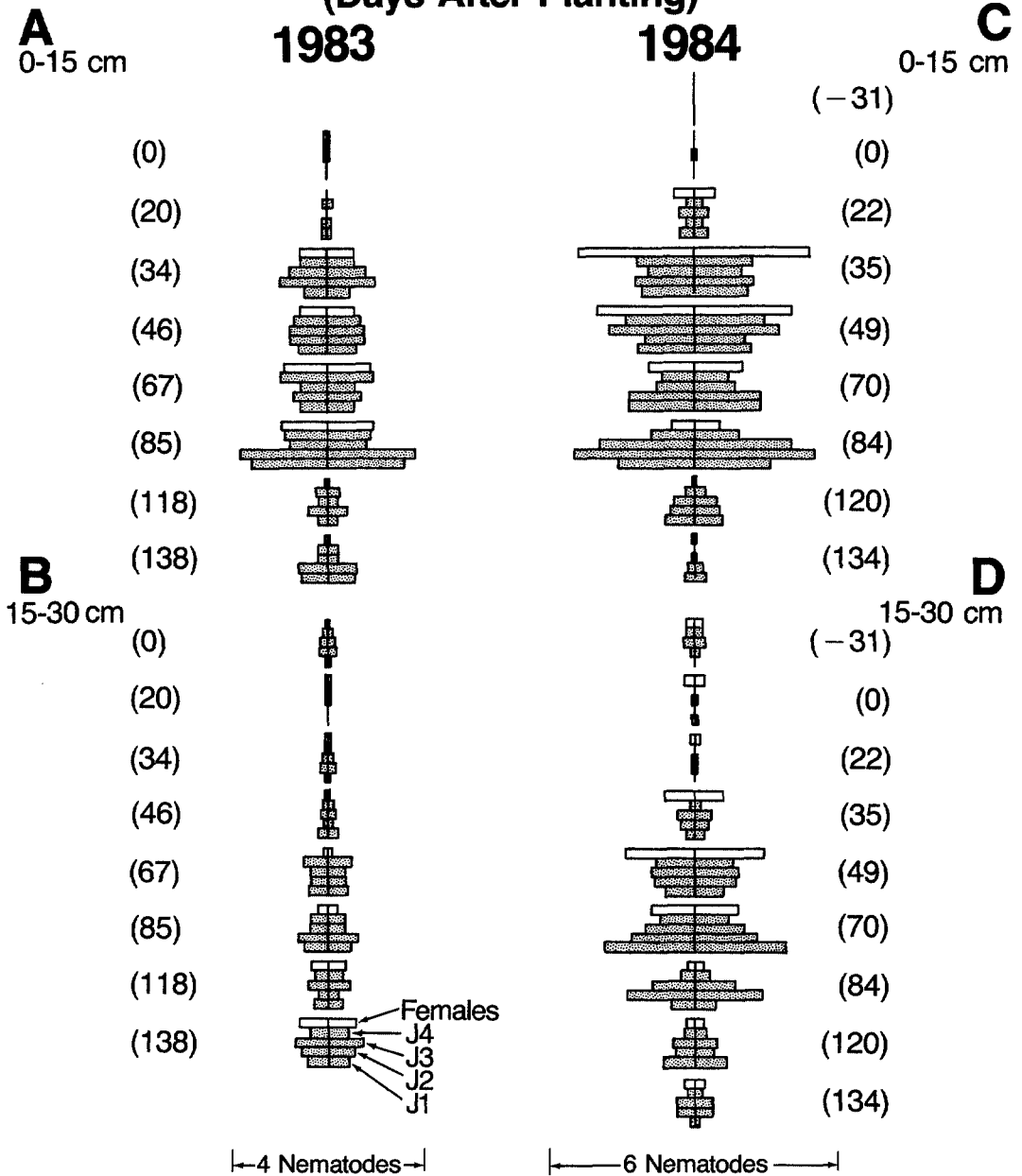


FIG. 2. Age structure (numbers) of *Longidorus breviannulatus* in soil around maize roots at two soil depths in 1983 and 1984, Butler County, Iowa.

Gravid females were not seen in nematodes extracted from the roots, but this could be because of methodology.

Overwintering: There were no significant differences in numbers of *H. galeatus* overwintering at either depth, but a significant

decline of females, juveniles, and total nematodes occurred between spring pre-planting and planting at the upper, but not lower, depth (Table 3). In contrast, *L. breviannulatus*, *P. scribneri*, and *X. americanum* were affected more at both depths by over-

XIPHINEMA AMERICANUM (Days After Planting)

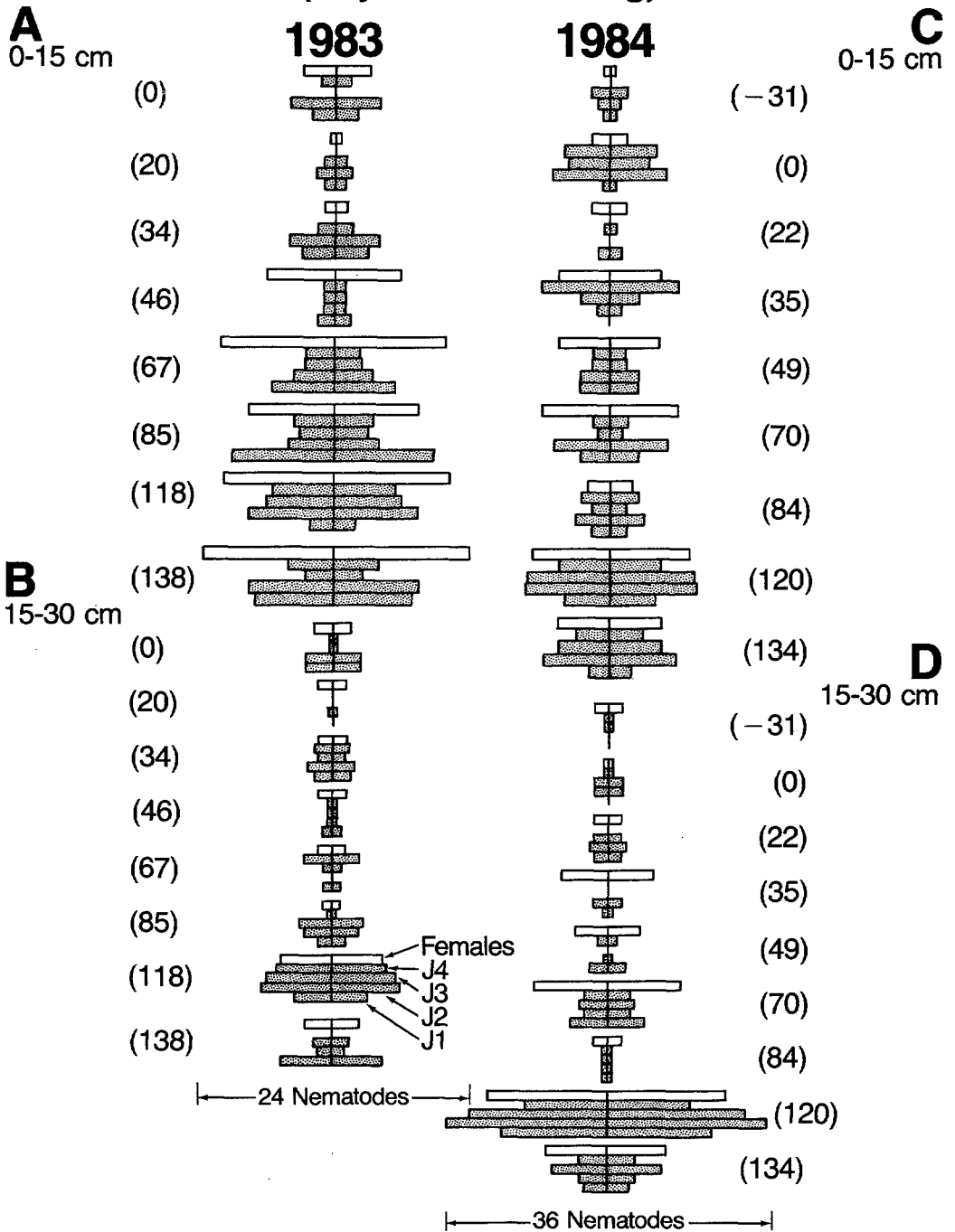


FIG. 3. Age structure (numbers) of *Xiphinema americanum* in soil around maize roots at two soil depths in 1983 and 1984, Butler County, Iowa.

HOPLOLAIMUS GALEATUS (SOIL) (Days After Planting)

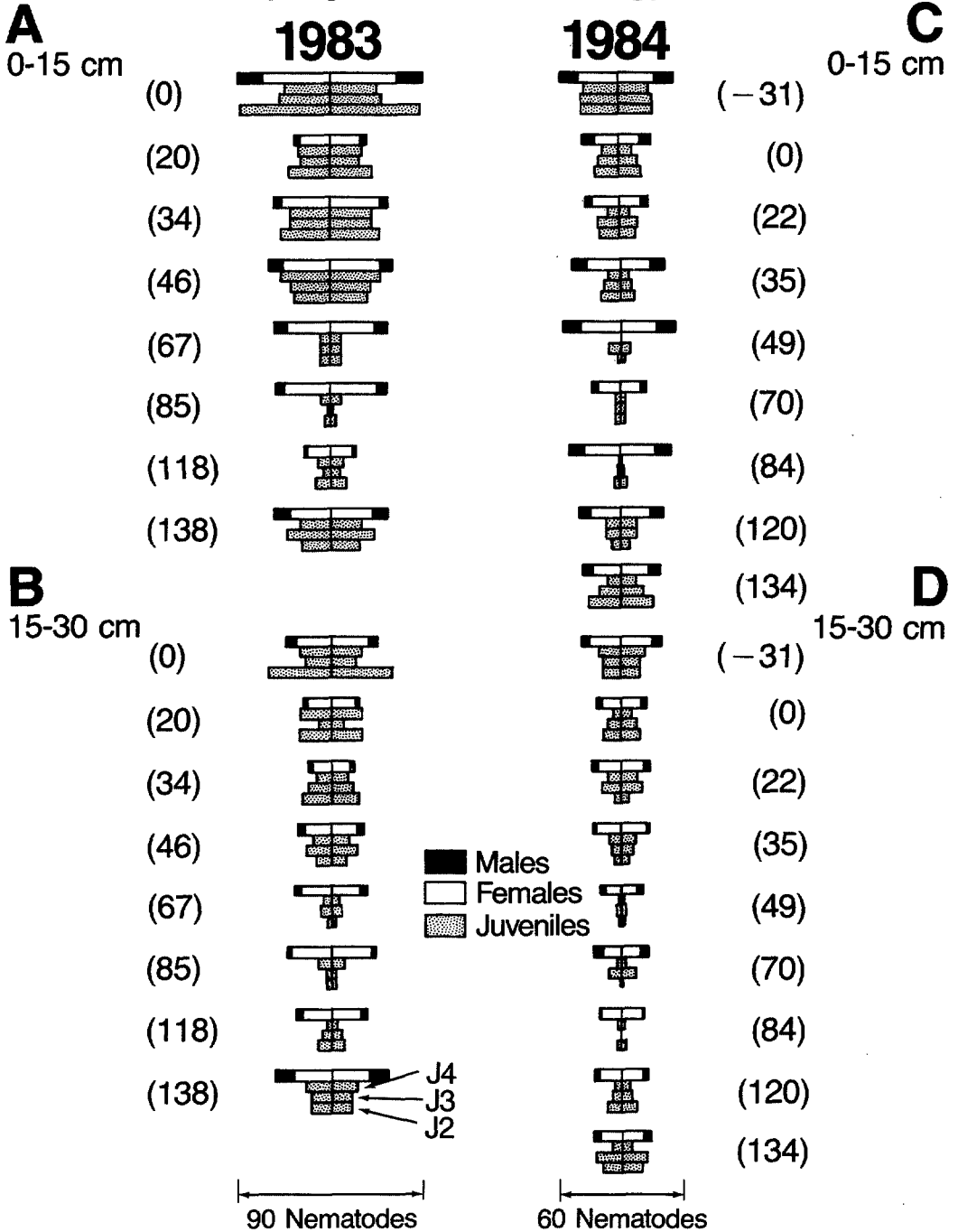


FIG. 4. Age structure (numbers) of *Hoplolaimus galeatus* in soil around maize roots at two soil depths in 1983 and 1984, Butler County, Iowa.

HOPLOLAIMUS GALEATUS (ROOTS) (Days After Planting)

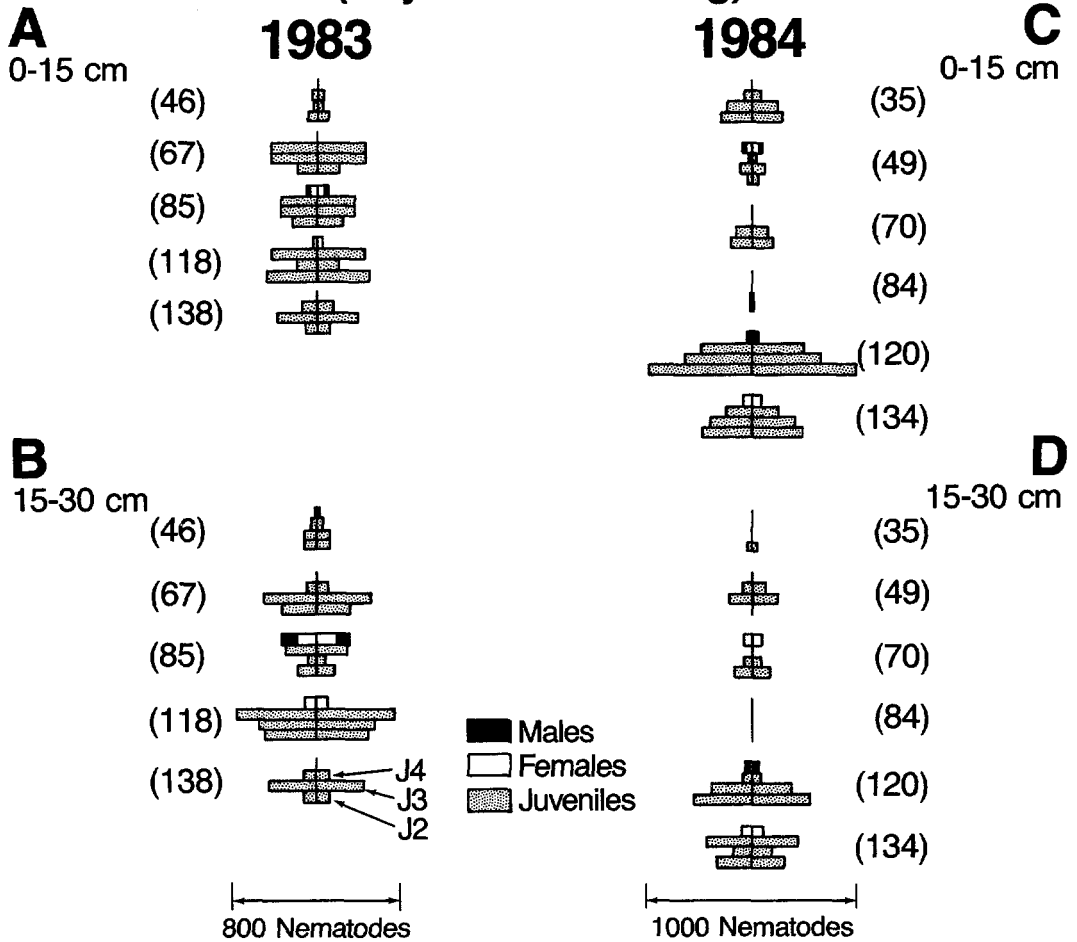


FIG. 5. Age structure (numbers) of *Hoplolaimus galeatus* in maize roots at two soil depths in 1983 and 1984, Butler County, Iowa.

wintering than by spring cultivation. A significant increase in *P. scribneri* juveniles and total *X. americanum* occurred between spring preplanting and planting at one or the other depths (Table 3).

Community diversity: Community diversity with the six plant-parasitic nematodes found was generally less when nematode biomass rather than number was used (Fig. 7). On the basis of noncorrected counts for extraction efficiency at all dates and at both levels, H' was greater with nematode num-

bers than with biomass in both years, except at the lower depth in September 1984 when the H' 's were the same on 120 DAP, and less with numbers than with biomass on 134 DAP (Fig. 7). Changes in the evenness index (J') generally followed changes in H' for both nematode numbers or biomass, whether corrected for 100% extraction efficiency or not as shown for biomass in 1983. H' and J' generally fluctuated more at the lower than at the upper depth in both years (Fig. 8).

PRATYLENCHUS SCRIBNERI (ROOTS)

(Days After Planting)

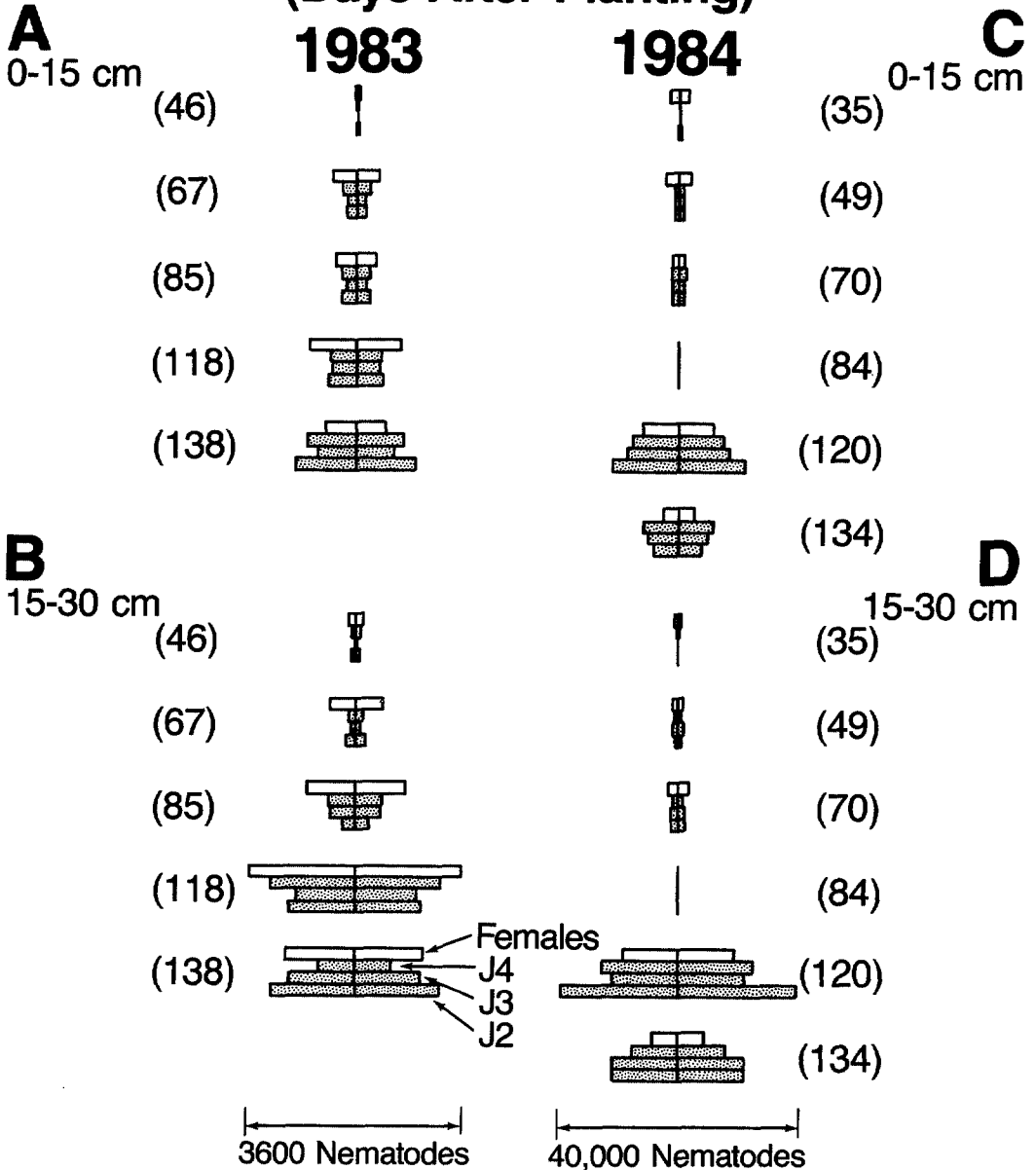


FIG. 6. Age structure (numbers) of *Pratylenchus scribneri* in maize roots at two soil depths in 1983 and 1984, Butler County, Iowa.

DISCUSSION

One value of descriptive population studies is to compare data with other reports so that, when enough comparisons

are made, one can tell whether a given pattern is exceptional or ordinary (4). Unfortunately, available data on nematodes are insufficient to make this judgment. Descriptive patterns are also important in

TABLE 3. Winter and spring survival of nematodes associated with maize in Butler County, Iowa, 1983-84.

	Fall 1983 to preplowing 1984†				Preplowing 1984 to postplowing 1984‡			
	0-15 cm		15-30 cm		0-15 cm		15-30 cm	
	a	b	a	b	a	b	a	b
<i>Hoplolaimus galeatus</i> , total	157	155	118	96	155	88	96	66
<i>H. galeatus</i> , female	40	38	35	31	38	22*	31	19
<i>H. galeatus</i> , juvenile	102	99	64	58	99	55**	58	41
<i>H. galeatus</i> , male	15	18	19	7	18	11	7	6
<i>Longidorus breviannulatus</i>	3.2	0.0**	5.4	1.2**	0.0	0.1	1.2	0.6
<i>Pratylenchus scribneri</i> , total	54	24**	63	15**	24	25	15	52*
<i>P. scribneri</i> , female	23	4**	22	3**	4	8	3	14
<i>P. scribneri</i> , juvenile	31	20	41	12*	20	17	12	38*
<i>Xiphinema americanum</i> , total	66	7**	24	5*	7	32*	5	8
<i>X. americanum</i> , female	24	1**	6	3	1	6	3	1
<i>X. americanum</i> , juvenile	42	6**	18	2**	6	26	2	7

* $P = 0.05$ of members of the second sampling compared with the first.

** $P = 0.01$ of members of the second sampling compared with the first.

† The a column is the number of nematodes 138 days after plowing in 1983; b column is the number of nematodes at 31 days before planting in 1984 and before spring cultivation.

‡ The a column is the number of nematodes at 31 days before planting in 1984; b column is the number at planting.

studying community classification and structure.

Certain results found here contrast with others. Malek et al. (8) found that populations of *L. breviannulatus* generally declined over the season. In this study, they frequently increased until 80-100 DAP. Some reports (3,10) indicate that *X. americanum* populations are greater at upper than lower depths, probably because the nematode is favored by greater oxygen concentrations (15) which would occur at the upper level. In this study, there was no significant seasonal difference in numbers of *X. americanum* at each depth, although, in general, numbers were greater at the upper depth except in late 1984. Whether this was because of migration or different rates of reproduction at different levels was not apparent. However, the increase in nematodes at the lower depth at 120 DAP in 1984 seems too great for much migration, considering the greater numbers at 84 DAP at the lower depth. Numbers of *P. scribneri* were generally greater at 15-30 than at 0-15 cm deep. This contrasts somewhat with Smolik and Evenson's (14) work with *P. hexincisus* on first year maize.

Sampling depths, soils, and other experimental conditions, however, were not identical in the two studies.

Stable age populations obviously did not exist in this study, although *L. breviannulatus* during 67-138 DAP at 15-30 cm deep in 1983 and some sequential samples of *H. galeatus* in the soil approached stability.

In this study, *H. galeatus* overwintered well but declined between the overwintering sampling and planting. If the decline of the nematode between the spring plowing and planting in 1984 resulted from the effects of plowing, then such treatments might be responsible for the erratic occurrence of this nematode compared with *P. scribneri* and *X. americanum*, which are generally more regular in occurrence. Another factor contributing to the nematode's erratic occurrence might be its dioecious nature because chance meetings of males and females are limited when numbers are few. Males and females of *H. galeatus* were few in the roots but common in the soil; thus, fertilization probably occurs mostly in the soil or while the nematodes are in the semiendoparasitic state. Based on populations of females, there is no evidence of discrete

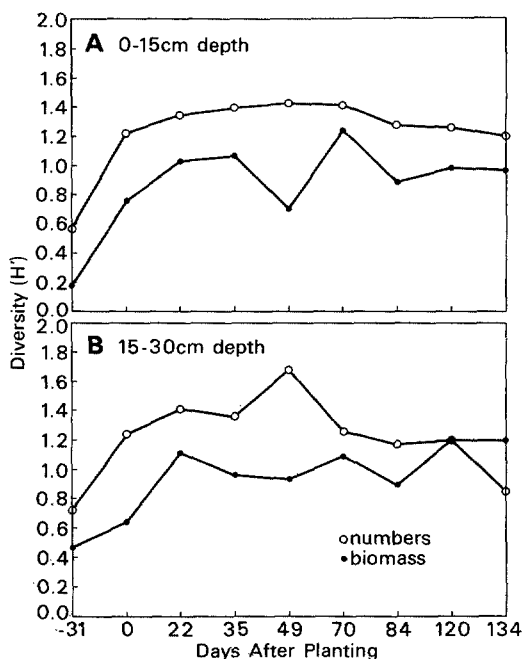


FIG. 7. Community diversity (H') of plant-parasitic nematode numbers and biomass around maize roots in 1984, Butler County, Iowa.

generations. The usually sharp decline of females in the roots after J4 indicates high mortality or migration to the soil.

Although the age pattern of *P. scribneri* at 67 DAP in 1983 would be classified as a declining population, the juveniles produced by the females at this date did not show up until later. Production of J2 increased and remained high as the season progressed and was greater at the lower than at the upper depth. The apparent declining population at 67 DAP probably was in its early stages of development.

Smaller community diversities result when nematode biomass rather than number is used because a few large nematodes, such as *H. galeatus* and *L. breviannulatus*, dominate community biomass, whereas when numbers are used, large nematodes generally constitute a small part of the community. This follows the corollary that large species contribute to a smaller diversity when compared with smaller species (5).

Although many scientists like to correct

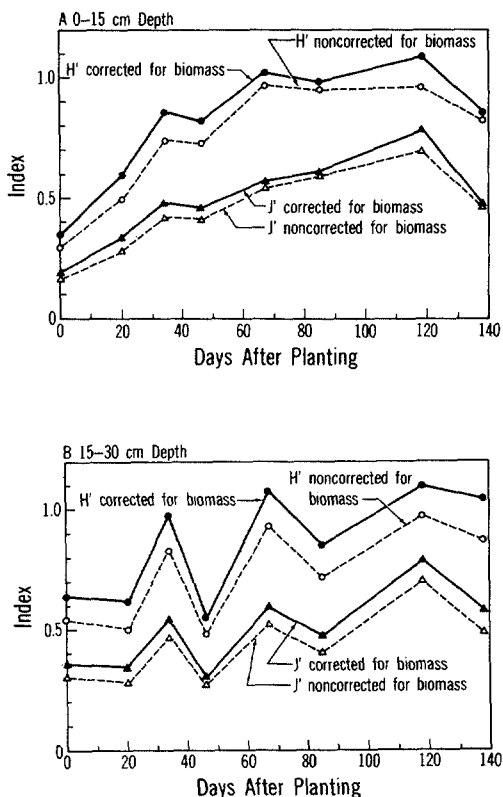


FIG. 8. Community diversity (H') and evenness (J') of plant-parasitic nematodes around maize roots in 1983, Butler County, Iowa.

to 100% recovery of nematodes, such a procedure made little difference concerning community analyses using H' and J' in this study.

When population changes are studied, inverse peaks between species are sometimes ascribed to competition between them. Competition with small animals in nature is difficult to prove, and such a phenomenon is often questioned (7,11). To have competition, there must be a shortage of substrate and a niche overlap (12). Although there were inverse nematode peaks in the present study, there was no evidence of a substrate shortage, and populations probably were not large enough to be affected by niche overlap. Although the maize field had a history of nematode damage, in no case were plants severely stunted to imply resource limitation. Nematicides were not applied to obtain different nema-

tode populations. The many tissues in a root system increase niche dimension allowing for several species to develop independently. Maize has an extensive root system, and unless severely pruned it can support a large nematode population. A clear distinction should be made between true competition and population changes resulting from natural cyclic patterns, periodic environmental changes, and morphological and physiological changes resulting from host-parasite interactions. Certainly there are situations where competition occurs (9). These are most apt to be where nematodes are confined such as in root-knot caused by *Meloidogyne* sp. (9). Based on the population studies reported here, there was no evidence of competition among the nematodes within this environment.

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