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Nematode Communities in Organically and Conventionally Managed Agricultural Soils[1]

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Abstract: Interpretation of nematode community indices requires a reference to a relatively undisturbed community. Maturity and trophic diversity index values were compared for five pairs of certified organically and conventionally managed soils in the Piedmont region of North Carolina. Available nitrogen (nitrate, ammonium) was estimated at various lag periods relative to times of sampling for nematode communities to determine the strength of correlative relationship between nematode communities and nitrogen availability. Soils were sampled six times yearly in 1993 and 1994 to determine the best time of year to sample. Maturity values for plant parasites were greater in organically than conventionally managed soils, and differences between management systems were greater in fall than spring months. However, other maturity and diversity indices did not differ between the two management practices. Differences in crop species grown in the two systems accounted for most differences observed in the community of plant-parasitic nematodes. Indices of free-living nematodes were correlated negatively with concentrations of ammonium, whereas indices of plant-parasitic nematodes were correlated positively with concentrations of nitrate. Due to the similarity of index values between the two systems, organically managed soils are not suitable reference sites for monitoring and assessing the biological aspects of soil quality for annually harvested crops.

Key words: community structure, conventional farming, ecology, maturity index, monitoring, nematode, ordination, organic farming, reference sites, trophic diversity.

Soil nematode communities are sensitive to changes in food supply (Yeates, 1987) and environment (Bongers et al., 1991; Ettema and Bongers, 1993; Freckman and Ettema, 1993; Samoiloff, 1987; Wasilewska, 1989). Thus, communities also have a significant role in regulating decomposition and nutrient cycling (Anderson et al., 1983; Ingham et al., 1985) and occupy a central position in the soil food web (Moore and de Ruiter, 1991). When attributes of soil nematode communities are quantified through measures such as a diversity index (Shannon and Weaver, 1949; Simpson, 1949) or maturity index (Bongers, 1990; Yeates, 1994), an indication of relative soil biological or ecological health is obtained, which can be used as one measure to address issues of change in ecological condition of soils in agricultural systems.

Ecological indices related to nematode communities do not provide absolute values of condition but require reference to some putatively undisturbed, baseline/reference community for interpretation or comparison (Karr, 1991, 1995). A previous study (Neher and Campbell, 1994) quantified the impact of cultivation on soil community structure and concluded that uncultivated pastures may serve as reference communities. A remaining question is whether a management system that abstains from applications of agrichemicals might also serve as a reference community. Among agroecosystems, organic farms may represent a source of nematode communities undisturbed by agricultural chemicals. Organic management minimizes or excludes synthetic chemical fertilizers and, instead, places an emphasis on the recycling of organic wastes and legume crops as green manure to supply nutrients on a schedule matching plant demand (USDA, 1980). With organic farming, soil microbes appear to play a more important role in plant nutrient cycling than in conventional systems (Allison, 1973). The

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conventional system supplies these plant nutrients in forms readily available for crop use, but their release and availability may not match plant uptake and excess may be lost through leaching or alter ecosystem function (Scow et al., 1994). Organic systems rely upon microbial degradation and mineralization of organic matter, especially leguminous green manure, to supply nutrients for subsequent crop use (Bolton et al., 1985). Nitrogen is mineralized by predators of bacteria and fungi, such as protozoa and microbivorous nematodes. Excess nitrogen generated by microbial grazing is released to the soil and becomes available for plant uptake. Farm practices that minimize the use of synthetic pesticides or inorganic fertilizers generally result in soils with ecological properties considered ''good'' or ''healthy,'' including significantly greater organic matter content and microbial activity, better soil structure, lower bulk density, easier penetrability, and thicker topsoil, than do farm practices that rely on intense use of synthetic fertilizers and pesticides (Bolton, 1983; Reganold et al., 1993). Greater organic matter content is usually related to higher levels of soil fertility, greater productivity, and improved tilth (USDA, 1980).

Additions of organic matter to soil are expected to increase numbers of bacterivorous and fungivorous nematodes and decrease numbers of plant-parasitic nematodes (Bohlen and Edwards, 1994; Freckman, 1988; Griffiths et al., 1994). Applications of manure add both organic matter and microbes, a source of food for the nematodes (Andrén and Lagerlöf, 1983; Weiss and Larink, 1991). Plant- and microbial-feeding nematodes have a high C:N ratio compared to their food sources and, thus, release nitrogen as a waste product. When bacteria are plentiful in soil, bacterivorous nematodes may discharge amino acids in substantial amounts. However, as bacterial populations decrease, nematodes begin to starve, and protein catabolism for maintenance energy requirements leads to increased ammonium excretion be nematodes (Anderson et al., 1983). Nitrogen content appears to be an important measure of potential microbial activity and, subsequently, the rate of decomposition (Neely et al., 1991).

In addition to increases in soil fertility, organic amendments may increase suppression of plant diseases by adding competitive, predaceous, or antagonistic microbes to soil (Clark et al., 1998). Some studies suggest that organic amendments with relatively low C:N ratios (i.e., 6–10) containing ammonium nitrogen may be used as nematicidal agents (Akhtar and Mahmood, 1996; Kaplan and Noe, 1993; Mian and Rodríguez-Kábana, 1982; Rao et al., 1997; Rodríguez-Kábana, 1986). For example, application of oilcakes of neem (*Axadirachta indica*), castor (*Ricinus communis*), composted manure and urea to pigeonpea (*Cajanus cajan*) fields resulted in a decrease in plant-parasitic nematodes and an increase in predatory and free-living nematodes (Akhtar and Mahmood, 1996). Amendments of composted manure and urea to soil were associated with increased numbers of free-living nematodes (Akhtar and Mahmood, 1996).

The primary objective of this study was to compare the structure and composition of nematode communities in soils of organically and conventionally managed agricultural fields. The goal was to ascertain whether certified organic farms could serve as a potential reference base for nematode community indicators for comparison of soils with annually harvested, herbaceous crops. Secondary objectives were to quantify temporal associations between nematode community index values and availability of nitrogen to crop plants, and determine the best time of year to sample nematode communities for environmental monitoring programs.

MATERIALS AND METHODS

Experimental design: To minimize the effects of differences in soil and climate, four fields with more than 8 years of organic management were paired with soils of similar soil map unit and geographic location that had been managed conventionally. It was not possible to identify a match for a fifth organically managed field. All fields were located in the Piedmont region of North Carolina (Table 1). Certification of organic fields was performed by Carolina Farm Stewardship Association, and sites were selected in collaboration with the USDA Natural Resources Conservation Service and county agents of the North Carolina Cooperative Extension Service. Differences between pairs of sites were attributed primarily to management approach. It was impossible to match crops planted in each type of management because all study sites were under commercial production. It was assumed that crop species had minimal influence on nematode community function based on similar maturity and trophic diversity index values observed among annual crops (i.e., wheat, soybean, corn) in a previous study (Neher and Campbell, 1994). It is important that environmental indicators for implementation on regional or national geographic scales allow for general application and assessment of ecological function among contrasting species and communities.

Two independent, composite soil samples were collected per farm. Soils were sampled in all fields monthly during spring (March, April, and May) and fall (September, October, and November) 1993 and 1994. These times were chosen because nematode populations are abundant and species richness is high (Yeates, 1984). Within each field, two independent linear transects were located randomly and diagonally to rows of the current or previous crop. Composite samples were collected along these transects; one core (2-cm diam., 20 cm deep) was collected at each of 20 equally spaced sites within a 2-ha area (Neher et al., 1995). The sampling depth was chosen because surface horizons of a soil profile have greater values of biological indicators (e.g., urease, phosphatase, dehydrogenase, microbial biomass) than deeper horizons (Dodds et al., 1996) and the sampling depth corresponded generally to the tillage depth (Bolton et al., 1985) for both management regimes. Cores for each transect were mixed thoroughly and gently by hand, after which a subsample of 500 ml of each soil sample was placed in a plastic bag and sent via overnight courier to the identification laboratory (N & A Nematode Identification Service, Davis, CA).

Laboratory analyses: Nematodes were extracted from each soil sample or subsample by a modified Cobb's sifting-and-gravity method followed by sugar flotation-centrifugation (Neher and Campbell, 1994, Neher

TABLE 1. Characteristics and locations of study sites in North Carolina.

				Soil parameters[c]			
Pair	County	Type[a]	Crops grown during study[b]	*Water pH*	*Percent organic matter*	*Electrical conductivity (dS/m)*	*Percent sand, percent clay*
1	Franklin	O	Mixed vegetables, herbs, grass cover crop	5.8 ± 1.2	2.4 ± 0.8	9.3 ± 10.7	72.7 ± 2.4, 10.3 ± 1.4
		C	Pumpkin	7.0 ± 0.2	1.9 ± 0.9	10.1 ± 10.6	71.3 ± 1.0, 11.8 ± 0.5
2	Orange	O	Mixed vegetables, fresh-cut flowers, rye/crimson clover cover crop	7.3 ± 0.1	4.4 ± 0.7	0.3 ± 0.1	33.3 ± 7.5, 22.3 ± 6.7
		C	Mixed vegetables	6.0 ± 0.2	3.7 ± 1.0	0.2 ± 0.0	24.0 ± 3.8, 32.3 ± 3.6
3	Chatham	O	Mixed vegetables, fresh-cut flowers	6.3 ± 0.2	3.1 ± 0.7	10.8 ± 11.1	54.8 ± 1.3, 13.8 ± 1.0
		C	Field corn, orchardgrass/clover cover crop	6.7 ± 0.2	4.7 ± 1.0	10.1 ± 10.2	30.3 ± 1.0, 30.0 ± 0.8
4	Alamance	O	Mixed greens, asparagus, oat cover crop	6.3 ± 0.3	5.1 ± 2.8	14.8 ± 16.4	41.5 ± 15.6, 22.5 ± 11.6
		C	Field corn = cereal rotation	6.4 ± 0.2	5.6 ± 0.7	11.1 ± 12.0	30.0 ± 5.9, 29.4 ± 3.4
5	Sampson	O	Mixed greens, oat, rye, crimson clover cover crop	6.1 ± 0.2	3.7 ± 0.8	13.2 ± 13.7	88.3 ± 1.7, 5.0 ± 0.8

[a] O = certified organic; C = conventional

[b] Mixed vegetables = summer squash, tomatoes, peppers, sweet corn, beans, garlic, leeks, carrot, okra, cabbage, broccoli, potatoes, cucumbers, snow peas, swiss chard; mixed herbs = basil, dill, cilantro; mixed greens = lettuce, arugula, kale.

[c] Numbers are mean ± standard deviation.

et al., 1995). Numbers of nematodes in each taxonomic family and trophic group were counted in 500 cm^3 soil; counts were not corrected for extraction efficiency. Taxonomic families were assigned to a trophic group (plant-parasitic, bacterivorous, fungivorous, omnivorous, or predatory; Yeates et al., 1993a) (Table 2). Taxonomic families were also assigned a colonizer-persister (CP) value (Bonger, 1990) (Table 2).

Soil physical and chemical properties were measured on additional subsamples from the composite samples. Available pools of nitrogen (i.e., nitrate, ammonium) were measured for all but the first three sampling dates. Nitrate concentrations were measured according to Cataldo et al. (1975), and ammonium concentrations were measured with the indophenol blue method (Keeney and Nelson, 1982). Samples for nitrogen analysis were stored at field moisture content at 5 °C for no more than 48 hours prior to preparation of soil extract. For further analysis, samples were air-dried and crushed with a hammer mill to a particle diameter ≤ 2 mm. All samples were dried at 90 °C for 48 hours before laboratory analyses were performed. Soil properties measured included organic carbon (Storer, 1984) with ashing temperature reduced to 360 °C to avoid dehydroxylation of kaolinitic clays (D. A. Storer, pers. comm.), pH (Smith and Doran, 1996), electrical conductivity (EC) (Smith and Doran, 1996), and soil texture (Gee and Bauder, 1985).

Statistical analyses: Five indices were computed for the nematode community in each soil sample: (i) maturity index for all free-living nematodes (Bongers, 1990), except that taxa with a CP value of 1 were excluded (MINO or ''maturity index with no ones'' (sensu Popovici, 1992); (ii) maturity index for all plant-parasitic nematodes (PPI) (Bongers, 1990); (iii) combined maturity index for free-living and plant-parasitic nematodes (ΣMI) (Yeates, 1994); (iv) diversity of trophic groups (H'; Shannon and Weaver, 1949); and (v) ratio of fungivorous to bacterivorous nematodes (FB) (Söhlenius et al., 1988). Opportunistic taxa (CP = 1) were not included in MINO because they are considered enrichment opportunists, and population densities increase rapidly in response to additions of nitrogen to soil and not necessarily to long-term changes in soil ecological condition (Bongers et al., 1995). Maturity indices (MINO, PPI, and ΣMI) were calculated as the weighted means of the values assigned constituent nematode families. Weighted means were expressed mathematically as $(\Sigma v_i \times f_i)/n$ where $\boldsymbol{v_i}$ = CP value assigned to family i, f_i = frequency of family i in a sample or sub-sample, and n = total number of individuals in a sub-sample). A PPI:MI ratio was calculated (Bongers and Korthals, 1995) because it shows effects of nutrient enrichment. Diversity of trophic groups was estimated by the Shannon-Weaver diversity index (H') or Hill's N1, i.e., H' = exp $[-\Sigma P_i(\ln P_i)]$, where P_i is the proportion of trophic group i in the total nematode community (Ludwig and Reynolds, 1988). The FB index was calculated on relative proportion values as (fungivores/(fungivores + bacterivores)) (sensu Yeates et al., 1993b). This ratio describes the decomposition pathway in detritus food webs (Söhlenius et al., 1988). Smaller ratios are associated with faster rates of decomposition and nutrient turnover.

Repeated measures analysis of variance (PROC GLM, SAS Ver. 6.08, SAS Institute, Cary, NC) was performed on nematode index values, proportions of trophic groups, and family abundance. No significant interactions between farm type and year sampled for indices and trophic groups were observed, so the interaction term was dropped from subsequent analyses. However, an interaction term was included for analysis of nematode abundance variables. Independent variables were defined as farm type (organic or conventional) and year sampled (1993 or 1994). Relative proportions of trophic groups of total nematode communities were transformed as arcsin of the square root of x, and abundances of nematode families were transformed as ln $(x + 1)$ prior to statistical analysis.

The best time of year was defined as the sampling time with the greatest difference observed between organically and conventionally managed soils. Values of nematode indices from conventional farms were subtracted from values from organic farms for each farm pair, replicate composite sample, month, and year of sampling. Difference data were analyzed as a two-way analysis of variance (PROC GLM) treating differences between farm pairs for each index as dependent variables and season (spring or fall) as an independent variable. Mean differences were analyzed as least-squared means to account for differences in sample size between seasons. The season with a significantly ($P <$ 0.05) greater absolute value was considered the optimum time for sampling.

Spearman rank correlations (PROC CORR) were performed to quantify associations between concentrations of nitrate and ammonium in soil and nematode community indices at the previous 0, 1, 2, 4, 5, and 6 months (sensu Yeates, 1982). Correlations were performed on data from both soil types combined because there were no significant ($P > 0.05$) differences in available nitrogen between systems.

Canonical correspondence analysis (CCA) was performed to explore the distribution of nematode families in relation to organic and conventional soil management and their associated environmental properties (e.g., pH, EC, available ammonium). A direct gradient procedure was performed with the Fortran package 'CANOCO' version 3.15 (ter Braak, 1992; ter Braak 1995). Site types (organic or conventional) were treated as nominal environmental variables (ter Braak, 1995). The program standardizes all environmental variables to a mean of 0.0 and variance of 1.0, and the dispersion of the family scores after standardization is used to express how well a variable explains the family data. In the final analysis, some soil environmental variables were omitted because they exhibited high variation inflation factors (VIF) that did not explain any additional variance of the nematode family data (ter Braak, 1986). Twenty-six nematode families and 11 environmental variables for 72 field site-month sampling combinations were included in the analysis.

RESULTS

Nematodes from a total of 27 and 29 families were found in soils managed conventionally and organically, respectively (Table 2). Bastianidae and Microlaimidae were collected only from organically managed soils. Genera of all families were reported previously (Neher et al., 1995) with the exception of *Oionchus* Cobb, 1913 (Mononchulidae) observed from one organically managed site. The most abundant families were Cephalobidae, Rhabditidae, and Tylenchidae for both management types. The least abundant families were Bunonematidae, Cylindrolaimidae, Diphtherophoridae, Leptolaimidae, Paraphelenchidae, Trichodoridae, Tylencholaimellidae, and Tylencholaimidae (Table 2). Numbers of Alaimidae, Anguinidae, Aphelenchoididae, Bunonematidae, Cephalobidae, Diploscapteridae, Heteroderidae, Monhysteridae, Paraphelenchidae, Plectidae, Prismatolaimidae, Rhabditidae, Tylenchidae and Tylenchulidae were consistently greater in 1993 than in 1994 for all sites, whether managed conventionally or organically ($P < 0.05$, Table 2). There was a significant interaction between management type and year sampled for Aphelenchidae and Panagrolaimidae ($P < 0.05$, Table 2). Both families were more abundant in conventionally than organically managed soils in 1993; the opposite was true in 1994. Values of PPI were greater in organically than conventionally managed soils ($P = 0.0005$, Fig. 1). In contrast, values of MINO, ΣMI, and PPI:MI were similar between management systems (Table 3). Greater abundances of Criconematidae and Heteroderidae were observed in organic soils compared to conventional soils ($P < 0.05$, Table 2). Although there were no differences in the maturity index of free-living nematodes, greater abundances of Plectidae, Prismatolaimidae, and Tylencholaimidae were observed in organically managed soils ($P <$ 0.05, Table 2).

Bacterivorous (55.7 ± 14.3%, mean ± standard deviation) and plant-parasitic (32.3 ± 14.0%) nematodes were the most abundant trophic groups in each soil management

TABLE 2. Nematodes per gram of dry soil for calculation of maturity and trophic diversity indices in 1993 and 1994.

Family	CP value[a]	Trophic group[b]	Farm type and year[c]				*P*-values[d]		
			Conventional		Organic				
			1993 (48)	1994 (36)	1993 (62)	1994 (48)	Type	Year	Type × year
Alaimidae	4	1	0.072	0.023	0.068	0.027	n.s.	**	n.s.
Anatonchidae	4	5	0.038	0.008	0.081	0.000	n.s.	n.s.	n.s.
Anguinidae	2	2	0.047	0.005	0.078	0.002	n.s.	**	n.s.
Aphelenchidae	2	2	0.580	0.079	0.361	0.136	n.s.	***	*
Aphelenchoididae	2	2	0.758	0.182	0.749	0.181	n.s.	***	n.s.
Bastianiidae	3	1	0.000	0.000	0.003	0.000	n.s.	n.s.	n.s.
Belonolaimidae	2	3	0.033	0.036	0.100	0.026	n.s.	n.s.	n.s.
Bunonematidae	1	1	0.009	0.001	0.003	0.000	n.s.	*	n.s.
Carcharolaimidae	4	5	0.000	0.000	0.009	0.001	n.s.	n.s.	n.s.
Cephalobidae	2	1	4.332	1.331	4.149	1.841	n.s.	***	n.s.
Chromadoridae	3	5	0.000	0.002	0.000	0.001	n.s.	n.s.	n.s.
Criconematidae	3	3	0.021	0.034	0.155	0.120	*	n.s.	n.s.
Cylindrolaimidae	3	1	0.000	0.002	0.000	0.002	n.s.	n.s.	n.s.
Diphtherophoridae	3	2	0.001	0.002	0.008	0.000	n.s.	n.s.	n.s.
Diplogasteridae	1	1	0.006	0.000	0.004	0.001	n.s.	n.s.	n.s.
Diploscapteridae	1	1	0.230	0.001	0.097	0.002	n.s.	*	n.s.
Dorylaimellidae	5	4	0.025	0.004	0.065	0.025	n.s.	n.s.	n.s.
Dorylaimidae	4	4	5.025	0.998	4.512	1.874	n.s.	n.s.	n.s.
Heteroderidae	3	3	0.093	0.002	0.156	0.039	*	***	n.s.
Hoplolaimidae	3	3	0.816	0.449	2.077	0.640	n.s.	n.s.	n.s.
Ironidae	4	5	0.000	0.000	0.607	0.000	n.s.	n.s.	n.s.
Leptolaimidae	3	1	0.000	0.001	0.004	0.001	n.s.	n.s.	n.s.
Leptonchidae	4	4	0.031	0.041	0.081	0.024	n.s.	n.s.	n.s.
Longidoridae	5	3	0.018	0.004	0.011	0.005	n.s	n.s	n.s
Microlaimidae	3	1	0.000	0.000	0.002	0.000	n.s	n.s	n.s
Monhysteridae	1	1	0.022	0.007	0.025	0.005	n.s	*	n.s
Mononchidae	4	5	0.867	0.537	2.195	0.795	n.s.	n.s.	n.s.
Mononchulidae	4	5	0.028	0.003	0.009	0.008	n.s.	n.s.	n.s.
Nygolaimidae	5	5	0.002	0.000	0.029	0.004	n.s.	n.s.	n.s.
Panagrolaimidae	1	1	0.077	0.001	0.017	0.006	n.s	**	*
Paraphelenchidae	2	2	0.004	0.000	0.003	0.001	n.s	*	n.s
Plectidae	2	1	0.190	0.069	0.354	0.113	*	***	n.s
Pratylenchidae	3	3	0.106	0.124	0.080	0.031	n.s	n.s	n.s
Prismatolaimidae	3	1	0.022	0.007	0.098	0.018	*	*	n.s
Rhabditidae	1	1	4.458	0.948	5.463	1.388	n.s	**	n.s
Seinuridae	2	5	0.068	0.028	0.076	0.022	n.s.	n.s.	n.s.
Tripylidae	3	4	0.592	0.081	0.349	0.070	n.s.	n.s.	n.s.
Trichodoridae	4	3	0.001	0.001	0.031	0.004	n.s	n.s	n.s
Tylenchidae	2	3	1.955	1.273	2.044	1.077	n.s	**	n.s
Tylencholaimellidae	4	2	0.004	0.001	0.035	0.001	n.s	n.s.	n.s
Tylencholaimidae	4	2	0.000	0.001	0.006	0.002	*	n.s	n.s
Tylenchulidae	2	3	0.133	0.047	0.215	0.048	n.s	*	n.s

[a] CP values are from Bongers (1990).

[b] Trophic groups are assigned as: 1 = bacterivorous, 2 = fungivorous, 3 = plant-parasitic, 4 = omnivorous, and 5 = predatory.

[c] Samples included in the statistical analyses.

[d] *P*-values are between subjects effects from repeated measures analysis of variance. *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$, n.s.: $P > 0.05$.

type. However, there were no differences in trophic composition, FB, or H' between soils managed conventionally or organically. Maximum differences in indices describing mostly free-living taxa (i.e., MINO, H') were observed in spring, whereas indices including large proportions of plant-parasitic taxa (i.e., PPI, ΣMI, and PPI:MI) were greatest during fall sampling periods (Table 4). There was no seasonal effect on FB measurements. Small coefficients of determination (R^2) indicated that differences between

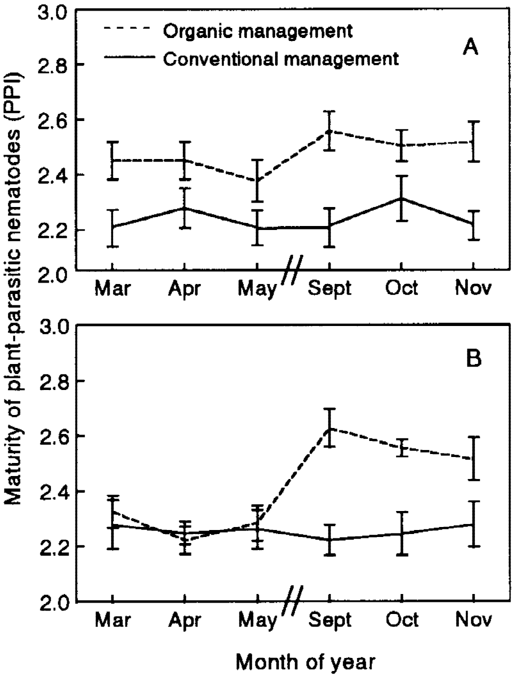

FIG. 1. Effect of soil management approach on plant-parasitic nematode maturity index in spring (March, April, May) and fall (September, October, November). A) 1993. B) 1994. Bars are standard error.

TABLE 3. Effect of organic or conventional farming practice on nematode community structure and ecosystem function.

	Organic vs. conventional[a]	1993 vs. 1994[a]
Successional maturity		
Maturity index (MINO)	0.8394	0.1448
Plant-parasitic index (PPI)	0.0005	0.6873
Combined maturity index (ΣMI)	0.0947	0.0892
PPI:MI	0.0670	0.2367
Trophic composition		
Bacterivores	0.6476	0.1854
Fungivores	0.1385	0.0331
Funigivore: Bacterivore (FB)	0.1334	0.0516
Omnivores	0.0736	0.0098
Predatory	0.8115	0.0325
Plant parasites	0.5254	0.0134
Shannon trophic diversity (H')	0.2227	0.9287
Available nitrogen (1994 only)		
Ammonium (µg/g dry soil)	0.0582	
Nitrate (µg/g dry soil)	0.8362	

[a] Numbers are *P*-values.

pairs of organic and conventional farms accounted for little of the variation associated with maturity and trophic indices.

Generally, maturity indices containing free-living nematodes were correlated negatively with values of available nitrate and ammonium (Table 5). Significant negative correlations were observed for nitrate concentrations measured subsequent to nematode indices by 0, 1, and 4 months for MINO and 1 month for ΣMI. Correlation coefficient values were greatest numerically for a lag time of 4 months. Significant negative correlations were observed for ammonium concentrations measured subsequent to nematode indices by 5 and 6 months for MINO and FB, respectively (Table 5). Positive correlation values were observed between maturity indices including plant-parasitic nematodes (PPI and PPI:MI) and available nitrate measured 0 and (or) 4 months after nematode communities. Values observed between plant-parasitic maturity and available ammonium content were not correlated (Table 5).

Canonical correspondence analysis results are displayed by an ordination diagram where environmental variables are depicted by vectors, and maximum numbers of specific nematode families are marked by points (Fig. 2). Numbers of each family decrease with increasing distance from each point in a unimodal fashion (ter Braak, 1986). The result is a bi-plot that approximates the weighted averages of each nematode family with respect to each of the environmental variables (including soil management style). Ordination axes are presented in sequence of variance explained by linear combination of environmental variables. In total, six environmental variables explained 81.5% of the variance of the family data. With CCA constrained to six environmental variables, the eigenvalues of CCA axes 1 (0.53, horizontal) and 2 (0.34, vertical) explained 52% of the cumulative variance of the nematode families data (Fig. 2). The family-environment correlations were large (axis 1 = 0.82 and axis 2 = 0.72). The projection of each family on each nominal environmental variable (organic or conventional) approximates the fraction of the total abundance of that family that is achieved

TABLE 4. Effect of season on the magnitude of difference in nematode community structure between organic and conventional farming practices.[a]

Index	Spring	Fall	P	R^2
Maturity index (MINO)	–0.055	0.016	0.0436	0.05
Plant-parasitic index (PPI)	0.036	0.278	0.0003	0.16
Combined maturity index (∑MI)	–0.104	0.172	0.0001	0.24
PPI:MI	0.010	0.027	0.0326	0.06
Funigivore: Bacterivore[a] (FB)	–0.060	–0.012	0.0523	0.05
Shannon trophic diversity (H')	–0.332	–0.043	0.0135	0.08

[a] Negative values indicate that conventional soils had greater index values than organic soils; the opposite was true for positive values.

at sites of that class (ter Braak, 1995). The ordination suggests Bastianidae, Bunonematidae, Diphtherophoridae, Prismatolaimidae, Microlaimidae, and Tylencholaimellidae are more common in organically managed soils. Alaimidae, Anguinidae, Aphelenchoididae, Leptolaimidae, Panagrolaimidae, Rhabditidae, and Heteroderidae are more common in conventionally managed soils. Environmental vectors point toward the maximum change of a parameter, and vector length indicates its importance in data interpretation. The position of the environmental vector depends on the eigenvalues of the axes and the intra-set correlations of that environmental vector (ter Braak, 1986). The length of a vector is equal to the rate of change in weighted average predicted from the bi-plot and, therefore, explains the extent of variation in family distribution along the parameter. Long vectors correlate more strongly with ordination axes than short vectors and have greater reliability in predictive applications. Relative contributions of the environmental variables to the CCA axes can be interpreted by examining the *t*-test scores of the canonical coefficients between the environmental variables and the ordination axes (ter Braak, 1992). Two variables—available ammonium ($t_{0.05(2)784} = 4.4$) and pH ($t_{0.05(2)784} = -2.1$)—contributed significantly to axis 1. Four variables—available ammonium ($t_{0.05(2)784} = 5.7$), percent sand ($t_{0.05(2)784} = 2.1$), EC ($t_{0.05(2)784} = -2.4$), and percent organic matter ($t_{0.05(2)784} = 2.8$)—contributed to axis 2. The first axis of the explanatory CCA could be interpreted as a gradient of ammonium

TABLE 5. Correlation of nematode community composition and time of subsequent nitrogen source availability (µg/g dry soil).

	Community index[a]				
Nitrogen sources, lag period	MINO	PPI	∑MI	PPI:MI	FB
Nitrate					
T-0[b] (136)[c]	–0.229**	0.195*	n.s.	0.3001***	n.s.
T-1 (90)	–0.230*	n.s.	–0.242*	n.s.	n.s.
T-2 (44)	n.s.	n.s.	n.s.	n.s.	n.s.
T-4 (45)	–0.415**	n.s.	n.s.	0.353*	n.s.
T-5 (43)	n.s.	n.s.	n.s.	n.s.	n.s.
T-6 (133)	n.s.	n.s.	n.s.	n.s.	n.s.
Ammonium					
T-0 (138)	n.s.	n.s.	n.s.	n.s.	n.s.
T-1 (92)	n.s.	n.s.	n.s.	n.s.	n.s.
T-2 (46)	n.s.	n.s.	n.s.	n.s.	n.s.
T-4 (45)	n.s.	n.s.	n.s.	n.s.	n.s.
T-5 (43)	–4.07**	n.s.	n.s.	n.s.	n.s.
T-6 (135)	n.s.	n.s.	n.s.	n.s.	–0.211*

[a] MINO = maturity index; PPI = plant parasite index; ∑MI = combined maturity index; PPI:MI = ratio of plant parasite index and maturity index; FB = ratio of fungivores to bacterivores.

[b] Values represent the number of months that nematode communities were measured prior to nitrogen.

[c] Values in parentheses are sample size for each time.

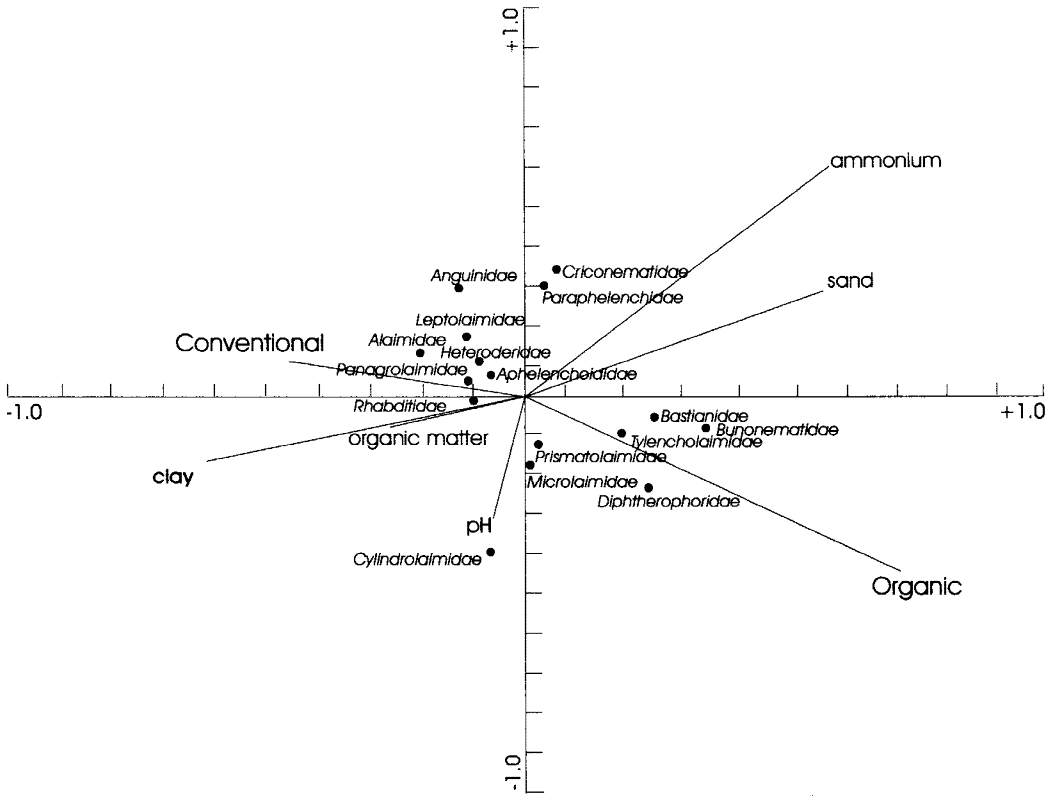

FIG. 2. Canonical correspondence analysis bi-plot of nematode families and environmental variables for soils managed organically or conventionally. Points represent numbers of collected nematodes in a family; abundances decrease with increasing distance from each point in a unimodal fashion (ter Braak, 1986). Data represent a compilation of all sites and times sampled.

availability. From Figure 2, it is evident that Criconematidae and Paraphelenchidae are more common in soils with greater availability of ammonium than are other families. The second axis appeared to be a gradient of cation exchange capabilities and suggests that Cylindolaimidae are common in soils with large nutrient exchange capabilities.

DISCUSSION

In this study, plant-parasitic and bacterivorous nematodes were the most abundant trophic groups present in organically and conventionally managed soils. Numbers of both trophic groups were greater in soils managed organically than conventionally. These results contrast with other reports that suggest that numbers of plant-parasitic nematodes decrease after additions of organic amendments (e.g., Bohlen and Edwards, 1994; Clark et al., 1998; Griffiths et al., 1994). No trophic group was a distinguishing characteristic of soils managed conventionally or organically. Fungivore: bacterivore ratios observed in this study were relatively small (median = 0.10), indicating a predominance of bacterivorous nematodes in both management systems. This study contrasts with that of Bohlen and Edwards (1994), who found smaller bacterivore:fungivore ratios in soils amended with leguminous green manures (1.45) and ammonium nitrate (1.66) than with cow manure (1.83). If Bohlen and Edwards' (1994) values are recalculated as FB (fungivores/ [bacterivores + fungivores]), they translate into values of 0.41, 0.38, and 0.35, respectively. Nevertheless, the ratios are an order of magnitude greater than observed in this study. Wide ranges of FB (0.15 to 2.30) have been observed in other studies where numbers of fungivores were twice as abundant in organically managed than conventionally managed soils (Porazinska and Coleman, 1995). Presumably, different mechanisms control bacterial and fungal populations. For example, small numbers of fungivores compared to bacterivores may reflect resource quality. Bacterial grazers ingest whole bacteria, and their prey have few defenses. Fungi contain anti-grazing chemicals, and fungivores must penetrate sometimes-resistant hyphal walls to obtain cell contents (Wardle and Yeates, 1993). Bacterivores may control the number of bacteria through grazing but will also control fungi by affecting the outcome of fungal-bacterial competition (Wardle and Yeates, 1993). Furthermore, applications of certain synthetic fertilizers, such as anhydrous ammonia, slow recovery of fungi more than bacteria (Eno and Blue, 1954). In this study, organic and conventional sites differed in the crops grown and whether or not synthetic herbicides and fertilizers were used as management tools. Therefore, FB respond to factors other than crop species and use of or abstinence from synthetic herbicides and fertilizers. Apparently, similarities between management practices outweighed their differences.

The results of the current study concur with other reports of the relative abundance of Prismatolaimidae in soils managed organically (Ferris et al., 1996; Yeates et al., 1997). In contrast to Ferris et al. (1996), I observed more Plectidae and Tylencholaimidae in organic than conventional management strategies instead of Rhabditidae. Plectidae and Prismatolaimidae are excellent colonizing taxa (Yeates and van der Meulen, 1996). Furthermore, a significant effect of year, but not management type, was observed for Cephalobidae, which contrasts with Yeates et al. (1997), who observed that numbers of Cephalobidae were consistently more numerous in soils under organic than conventional management. Numbers of microbial-feeding nematodes indicate an important role in nitrogen mineralization (Ingham et al., 1985). However, it is not clear whether nematode populations reflect relative grazing activities, competition, antagonism, or simply the abundance of suitable food (Scow et al., 1994). Often, there is no significant correlation between microbial-feeding nematodes and the biomass of their food source, bacteria, and fungi (e.g., Bostrom and Söhlenius, 1986; Neher and Campbell, 1994; Neher et al., 1995; 1998). Perhaps the lack of association observed for concurrent measures supports the hypothesis of asynchronous peaks in populations of predator and prey.

No differences in values of maturity indices for free-living nematodes were observed between soils managed organically or conventionally. These results may reflect similar frequencies of disturbance in both management systems even though the type of management differed. For example, soils managed organically underwent frequent cultivation, and herbicides were substituted for cultivation in soils managed conventionally. Cultivation decreases maturity and trophic diversity index values (Neher and Campbell, 1994). The results of this study support Yeates et al. (1997), who observed similar proportions of free-living nematodes in the CP = 1, CP = 4, and CP = 5 groups in soils managed organically or conventionally. In contrast, I observed significantly greater PPI values in soils managed organically than conventionally, which concurs with Yeates et al. (1997). Much of the contrast in PPI values between management approaches can be attributed to greater numbers of Hoplolaimidae and Trichodoridae in organic than conventional soils. The relative abundance of these families likely reflects the host species present (Maggenti, 1981). Clark et al. (1998) noted increases in particular plant-parasitic taxa corresponding to the host species rotation sequence in their comparison of conventional and alternative tomato ecosystems. As a measurement including both free-living and plant-parasitic nematodes, ΣMI did not detect differences between soil managed conventionally and organically. These results concur with those of Porazinska and Coleman (1995), who measured similar ΣMI values for cucumber plantings grown under synthetic fertilizer and organic poultry manure regimes. In contrast, Yeates et al. (1997) found somewhat greater ΣMI values for organically than conventionally managed systems in silt and loam soils but not sandy soils.

Understanding the relationships among members of the soil community and the factors controlling the timing and release of nutrients by biological processes is important for optimal management of cropping systems (Scow et al., 1994). Nematodes may play a role in appropriate timing and release of nitrogen. The current study and others (Wardle et al., 1995; Yeates et al., 1993b) have demonstrated significant temporal lag effects between nematode populations and nitrogen availability. For instance, *Bursilla* Andrássy, 1976 (Rhabditidae) is a major contributor to nitrogen mineralization by mobilizing nitrogen previously bound by bacteria (Ferris et al., 1996), but contributions of other nematode taxa to nitrogen mineralization have yet to be quantified.

Population differences between years of the study correspond with those observed by Yeates (1984) in pasture soils. For taxa common to both studies, annual fluctuations were observed for Tylenchidae, Heteroderidae, Rhabditidae, Panagrolaimidae, Cephalobidae, Plectidae, and Monhysteridae. In contrast, annual population differences were observed for Aphelenchidae and Aphelenchoididae in this study and Pratylenchidae in Yeates' (1984). Use of community structure indices are more robust to annual fluctuations and thus, more reliable than genera or families of nematodes for regional or national monitoring programs (Neher and Campbell, 1994; Neher et al., 1995).

Indices that describe the majority of variance within nematode communities appeared to have greater ability to differentiate between management type in fall than in spring months. These results correspond to the greater total abundances of nematodes during the fall. Peaks in nematode populations in fall months can be related to two factors: (i) the input of crop residue following harvest of crops (Kastner and Germershausen, 1989) and (ii) more favorable soil temperatures in fall than in spring (Stinner and Crossley, 1982). The decline of nematode numbers during spring (March–May) roughly follows the loss of crop residue through decomposition, correlated to the large proportion of fauna being free-living rather than plant-parasitic (Stinner and Crossley, 1982). These seasonal patterns are also apparent in forest ecosystems (Popovici, 1984). Based on these findings, the best time to measure successional maturity or trophic diversity of temperate-zone nematode communities is during fall months because differences between organically and conventionally managed agricultural soils are most evident at this time.

Of the environmental factors measured, available ammonium, pH, EC, and soil texture were the features of the environment correlated with nematode families. It is critical to consider soil texture when interpreting maturity indices (Yeates, 1984; Yeates et al., 1997). For example, nematode community composition will be different in soils with sand, silt, or loam texture, even with similar management practices (Yeates et al., 1997). In this study, conventionally and organically managed sites were paired by soil type, including texture. Differences between management practice were unable to surpass effects of soil properties.

Based on the similarity of index values between soil management practices, organic farms are not useful as a reference base for maturity and trophic diversity indices for annual crops in conventional farms. Differences observed in plant-parasitic nematode communities can be attributed primarily to the different host crops present in the contrasting management practices. Physical disturbances such as cultivation disturb soil nematode community structure and function as much or more than applications of synthetic chemicals such as fertilizers and pesticides (Neher, 1995; Neher and Campbell, 1994). Sites with minimal or no physical disturbance may serve as better reference sites in environmental monitoring programs than sites without application of synthetic chemicals. These conclusions were robust enough to cross a wide range of soil textures and seasons.

LITERATURE CITED

Akhtar, M., and I. Mahmood. 1996. Control of plant-parasitic nematodes with organic and inorganic amendments in agricultural soil. Applied Soil Ecology 43:243–247.

Allison, F. E. 1973. Organic farming. Pp. 558–582 *in* F. E. Allison, ed. Developments in soil science. III. Soil organic matter and its role in crop production. Amsterdam: Elsevier Science Publishing.

Anderson, R. V., W. D. Gould, L. E. Woods, C. Cambardella, R. E. Ingham, and D. C. Coleman. 1983. Organic and inorganic nitrogenous losses by microbivorous nematodes in soil. Oikos 40:75–80.

Andrén, O., and J. Lagerlöf. 1983. Soil fauna (microarthropods, enchytraeids, nematodes) in Swedish agricultural cropping systems. Acta Agriculturae Scandinavica 33:33–52.

Bohlen, P. J., and C. A. Edwards. 1994. The response of nematode trophic groups to organic and inorganic nutrient inputs in agroecosystems. Pp. 235–244 *in* J. W. Doran, D. C. Coleman, D. F. Bezdicek, and B. A. Stewart, eds. Defining soil quality for a sustainable environment . Madison, WI: Agronomy Society of America.

Bolton, H., Jr. 1983. Soil microbial biomass and selected soil enzyme activities on an alternatively and a conventionally managed farm. M. S. thesis, Washington State University, Pullman, WA.

Bolton, H., Jr., L. F. Elliott, R. I. Papendick, and D. F. Bezdicek. 1985. Soil microbial biomass and selected soil enzyme activities: Effect of fertilization and cropping practices. Soil Biology and Biochemistry 17:297–302.

Bongers, T. 1990. The maturity index: An ecological measure of environmental disturbance based on nematode species composition. Oecologia 83:14–19.

Bongers, T., R. Alkemade, and G. W. Yeates. 1991. Interpretation of disturbance-induced maturity decrease in marine nematode assemblages by means of the Maturity Index. Marine Ecology Progress Series 76: 135–142.

Bongers, T., R. G. M. de Goede, G. W. Korthals, and G. W. Yeates. 1995. Proposed changes of *c-p* classification for nematodes. Russian Journal of Nematology 3: 61–62.

Bongers, T., and G. Korthals. 1995. The behaviour of MI and PPI under enriched conditions. Nematologica 41:286.

Boström, S., and B. Söhlenius. 1986. Short-term dynamics of nematode communities in arable soil: Influence of a perennial and an annual cropping system. Pedobiologia 29:345–357.

Cataldo, D. A., M. Haroon, L. E. Schrader, and V. L. Youngs. 1975. Rapid colorimetric determination of nitrate in plant tissue by titration of salicylic acid. Communications in Soil Science and Plant Analysis 6:71–80.

Clark, M. S., H. Ferris, K. Klonsky, W. T. Lanini, A. H. C. van Bruggen, and F. G. Zalom. 1998. Agronomic, economic, and environmental comparison of pest management in conventional and alternative tomato and corn systems in northern California. Agriculture, Ecosystems and Environment 68:51–71.

Dodds, W. K., M. K. Banks, C. S. Clenan, C. W. Rice, D. Sotomayor, E. A. Strauss, and W. Yu. 1996. Biological properties of soil and subsurface sediments under abandoned pasture and cropland. Soil Biology and Biochemistry 28:837–846.

Eno, C. F., and W. G. Blue. 1954. The effect of anhydrous ammonia on nitrification and the microbiological population in sandy soils. Soil Science Society of America Proceedings 18:178–181.

Ettema, C. H., and T. Bongers. 1993. Characterization of nematode colonization and succession in disturbed soil using the Maturity Index. Biology and Fertility of Soils 16:79–85.

Ferris, H., R. C. Venette, and S. S. Lau. 1996. Dynamics of nematode communities in tomatoes grown in conventional and organic farming systems, and their impact on soil fertility. Applied Soil Ecology 3:161–175.

Freckman, D. W. 1988. Bacterivorous nematodes and organic-matter decomposition. Agriculture, Ecosystems and Environment 24:195–217.

Freckman, D. W., and C. H. Ettema. 1993. Assessing nematode communities in agroecosystems of varying human intervention. Agriculture, Ecosystems and Environment 45:239–261.

Gee, G. W., and J. W. Bauder. 1985. Particle-size analysis. Pp. 383–411 *in* A. Klute, ed. Methods of soil analysis, Part 1. Agronomy Monograph No. 9, 2nd ed. Madison, WI: American Society of Agronomy.

Griffiths, B. S., K. Ritz, and R. E. Wheatley. 1994. Nematodes as indicators of enhanced microbiological activity in a Scottish organic farming system. Soil Use and Management 10:20–24.

Ingham, R. E., J. A. Trofymow, E. R. Ingham, and D. C. Coleman. 1985. Interactions of bacteria, fungi, and their nematode grazers: Effects on nutrient cycling and plant growth. Ecological Monographs 55:119–140.

Kaplan, M., and J. Noe. 1993. Effects of chicken-excrement amendments on *Meloidogyne arenaria*. Journal of Nematology 25:71–77.

Karr, J. R. 1991. Biological integrity: A long-neglected aspect of water resource management. Ecological Application. 1:66–84.

Karr, J. R. 1995. Ecological integrity and ecological health are not the same. Pp. 1–15 *in* P. Schulze, ed. Engineering within ecological constraints. Washington, DC: National Academy Press.

Kastner, V. A., and K. Germershausen. 1989. Struktur und Abundanzdynamik der Nematodenfauna in einem Schwarzerde-Loßboden. Hercynia 26:71–93.

Keeney, D. R., and D. W. Nelson. 1982. Nitrogen—inorganic forms. Pp. 643–698 *in* A. L. Page, R. H. Miller, and D. R. Keeney, eds. Methods of soil analysis, Part 2. Chemical and microbiological properties. Agronomy Monograph No. 9, 2nd ed. Madison, WI: American Society of Agronomy.

Ludwig, J. A., and J. F. Reynolds. 1988. Statistical ecology: A primer on methods and computing. New York: John Wiley.

Maggenti, A. R. 1981. General nematology. New York: Springer-Verlag.

Mian, I. H., and R. Rodríguez-Kábana. 1982. Soil amendments with oil cakes and chicken litter for control of *Meloidogyne arenaria*. Nematropica 12:205–220.

Moore, J. C., and P. C. de Ruiter. 1991. Temporal and spatial heterogeneity of trophic interactions within below-ground food webs. Agriculture, Ecosystems and Environment 34:371–397.

Neely, C. L., M. H. Beare, W. L. Hargrove, and D. C. Coleman. 1991. Relationships between fungal and bacterial substrate-induced respiration, biomass and plant residue composition. Soil Biology and biochemistry 23: 947–954.

Neher, D. A. 1995. Biological diversity in soils of agricultural and natural ecosystems. Pp. 55–72 *in* R. K. Olson, C. A. Francis, and S. Kaffka, eds. Exploring the role of diversity in sustainable agriculture. Madison, WI: American Society of Agronomy.

Neher, D. A., and C. L. Campbell. 1994. Nematode communities and microbial biomass in soils with annual and perennial crops. Applied Soil Ecology 1:17–28.

Neher, D. A., K. N. Easterling, D. Fiscus, and C. L. Campbell. 1998. Comparison of nematode communities in agricultural soils of North Carolina and Nebraska. Ecological Applications 8:213–223.

Neher, D. A., S. L. Peck, J. O. Rawlings, and C. L. Campbell. 1995. Measures of nematode community structure and sources of variability among and within fields. Plant and Soil 170:167–181.

Popovici, I. 1984. Nematode abundance, biomass and production in a beech forest ecosystem. Pedobiologia 26:205–219.

Popovici, I. 1992. Nematodes as indicators of ecosystem disturbance due to pollution. Studia Universitatea Babes-Bolyai, Biologia 37:15–27.

Porazinska, D. L., and D. C. Coleman. 1995. Ecology of nematodes under influence of *Curcurbita* spp. and different fertilizer types. Supplement to the Journal of Nematology 27:617–623.

Rao, M. S., P. P. Reddy, and M. Nagesh. 1997. Management of root-knot nematode, *Meloidogyne incognita* on tomato by integration of *Trichoderma harzianum* with neem cake. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz 104:423–425.

Reganold, J. P., A. S. Palmer, J. C. Lockhart, and A. N. Macgregor. 1993. Soil quality and financial performance of biodynamic and conventional farms in New Zealand. Science 260:344–349.

Rodríguez-Kábana, R. 1986. Organic and inorganic nitrogen amendments to soil as nematode suppressants. Journal of Nematology 18:129–135.

Samoiloff, M. R. 1987. Nematodes as indicators of toxic environmental contaminants. Pp. 433–439 *in* J. A. Veech and D. W. Dickson, eds. Vistas on nematology. Hyattsville, MD: Society of Nematologists.

Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. Urbana: University of Illinois.

Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.

Scow, K. M., O. Somasco, N. Gunapala, S. Lau, R. Venette, H. Ferris, R. Miller, and C. Shennan, 1994. Transition from conventional to low-input agriculture changes soil fertility and biology. California Agriculture 48:20–26.

Smith, J. L., and J. W. Doran. 1996. Measurement and use of pH and electrical conductivity for soil quality analysis. Pp. 169–185 *in* J. W. Doran and A. J. Jones, eds. Methods for assessing soil quality. Soil Science Society of America Special Publication. Madison, WI: Soil Science Society of America.

Söhlenius, B., S. Boström, and A. Sandor. 1988. Carbon and nitrogen budgets of nematodes in arable soil. Biology and Fertility of Soils 6:1–8.

Stinner, B. R., and D. A. Crossley, Jr. 1982. Nematodes in no-tillage agroecosystems. Pp. 14–28 *in* D. W. Freckman, ed. Nematodes in soil ecosystems. Austin, TX: University of Texas Press.

Storer, D. A. 1984. A simple high-sample-volume ashing procedure for determination of soil organic matter. Communications in Soil Science and Plant Analysis 15: 759–772.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.

ter Braak, C. J. F. 1992. CANOCO-A Fortran Program for Canonical Community Ordination (vers 3.12). Ithaca, NY: Microcomputer Power.

ter Braak, C. J. F. 1995. Ordination. Pp. 91–173 *in* R. H. G. Jongman, C. J. F. ter Braak, and O. F. R. van Tongeren, eds. 1995. Data analysis in community and landscape ecology. Cambridge, UK: Cambridge University Press.

United States Department of Agriculture. 1980. Report and recommendations on organic farming. Washington, DC: United States Government Printing Office.

Wardle, D. A., and G. W. Yeates. 1993. The dual importance of competition and predation as regulatory forces in terrestrial ecosystems: Evidence from decomposer food-webs. Oecologia 93:303–306.

Wardle, D. A., G. W. Yeates, and R. N. Watson. 1995. The detritus food-web and the diversity of soil fauna as indicators of disturbance regimes in agro-ecosystems. Plant Soil 170:35–43.

Wasilewska, L. 1989. Impact of human activities on nematodes. Pp. 123–132 *in* M. Charholm and L. Bergstrom, eds. Ecology of arable land. Dordrecht, The Netherlands: Kluwer.

Weiss, B., and O. Larink. 1991. Influence of sewage sludge and heavy metals on nematodes in an arable soil. Biology and Fertility of Soils 12:5–9.

Yeates, G. W. 1982. Variation of pasture nematode populations over thirty-six months in a summer dry silt loam. Pedobiologia 24:329–346.

Yeates, G. W. 1984. Variation in soil nematode diversity under pasture with soil and year. Soil Biology and Biochemistry 16:95–102.

Yeates, G. W. 1987. How plants affect nematodes. Advances in Ecological Research 17:61–113.

Yeates, G. W. 1994. Modification and qualification of the nematode maturity index. Pedobiologia 38:97–101.

Yeates, G. W., R. D. Bardgett, R. Cook, P. J. Hobbs, P. J. Bowling, and J. F. Potter. 1997. Faunal and microbial diversity in three Welsh grassland soils under conventional and organic management regimes. Journal of Applied Ecology 34:453–470.

Yeates, G. W., T. Bongers, R. G. M. de Goede, D. W. Freckman, and S. S. Georgieva. 1993a. Feeding habits in soil nematode families and genera—an outline for soil ecologists. Journal of Nematology 25:315–331.

Yeates, G. W., and H. Van der Meulen. 1996. Recolonization of methyl-bromide sterilized soils by plant and soil nematodes over 52 months. Biology and Fertility of Soils 21:1–6.

Yeates, G. W., D. A. Wardle, and R. N. Watson. 1993b. Relationships between nematodes, soil microbial biomass, and weed-management strategies in maize and asparagus cropping systems. Soil Biology and Biochemistry 25:869–876.