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Nematode community structure in rows and between rows of a soybean field

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Summary – Densities of nematode genera in six trophic groups were compared in rows and between rows of a soybean *(Glycine max)* crop in Florida, U.S.A., in 1992. Regardless of trophic group, densities of the most common genera were greater ($P \# 0.10$) in soybean rows than between rows during the latter half of the soybean crop. When a subsequent crop of rye *(Secale cereale)* was planted in broadcast fashion (i.e., no defined rows of rye), few differences were observed in nematode population densities in locations of the former soybean rows and former locations between rows. Various indices were used to compare nematode community structure in rows and between rows. Among the indices tested, evenness, richness, and Shannon-Weaver and Simpson indices were effective in distinguishing differences in nematode community structure during the second half of the soybean season. Results confirmed the importance of rhizosphere effects in stratification of nematodes of most trophic groups.

Résumé – ***Structure d'une communauté de nématodes dans les rangs et entre les rangs d'un champ de soja*** – En 1992, les densités de genres de nématodes appartenant à six groupes trophiques présents dans les rangs et entre les rangs d'un champ de soja de Floride ont été comparées. La densité des genres les plus communs était plus importante ($P \# 0.10$) dans les rangs de soja qu'entre les rangs pendant la deuxième période de la croissance du soja. Cependant, lorsque du seigle a été semé à la volée (sans rangs bien définis) après la culture de soja, peu de différences sont observées entre les densités de nématodes aux endroits correspondant aux rangs et entre les rangs de la culture de soja précédente. Plusieurs indices ont été utilisés pour comparer la structure de la communauté des nématodes dans les rangs et entre les rangs. Parmi ceux employés, l'indice de Shannon-Weaver, l'indice de Simpson, et des indices de richesse des genres et d'équitabilité, ont permis de déceler des différences de structure de la communauté de nématodes pendant la deuxième période de la croissance de la culture de soja. Les résultats obtenus confirment l'importance des effets de la rhizosphère sur la stratification des nématodes des grands groupes trophiques.

Key words : Community structure, diversity, ecology, nematodes.

Because the rhizosphere is a region of intense biological activity and a rich source of nutrients for soil organisms, population densities of most soil microflora and microfauna are usually greater there than in non-rhizosphere soil (Curl & Truelove, 1986; Lee & Pankhurst, 1992). In row-crop agriculture, this rhizosphere effect favors greater nematode densities in plant rows than between rows, a pattern which has been observed to some extent with plant-parasitic nematodes (Ferris & McKenry, 1976; Francl, 1986). Less information is available on the comparative distribution of other nematode trophic groups between and within plant rows. Presumably, these groups may be more abundant in plant rows because abundance of microbial food sources such as bacteria and fungi is greater in the rhizosphere (Lee & Pankhurst, 1992). However, accumulation of organic material between rows may result in abundant populations of microbivorous nematodes in this zone as well (Ferris & McKenry, 1976).

Recent ecological studies of soil nematode communities have focused on individual taxa and on indices of community structure (Wasilewska, 1991; Freckman & Ettema, 1993; McSorley, 1993; Neher & Campbell, 1994; Wasilewska, 1994; Yeates & Bird, 1994). Such indices may prove useful as indicators of agricultural management (Freckman & Ettema, 1993; Yeates & Bird, 1994) or ecosystem health (Neher & Campbell, 1994). Although relationships between crop performance and densities of single plant-parasitic nematode species are well-recognized (McSorley & Phillips, 1993), probably not enough is known at present to relate specific aspects of nematode community structure to the stability and productivity of an agroecosystem. The objectives of the present study were to compare nematode densities and community structure in plant rows of a field crop with those between rows, and to provide background data on nematode community structure in an agroecosystem subject to serious damage from plant-parasitic nematodes.

Materials and methods

Site description and crop maintenance

The experimental site was located in Alachua County, Florida, U.S.A., at approximately 29°40'N and 82°30'W. The soil was an Arredondo fine sand (91 % sand, 4.5 % silt, 4.5 % clay) with 1.8 % organic matter

and pH 5.7. The field was planted with soybean [*Glycine max* (L.) Merr.] in 1991 and with rye (*Secale cereale* L. cv. Wrens Abruzzi) during the winter of 1991-92. Rye was harvested and the field plowed in late March. The site was disked in April, and 42 kg P/ha was applied to the site in late May and incorporated by disking. The soybean cv. Cobb was planted 5 June 1992. Individual plots consisted of four rows, 9 m long and 76 cm apart, and plots were replicated six times. Crop management practices were as recommended for soybean production in the region (Bailey *et al.,* 1980).

The relatively unproductive soybeans were not harvested, but heights of three plants per plot were measured on 1 October and then all plants were mowed. Locations of the soybean rows were marked with permanent stakes at the end of the field so that locations of the former rows could be determined accurately in the future. The site was disked to a depth of 15 cm in mid-October, and seed of the rye cv. Wrens Abruzzi was broadcast at 50 kg/ha over the entire site on 6 November. Rye was harvested from the plots on 3 February 1993 and dry above-ground biomass determined from 1 m^2 from each plot.

Sampling and processing

Soil samples for nematode analysis were collected on 5 June, 14 July, 20 August, 1 October, 12 November, and 30 December 1992, and on 2 February 1993. An individual soil sample consisted of six soil cores, 2.5 cm in diameter and 0-20 cm deep. Separate samples were collected at two locations within each plot. The " in row " sample was collected by removing the six cores at 0.5-m intervals along a 3.0-m transect positioned directly over the second row (counting from north) of plants in each plot. The " between row " sample was collected by removing the six cores at 0.5-m intervals along a 3.0-m transect positioned parallel to and equidistant from the second and third rows (i.e., 38 cm from each row) of each plot. Samples were always collected from the middle 5.0-m segment of the 9.0-m-long plot. However, the location of the 3.0-m sampling transect within the 5.0-m segment varied slightly on each sampling date, to avoid previous sampling holes.

The cores comprising each sample were mixed and stored in plastic bags at 10 °C for 3-5 days prior to extraction. Nematodes were extracted from a 100-cm^3 soil subsample using a sieving and centrifugation procedure (Jenkins, 1964). All nematodes from the subsample were counted at 100 × on a Nikon inverted microscope, equipped such that individual specimens could be examined in place at 400 × to facilitate identification to genus level.

Analysis

The population density of each nematode genus (numbers/100 cm^3), the total number of genera (s), and the total number of nematodes (N) in each sample were determined. Nematode genera were assigned to one of six trophic groups (bacterivores, fungivores, plant parasites, predators, omnivores, plant associates) based on the classification system of Yeates *et al.* (1993). *Tylenchus sensu lato* and a few related genera were considered " plant associates ", although their food habits are unclear (Yeates *et al.,* 1993). The total number and percentage of nematodes in each trophic group were determined for each sample.

Several indices of nematode community structure or composition were calculated from data on density of the nematode genera. Margalef's (1958) index of taxon richness, as used by Yeates and Bird (1994), was calculated as :

$$\text{richness} = (s - 1)/\log_e N$$

The Shannon-Weaver (1949) diversity index was used to measure diversity among nematode genera :

$$\text{genus diversity} = H'_g = -\Sigma p_i \log_e p_i$$

where P_i is the proportion of the ith genus in the sample and the term $p_i \log_e p_i$ is summed over all genera. Evenness (Pielou, 1975) was determined from the diversity index as

$$\text{evenness} = J = H'_g/\text{maximum } H'_g = H'_g/\log_e s$$

Simpson's (1949) index was used to assess dominance across all nematode genera in the sample :

$$\text{genus dominance} = \lambda_g = \Sigma(p_i)^2$$

Diversity and dominance were also determined across trophic groups, rather than across individual genera, to obtain measures of trophic diversity (H'_t) and trophic dominance (λ_t). In these instances, p_i becomes the proportion of the ith trophic group in the total nematode community (Neher & Campbell, 1994).

The maturity index (Bongers, 1990) was calculated across all nematode genera except plant parasites :

$$\text{maturity index} = MI = \Sigma v_i p_i$$

where v_i is the *c-p* value of the ith genus, using *c-p* values from 1 to 5 as defined by Bongers (1990) to reflect a relative degree of colonization or persistence (abbreviated as *c-p*) of the genus. The plant parasite index (*PPI*) was determined in a similar manner for the plant-parasitic genera (Bongers, 1990). In addition, a modified maturity index (*SMI*) was determined across all nematode genera (including plant parasites), as was done by Wasilewska (1994) and by Yeates (1994). Note that *SMI* includes all nematodes, whereas *MI* includes only non-parasites and *PPI* includes only plant parasites. The ratio of bacterivores and fungivores to plant parasites [(B + F)/PP], introduced by Wasilewska (1994), and the ratio of fungivores to bacterivores (F/B), used by other authors (Freckman & Ettema, 1993; Yeates & Bird, 1994), were calculated for each sample. Since the trophic status of *Tylenchus* and related plant associates remains unclear (Yeates *et al.,* 1993), a modified *F/B* ratio in which these plant associates were included as fungivores was also determined.

Nematode densities and ecological indices in rows were compared with those between rows using analysis

of variance (Freed *et al.*, 1991). Density data for individual nematode genera were transformed by $log_{10}(x + 1)$ prior to analysis, but untransformed arithmetic means ± standard errors are presented.

Results

Crop performance

Soybean plants were severely damaged by plant-parasitic nematodes, and many showed root symptoms typical of damage (Christie, 1959) by *Belonolaimus longicaudatus* and *Paratrichodorus* spp. Soybean plants did not produce yield, and were not harvested. At the end of the season on 1 October, mean plant height per plot averaged only 42 cm, with a range of 0-72 cm over the six plots. Rye yield per plot averaged only 67 g dry wt/m^2, with a range of 23-138 g/m^2.

Nematode densities

A variety of nematode genera were present at this site, and density data on the more common genera are summarized (Tables 1-3). Some genera were represented only by occasional specimens, or occurred in very few samples. These are not shown in the tables but are included in the totals for their appropriate feeding habits. These rare genera included *Bunonema, Chronogaster, Isolaimium* (bacterivores); *Deladenus, Thada, Tylencholaimus* (fungivores); *Cobbonchus, Discolaimus, Iotonchus, Mylonchulus, Seinura, Sporonchulus, Tobrilus* (predators); *Actinolaimus,* unidentified diplogasterid, *Enchodelus, Mesodorylaimus* (omnivores); *Ecphyadophora, Psilenchus* (plant associates).

No differences ($P \# 0.10$) in nematode population densities in rows and between rows were observed in the initial samples, collected at the time of soybean planting (Table 1). However, differences in nematode densities in rows and between rows increased as the soybean growing season progressed (Tables 1, 2), with many genera becoming more abundant in the plant rows. Of the fourteen most common bacterivorous genera (Table 2), seven (50 %) had lower numbers ($P \# 0.10$) between rows than in rows on 20 August, and the same trend occurred with four of fourteen (29 %) genera in October. *Teratocephalus* showed the opposite trend and was consistently more common between rows than in rows during the latter half of the soybean crop. Among the plant parasites, *Belonolaimus, Meloidogyne,* and *Pratylenchus* were consistently more common ($P \# 0.10$) in soybean rows than between rows in August and October. The two most common fungivores *(Aphelenchoides, Aphelenchus)* and the two most common omnivores *(Aporcelaimellus, Eudorylaimus)* were more common in rows at the end of the soybean season. Thus the trend toward greater abundance in plant rows as the soybean season progressed was observed in most feeding groups.

Standard errors associated with the various means tended to decrease between rows in those instances when mean density was lower between rows than in rows (Table 2). However, in most of these instances, the ratio between the standard error and the mean was fairly similar in the row and between rows.

The rye crop was not stratified into rows and spaces between rows, but the locations of the former soybean rows were marked so that these could be sampled as before. Differences ($P \# 0.10$) between nematode densities in and between rows of the former soybean crop diminished in the subsequent rye crop (Table 3). In the rye crop, few consistent differences ($P \# 0.10$) were evident in densities of nematode genera in locations of the old soybean rows compared to locations between old soybean rows. The soybean cyst nematode, *Heterodera glycines,* showed the greatest tendency toward increased abundance in the sites of the old soybean rows.

Indices of community structure

Total numbers of nematodes per 100 cm^3 of soil ranged from 836 (= 1.67 million/m^2) to 2 919 (= 5.89 million/m^2), both occurring in the 20 August sampling (Table 4). On this date and on 1 October, total numbers in the soybean rows were greater ($P \# 0.05$) than numbers between rows. Despite these differences in nematode numbers, the percent composition of the various trophic groups within the community was not very different in rows and between rows. The nematode community consisted primarily of plant parasites and bacterivores, with these two groups accounting for 72.3-87.5 % of all nematodes in the soybean crop (Table 4) and 81.8-87.0 % of all nematodes recovered from the rye crop (Table 5). The number of genera recovered per sample increased by about three from the beginning to the end of the soybean crop, but was significantly lower ($P \# 0.05$) between rows than in rows on only one sampling date (Table 4). Richness was greater between rows on 20 August and 1 October because the total numbers of nematodes in rows were so much larger than the numbers between rows on those two dates (Table 4). Diversity calculated across genera, H'_g, tended to be greater between rows than within rows late in the soybean season (Table 4), because several of the most common genera (e.g. *Cervidellus, Rhabditis, Meloidogyne*) were much more abundant in rows than between rows at that time. Evenness, which is calculated from H'_g, followed a similar trend. Trophic diversity, H'_t, was low because of the great abundance of plant parasites and bacterivores relative to the other trophic groups, and was lower in rows than between rows at the end of the soybean crop. Genus dominance (1_g) and trophic dominance (1_t) showed opposite trends to H'_g and H'_t, respectively. The maturity indices *MI* and *SMI* did not show consistent patterns with sample location, however the plant parasite index *(PPI)* was greater between rows than in rows of the soybean crops (Table 4). Most plant parasites sampled here have *c-p* values of 3, but *Paratrichodorus* has a *c-p* value of 4. *Paratrichodorus* densities

Table 1. *Nematode density per 100 cm³ soil in rows and between rows of soybeans at planting and early season. Data are arithmetic means ± standard errors of nematode densities per 100 cm³ from six replications on each date;* c-p *values from Bongers (1990).*

Nematode genus	c-p value	5 June 1992		14 July 1992	
		In row	Between rows	In row	Between rows
BACTERIVORES					
Acrobeles	2	76.8 ± 21.1	122.0 ± 34.4	61.5 ± 23.5	45.2 ± 18.6
Acrobeloides	2	84.5 ± 19.1	38.3 ± 11.6	72.3 ± 19.1	58.2 ± 13.5
Alaimus	4	3.5 ± 1.2	8.3 ± 2.9	8.0 ± 1.8	5.8 ± 2.4
Cephalobus	2	2.3 ± 1.3	1.2 ± 0.3	13.7 ± 6.5	8.2 ± 2.4
Cervidellus	2	134.0 ± 22.4	182.3 ± 52.2	195.2 ± 35.9	115.3 ± 25.8 *
Chiloplacus	2	6.5 ± 5.1	2.0 ± 0.6	13.3 ± 7.5	6.8 ± 2.5
Eucephalobus	2	155.7 ± 16.0	155.2 ± 31.4	133.8 ± 30.4	104.7 ± 30.2
Panagrolaimus	1	0.5 ± 0.3	2.7 ± 0.8	3.2 ± 1.0	3.7 ± 1.8
Plectus	2	16.0 ± 11.1	7.2 ± 5.2	0.3 ± 0.2	1.5 ± 1.0
Prismatolaimus	3	4.5 ± 2.3	3.8 ± 2.9	14.8 ± 12.1	12.2 ± 9.5
Rhabditis s.l.	1	207.3 ± 45.2	179.5 ± 36.6	96.2 ± 19.3	94.3 ± 12.5
Teratocephalus	3	0	1.5 ± 1.1	0	0.7 ± 0.5
Wilsonema	2	4.2 ± 1.0	5.8 ± 2.9	3.0 ± 0.9	2.0 ± 0.7
Zeldia	2	14.2 ± 2.4	13.8 ± 1.8	40.2 ± 14.1	8.3 ± 3.4 *
Total bacterivores		710.0 ± 80.6	737.7 ± 125.8	655.5 ± 100.4	466.8 ± 81.7 *
PLANT PARASITES					
Belonolaimus	3	9.3 ± 6.2	12.2 ± 8.2	7.5 ± 4.8	1.2 ± 1.0 †
Criconemella	3	491.8 ± 481.5	83.3 ± 82.5	58.0 ± 46.3	220.3 ± 210.1 *
Helicotylenchus	3	0	22.7 ± 22.7	1.0 ± 0.8	1.3 ± 1.3
Heterodera	3	12.3 ± 10.9	60.7 ± 60.7	12.3 ± 11.0	6.2 ± 4.5
Meloidogyne	3	10.2 ± 5.5	2.0 ± 0.7	26.5 ± 13.9	3.5 ± 1.7
Paratrichodorus	4	129.2 ± 37.1	137.7 ± 35.6	76.0 ± 16.1	106.8 ± 20.7 †
Pratylenchus	3	10.0 ± 6.0	5.3 ± 3.0	4.3 ± 3.5	13.0 ± 8.9
Xiphinema	5	0.7 ± 0.3	0.2 ± 0.2	0.3 ± 0.3	0.5 ± 0.5
Total plant parasites		663.5 ± 516.0	324.0 ± 115.2	186.0 ± 57.5	352.8 ± 212.5
FUNGIVORES					
Aphelenchoides	2	176.5 ± 46.2	143.8 ± 22.2	74.7 ± 27.8	58.0 ± 19.8
Aphelenchus	2	8.7 ± 3.5	5.0 ± 2.2	12.8 ± 6.5	14.0 ± 7.7
Diphtherophora	3	6.2 ± 3.1	4.7 ± 2.0	4.7 ± 2.0	13.2 ± 5.4
Ditylenchus	2	2.2 ± 1.0	0.8 ± 0.5	5.8 ± 2.5	3.7 ± 1.0
Leptonchus	4	0	0	0	0.2 ± 0.2
Nothotylenchus	2	33.8 ± 6.6	44.7 ± 12.4	41.3 ± 19.8	15.0 ± 6.8
Total fungivores		234.7 ± 52.8	203.8 ± 34.3	141.5 ± 39.1	104.7 ± 28.0
PREDATORS					
Miconchus	4	4.3 ± 1.8	3.3 ± 2.0	2.7 ± 0.8	2.2 ± 0.7
Mononchus	4	6.0 ± 2.6	2.0 ± 1.1	3.8 ± 1.9	0.5 ± 0.3 †
Nygolaimus	5	0	0	0	0
Total predators		10.5 ± 3.6	6.2 ± 2.1	6.7 ± 1.9	2.8 ± 0.8 *
OMNIVORES					
Aporcelaimellus	5	38.0 ± 3.4	41.3 ± 3.0	46.2 ± 9.5	25.8 ± 5.8 **
Eudorylaimus	4	34.0 ± 6.1	25.3 ± 2.3	21.5 ± 5.4	7.2 ± 1.9 **
Total omnivores		72.8 ± 5.5	68.7 ± 5.0	68.3 ± 10.2	33.2 ± 6.7 **
PLANT ASSOCIATES					
Tylenchus s.l.	2	60.2 ± 14.2	70.7 ± 18.0	39.0 ± 16.4	33.0 ± 7.9
Total root associates		61.5 ± 13.8	70.7 ± 18.0	39.5 ± 16.2	33.2 ± 7.8

*, ** Nematode densities in row and between rows differ at $P \# 0.05$ and $P \# 0.01$, respectively.
† Nematode densities in row and between rows differ at $P \# 0.10$.

Table 2. *Nematode density per 100 cm³ soil in rows and between rows of soybeans at late season and harvest. Data are arithmetic means ± standard errors of nematode densities per 100 cm³ from six replications on each date.*

Nematode genus	20 August 1992		1 October 1992	
	In row	Between rows	In row	Between rows
BACTERIVORES				
Acrobeles	43.7 ± 11.5	6.0 ± 1.6 **	10.8 ± 5.4	6.3 ± 3.4
Acrobeloides	229.2 ± 61.1	61.5 ± 16.6 *	111.7 ± 52.9	56.0 ± 23.7
Alaimus	2.8 ± 1.2	8.5 ± 2.3 †	2.2 ± 1.0	2.3 ± 0.7
Cephalobus	17.8 ± 5.4	23.5 ± 7.2	142.7 ± 80.5	23.8 ± 6.5
Cervidellus	340.0 ± 47.9	119.3 ± 19.8 **	311.8 ± 99.6	82.7 ± 11.0 *
Chiloplacus	12.0 ± 3.2	11.8 ± 4.2	4.8 ± 2.3	4.8 ± 1.6
Eucephalobus	94.7 ± 12.0	78.0 ± 14.4 †	84.7 ± 10.4	66.5 ± 14.3
Panagrolaimus	3.7 ± 1.9	2.8 ± 1.5	52.0 ± 36.2	2.0 ± 1.1 †
Plectus	0.7 ± 0.3	0 †	0.2 ± 0.2	0.7 ± 0.5
Prismatolaimus	6.2 ± 3.6	2.8 ± 1.2	6.8 ± 4.1	4.5 ± 2.3
Rhabditis s.l.	125.0 ± 20.1	71.7 ± 17.6 †	245.7 ± 76.8	85.3 ± 24.4 *
Teratocephalus	0.2 ± 0.2	2.3 ± 1.1 *	0.3 ± 0.3	7.7 ± 6.5 *
Wilsonema	10.2 ± 3.2	3.0 ± 1.2 **	5.3 ± 2.6	5.8 ± 1.8
Zeldia	69.2 ± 52.1	3.7 ± 2.3	39.7 ± 15.8	3.3 ± 2.1 **
Total bacterivores	955.2 ± 114.5	395.0 ± 43.4 **	1019.2 ± 223.4	351.8 ± 55.2 **
PLANT PARASITES				
Belonolaimus	17.8 ± 9.6	5.2 ± 2.8 †	22.2 ± 9.2	3.3 ± 1.4 †
Criconemella	44.7 ± 37.1	40.0 ± 34.0	22.2 ± 18.9	35.7 ± 25.0
Helicotylenchus	0.3 ± 0.3	0	20.5 ± 20.5	2.5 ± 2.3
Heterodera	53.0 ± 44.2	15.0 ± 13.0	86.8 ± 59.3	22.0 ± 16.4
Meloidogyne	1186.2 ± 524.0	46.7 ± 14.0 †	593.2 ± 161.1	212.0 ± 111.0 *
Paratrichodorus	274.2 ± 124.4	131.5 ± 35.7	74.3 ± 8.5	68.2 ± 18.1
Pratylenchus	30.5 ± 18.2	4.2 ± 1.7 †	89.5 ± 56.3	10.7 ± 4.2 *
Xiphinema	0	0.2 ± 0.2	0.7 ± 0.7	0.5 ± 0.5
Total plant parasites	1606.7 ± 622.0	242.7 ± 65.6 *	909.3 ± 213.8	354.8 ± 142.8 *
FUNGIVORES				
Aphelenchoides	50.0 ± 10.0	21.0 ± 7.1 *	44.7 ± 19.6	9.8 ± 1.8 †
Aphelenchus	67.0 ± 12.2	21.8 ± 9.9 *	90.8 ± 29.9	25.8 ± 14.1 *
Diphtherophora	18.5 ± 5.0	20.0 ± 5.4	4.2 ± 1.1	8.5 ± 3.0
Ditylenchus	5.7 ± 2.1	7.0 ± 2.2	5.7 ± 1.7	6.7 ± 2.6
Leptonchus	0.3 ± 0.2	0.2 ± 0.2	0	0
Nothotylenchus	13.5 ± 6.8	5.0 ± 2.0 †	5.0 ± 1.4	3.5 ± 1.1
Total fungivores	159.0 ± 19.9	76.5 ± 17.2 **	155.8 ± 47.1	57.8 ± 14.2 **
PREDATORS				
Miconchus	1.7 ± 0.8	4.3 ± 3.0	0.7 ± 0.3	3.0 ± 1.4 †
Mononchus	2.0 ± 0.7	7.0 ± 3.8	2.5 ± 0.8	10.0 ± 3.8
Nygolaimus	0	0	10.0 ± 4.2	3.3 ± 1.4
Total predators	11.3 ± 1.9	12.2 ± 3.6	20.8 ± 5.1	17.8 ± 4.6
OMNIVORES				
Aporcelaimellus	53.0 ± 13.4	21.8 ± 1.4 *	37.5 ± 10.2	19.5 ± 4.6 †
Eudorylaimus	34.0 ± 12.6	13.5 ± 1.8	13.7 ± 5.0	3.3 ± 1.5 *
Total omnivores	87.5 ± 24.5	25.7 ± 1.5 †	52.7 ± 9.2	23.5 ± 4.9 *
PLANT ASSOCIATES				
Tylenchus s.l.	69.2 ± 18.8	65.0 ± 17.1	33.0 ± 7.6	78.2 ± 15.6
Total root associates	69.2 ± 18.8	65.2 ± 17.0	34.0 ± 7.5	78.7 ± 15.9

*, ** Nematode densities in row and between rows differ at $P \# 0.05$ and $P \# 0.01$, respectively.
† Nematode densities in row and between rows differ at $P \# 0.10$.

Table 3. *Nematode densities per 100 cm³ soil after planting, at midseason, and at harvest of rye crop in locations of rows and between rows of previous soybean crop. Data are arithmetic means ± standard errors of nematode densities per 100 cm³ from six replications on each date.*

Nematode genus	12 November 1992		30 December 1992		2 February 1993	
	In row	Between rows	In row	Between rows	In row	Between rows
BACTERIVORES						
Acrobeles	5.0 ± 1.1	3.7 ± 0.8	8.2 ± 2.8	5.2 ± 2.5 *	4.0 ± 0.6	6.3 ± 2.1
Acrobeloides	72.2 ± 14.3	80.8 ± 28.3	188.2 ± 69.4	300.7 ± 109.3	161.8 ± 37.5	209.2 ± 56.8
Alaimus	1.2 ± 0.5	3.2 ± 0.6 **	1.8 ± 0.9	2.3 ± 1.1	2.8 ± 0.6	2.3 ± 1.1
Cephalobus	22.0 ± 10.7	11.0 ± 3.4	15.8 ± 4.5	15.0 ± 3.2	21.2 ± 7.8	7.8 ± 1.6
Cervidellus	140.8 ± 37.0	112.8 ± 22.4	277.5 ± 70.0	252.3 ± 68.2	230.5 ± 50.6	200.2 ± 48.8
Chiloplacus	4.8 ± 2.0	5.0 ± 1.8	2.7 ± 1.1	1.5 ± 0.9	1.7 ± 0.7	2.0 ± 1.6
Eucephalobus	104.7 ± 24.6	119.3 ± 31.0	200.0 ± 35.2	144.7 ± 27.5	261.0 ± 58.2	257.3 ± 69.7
Panagrolaimus	9.7 ± 3.6	6.5 ± 1.9	67.3 ± 18.0	63.3 ± 22.6	38.2 ± 23.3	8.3 ± 3.2
Plectus	0.3 ± 0.3	0.5 ± 0.5	1.0 ± 0.8	0.5 ± 0.5	0.3 ± 0.3	0
Prismatolaimus	1.5 ± 1.1	2.3 ± 2.2	1.5 ± 1.0	0	8.0 ± 7.8	1.8 ± 0.8
Rhabditis s.l.	101.8 ± 23.0	174.7 ± 52.8	207.7 ± 43.9	202.7 ± 38.5	250.2 ± 44.7	226.7 ± 59.7
Teratocephalus	4.7 ± 3.5	6.0 ± 3.6 †	0.8 ± 0.5	6.2 ± 5.0	0.7 ± 0.3	9.0 ± 6.2
Wilsonema	3.2 ± 1.8	4.0 ± 2.6	5.3 ± 2.0	2.8 ± 0.9	5.0 ± 1.5	1.8 ± 0.6
Zeldia	6.7 ± 3.7	6.3 ± 2.1	30.2 ± 13.5	22.0 ± 10.9	34.5 ± 15.6	11.3 ± 5.7 †
Total bacterivores	479.2 ± 86.7	536.2 ± 131.5	1008.0 ± 180.0	1019.3 ± 187.3	1020.8 ± 141.4	944.2 ± 139.3
PLANT PARASITES						
Belonolaimus	11.0 ± 8.9	4.0 ± 2.5	14.7 ± 8.6	9.8 ± 3.7	12.2 ± 7.7	13.8 ± 5.6
Criconemella	161.0 ± 131.7	169.0 ± 149.1	123.5 ± 104.0	30.5 ± 22.2	32.8 ± 30.1	33.3 ± 30.0
Helicotylenchus	0.2 ± 0.2	8.5 ± 8.5	1.0 ± 1.0	4.5 ± 4.3	0.2 ± 0.2	9.3 ± 9.1
Heterodera	28.2 ± 18.3	13.8 ± 9.1 †	34.3 ± 19.9	6.2 ± 4.2 *	8.2 ± 6.4	10.2 ± 10.0
Meloidogyne	398.7 ± 136.5	529.3 ± 114.1	352.7 ± 157.8	425.5 ± 174.9	228.8 ± 72.0	321.0 ± 92.7
Paratrichodorus	103.8 ± 28.7	87.2 ± 18.8	99.5 ± 14.2	108.7 ± 19.9	160.0 ± 17.0	150.8 ± 48.6
Pratylenchus	208.3 ± 170.8	263.0 ± 237.2	114.3 ± 79.3	88.0 ± 79.1	129.8 ± 111.9	52.7 ± 44.8
Xiphinema	1.5 ± 1.0	0.2 ± 0.2	3.2 ± 2.4	0.3 ± 0.2	0.3 ± 0.2	0.2 ± 0.2
Total plant parasites	912.7 ± 209.0	1075.0 ± 307.8	743.2 ± 104.1	673.5 ± 151.5	572.3 ± 98.1	591.3 ± 74.9
FUNGIVORES						
Aphelenchoides	29.2 ± 8.8	30.0 ± 9.9	126.5 ± 51.8	114.5 ± 29.7	64.8 ± 14.6	156.2 ± 56.4
Aphelenchus	36.7 ± 13.0	47.0 ± 8.1 †	29.8 ± 9.4	67.2 ± 17.4 *	41.2 ± 18.1	55.8 ± 11.1
Diphtherophora	7.7 ± 2.9	16.8 ± 6.0	8.8 ± 2.8	9.2 ± 3.5	19.0 ± 4.0	28.3 ± 6.7
Ditylenchus	10.2 ± 3.5	6.7 ± 3.0	12.8 ± 8.2	10.8 ± 3.1	12.7 ± 3.2	6.3 ± 2.9
Leptonchus	1.2 ± 1.0	0.8 ± 0.8	0	0	0.5 ± 0.5	4.0 ± 3.8
Nothotylenchus	8.8 ± 2.4	5.7 ± 1.9	27.2 ± 18.0	4.3 ± 1.6 *	11.7 ± 3.9	9.8 ± 4.2
Total fungivores	97.0 ± 16.4	110.0 ± 25.4	209.3 ± 80.5	209.5 ± 51.0	152.2 ± 31.7	263.0 ± 76.7
PREDATORS						
Miconchus	0.5 ± 0.3	1.2 ± 0.6	0.5 ± 0.5	0.7 ± 0.5	0.3 ± 0.3	0.5 ± 0.3
Mononchus	0.8 ± 0.3	1.0 ± 0.4	3.5 ± 1.9	8.3 ± 4.3	3.0 ± 1.8	5.2 ± 2.2
Nygolaimus	16.5 ± 4.8	15.2 ± 2.7	16.3 ± 5.0	14.3 ± 3.6	16.7 ± 5.1	12.8 ± 2.8
Total predators	18.7 ± 5.3	19.2 ± 2.7	22.7 ± 4.9	26.5 ± 6.5	22.7 ± 3.4	19.5 ± 3.4 †
OMNIVORES						
Aporcelaimellus	18.0 ± 3.8	20.3 ± 8.6	11.0 ± 4.1	7.3 ± 3.6	15.0 ± 3.2	3.8 ± 0.7 *
Eudorylaimus	10.7 ± 3.7	8.0 ± 4.2	21.8 ± 15.0	6.7 ± 3.5	13.5 ± 6.7	10.5 ± 4.9
Total omnivores	30.2 ± 4.9	30.8 ± 8.6	32.8 ± 18.6	15.2 ± 5.6	32.8 ± 7.4	20.3 ± 6.1 *
PLANT ASSOCIATES						
Tylenchus s.l.	40.3 ± 6.9	75.5 ± 28.1	47.8 ± 8.8	55.7 ± 12.6	56.2 ± 21.7	52.5 ± 12.3
Total root associates	42.7 ± 5.7	78.0 ± 29.6	48.3 ± 9.1	58.8 ± 14.7	56.2 ± 21.7	52.7 ± 12.3

*, ** Nematode densities in previous soybean row locations and between previous rows differ at $P \# 0.05$ and $P \# 0.01$, respectively.
† Nematode densities in previous soybean row locations and between previous rows differ at $P \# 0.10$.

Table 4. *Indices of nematode community composition in rows and between rows of soybeans at planting, during season, and at harvest. Data are means from six replications on each sampling date (See text for definitions of indices).*

Index measured	5 June 1992		14 July 1992		20 August 1992		1 October 1992	
	In row	Between rows	In row	Between rows	In row	Between rows	In row	Between rows
Total nematodes (per 100 cm^3)	1776	1423	1118	1004	2919	836 *	2205	894 **
% bacterivores	49.6	51.2	58.3	52.7	40.9	47.6	44.9	43.2
% plant parasites	22.9	21.1	17.5	26.9	42.4	28.5	42.6	32.0
% fungivores	16.2	14.6	11.9	11.7	8.0	9.3	6.5	6.8
% predators	0.9	0.5	0.7	0.3 †	0.4	1.6	1.0	2.2 *
% omnivores	5.2	5.3	6.4	3.5 *	3.0	4.5 *	2.6	2.9
% plant associates	3.6	5.3	3.1	3.6	3.7	7.7	1.9	11.0 *
Number of genera	26.5	27.5	26.5	26.3	29.5	27.3 *	30.5	29.3
Richness	3.48	3.63	3.67	3.73	3.66	3.92 †	3.87	4.25 †
H'_g	2.28	2.37	2.52	2.31	2.13	2.52 *	2.25	2.45
J'	0.70	0.72	0.77	0.71	0.63	0.76 *	0.66	0.73 †
λ_g	0.17	0.12	0.10	0.17	0.22	0.11 †	0.17	0.13
H'_t	1.11	1.22	1.13	1.07	1.01	1.26 †	1.05	1.23 †
λ_t	0.43	0.36	0.41	0.44	0.46	0.36 †	0.44	0.36 †
MI	2.00	2.00	2.11	2.05 †	2.07	2.14	1.97	2.04
PPI	3.58	3.68	3.49	3.64 *	3.23	3.54 *	3.11	3.32 *
SMI	2.30	2.33	2.34	2.40	2.52	2.54	2.43	2.43
(B + F)/PP	8.80	5.32	6.06	4.13 †	3.44	3.14	1.55	2.43
F/B	0.32	0.28	0.20	0.21	0.18	0.19	0.15	0.16
Modified *F/B*	0.41	0.39	0.26	0.28	0.27	0.36	0.20	0.42 **

*, ** Indices measured in rows and between rows differ at $P \# 0.05$ and $P \# 0.01$, respectively.
† Indices measured in rows and between rows differ at $P \# 0.10$.

were similar in rows and between rows, but the greater abundance of genera such as *Meloidogyne* (*c-p* value = 3) in rows resulted in a lower value of *PPI* there. The ratio of fungivores and bacterivores to plant parasites and the F/B ratio both declined from the beginning to the end of the soybean crop. In the rye crop, few differences in indices of community structure were observed when comparing locations in rows and between rows of the previous soybean crop (Table 5).

Discussion

During growth of a soybean crop, nematode distribution became stratified along plant rows, so that many different genera were more abundant in the plant row than between rows. Among the plant parasites, this effect was most evident with the endoparasites *Meloidogyne* and *Pratylenchus* and with *Belonolaimus,* an ectoparasite which is often found in particularly close association with the root hairs (Kaplan, 1985; McSorley & Dickson, 1989). The intense biological activity and availability of organic material within the rhizosphere supports an abundance of decomposer bacteria and fungi (Curl & Truelove, 1986), which in turn support local abundance of nematode fungivores and bacterivores (Freckman, 1988) which feed on these microorganisms. In our study, the trend toward greater abundance in plant rows than between rows was actually more frequent among those nematodes which do not feed directly on the root system than among the plant parasites. On 20 August (Table 2), five of the six most common bacterivores, the two most common fungivores, and the most common omnivore were all significantly more abundant in the plant rows than between rows. Two of the less common bacterivores *(Alaimus, Teratocephalus)* were exceptions to this trend and both have higher *c-p* values than most other bacterivores (Bongers, 1990). It was not possible to know whether they did not compete well with the more common genera in the rows, or if their food source was different.

From a practical standpoint, the fact that most genera in most trophic groups are more abundant in rows suggests that the plant row is the preferred sampling site for population estimation. However, a reliable sampling plan must consider the variance among samples as well as the mean. Could sampling error be greater in the rows, with their possible patches of high and low root

Table 5. *Indices of nematode community composition after planting, at midseason, and at harvest of a rye crop in locations of rows and between rows of previous soybean crop. Data are means from six replications on each sampling date (See text for definitions of indices).*

Index measured	12 November 1992		30 December 1992		2 February 1993	
	In row	Between rows	In row	Between rows	In row	Between rows
Total nematodes (per 100 cm^3)	1586	1857	2077	2015	1869	1900
% bacterivores	33.3	31.0	47.2	50.7	53.8	49.4
% plant parasites	53.7	54.4	38.3	34.0	31.3	32.4
% fungivores	6.6	6.8	8.9	10.0	8.5	12.8
% predators	1.1	1.2	1.2	1.3	1.2	1.0
% omnivores	1.9	1.9	1.5	0.7	1.7	1.1 *
% plant associates	3.0	4.3	2.3	2.7	2.8	2.8
Number of genera	29.0	30.0	28.5	28.0	31.2	29.3
Richness	3.82	3.90	3.61	3.58	4.03	3.77
H_g^{**}	2.15	2.10	2.28	2.24	2.37	2.31
J	0.64	0.62	0.68	0.67	0.69	0.68
λ_g	0.21	0.22	0.17	0.18	0.13	0.14
H_t^{**}	1.02	1.03	1.07	1.07	1.08	1.15
λ_t	0.47	0.47	0.42	0.42	0.42	0.38
MI	2.08	2.02	1.90	1.86	1.90	1.92
PPI	3.16	3.14	3.15	3.22	3.35	3.28
SMI	2.62	2.60	2.37	2.30	2.34	2.36
(B + F)/PP	1.01	1.06	1.97	2.39	2.64	2.04
F/B	0.21	0.21	0.18	0.20	0.15	0.27 †
Modified *F/B*	0.34	0.34	0.23	0.25	0.21	0.32

* Indices measured in previous soybean row locations and between previous rows differ at $P \# 0.05$.
** Indices measured in previous soybean row locations and between previous rows differ at $P \# 0.10$.

density, than in the areas between rows, which may be more uniform? Our data suggest that when density in the row is greater than density between rows, the standard error in the row was larger as well. However, the ratio of the standard error to the mean remained nearly constant. Since the ratio of the standard error to the mean is an important and often-used measure of sampling precision (McSorley, 1987), the precision of the estimate should be similar whether a sample is collected in the rows or between the rows. However, the sample in the rows offers the better chance to detect the range of nematode genera, since means are generally greater.

Differences in nematode densities in rows and between rows vanished quickly in the next crop (rye) when distinct rows were not maintained. With the exception of *H. glycines,* there was almost no evidence that peaks in nematode density persisted in the former row sites. The disruptive effects of cultivation on nematode communities are recognized by many authors (Wasilewska, 1979; Freckman & Ettema, 1993; Neher & Campbell, 1994) who concluded that perennial crops were more suitable than annual crops for monitoring changes in nematode community structure.

There is much recent interest in using indices of nematode community structure as indicators of biodiversity, ecosystem disturbance, and agricultural productivity and sustainability (Ettema & Bongers, 1993; Freckman & Ettema, 1993; Neher & Campbell, 1994; Wasilewska, 1994; Yeates & Bird, 1994). Yet, while differences in indicators may be apparent in response to many factors, a fundamental problem is to define a " productive " or " sustainable " agroecosystem. The present study may be useful as a reference point in providing background data on nematode community structure in an extremely undesirable agroecosystem. At the time of planting, densities of four plant-parasitic nematodes (*B. longicaudatus, H. glycines, M. incognita, P. minor)* exceeded the damage thresholds for soybean in the southeastern United States (Rickard & Barker, 1982), and density of one of these *(P. minor)* was over ten times the threshold density. Damage to soybean was severe, and no marketable yield was obtained. As a result, soybean production was abandoned in this site in 1993.

Ferris and Ferris (1974) observed that, in an unproductive soybean field with very poor growth, 96 % of the nematode community consisted of Tylenchida (primar-

ily plant parasites). The present site contained only 21-23 % plant parasites at the time of planting, increasing to 43 % in the rows by the end of the soybean season. These proportions do not seem unusual compared to other agricultural and natural sites (Ferris & Ferris, 1974; McSorley, 1993; Yeates & Bird, 1994). The percentage of bacterivores and plant parasites together appear high in the soybean (72-88 %) and rye (82-87 %) crops. Comparable proportions from a forest site in the same county ranged from 56 to 68 % (McSorley, 1993). However, bacterivore plus plant parasite levels of 70-80 % may not be unusual in nematode communities. Levels approached 70 % at several productive agricultural sites in Michigan (Freckman & Ettema, 1993), exceeded 70 % at several locations in South Australia (Yeates & Bird, 1994), and approached 80 % in pastures in Florida and Honduras (Powers & McSorley, 1994).

Numbers of genera recovered in our site are comparable to those of other, more productive locations (Freckman & Ettema, 1993), as are total numbers of nematodes (Yeates & Bird, 1994). Means in taxon richness in our soybean and rye plots ranged from 3.48-4.25, within the ranges of 2.60-4.69 and 1.49-5.02 observed for this index in New Zealand (Yeates, 1984) and Australia (Yeates & Bird, 1994), respectively.

Values of the Shannon-Weaver diversity index *(H'_g)* obtained in the soybean and rye crops here (range in mean values : 2.10-2.52) were comparable to the mean values of 2.10 and 2.15 obtained by Freckman and Ettema (1993) from annual and perennial systems, respectively. Our values were within the range of 1.25-2.97 obtained across several sites in Australia (Yeates & Bird, 1994), but less than those (3.0-4.4) obtained by Wasilewska (1994) from pastures, although she used log_2 rather than log_e, and her pasture sites contained more genera than our fields. Evenness *(J')* is used to facilitate comparison of H'_g values from samples with different numbers of genera. The range in J' obtained here (0.62-0.77) was within the range of 0.51-0.94 obtained across locations in South Australia (Yeates & Bird, 1994). Trophic diversity, H'_t, was considerably lower in the present study (range in mean values 1.01-1.26) than in agricultural sites in North Carolina (Neher & Campbell, 1994), but H'_t values are not available from many studies for comparaison. Simpson's index, λ_g, is a measure of dominance by the more common taxa, and its reciprocal, $1/\lambda_g$, can be used as a diversity index, referred to as the Simpson diversity index by Freckman and Ettema (1993). Values of 6.54-6.73 obtained for $1/\lambda_g$ by Freckman and Ettema (1993) give a λ_g value of 0.15, which is within the range (0.10-0.22) of mean λ_g values obtained here or the range (0.09-0.36) obtained by Yeates and Bird (1994). Trophic diversity as used by other authors (Freckman & Ettema, 1993; Yeates & Bird, 1994) is the same as $1/\lambda_t$. Values of trophic diversity of 2.94 and 3.14 (Freckman & Ettema, 1993) correspond to λ_t of 0.34 and 0.32, and the range in trophic diversity values of 2.18-3.83 (Yeates & Bird, 1994) corresponds to a range in λ_t of 0.26-0.46. Thus λ_t values from both studies do not differ much from our range in mean values of 0.36-0.47.

As originally defined, the maturity index *(MI)* did not include plant parasites (Bongers, 1990), but recent authors (Wasilewska, 1994; Yeates, 1994) have included them in the maturity index calculation, designated as *SMI* using the terminology of Yeates (1994). Since many nematode communities contain substantial numbers of bacterivores with *c-p* values of 1-2, and since most common plant parasites tend to have a *c-p* value of 3 (Table 1; Yeates & Bird, 1994), *SMI* will almost always be slightly larger than *MI*. Our range in mean values of *MI* (1.86-2.11) is comparable to the 1.67-2.69 range for sites in South Australia (Yeates & Bird, 1994). Our range for *SMI* (2.30-2.62) is comparable to that for meadows more than 4 years old in Poland (Wasilewska, 1994) and that of sites in South Australia (Yeates & Bird, 1994). The plant-parasite index *(PPI)* tends to converge to a value of 3, and in our system is simply an indicator of abundance of *Paratrichodorus* (*c-p* = 4) relative to the other plant parasites. This result suggests that the *PPI* may be of limited use, and probably should be re-examined and refined. The Trichodoridae were originally assigned a *c-p* value of 4 (on a 1-5 scale), which is typical for many Dorylaimida (Bongers, 1990). However, the ability of *P. minor* to quickly recolonize fumigated soil is well known (Perry, 1953; Weingartner *et al.*, 1983); this is a characteristic of a colonizer, for which a low *c-p* value is more realistic.

Yeates and Bird (1994) found that values of the *F/B* ratio varied widely (0.13-4.19) with environment and soil type. Our range in mean values was narrow (0.15-0.32) and slightly above values reported by Neher and Campbell (1994) but slightly below values reported by Freckman and Ettema (1993). Wasilewska's (1994) ratio of *(B + F)/PP* showed a rapid decrease in our soybean field as the plants aged and plant parasites became more abundant. Our range in mean values of 1.01-8.80 is comparable to the range (0.8-8.7) of values obtained by Wasilewska (1994) for meadow communities.

These comparisons of our values obtained for various indices of community structure with values obtained by other authors revealed no obvious discrepancies. Of course, ranges in means of index values are not the best nor most precise measure for making such comparisons. Each mean value (Tables 4, 5) was itself derived from six plots, among which variability in measured values occurred. When variability in densities of certain common nematodes was high (e.g., *Criconemella* in the soybean field on 5 June), the magnitudes and ranges of derived indices were affected as well. More reliable comparisons should be made from experiments in which the many sources of variation (season, climate, soils, etc.) are controlled, since these may affect ranges. However, based on our comparisons, we cannot suggest that any

of these indices had unusual values in the extremely poor agricultural site examined here. A better indicator of crop productivity may be the density of key genera or species of plant parasites, such as *P. minor*. Our observations suggest that nematode community structure in a nematode-damaged crop may not be much different from that in other crops and habitats. Additional studies are necessary to support or confirm these observations and to determine which indices of nematode community structure may be the best indicators of agricultural productivity or disturbance.

It is difficult to generalize the performance of indices of community structure across a wide range of geographical locations and environmental conditions (Yeates & Bird, 1994). However, many of these indices have been useful in distinguishing differences in community structure on a local level (Ettema & Bongers, 1993; Freckman & Ettema, 1994; Neher & Campbell, 1994; Wasilewska, 1994; Yeates & Bird, 1994). Among several indices examined, richness, H', J, and 1 were the most descriptive of the degree of disturbance to several sites in South Australia (Yeates & Bird, 1994). For our purposes, richness and those indices derived from the Shannon-Weaver or Simpson indices (H'_g, H'_t, J, 1_g, 1_t) were the most effective in distinguishing differences in rows *vs* between rows.

Conclusions

At a field location in Florida, U.S.A., densities of common nematode genera in most trophic groups became greater in rows than between rows of a soybean crop as the season progressed. For most nematode genera, the ratio of the standard error to the mean from samples collected between rows and those collected in rows were similar, indicating that sample precision was similar in both locations and suggesting that row locations were preferable for sampling due to higher densities. Of several indices of nematode community structure, richness, evenness, and the Shannon-Weaver and Simpson indices were effective in distinguishing differences in community structure in rows and between rows. Stratification of nematodes along plant rows disappeared quickly if rows were not maintained, as observed in a subsequent crop of rye, which was sown in broadcast fashion.

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References

Bailey, B. A., Whitty, E. B., Teem, D. H., Johnson, F. A., Dunn, R. A., Kucharek, T. A., & Cromwell, B. P. (1980). *Soybean production guide.* Circ. C77E. Inst. Food & agric. Sci., Univ. Florida, Gainesville.

Bongers, T. (1990). The maturity index : an ecological measure of environmental disturbance based on nematode species composition. *Oecologia,* 83 : 14-19.

Christie, J. R. (1959). *Plant nematodes, their bionomics and control.* Agric. Exp. Statns, Univ. Florida, Gainesville, 256 p.

Curl, E. A., & Truelove, B. (1986). *The rhizosphere.* Berlin, Springer-Verlag, 288 p.

Ettema, C. H., & Bongers, T. (1993). Characterization of nematode colonization and succession in disturbed soil using the maturity index. *Biol. & Fertility Soils,* 16 : 79-85.

Ferris, H., & McKenry, M. V. (1976). Nematode community structure in a vineyard soil. *J. Nematol.,* 8 : 131-137.

Ferris, V. R., & Ferris, J. M. (1974). Interrelationships between nematode and plant communities in agricultural ecosystems. *Agro-Ecosyst.,* 1 : 275-299.

Francl, L. J. (1986). Spatial analysis of *Heterodera glycines* populations in field plots. *J. Nematol.,* 18 : 183-189.

Freckman, D. W. (1988). Bacterivorous nematodes and organic-matter decomposition. *Agric., Ecosyst. & Envir.,* 24 : 195-217.

Freckman, D. W., & Ettema, C. H. (1993). Assessing nematode communities in agroecosystems of varying human intervention. *Agric., Ecosyst. & Envir.,* 45 : 239-261.

Freed, R., Eisensmith, S. P., Goetz, S., Reicosky, D., Smail, V. W., & Wolberg, P. (1991). *User's guide to MSTAT-C.* East Lansing, Michigan St. Univ.

Jenkins, W. R. (1964). A rapid centrifugal-flotation technique for separating nematodes from soil. *Pl. Dis. Reptr,* 48 : 692.

Kaplan, D. T. (1985). Influence of the sting nematode, *Belonolaimus longicaudatus,* on young citrus trees. *J. Nematol.,* 17 : 408-414.

Lee, K. E., & Pankhurst, C. E. (1992). Soil organisms and sustainable productivity. Australian. *J. Soil Res.,* 30 : 855-892.

Margalef, R. (1958). Information theory in ecology. *Gen. Syst.,* 3 : 36-71.

McSorley, R. (1987). Extraction of nematodes and sampling methods. *In :* Brown, R. H., & Kerry, B. R. (Eds). *Principles and practice of nematode control in crops.* Sydney, Academic Press : 13-47.

McSorley, R. (1993). Short-term effects of fire on the nematode community in a pine forest. *Pedobiologia,* 37 : 39-48.

McSorley, R., & Dickson, D. W. (1989). Effects and dynamics of a nematode community on maize. *J. Nematol.,* 21 : 462-471.

McSorley, R., & Phillips, M. S. (1993). Modelling population dynamics and yield losses and their use in nematode management. *In :* Evans, K., Trudgill, D. L., & Webster, J. M. (Eds). *Plant parasitic nematodes in temperate agriculture.* Wallingford, UK, CAB International : 61-85.

Neher, D. A., & Campbell, C. L. (1994). Nematode communities and microbial biomass in soils with annual and perennial crops. *Appl. Soil Ecol.,* 1 : 17-28.

PERRY, V. G. (1953). Return of nematodes following fumigation of Florida soils. *Proc. Florida St. hortic. Soc.,* 66 : 112-114.

PIELOU, E. C. (1975). *Ecological diversity.* New York, John Wiley, 165 p.

POWERS, L. E., & MCSORLEY, R. (1994). Soil nematode community structure in two tropical pastures. *Nematropica,* 24 : 133-142.

RICKARD, D. A., & BARKER, K. R. (1982). Nematode assays and advisory services. *In :* Riggs, R. D. (Ed.). *Nematology in the southern region of the United States.* South. *coop.* Ser. Bull. 276, Fayetteville, Arkansas agric. Exp. Statn : 8-20.

SHANNON, C. E., & WEAVER, W. (1949). *The mathematical theory of communication.* Urbana, Univ. Illinois, 117 p.

SIMPSON, E. H. (1949). Measurement of diversity. *Nature,* 163 : 688.

WASILEWSKA, L. (1979). The structure and function of soil nematode communities in natural ecosystems and agrocenoses. *Polish ecol. Studies,* 5 : 97-145.

WASILEWSKA, L. (1991). Long term changes in communities of soil nematodes in fen peat meadows due to the time since their drainage. *Ekol. polska,* 39 : 59-104.

WASILEWSKA, L. (1994). The effect of age of meadows on succession and diversity in soil nematode communities. *Pedobiologia,* 38 : 1-11.

WEINGARTNER, D. P., SHUMAKER, J. R., & SMART, G. C. Jr. (1983). Why soil fumigation fails to control potato corky ringspot disease in Florida. *Pl. Dis.,* 67 : 130-134.

YEATES, G. W. (1984). Variation in soil nematode diversity under pasture with soil and year. *Soil Biol. & Biochem.,* 16 : 95-102.

YEATES, G. W. (1994). Modification and qualification of the nematode maturity index. *Pedobiologia,* 38 : 97-101.

YEATES, G. W., & BIRD, A. F. (1994). Some observations on the influence of agricultural practices on the nematode faunae of some South Australian soils. *Fundam. appl. Nematol.,* 17 : 133-145.

YEATES, G. W., BONGERS, T., DE GOEDE, R. G. M., FRECKMAN, D. W., & GEORGIEVA, S. S. (1993). Feeding habits in soil nematode families and genera - an outline for soil ecologists. *J. Nematol.,* 25 : 315-331.