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Nematode communities and microbial biomass in soils with annual and perennial crops

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Abstract

Soils from medium- (alfalfa) or long-term (tall-fescue pasture) perennial cropping systems, which represent systems with relatively little disturbance, were collected across the three geographic regions of North Carolina and evaluated as potential reference sites for monitoring the ecological condition of soils for annual crops (e.g. soybeans). Maturity (based on life history characteristics) and trophic diversity indices of soil nematode communities were quantified for all soils to determine the successional status and relative abundance of trophic groups, respectively, in agricultural soils. The distribution and range of maturity index values for plant-feeding nematodes were greater for perennial than annual crops. The relative distribution of nematode trophic groups (bacterial-feeders, fungal-feeders, plant-feeders, omnivores, and predators) was similar among annual and perennial cropping systems. The ratios of fungal-feeding to bacterial-feeding nematodes were greater in perennial than annual cropping systems indicating that the decomposition pathway was dominated more by fungi and fungal-feeding nematodes in alfalfa and pastures than soybean cropping systems. Ratios of total fungal- to total bacterial-biomass were greater for pasture and soybean than for alfalfa cropping systems and, therefore, did not clearly differentiate perennial and annual crops. Based on the maturity index for plant-feeding nematodes, and the ratio of fungal-feeding to bacterial-feeding nematodes, fields with alfalfa or in pasture may be suitable for use as reference sites in monitoring the ecological condition of soil associated with annual crops for the Agroecosystem component of the Environmental Monitoring and Assessment Program (EMAP), a national monitoring program initiated and sponsored by the U.S. Environmental Protection Agency.

Key words: Biomonitoring; EMAP; Fungal-to-bacterial biomass ratios; Maturity index; Trophic diversity

1. Introduction

The Agroecosystem component of the Environmental Monitoring and Assessment Program (EMAP), initiated by U.S. EPA (Kutz and Linthurst, 1990; Messer et al., 1991), is being developed as an interagency monitoring and assessment program to estimate the current status, trends, and changes in selected indicators of the condition of the Nation's agroecological resources on a regional basis with known statistical confidence. A primary question to be answered by this monitoring and assessment effort is: What proportion of agroecosystems in the United States are ecologically sustainable? The development and evaluation of a suite of indicators to

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assess the condition of the fundamental components of agroecosystems is critical to answering this question. Indicators may be biological or abiotic characteristics of the condition of a resource at the organism, population, community or ecosystem level of organization (Heck et al., 1993).

Soil is a critical component in the structure and function of agroecosystems and the condition of soil biological communities is important to both the structure and function of soils. An indicator of soil ecological condition would be helpful to measure the current status of vital ecological processes in soil and changes in function through time. For a monitoring effort such as the Agroecosystem component of EMAP, a biological indicator of soil condition must meet several criteria. The indicator should: (1) reflect the structure and/or function of ecological processes in soils no matter what soil series or geographic location is sampled; (2) be responsive to changes in soil condition; (3) be measurable with only one or two sampling periods per year; (4) have available methodologies for requisite measurements; (5) be interpretable. For practical purposes in a national program, it is also desirable that samples can be obtained by a non-scientist at a reasonable cost.

Nematodes (free-living and plant-parasitic) possess several attributes that make them useful as ecological indicators and thus, show promise as an indicator of soil ecological condition (Freckman, 1988). Functional groups of nematodes are present in three positions in the soil food chain (Moore and de Ruiter, 1991). Plant-feeding nematodes are primary herbivores that feed on plant roots or shoots. Bacterial-feeding and fungal-feeding nematodes consume bacteria and fungi (including mycorrhiza) and are indirectly involved with decomposition (Yeates and Coleman, 1982) and nitrogen mineralization owing to their interaction with the microflora (Ingham et al., 1985). Some nematodes are predacious and feed upon nematodes in the other functional groups and other soil invertebrates including enchytraeids, tardigrades and protozoa (Moore and de Ruiter, 1991). Omnivores do not hold a separate position in the food chain, but add 'connectedness' to the food web (Coleman et al., 1983) by feeding on more than one food source, including bacteria, fungi, algae, protozoa, and rotifers.

Food webs in cultivated agricultural soils are typically bacterial- rather than fungal-based (Hendrix et al., 1986). Abundance of bacterial- and fungal-feeding nematodes may or may not be correlated with microbial populations (Ingham et al., 1985). However, the ratio of total fungal- to total bacterial-biomass is an index that reflects the structure of the microbial community (Ingham and Horton, 1987; Yeates et al., 1993a).

Indices of nematode community structure show promise for monitoring the ecological condition of soils because of their ability to reflect change in soil condition (Bongers, 1990; De Goede, 1993; Ettema and Bongers, 1993; Freckman and Ettema, 1993; Neher et al., 1994). Perturbation to soils, such as addition of mineral nitrogen fertilizers (Wasilewska, 1989), cultivation (Hendrix et al., 1986), liming (Hyvonen and Persson, 1990), and accumulation of heavy metals (Samoiloff, 1987; Bongers et al., 1991), affects species richness and trophic structure (Wasilewska, 1989). In several experiments in which the recovery of nematodes was studied after disturbance, changes in successional status of nematode communities were evident. Over a period of 60 weeks after soil fumigation and manuring, community composition progressed from colonizer taxa to more specialized, later successional taxa (Ettema and Bongers, 1993).

Indices of maturity (calculated separately for plant-feeding or plant-parasitic, PPI, and free-living, MI, nematode taxa) and trophic diversity are less variable than ratios of trophic groups and populations of individual trophic groups and, thus may be more likely to detect true trends in the ecological condition of soil (Neher et al., 1994). Bongers (1990) based maturity indices on life strategy characteristics of nematode taxonomic families with colonizers (short life-cycle, high reproductive rates, tolerant to disturbance) weighted as one and persisters (long life-cycles, low colonization ability, few offspring, sensitive to disturbance) weighted as five. Plant-feeding

taxa were assigned colonizer-persister values only from two to five (Bongers, 1990). Maturity indices of free-living taxa, MI, may be viewed as a measure of disturbance, with lower values indicative of a more disturbed environment and higher values characteristic of a less disturbed environment. Conversely, PPI would increase with increased disturbance such as ammonia fertilization which increases primary production, particularly of roots (Bongers, 1990).

Trophic diversity can be expressed with a Shannon or Simpson diversity index (Shannon and Weaver, 1949; Simpson, 1949). Higher diversity may imply a relatively higher abundance of the rarer trophic groups such as omnivorous and predacious nematodes in arable soils (Wasilewska, 1979). The Shannon index gives weight to rarer taxa e.g. omnivores and predators, whereas the Simpson index gives weight to the more abundant taxa e.g. bacterial- and plant-feeding nematodes (Ludwig and Reynolds, 1988). Because of the typically unequal distribution of trophic groups within nematode communities in agroecosystems (Wasilewska, 1979), the Shannon index may be more applicable than the Simpson index of diversity.

Interpretation and comparison of nematode community indices require a reference base. Ideally, a reference base for soil ecological condition is an ecosystem in which the soil has never been cultivated or otherwise disturbed. Such a reference site, however, would be unrealistic for agroecosystems which are disturbed intentionally for human purposes. Realistically, an agroecosystem that includes medium- or long-term perennial crops could be considered as a reference base or a point of comparison. For example, crops of alfalfa (*Medicago sativa* L.) and permanent pastures (e.g. tall-fescue grass *Festuca arundinacea* Schreb. alone and mixed with legumes) might serve as reference bases. Crops such as these would be practical choices, because they occur frequently in agroecosystems and are widespread geographically.

Soils of perennial crops such as 3 and 5 year old alfalfa may have a nematode species diversity that is greater than that of soils of annual crops and is comparable with that in soils of undisturbed areas (Ferris and Ferris, 1974; Wasilewska, 1979). Although bacterial- and plant-feeding nematodes are more abundant than predatory and omnivorous nematodes in soils cropped to annual crops, grasslands, and perennial crops (Wasilewska, 1979), there is a greater abundance of omnivorous and predatory nematodes in soils with perennial than with annual crops (Wasilewska, 1979; Bostrom and Sohlenius, 1986). Omnivorous and predacious nematodes have a longer life span and rely on a variety of foods, making them more sensitive to disturbance than fungal-feeding and bacterial-feeding nematodes (Wasilewska, 1979). In this study, we evaluated soils with a medium- or long-term perennial crop as potential reference sites of ecological condition of soil with annual crops. We used indices of nematode communities and microbial biomass to compare soils with perennial and annual crops. The indices we used were maturity of plant-feeding nematodes, trophic diversity of nematode communities, ratios of fungal-feeding to bacterial-feeding nematodes, and ratios of fungal- to bacterial-biomass.

2. Materials and methods

2.1. Experimental design

Ninety-two fields of annual crops (soybean, *Glycine max* (L.) Merr.); corn, *Zea mays* L.; wheat, *Triticum aestivum* L.) were sampled in December 1990 for comparison of nematode communities. These three crops were selected because they had more hectarage in North Carolina than any other annual crops (North Carolina Agricultural Statistics Division, 1990). Because there were no differences in nematode community indices (PPI: $P=0.3307$, trophic diversity: $P=0.5011$) among the annual cropping systems in 1990, soybean ($n=47$) was chosen as the representative annual crop for comparison with perennial crops for a comparative study between annual and perennial crops in 1991.

A total of 27 soybean fields, 25 alfalfa fields at least 5 years old, and 28 tall-fescue grass and tall-fescue grass plus legume pastures at least 10 years

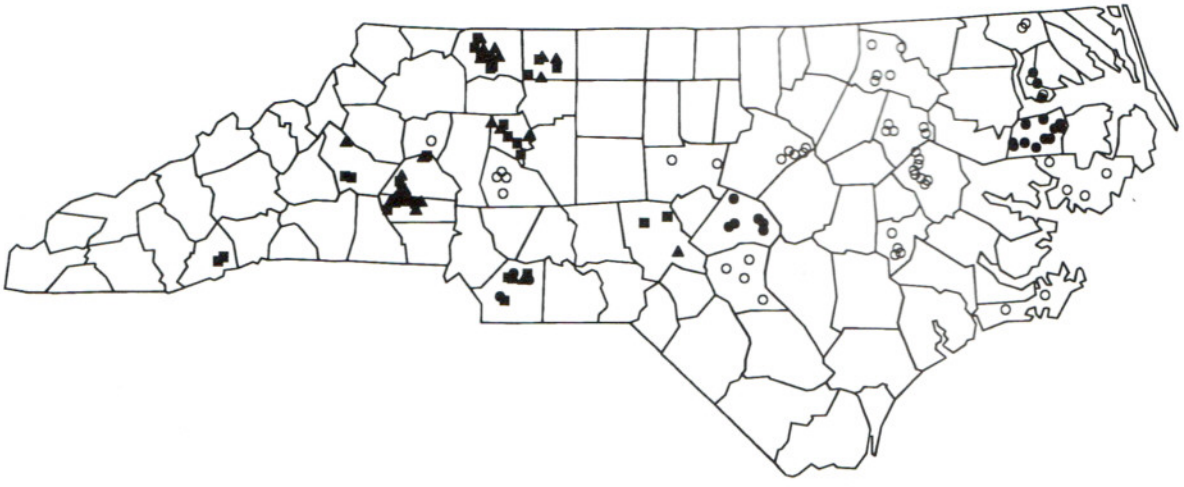

Fig. 1. Sampling locations in the state of North Carolina for soybean (○, 1990: ●, 1991), alfalfa (▲), and pasture (■). Distribution of fields within counties across the state of North Carolina was proportional to the intensity of cropped hectarage of each cropping system during the previous year.

old were sampled in December 1991. Number of years in annual crop production were recorded for soybean and years since cultivation were recorded for the alfalfa and pastures. Distribution of selected fields within counties across the state of North Carolina was proportional to the hectarage of each cropping system during the previous year (U.S. Department of Commerce, 1987; North Carolina Agricultural Statistics Division, 1991). County extension agents were consulted for selection of fields. Multiple fields of the same crop within a county were scattered across the county. Fields of different crops were sometimes located on a single farm but were not adjacent to one another. Because no significant differences in nematode community indices in soils with soybean were detected between sampling years, data from soybean fields in 1990 were combined with data from the 1991 survey for comparisons of annual and perennial crops (Fig. 1).

Soil in each field was sampled by taking one core (2 cm in diameter and 20 cm deep) at each of 20 equally-spaced locations in a systematic, serpentine (grid) design established within 2 ha in each field (Neher et al., 1994). For fields less than 2 ha, the size of the grid was adjusted and the entire field was sampled. The starting point of the serpentine pattern i.e. number of paces along and into a field, was determined by a draw from a random number table. The 20 soil cores from each field were bulked into a single composite sample to reduce variance associated with the aggregated spatial pattern of nematodes in soil (McSorley and Walter, 1991) and to obtain a representative estimate of the nematode community in the field. Composite soil samples were mixed and then stored at the existing moisture and 15°C to minimize changes in nematode populations (Barker et al., 1986). Nematodes were extracted within 14 days after sampling.

2.2. Laboratory analyses

Nematodes in 500 cm^3 of soil were extracted by means of semi-automatic elutriation followed by sucrose centrifugation (Barker, 1985); nematode counts were not corrected for extraction efficiency. Extracted nematodes were examined and assigned to one of five trophic groups: (1) plant-feeder; (2) bacterial-feeder; (3) fungal-feeder; (4) omnivore; (5) predator according to the system of Yeates et al. (1993b). Nematodes were counted by taxonomic family for plant-feeders but not for other trophic groups. Therefore, it was possible to calculate family-level in-

dices e.g. the maturity index for plant-feeding, but not free-living, nematode taxa. A list of genera within each family and trophic group can be found in Neher et al. (1994).

Subsamples (50 ml) of soil were removed from each composite sample for measurement of microbial biomass in the 1991 survey only. Measurements of soil microbial biomass were obtained by direct microscopy coupled with staining techniques (Microbial Biomass Service, Oregon State University). Bacteria in soil suspensions were stained with fluorescein isothiocyanate (FITC) and filtered onto Nucleopore, black-stained filters (Babiuk and Paul, 1970). Total bacterial biomass was determined by counting numbers and measuring the diameters of bacteria. Active bacterial biomass was determined by counting bacteria stained with fluorescein diacetate (FDA) in agar-film soil suspensions (Lodge and Ingham, 1991). Active fungal biomass was determined by measuring the length and diameter of FDA-stained hyphae. Total fungal biomass was determined by measuring the length and diameter of hyphae in agar-film soil suspensions using a combination of epi-fluorescent and phase contrast microscopy (Ingham and Klein, 1984; Lodge and Ingham, 1991).

Additional subsamples of soil from the composite sample were air-dried, crushed with a hammer mill to a diameter of less than 2 mm, and analyzed for chemical and physical properties including organic matter, extractable phosphorus, pH, cation exchange capacity (CEC), exchangeable cations, percent base saturation, electrical conductivity, and concentrations of trace metals (copper, zinc, aluminum) (Brookside Farms Laboratory Association, New Knoxville, OH). Soil texture was measured by the authors for two subsamples from each composite sample with the hydrometer method (Gee and Bauder, 1982).

2.3. Statistical methods

Nematode community structure was described by maturity of communities of plant-feeding or plant-parasitic nematodes (PPI) and trophic diversity. PPI was calculated as the weighted mean of the values assigned to constituent nematode families (and the genera and species they contain) (Bongers, 1990), such that

$$\mathrm{PPI} = (\Sigma v_i * f_i)/n$$

where v_i is the colonizer–persister (c–p) value assigned to family i, f_i is the frequency of family i in a sample, and n is the total number of individuals in a sample. Trophic diversity was estimated with the Shannon diversity index (N1) where

$$\mathrm{N1} = \exp(-\Sigma P_i(\ln P_i))$$

and P_i is the proportion of trophic group i in the total nematode community (Ludwig and Reynolds, 1988). In addition, a ratio of the proportion of fungal-feeding to bacterial-feeding nematodes was calculated as (fungal-feeders/(fungal-feeders + bacterial-feeders)) (sensu Yeates et al., 1993a).

Prey–predator ratios were estimated to describe the relationship between nematodes and microbial biomass. Fungal-feeding and bacterial-feeding nematode populations were transformed to numbers per gram of dry soil and microbial biomass to milligrams per gram of dry soil + 0.0001 for analysis. A ratio of fungal- to bacterial-biomass was calculated (fungal biomass/(fungal biomass + bacterial biomass)) to describe the structure of the microbial community. Associations between abundances of bacterial-feeding and fungal-feeding nematodes and bacterial- and fungal-biomass were examined with Spearman rank correlations. Differences in nematode community indices, abundance of nematodes by trophic groups, and microbial biomass among the pasture, alfalfa, and soybean cropping systems were estimated with least-squares means of the general linear model (GLM) procedure (Statistical Analysis Systems Institute Inc. (SAS), 1989).

Cumulative distribution functions (CDF) were constructed to illustrate the proportion of cropped land area that had an index of a certain value or less. CDF were calculated for PPI, trophic diversity, the ratio of fungal-feeding to bacterial-feeding nematodes, and the ratio of total fungal- to total bacterial-biomass.

Canonical correlation procedures were used to

quantify the relationship between abundance of nematodes in each of three trophic groups (bacterial-feeding, fungal-feeding, and plant-feeding nematodes) and a group of environmental variables (i.e. soil sand content, soil clay content, soil pH, and the ratio of total fungal- to total bacterial biomass) (Afifi and Clark, 1990). All variables were selected based on their relatively high correlations with the canonical variables in earlier runs of the canonical correlation analysis. Nematode trophic groups, sand content, and clay content were transformed as the square root of x, $x/10$, and $x/10$, respectively, so that all variables within each canonical variable would be on a similar scale. Because of intercorrelation among variables within a canonical variable, canonical variable correlations rather than canonical variable coefficients were presented (Affifi and Clark, 1990). A likelihood ratio statistic was used to test for significance of canonical correlations using the canonical correlation (CANCORR) procedure (SAS, 1989).

3. Results

Perennial crops had a wider and higher range of maturity index values (PPI) than annual crops ($P=0.0001$, Fig. 2a). PPI values were 3.27 ± 0.10 (mean $\pm$ standard error) and 2.82 ± 0.03 for perennial and annual crops, respectively. Distribution of trophic diversity was similar between annual and perennial crops ($P=0.0897$, Fig. 2b) and overall estimates of trophic diversity were 2.78 ± 0.09 (mean $\pm$ standard error) and 2.54 ± 0.07 for perennial and annual crops, respectively. Trophic diversity was correlated ($P<0.05$) positively with population levels of fungal-feeding ($r=0.40$), omnivorous ($r=0.51$), and predacious ($r=0.34$) nematodes and negatively with population levels of bacterial-feeding ($r=-0.25$) nematodes. The ratio of fungal-feeding to bacterial-feeding nematodes was greater in perennial than annual crops ($P=0.0001$, Fig. 2c). Overall mean estimates of this ratio were 0.21 ± 0.02 and 0.11 ± 0.01 (mean $\pm$ standard error) for perennial and annual crops, respectively. There were no statistical differences in the values of all three indices between alfalfa and pastures.

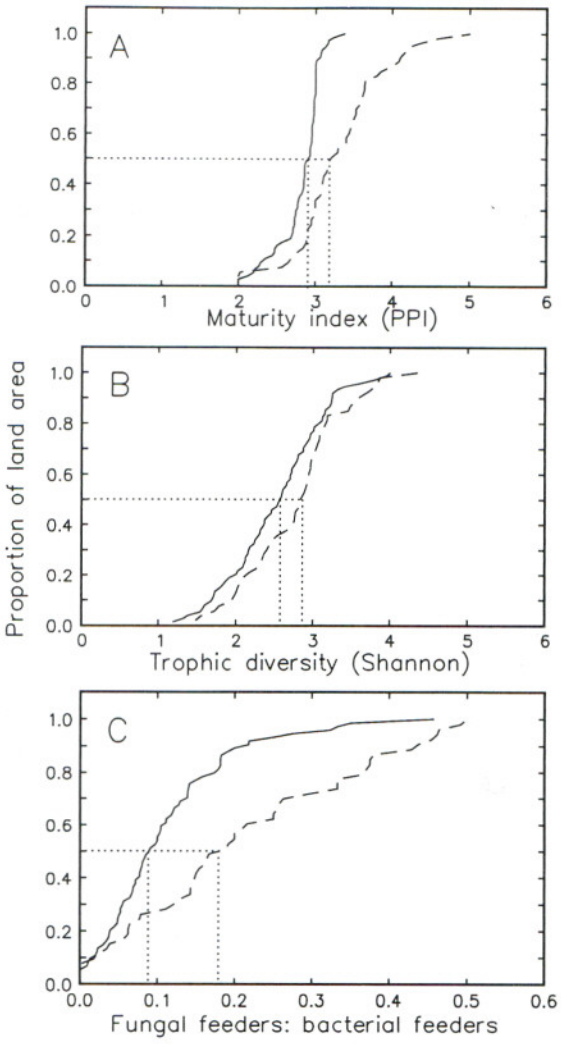

Fig. 2. Cumulative distribution function of the (a) maturity index of plant–feeding nematodes, (b) Shannon trophic diversity, and (c) fungal- to bacterial-feeding nematodes for soybean (solid line) and perennial (dashed line) crops sampled in North Carolina. Sampling locations are illustrated in Fig. 1. Dotted lines represent median values.

The ratio of bacterial-feeding nematodes to total bacterial biomass was greater for soybean than for alfalfa or pasture systems ($P=0.0012$, Table 1). However, no differences were detected among cropping systems for the ratio of bacterial-feeding nematodes to active bacterial biomass

Table 1
Mean ratio of microbial-feeding nematodes[1] to total microbial biomass[2] (mean ± SE) and ratio of total fungal- to total bacterial biomass for soybean ($n=27$), alfalfa ($n=25$), and permanent pasture ($n=28$) cropping systems sampled across North Carolina in December 1991. Actual means are presented, although statistical analysis was performed on least-squares means

Crop	Bacterial-feeding nematode numbers to total bacterial biomass	Fungal-feeding nematode numbers to total fungal biomass	Total fungal biomass to total bacterial biomass
Soybean	3.48 ± 0.56^a	26.41 ± 15.39^a	0.116 ± 0.015^a
Alfalfa	1.12 ± 0.32^b	8.74 ± 2.17^a	0.057 ± 0.009^b
Pasture	1.76 ± 0.42^b	22.26 ± 10.88^a	0.120 ± 0.019^a

[1]Number of nematodes per gram of dry soil.
[2]Milligrams of biomass + 0.0001 per gram of dry soil.
Different letters indicate there were statistical differences ($P<0.05$) between least-squares means of cropping systems.

($P=0.1527$) or the ratios of fungal-feeding nematodes to total ($P=0.5221$) or active ($P=0.4619$) fungal biomass. The only significant correlation between nematode communities and microbial biomass was the positive correlation of numbers of fungal-feeding nematodes to active fungal biomass in alfalfa systems (Table 2). The ratios of fungal-feeding nematodes to total fungi were numerically greater than the ratios of bacterial-feeding nematodes to total bacteria in all cropping systems (Table 1).

There was a significant correlation between active and total fungal biomass for all crops, individually, but no significant relationship between active and total bacterial biomass (Table 2). The ratio of total fungal- to total bacterial-biomass was greater for pasture and soybean than alfalfa cropping systems ($P=0.0086$, Table 1). The ratio of active fungal- to active bacterial-biomass was not different among cropping systems ($P=0.5804$). Within the soybean cropping system, the active bacterial biomass was greater for fields in cultivation for more than 50 years ($n=17$, 0.063 ± 0.023, mean ± standard error) than for fields in cultivation less than 50 years ($n=57$, 0.030 ± 0.004, mean ± standard error).

The canonical variables for trophic structure and environment (Table 3) were correlated positively (first canonical correlation = 0.70, second canonical correlation = 0.48, $P=0.0001$) indicating there was an association between trophic structure of nematode communities and their environment (soil chemical properties and microbial biomass). Bacterial-feeding and fungal-feeding nematodes had the largest loading in the first and second canonical variables of nematode communities, respectively, and were correlated positively with their respective canonical variable (Table 3). The first environmental canonical variable was correlated negatively with soil clay content and soil pH and correlated positively with soil sand content (Table 3). The second environmental canonical variable was correlated positively with soil pH and correlated negatively with soil sand content (Table 3). Soil clay content had a small correlation coefficient

Table 2
Spearman rank correlation coefficients between microbial biomass, microbial-feeding and predatory nematode trophic groups for soybean ($n=27$), alfalfa ($n=25$), and permanent pasture ($n=28$) cropping systems sampled across North Carolina in December 1991

Variable 1	Variable 2	Soybean	Alfalfa	Pasture
Active bacteria	Total bacteria	−0.108	0.091	0.239
Active fungi	Total fungi	0.736**	0.475*	0.726**
Bacterial-feeding	Active bacteria	0.010	0.015	0.032
Fungal-feeding	Active bacteria	−0.191	0.326	−0.060
Bacterial-feeding	Active fungi	0.090	0.311	−0.327
Fungal-feeding	Active fungi	−0.116	0.459*	0.018

*$P<0.05$; **$P=0.0001$.

Table 3
Correlations between canonical variables and corresponding variables. Canonical correlations were estimated for a set of nematode trophic groups and a set of environmental parameters including soil chemical properties and the ratio of total fungal to bacterial biomass

Nematode trophic groups	N1[1]	N2[2]
Bacterial-feeding nematodes	0.8986	0.2790
Fungal-feeding nematodes	0.2128	0.8353
Plant-root feeding nematodes	0.6649	−0.3803
Environmental parameters	**E1[1]**	**E2[2]**
Sand content (%)	0.6189	−0.4972
Clay content (%)	−0.9989	−0.0178
pH	−0.6278	0.5917
Fungal-to-bacterial biomass ratio	0.3288	−0.2257

[1]First canonical variable.
[2]Second canonical variable.

in the second canonical variable and the ratio of fungal- to bacterial-biomass had a relatively small correlation coefficient in both the first and second canonical variables. Organic matter content ranged from 0.6 to 45.7% and was not included in the environmental canonical variables because it had a small correlation in preliminary runs of the canonical correlation. The first two environmental canonical variables predicted 47.1 and 16.2% of their own variability but only 23.2 and 0.04% of the variation associated with the nematode trophic group variables in the first and second canonical correlations, respectively.

4. Discussion

In this study, maturity index values of plant-feeding nematodes, PPI, were greater for perennial crops (mean = 3.27) than for annual crops (mean = 2.82). These magnitudes and ranking of values of PPI were not expected based upon the work of Freckman and Ettema (1993) who estimated a range of 2.42–2.65 for annual crops, an average of 2.16 for alfalfa and poplar combined, and about 2.35 for abandoned or never-tilled successional treatments in Michigan. However, overall our soil samples contained more nematodes with relatively higher c–p values such as those in the families Heteroderidae (i.e. *Meloidogyne* and *Heterodera* spp.), Hoplolaimidae (i.e. *Helicotylenchus* spp.), and Longidoridae (i.e. *Xiphinema* spp.) than soils collected by Freckman and Ettema (1993). Bongers (1990) predicted that disturbance of soil through cultivation and nutrient amendments, which is often associated with an increase in production of annual crops, would result in higher PPI values than cropping systems with less disturbance.

Bongers (1990) originally separated plant-feeding nematodes from the other trophic groups in the calculation of the maturity index on the basis that the life strategy of plant-feeding nematodes was not comparable with that of free-living taxa. However, Yeates (1994) argued that combining the plant-feeding and free-living nematode taxa into a single maturity index enhanced the biological validity of the index by its holistic nature. Yeates (1994) observed that maturity index values for plant-feeding nematodes were similar to that of MI in New Zealand for permanent pasture. Values for the combined maturity index (including plant-feeding and free-living nematode communities) decreased with disturbances such as pesticide application, tillage, heavy metal contamination, and burning of tussock grass (Yeates, 1993). Although in our study PPI included only plant-feeding nematodes, our results support the work of Yeates (1994) who observed a decrease in the maturity of nematode communities that included plant-feeding nematodes with an increase in disturbance, e.g. repeated cultivation.

Although not statistically significant, nematode trophic diversity in our study was slightly greater in perennial (mean = 2.78) than annual (mean = 2.54) crops. Our results were in general agreement with those from previous studies (Sohlenius and Sandor, 1987; Freckman and Ettema, 1993) and with those of Yeates et al (1993a) who found Shannon indices of nematode diversity ranged from 2.02–2.29 for maize and about 2.80 for asparagus in late fall to early winter, the same time of year as we sampled. The difference in species diversity between perennial (e.g. meadow fescue (*Festuca pratensis* L.)) and annual crops (e.g. barley, *Hordeum distichum* L.)

may be less pronounced for perennial crops that are 3 years old or less (Bostrom and Sohlenius, 1986). Trophic diversity was greater in perennial cropping systems that had a longer period since the last cultivation (e.g. abandoned or never-tilled successional systems) than annual or perennial systems with a shorter period since the last cultivation (e.g. alfalfa, poplar, and no-till) (Freckman and Ettema, 1993).

The ratio of fungal-feeding to bacterial-feeding nematodes may be an important description of the decomposition pathway in the detritus food webs (Sohlenius and Sandor, 1987). Our estimates (0.21 and 0.11 for perennial and annual crops, respectively) of the ratio of fungal-feeding to bacterial-feeding nematodes (Fig. 2c) were mostly lower than those estimated for soybean (0.45) by Freckman and Ettema (1993) but were more similar to those measured for maize (*Zea mays* L.) (0.16–0.17) and asparagus (*Asparagus* spp.) (0.28) by Yeates et al (1993a). Although Bostrom and Sohlenius (1986) found that fungal-feeding nematodes were relatively more abundant in some perennial than annual cropping systems, we did not find any significant effect of cropping system on abundance of fungal-feeding nematodes. Therefore, the ratio of fungal-feeding to bacterial-feeding nematodes was due mostly to changes in numbers of bacterial-feeding not fungal-feeding nematodes.

Reports in the literature have conflicting results concerning the relationship between microbial-feeding nematodes and their food source in soil (Ingham et al. 1985). Our results generally support those of Bostrom and Sohlenius (1986) who found no clear connections between numbers of bacterial-feeding and fungal-feeding nematodes and the biomass of their food source, bacteria and fungi. In contrast, Trofymow and Coleman (1982) observed a positive relationship between bacterial-feeding nematodes and bacterial numbers in soils amended with chitin and/or cellulose. Wardle and Yeates (1993) proposed that numbers of predatory nematodes were correlated more strongly with microbial biomass than the microbial-feeding nematodes, owing to the regulatory pressures of grazing and competition for bacterial- and fungal-biomass, respectively. Perhaps one reason we did not observe a relationship between microbial grazers and microbial populations is that our data was restricted to one sample period per year.

Bacteria were clearly the dominant microorganisms in the cropping systems during the late fall sampling time. We are unable to explain why the fungal- to bacterial-biomass ratio was significantly lower in soils with alfalfa than in soils with soybean and alfalfa. We expected a greater fungal- to bacterial-biomass ratio in alfalfa and pasture than in cultivated soybean fields. Cultivation of soils distributes plant residue throughout the plowed layer which promotes bacterial activity and abundance (Neely et al., 1991; Beare et al., 1992) and development of a bacterial-based food web (Hendrix et al., 1986). Perennial crops e.g. alfalfa and pastures, were not cultivated and allowed accumulation of plant residue on the soil surface which can promote fungal growth and lead to a food web with a more even balance of fungi and bacteria (Hendrix et al., 1986).

Generally, fungal- to bacterial-biomass ratios increase with increasing C:N ratios in soil (Ingham and Horton, 1987). A fungal- to bacterial-biomass ratio between 0.1 and 1.0 is generally considered good for growing crops, especially if bacterial and fungal populations are relatively high. A ratio less than 0.05 may indicate that soil fertility is declining. In our study, approximately 60 and 25% of the land area cropped to annual and perennial cropping systems, respectively, had fungal- to bacterial-biomass ratios less than 0.05 (Fig. 3) and approximately 20 and 50% of the land area cropped to annual and perennial cropping systems, respectively, had ratios between 0.1 and 1.0 (Fig. 3) indicating that many of the soils sampled may be declining in fertility. The fertility in perennial crops may be generally greater than annual crops because they are less disturbed. Our estimates of the ratios total fungal- to total bacterial-biomass were less than those of Beare et al (1992) who estimated microbial biomass in soybean/rye (*Secale cereale* L.) and sorghum/rye cropping systems using the same methods that we did and those of Anderson and Domsch (1975) who measured microbial respi-

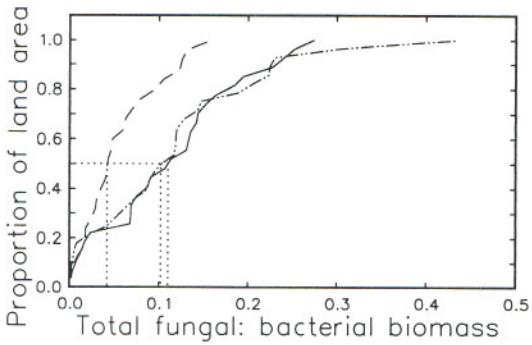

Fig. 3. Cumulative distribution function of the ratio of total fungal to total bacterial biomass in alfalfa (dashed line), pasture (alternating long and short dashed line), and soybean (solid line) cropping systems in 1991. There was a significant difference ($P=0.0001$) between alfalfa and the other two cropping systems, but no significant difference between pasture and soybean. Sampling locations are illustrated in Fig. 1. Dotted lines represent median values.

ration of four agricultural soils at depths of 0–10 cm.

We did not observe any obvious relationship between organic matter content (ranging from 0.6 to 45.7%), microbial populations, or nematode trophic groups. Numbers of bacterial-feeding nematodes should increase with additions of organic matter (Wasilewska, 1979) including input from the roots in the form of exudates and dead tissues (Hendrix et al., 1990). Other factors such as soil texture may have masked relationships between organic matter and these groups in our study.

Measurement of the soil environment was not a very reliable estimate of nematode community structure. Based on canonical correlation, nematode trophic groups and environmental variables were correlated in our study, but were not strong predictors of each other, at least when quantified at the same sampling time. However, Yeates et al. (1993a) showed that nematode populations sampled on 10 October were more strongly related to environmental factors at the prior sampling on 25 July than those at 10 October in maize and asparagus cropping systems. Nematode community structure may thus depend more on past than current environmental conditions.

5. Conclusions

Our data suggest that forage and pasture crops may be suitable for use as reference crops in monitoring the ecological condition of soils associated with annual crops. We observed significant differences between annual and perennial cropping systems in the maturity index for plant-feeding nematodes and the ratio of fungal- feeding to bacterial-feeding nematodes (Fig. 2a,c). However, the period of time (1–5 years) that a perennial crop (e.g. alfalfa) has been in place without disturbance influences the number of species and structure of the nematode community (Wasilewska, 1979) and may affect its usefulness as a reference. A long-term perennial crop is more closely related to an undisturbed site than is a medium-term perennial crop. Crop land that has never been tilled or has been abandoned for a long period of time would be the best reference (Freckman and Ettema, 1993). However, for a large-scale monitoring program for agroecosystems, sites that have never been cultivated may be impractical to locate, and perennial agricultural fields may provide the best reference sites.

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