

Nematode Communities as Ecological Indicators of Agroecosystem Health

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CONTENTS

7.1	Introduction.....	105
7.2	Nematodes and Their Role in the Soil Ecosystem.....	106
7.3	Nematode Community Indices.....	107
	7.3.1 Maturity Indices.....	107
	7.3.2 Trophic Diversity Indices.....	109
7.4	Relationship of Nematode Communities to Ecosystem Function.....	110
	7.4.1 Nutrient Availability.....	110
	7.4.2 Decomposition of Organic Matter.....	111
7.5	Index Calibration.....	111
	7.5.1 Perennial Crops.....	112
	7.5.2 Organic Production.....	112
	7.5.3 Confounded Disturbance Regimes.....	115
7.6	Regional Scale Application.....	115
7.7	Future Research.....	116
	References.....	117

7.1 INTRODUCTION

In the search for ways to measure the sustainability of agroecosystems, the soil has often been ignored. However, soil supports essential ecosystem functions, such as promoting plant productivity, enhancing water relations, regulating nutrient mineralization, permitting decomposition, and acting as an environmental buffer (Neher,

1999a). The relative health and quality of an agroecosystem's soil, especially its biological and ecological components, should correlate closely with the overall health and sustainability of the system.

Biologically, soil ecosystems support a great diversity of both microfauna (fungi, bacteria, protozoa, and algae) and mesofauna (protozoa, arthropods, and nematodes). The author's research suggests that measures of the community structure of one of these biological components, namely nematodes, may serve as useful indicators of the health of agricultural soils, and therefore have promise as indicators of sustainability.

7.2 NEMATODES AND THEIR ROLE IN THE SOIL ECOSYSTEM

Soil nematodes (roundworms) are relatively abundant (6×10^4 to 9×10^6 per m^2), small (300 μm to 4 mm) animals with short generation times (days to a few weeks) that allow them to respond to changes in food supply (Wasilewska, 1979; Bongers, 1990). Relative to other soil micro and mesofauna, trophic or functional groups of nematodes can be identified easily, primarily by morphological structures associated with various modes of feeding (Yeates and Coleman, 1982). Nematode species with a buccal stylet (spear like structure) feed on cell contents and juices obtained by piercing the cellular walls of plant roots or fungal mycelium. Other species have no stylets and feed on particulate food such as bacteria and small algae (Vinciguerra, 1979). Agricultural soil communities often have large numbers of bacterial and plant feeding nematodes and smaller numbers of fungal feeding, omnivorous, and predaceous nematodes (Wasilewska, 1979; Hendrix, et al., 1986).

Nematodes are part of a complex soil ecosystem. A small fraction of soil fauna depends upon primary producers, feeding on plant roots and their exudates. The subgroups of these organisms that form parasitic relationships with plants and their roots are the best known of soil organisms because of the damage they cause to agricultural crops. They decrease plant production, disrupt plant nutrient and water transfer, and decrease fruit and tuber quality and size (Yeates and Coleman, 1982; Brussaard et al., 1997). Most soil organisms perform beneficial roles in ecosystem function and are not parasites or pests. For example, most soil bacteria, actinomycetes, fungi, algae, and protozoa are decomposers of organic matter. These microorganisms are involved directly with production of humus, cycling of nutrients and energy flow, elemental fixation, metabolic activity in soil, and the production of complex chemical compounds that cause soil aggregation. Microbial grazing mesofauna (e.g., Collembola, mites, nematodes, and protozoa) affect growth and metabolic activities of microbes and alter the microbial community, thus regulating decomposition rate (Wasilewska et al., 1975; Trofymow and Coleman, 1982; Whitford et al., 1982; Yeates and Coleman, 1982; Seastedt, 1984) and nutrient mineralization (Seastedt et al., 1988; Sohlenius et al., 1988).

It should be noted that only 10% of soil dwelling species have been identified (Hawksworth and Mound, 1991). Our knowledge of soil organisms has been limited by our inability to extract organisms from soil efficiently and by difficulties in

involved in identification of new species, determining their food preferences, quantifying interactions among organisms in soil communities, and defining specific functions in ecosystems (de Bruyn, 1997).

Soil dwelling organisms are linked through detrital food webs, which consist of pathways centered on plant roots, bacteria, and fungi (Moore et al., 1988; see Figure 7.1). Protozoa feed primarily within the bacterial pathway. Microarthropods feed primarily within the fungal pathway. Bacterial and fungal pathways unite higher in the food chain at the trophic level of predaceous nematodes and mites (Whitford, 1989). Arthropods and nematodes have the potential to feed upon, or otherwise affect, organisms in all three pathways.

7.3 NEMATODE COMMUNITY INDICES

Nematodes have attributes that make them useful as ecological indicators (Freckman, 1988; Neher and Campbell, 1994). Various kinds of perturbations 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) affect the species richness, trophic structure, and successional status of nematode communities. Because they reflect changes in soil structure and function related to these perturbations, indices of nematode community structure show promise for monitoring the ecological condition of the soil (Bongers, 1990; de Goede, 1993; Ettema and Bongers, 1993; Freckman and Ettema, 1993).

There are many methods of measuring nematode community structure. Through a series of experiments on sampling and experimental design at various spatial scales, the author concluded that maturity (Bongers, 1990) and trophic diversity indices are capable of differentiating among sampling sites better and more efficiently than measures based on populations or ratios of individual trophic groups (Neher et al., 1995). Maturity and trophic diversity indices measure different aspects of soil communities and are complementary when used together. "Maturity" is a measure of successional status and trophic diversity measures food web structure.

7.3.1 Maturity Indices

Maturity indices are a measure of the ecological successional status of a soil community. They are based on the principle that different taxa have different sensitivities to stress or disruption of the successional sequence because of differences in their life history characteristics. Because succession can be interrupted at various stages by common agricultural practices, such as cultivation and applications of fertilizer and pesticides (Ferris and Ferris 1974; Wasilewska, 1979), the successional status of a soil community may reflect the history of disturbance.

The maturity index is a weighted mean frequency of taxa assigned weights ranging from 1 to 5, with smaller weights assigned to taxa with relative tolerance to disturbance and larger weights representing taxa more sensitive to disturbance (Bongers, 1990). A maturity index for free living taxa (MI) may be viewed as a

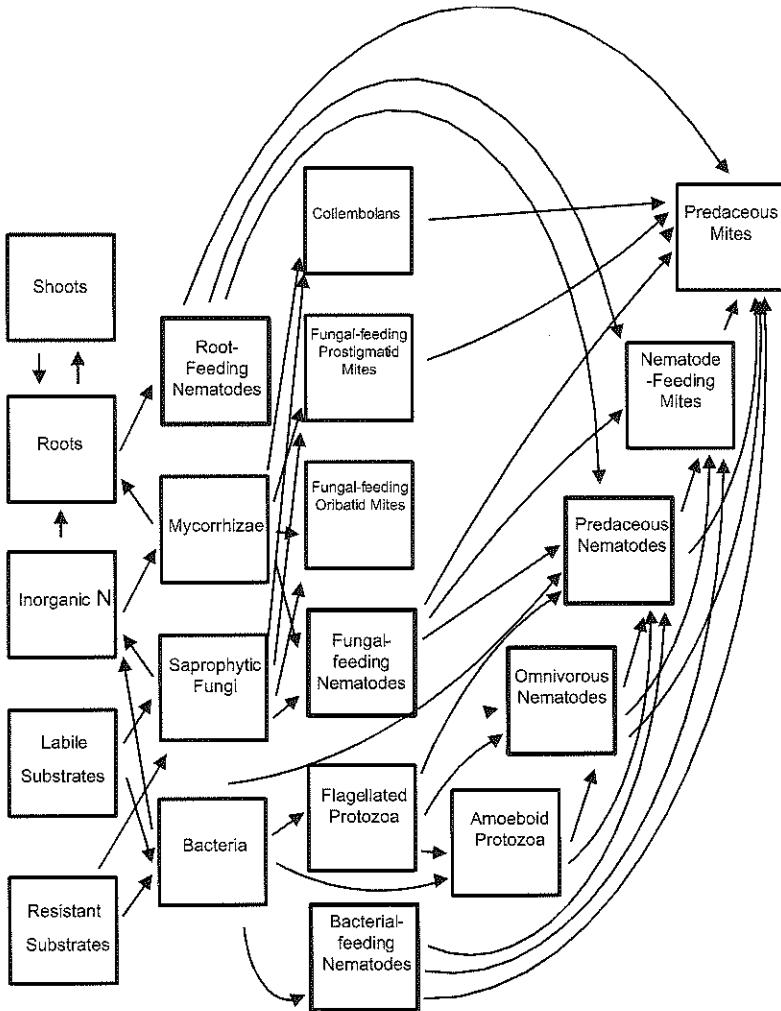


Figure 7.1 Soil food web in native North American shortgrass steppe prairie in eastern Colorado. Arrows indicate potential feeding relationships that were quantified. Five trophic groups of nematode communities are highlighted. (From Moore, J.C. and de Ruiter, P.C., Temporal and spatial heterogeneity of trophic interactions within below ground food webs, in *Agriculture, Ecosystems and Environment*, 34, 391–397, 1991. With permission.)

measure of disturbance, with smaller values indicative of a more disturbed environment and larger values characteristic of a less disturbed environment (Freckman and Ettema, 1993). A maturity index for plant parasitic taxa (PPI) may or may not correlate positively with MI (Bongers, 1990; Freckman and Ettema, 1993; Neher and Campbell, 1994).

Following a disturbance, such as the addition of animal manure to soil, progressive increases in the abundance of nematodes with large maturity index values have

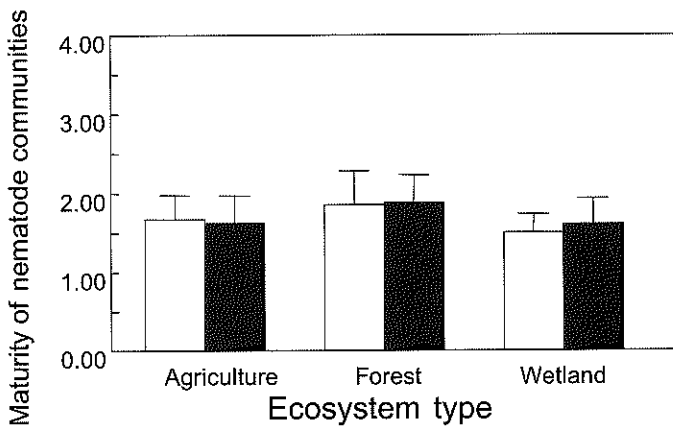


Figure 7.2 Means and standard errors of nematode community composition measured as successional maturity (ΣMI_{25}) in disturbed (open bars) and undisturbed (solid bars) soils of North Carolina. Disturbed is defined as annually cultivated arable soils, 1- to 3-year-old forests, and functioning wetlands. Undisturbed is defined as 10+-year-old pastures, 30+-year-old forests, and wetlands converted to agricultural production.

been documented, following the initial predominance of nematodes with smaller values (Ettema and Bongers, 1993). Similarly, soil communities in uncultivated or no-till agricultural systems have been considered successional more mature than those in frequently cultivated agricultural soil (Hendrix et al., 1986; Freckman and Ettema, 1993). Likewise, soils with perennial crops are successional more mature than soils with annual crops (Freckman and Ettema, 1993; Neher and Campbell, 1994). Interpretation of maturity indices, however, depends on ecosystem type (D. A. Neher, M. E. Barbercheck, and O. Anas, unpublished data). Successional maturity is greater in forest soils than in wetland and agricultural soils (Figure 7.2).

7.3.2 Trophic Diversity Indices

Trophic diversity indices describe the relative abundance and evenness (Ludwig and Reynolds, 1988) of the occurrence of five nematode trophic groups (see Figure 7.1). Trophic diversity can be expressed with either a Shannon or a Simpson diversity index (Shannon and Weaver, 1949; Simpson, 1949). In agricultural soils, greater diversity of trophic groups is correlated with an increase in the frequency of occurrence of generally less abundant trophic groups (i.e., fungal feeding, omnivores, and predators) relative to that of generally more abundant trophic groups (i.e., bacterial and plant feeding groups) (Wasilewska, 1979). Due to the typically unequal distribution of trophic groups within nematode communities in agroecosystems (Wasilewska, 1979), the Shannon index — which gives more weight to abundant taxa (Ludwig and Reynolds, 1988) — may be more applicable than the Simpson index of diversity (Neher and Campbell, 1994).

It has been demonstrated that disturbances such as cultivation (Freckman and Ettema, 1993) and addition of manure (Neher and Olson, 1999) decrease trophic

diversity. Also, trophic diversity tends to be greater in soils with perennial crops than it is in soils with annual crops (Neher and Campbell, 1994). These apparent differences are attributed mostly to a decline in numbers of omnivorous and predaceous nematodes and increases in numbers of bacterial-feeding nematodes (Wasilewska, 1979; Hendrix et al., 1986; Neher and Campbell, 1994). To date, no study has been published that tracks temporal changes in trophic diversity after a disturbance in as much detail as changes in maturity indices (Ettema and Bongers, 1993).

Appropriate caution must be taken when applying trophic designations to nematode species and genera because recent ecological studies have revealed that feeding habit groupings may be ambiguous in some cases. For example, abundant populations of *Aphelenchoides*, *Tylenchus*, *Tylencholaimus*, and *Ditylenchus* can be classified as "plant/fungal feeding" nematodes (Sohlenius et al., 1977) or some "predaceous" mononchids can grow and reproduce by feeding on bacteria (Yeates, 1987b). Current assignments of many nematode feeding groups have been inferred rather than confirmed by maintenance of nematodes over many generations under biologically defined conditions (Yeates et al., 1993). The problem could be minimized if supplementary studies were conducted to examine critically the feeding preferences of nematode taxa in defined environments.

7.4 RELATIONSHIP OF NEMATODE COMMUNITIES TO ECOSYSTEM FUNCTION

Indices of nematode community structure can be considered appropriate and successful indicators of soil quality if they correspond with ecological processes occurring in the soil; that is, nutrient mineralization and decomposition of organic matter. It is too soon to claim that this is the case, because initial experiments have been correlative in nature. Nevertheless, the studies point to a direct relationship between the structure of soil nematode communities and ecological processes.

7.4.1 Nutrient Availability

Nematodes have been demonstrated to affect plant productivity by increasing nutrient availability through regulation of mineralization processes. For example, shoot biomass and nitrogen content of plant shoots grown in the presence of protozoans and free living nematodes are greater than those of plants grown without mesofauna (Verhoef and Brussaard, 1990; Yeates and Wardle, 1996). Associations between nematode presence and increased availability of nitrogen were determined in experiments performed in petri dishes (Trofymow and Coleman, 1982), and field studies have confirmed these findings (Neher, 1999b). The basis of this relationship is that grazing on microbes by mesofauna releases and mineralizes nutrients immobilized in microbes, subsequently converting nitrogen from organic to inorganic forms that plants can utilize (Trofymow and Coleman, 1982; Seastedt et al., 1988; Sohlenius et al., 1988).

Soil fauna are responsible for approximately 30% of nitrogen mineralization in agricultural and natural ecosystem soils. Protozoans and bacterial-feeding nematodes

the main consumers of bacteria, account for 83% of this nitrogen mineralization (Elliott, et al., 1988), and are estimated to contribute about 8 to 19% of nitrogen mineralization in conventional and integrated farming systems (Beare, 1997). Nematodes contribute directly to nitrogen mineralization by excretion of nitrogenous wastes, mostly as ammonium ions (Anderson et al., 1983; Ingham et al., 1985; Hunt et al., 1987). In addition to serving as a stimulatory force in net mineralization of nutrients, nematodes also promote nutrient immobilization because their bodies constitute reservoirs of nutrients. When nematodes die nutrients immobilized in their tissues are mineralized and subsequently become available to plants.

Although nematode presence is correlated positively with increased availability of nutrients, the relationship between nematode community structure and nutrient availability is less clear. In agricultural soils, increased nitrogen fertilization, a disturbance to the ecosystem, returns nematode community structure to an earlier successional state, similar to additions of manure (Ettema and Bongers, 1993). Negative correlations occur between successional maturity of nematode communities and concentrations of nitrate and ammonium, two forms of nitrogen available to plants (Neher, 1999b). The causality in this relationship, however, is unclear. In general, the actual mechanisms of soil organisms' impact on soil fertility are not well understood (Giller et al., 1997).

7.4.2 Decomposition of Organic Matter

The process of organic matter decomposition is closely linked to nutrient mineralization and immobilization. Cellulose and lignin represent two abundant molecules present in organic matter that must be decomposed. Cellulose is composed of labile compounds and is, therefore, decomposed easily by a wide variety of microorganisms. Lignin is more resistant to decay, and only specialized fungal species can decompose it (Dix and Webster, 1995).

The author conducted an experiment in agricultural systems in North Carolina measuring nematode communities and decomposition of cellulose and lignin as mass loss through time. Positive correlations ($p < 0.05$) were observed between successional maturity of nematode communities and decomposition of cellulose in non-cultivated, perennial agricultural systems (D. A. Neher, M. E. Barbercheck, and O. Anas, unpublished data). This result suggests a direct association between successional maturity of soil communities and ecosystem function. However, this association was decoupled in cultivated soils with annual crops ($p > 0.05$). No correlation was observed between nematode community composition and lignin decomposition.

7.5 INDEX CALIBRATION

Ecological indices related to nematode communities do not provide absolute values of condition but require reference to some putatively undisturbed community for interpretation or comparison (de Bruyn, 1997; Neher, 1999b). Use of an undisturbed community for a reference point is unrealistic, because agroecosystems are disturbed intentionally for human purposes.

Two types of agroecosystems, perennial crop systems and organic systems, may serve as bases of comparison when using nematode community indices to measure the health of soils cultivated with annual crops. The argument for using perennial systems as the basis of comparison is based on the claim that farming systems that include soil conservation practices, such as zero or minimum tillage, are more sustainable than those employing conventional practices (de Bruyn, 1997). The argument for using organic systems rests on the claim that organic farms support nematode communities undisturbed by agricultural chemicals.

7.5.1 Perennial Crops

Research suggests that forage and pasture agroecosystems may be suitable for use as a reference point in monitoring the ecological condition of soils associated with annual crops. The PPI and the ratio of fungal feeding to bacterial feeding nematodes for annual crops (soybean, corn, wheat) were found to be significantly different from those for perennial crops (alfalfa and tall fescue grass, alone or mixed with legumes). Trophic diversity was similar in the two systems, suggesting no differences in food web structure. Results indicate that soils with perennial crops are more mature successional than soils with annual crops and that the ratio of fungal to bacterial feeding nematodes may be an important description of the decomposition pathway in detritus food webs (Sohlenius and Sandor, 1987). Data from this study are summarized in Figure 7.3.

When using a perennial system as a base of comparison, the period of time that the system has been undisturbed must be considered (Wasilewska, 1979; 1994). A long-term perennial crop (> 10 years) is related more closely to an undisturbed site than a medium term (2 to 5 years) perennial crop. Crop land that has never been cultivated or has been abandoned for a long period may be the best reference (Freckman and Ettema, 1993). These sites may be difficult to locate. Perennial agriculture fields such as those described above would be practical choices for a large scale monitoring program because they occur frequently in agroecosystems and are widespread geographically (Neher and Campbell, 1994).

7.5.2 Organic Production

Organic management minimizes or excludes synthetic chemical fertilizers. It places an emphasis on the recycling of organic wastes and the use of legume crops as green manure to supply nutrients on a schedule matching plant demand (USDA, 1980). In organic farming systems, soil microbes appear to play a more important role in plant nutrient cycling than they do in conventional systems (Allison, 1973). Farm practices that minimize the use of synthetic pesticides or inorganic fertilizers generally result in soils with ecological properties considered "good" or "healthy" (Bolton, 1983; Reaganold et al., 1993).

The author participated in two studies that compared successional maturity and trophic diversity of nematode communities in organic and conventional farming systems. The first experiment compared soils from 5 pairs of organically and conventionally managed fields in the Piedmont region of North Carolina (Olsen, 1990). The

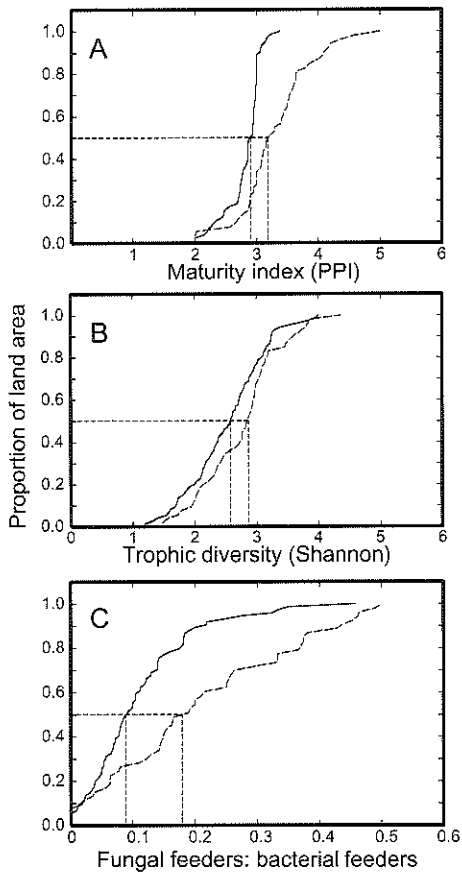


Figure 7.3 Cumulative distribution function of the (A) maturity index of plant-parasitic nematodes, (B) Shannon trophic diversity index, and (C) fungal to bacterial feeding nematodes ratio for annual (solid line) and perennial (dashed line) crops sampled in North Carolina. Dotted lines represent median values. (From Neher, D.A. and Campbell, C.L., Nematode communities and microbial biomass in soils with annual and perennial crops, *Appl. Soil Ecol.*, 1, 17–28, 1994. With permission.)

second experiment compared effects of 4 different farming systems (manure only [O]; mineral fertilizer only [F]; mineral fertilizer plus herbicides [HF]; and mineral fertilizer plus herbicides plus insecticides [HFI] near Ithaca, Nebraska) (Neher and Olson, 1999).

In the first experiment, values of PPI were greater in soils managed organically than they were in those managed conventionally, but no differences in MI were observed between farming systems (see Figure 7.4). In the second experiment, successional maturity did not differ among management systems, but populations of early successional taxa (weights = 1–2) were greater in the higher input farming systems, suggesting that soils amended with mineral fertilizer and pesticides were at a less mature stage than soils amended with organic matter only. Contrary to predictions, trophic diversity was greatest in the HFI system and least in the O system (Neher and Olson, 1999).

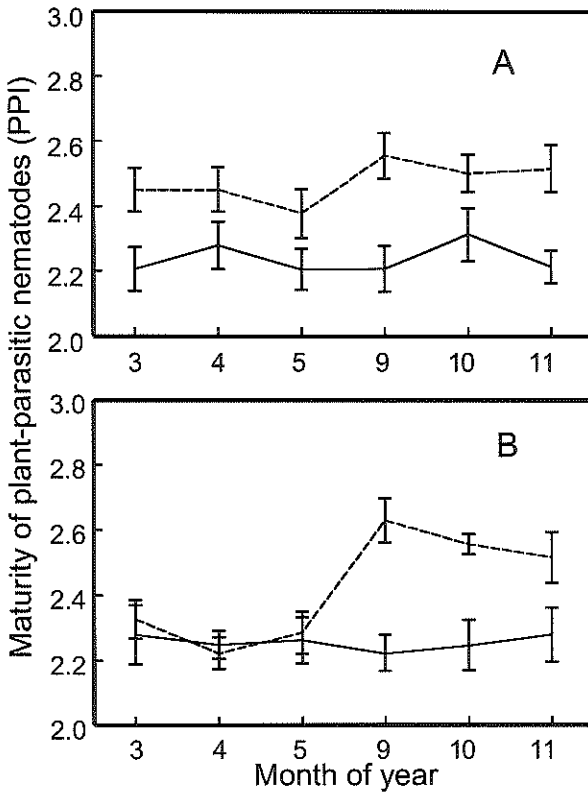


Figure 7.4 Mean values of the plant parasitic maturity index (PPI) in soils managed organically (dashed line) and conventionally (solid line) in spring (3 = March, 4 = April, 5 = May) and fall (9 = September, 10 = October, 11 = November) of (A) 1993 and (B) 1994. Standard error bars are illustrated. (From Neher, D.A., Nematode communities in organically and conventionally managed agricultural soils, *J. Nematol.*, 31, 142–154, 1999b.)

Results from both experiments may reflect similar frequencies of disturbance in all management systems. For example, soils managed organically underwent frequent cultivation. The cultivation was replaced by the use of herbicides in soils managed conventionally. Cultivation decreases maturity and trophic diversity index values (Neher and Campbell, 1994). Based on the similarity of index values for the different soil management practices, it is possible to conclude that organically managed systems are not useful as a reference base for maturity indices for annual crops in conventionally managed soils (Neher, 1999b). Physical disturbances such as cultivation disturb soil nematode community structure and function as much as, or more than, applications of synthetic chemicals such as fertilizers and pesticides (Neher and Campbell, 1994; Neher, 1995). Sites with minimal to no physical disturbance may serve as better reference sites in environmental monitoring programs than sites without application of synthetic chemicals (Neher, 1999b).

7.5.3 Confounded Disturbance Regimes

As suggested above, a major challenge in assessing soil quality is the confounded nature of physical and chemical disruption in most management practices. Some taxa may be sensitive to one or both types of disturbance, with similar or inverse associations (Fiscus, 1997). Fiscus hypothesizes that physical changes in soil can act as a disturbance while chemical/nutrient changes can act as an enrichment, leading to qualitatively different impacts on nematode communities. Indirect impacts of disturbance on nematode community composition often exceed direct impacts. Greater sensitivity to indirect effects suggests that nematode communities are more responsive to the secondary impacts (those mediated by the soil environment) of agricultural management than the impacts of cultivation or chemical/nutrient applications themselves (Fiscus, 1997).

7.6 REGIONAL SCALE APPLICATION

The goal of contemporary environmental monitoring programs is to compare nematode communities in soils between geographic regions ranging in size from 375,000 to 600,000 km² (Neher et al., 1998). The author participated in a multiple region survey to determine the feasibility of using maturity and trophic diversity indices of nematode communities on large geographic scales. In these surveys, soil samples were collected from fields that were planted with annual row crops or an annually harvested perennial crop such as hay or alfalfa in North Carolina (n = 164) and Nebraska (n = 154) (Neher et al., 1998). Fields were selected using an area frame design (Cotter and Nealon, 1987). Within every field, soils were sampled by taking one core at each of 20 equally spaced sites along one 90-m linear transect across a random 2-ha area to obtain data to measure variation among fields (Neher et al., 1995; 1998). Cores for each transect were mixed thoroughly by hand to form a composite sample to reduce variance associated with the aggregated spatial pattern of nematodes in soil (Barker and Campbell, 1981) and obtain a realistic representation of the nematode community in the field. In every sixth field, a second transect was also sampled to quantify variability within fields. Variability within composite samples was quantified by splitting composite soil samples of double volume taken from a second independent transect in every twelfth field (Neher and Campbell, 1996; Neher et al., 1998).

Modifications of maturity indices increased reliability (signal to noise ratio) and thus improved performance on a regional scale (Neher and Campbell, 1996). In one modification, values for the early colonizing taxa (weight = 1) (Popovici, 1992) were removed from the original MI index (Bongers, 1990) to give a new index, MI25 (Bongers et al., 1995; described as "MINO" in Neher and Campbell, 1996). In the other modification, plant feeding and free living taxa of nematodes were combined in a single index, ΣMI (Yeates, 1994). Relatively large total and within sample variance for the original MI index compared to the modified MI25 index suggest that inclusion of the free living opportunists (weight = 1) decreases the reliability of detection by inflating the noise factor (Neher and Campbell, 1996).

Differences in successional maturity and trophic diversity of nematode communities between North Carolina and Nebraska, two states of contrasting climates and soil types, exceeded those among Land Resource Regions (LRRs) within states. LRRs represent geographic areas with unique soil type, topography, climate, and water resources (USDA-SCS, 1981). These relatively large differences suggest that maturity and trophic diversity indices of soil quality need not be calibrated independently when applied in geographic areas smaller than the land area of North Carolina (126,180 km²) and Nebraska (199,120 km²) (Neher and Campbell, 1996). It has yet to be determined how large a region or state can be before subdivision is necessary for independent calibrations of indices.

Based upon the results of the regional surveys, it appears that regional studies require a minimum sampling of 50 to 100 fields, with three independent samples (transects) per field and two subsamples assayed per sample. If cost is a major limiting factor, an alternative would be to sample a larger number of fields with only one subsample for each of two samples assayed per field (Neher and Campbell, 1996). The information obtained using this option would have a smaller degree of reliability; however, cost is often a driving factor in sampling programs. For states or regions such as North Carolina, in which plant feeding nematodes are major agricultural pests, an index such as MI or MI25 may be a better choice than PPI if the focus of the study is to examine overall maturity or stability of nematode communities. For states or regions such as Nebraska, in which plant feeding nematodes occur but are less prevalent, ecological indices that include plant parasitic nematodes, such as PPI and Σ MI, may be the better choices because they indicate variability among fields more reliably than indices that only include free living nematodes (Neher and Campbell, 1996).

7.7 FUTURE RESEARCH

Many challenges remain to be overcome before it is possible to fully understand and interpret maturity and trophic diversity indices.

- First, our ability to resolve trophic or functional groups must be improved, because it limits our current understanding. Many species have yet to be assigned to trophic or functional groups (Brussaard et al., 1997). Ultimately, resolution at a species level is desirable (Neher, 1999a). However, before this is possible, experiments must be conducted to learn the natural history traits of free living species and the response of each species to various types of environmental stresses. These experiments will help us to understand and identify which species or groups of species have key functions in the maintenance of energy and material flow through an ecosystem (de Bruyn, 1997).
- Second, a more thorough understanding of the sequence of community succession relative to soil function dynamics would be useful in establishing the kinds of community composition associated with ecologically sound agricultural systems (Neher, 1999a). These associations can only be revealed with appropriate sampling schedules that consider the lag periods that may occur between nematode population peaks and subsequent ecological process change.

- Third, quantitative associations that reveal cause/effect relationships or mechanisms between nematodes and ecosystem function are necessary for complete understanding of indicator performance.
- Fourth, alternative indices for describing how nematode communities respond to environmental stress must be developed and evaluated. For example, an alternative to the maturity index is an index based on reproductive, gender determination, and dispersal traits (Siepel, 1995). The index would be sensitive to how these characteristics vary among the different stages of the nematode life cycle and how the dominant versions of these traits change with different types and frequencies of disturbance and stress.

REFERENCES

- Allison, F.E., Soil organic matter and its role in crop production. *Dev. Soil Sci.*, Vol. 3, Elsevier, Amsterdam, 1973.
- Anderson, R.V., Gould, W.D., Woods, L.E., Cambardella, C., Ingham, R.E., and Coleman, D.C., Organic and inorganic nitrogenous losses by microbivorous nematodes in soil, *Oikos*, 40, 75–80, 1983.
- Barker, K.R. and Campbell, C.L., Sampling nematode populations, in Zuckerman, B.M., and Rohde, R.A., Eds., *Plant Parasitic Nematodes*, Academic Press, NY, Vol. 3, 51–474, 1981.
- Beare, M.H., Fungal and bacterial pathways of organic matter decomposition and nitrogen mineralization in arable soil, in Brussaard, L. and Ferrera-Cerrato, R., Eds., *Soil Ecology in Sustainable Agricultural Systems*, Lewis Publishers, Boca Raton, FL, 37–70, 1997.
- Bolton, H., Jr. Soil microbial biomass and selected soil enzyme activities on an alternatively and a conventionally managed farm, M.S. thesis, Washington State University, Pullman, 1983.
- Bongers, T., The maturity index: an ecological measure of environmental disturbance based on nematode species composition, *Oecologia*, 83, 14–19, 1990.
- Bongers, T., Alkemade, R., and Yeates, G.W., Interpretation of disturbance-induced maturity decrease in marine nematode assemblages by means of the Maturity Index, *Mar. Ecol. Prog. Ser.*, 76, 135–142, 1991.
- Bongers, T., de Goede, R.G.M., Korthals, G.W., and Yeates, G.W., Proposed changes of c-p classification for nematodes, *Russian J. Nematol.*, 3, 61–62, 1995.
- Brussaard, L., Behan-Pelletier, V.M., Bignell, D.W., Brown, V.K., Didden, W., Folgarait, P., Fragoso, C., Freckman, D.W., Gupta, V.V.S.R., Hattori, T., Hawksworth, D.L., Klopatek, C., Lavelle, P., Malloch, D.W., Rusek, J., Söderström, B., Tiedje, J.M., and Virginia, R.A., Biodiversity and ecosystem functioning in soil, *Ambio*, 26, 563–570, 1997.
- Cotter, J., and Nealon, J., Area frame design for agricultural surveys, USDA, National Agricultural Statistics Service, Research and Applications Division, Washington, D.C., 1987.
- de Bruyn, L.A.L., The status of soil macrofauna as indicators of soil health to monitor the sustainability of Australian agricultural soils, *Ecol. Econ.*, 23, 167–178, 1997.
- de Goede, R., *Terrestrial Nematodes in a Changing Environment*, CIP-gegevens Koninklijke Bibliotheek, Den Haag, Wageningen, The Netherlands, 1993.
- Dix, N.J. and Webster, J., *Fungal Ecology*, Chapman and Hall, London, UK, 1995.
- Elliott, E.T., Hunt, H.W., and Walter, C.E., Detrital food web interactions in North American grassland ecosystems, *Agric. Ecosystems Environ.*, 24, 41–56, 1988.
- Ettema, C.H. and Bongers, T., Characterization of nematode colonisation and succession in disturbed soil using the Maturity Index, *Biol. Fertil. Soils*, 16, 79–85, 1993.

- Ferris, V.R. and Ferris, J.C., Inter-relationships between nematode and plant communities in agricultural ecosystems, *Agro-Ecosystems*, 1, 275–299, 1974.
- Fiscus, D.A., Development and evaluation of an indicator of soil health based on nematode communities, M.S. thesis, North Carolina State University, Raleigh, NC, 1997.
- Freckman, D.W., Bacterivorous nematodes and organic-matter decomposition, *Agric. Ecosystems Environ.*, 24, 195–217, 1988.
- Freckman, D.W. and Ettema, C.H., Assessing nematode communities in agroecosystems of varying human intervention, *Agric. Ecosystems Environ.*, 45, 239–261, 1993.
- Giller, K.E., Beare, M.H., Lavelle, P., Izac, A.M.N., and Swift, M.J., Agricultural intensification, soil biodiversity and agroecosystem function, *Appl. Soil Ecol.*, 6: 3–16, 1997.
- Hassink, J., Bouwman, L.A., Zwart, K.B., and Brussaard, L., Relationships between habitable pore space soil biota and mineralization rates in grassland soils, *Soil Biol. Biochem.*, 25, 47–55, 1993.
- Hawksworth, D.L. and Mound, L.A., Biodiversity databases: the crucial significance of collections, in Hawksworth, D.L., Ed., *The Biodiversity of Microorganisms and Invertebrates: Its Role in Sustainable Agriculture*, CAB International, Wallingford, UK, 1991, 17–29.
- Hendrix, P.F., Parmelee, R.W., Crossley, D.A., Jr., Coleman, D.C., Odum, E.P., and Groffman, P.M., Detritus food webs in conventional and no-tillage agroecosystems, *BioScience*, 36, 374–380, 1986.
- Hunt, H.W., Coleman, D.C., Ingham, E.R., Ingham, R.E., Elliott, E.T., Moore, J.C., Rose, S.L., Reid, C.P.P., and Morley, C.R., The detrital food web in a shortgrass prairie, *Biol. Fertil. Soils*, 3, 57–68, 1987.
- Hyvonen, R. and Persson, T., Effects of acidification and liming on feeding groups of nematodes in coniferous forest soils, *Biol. Fertil. Soils*, 9, 205–210, 1990.
- Ingham, R.E., Trofymow, J.A., Ingham, E.R., and Coleman, D.C., Interactions of bacteria, fungi, and their nematode grazers: Effects on nutrient cycling and plant growth, *Ecol. Monogr.*, 55, 119–140, 1985.
- Lubchenco, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., MacMahon, J.A., Matson, P.A., Melillo, J.M., Mooney, H.A., Peterson, C.H., Pulliam, H.R., Real, L.A., Regal, P.J., and Risser, P.G., The sustainable biosphere initiative: an ecological research agenda, *Ecology*, 72, 371–412, 1991.
- Ludwig, J.A. and Reynolds, J.F., *Statistical Ecology: A Primer on Methods and Computing*, Wiley, New York, 1988.
- Moore, J.C. and P.C. de Ruiter, Temporal and spatial heterogeneity of trophic interactions within below-ground food webs, *Agric. Ecosystems Environ.*, 34: 371–397, 1991.
- Moore, J.C., Walter, D.E., and Hunt, H.W., Arthropod regulation of micro- and mesobiota in below-ground detrital food webs, *Annu. Rev. Entomol.*, 33, 419–439, 1988.
- Neher, D.A., Biological diversity in soils of agricultural and natural ecosystems, in Olson, R.K., Francis, C.A., and Kaffka, S., Eds., *Exploring the Role of Diversity in Sustainable Agriculture*, American Society of Agronomy, Madison, WI, 1995, 55–72.
- Neher, D.A., Soil community composition and ecosystem processes: Comparing agricultural ecosystems with natural ecosystems, *Agroforestry Syst.*, 45, 159–185, 1999a.
- Neher, D.A., Nematode communities in organically and conventionally managed agricultural soils, *J. Nematol.*, 31, 142–154, 1999b.
- Neher, D.A. and Campbell, C.L., Nematode communities and microbial biomass in soils with annual and perennial crops, *Appl. Soil Ecol.*, 1, 17–28, 1994.
- Neher, D.A. and Campbell, C.L., Sampling for regional monitoring of nematode communities in agricultural soils, *J. Nematol.*, 28, 196–208, 1996.

- Neher, D.A. and Olson, R.K., Nematode communities in soils of four farm cropping management systems, *Pedobiologia*, 43, 430–438, 1999.
- Neher, D.A., Peck, S.L., Rawlings, J.O., and Campbell, C.L., Measures of nematode community structure for an agroecosystem monitoring program and sources of variability among and within agricultural fields, *Plant Soil*, 170, 167–181, 1995.
- Neher, D.A., Easterling, K.N., Fiscus, D., and Campbell, C.L., Comparison of nematode communities in agricultural soils of North Carolina and Nebraska, *Ecol. Appl.*, 8, 213–223, 1998.
- Popovici, I., Nematodes as indicators of ecosystem disturbance due to pollution, *Stud. Univ. Babeş-Bolyai Ser. Biol.*, 37, 15–27, 1992.
- Samoiloff, M.R., Nematodes as indicators of toxic environmental contaminants, in Veech, J.A. and Dickson, D.W., Eds., *Vistas on Nematology*, Society of Nematologists, Hyattsville, MD, 1987, 433–439.
- Seastedt, T.R., The role of microarthropods in decomposition and mineralization processes, *Annu. Rev. Entomol.*, 29, 25–46, 1984.
- Seastedt, T.R., James, S.W., and Todd, T.C., Interactions among soil invertebrates, microbes and plant growth in the tallgrass prairie., *Agric. Ecosystems Environ.*, 24, 219–228, 1988.
- Shannon, C.E. and Weaver, W., *The Mathematical Theory of Communication*, University of Illinois, Urbana, 1949.
- Siepel, H., Applications of microarthropod life-history tactics in nature management and ecotoxicology, *Biol. Fertil. Soils*, 19, 75–83, 1995.
- Simpson, E.H., Measurement of diversity, *Nature*, 163, 688, 1949.
- Sohlenius, B. and Sandor, A., Vertical distribution of nematodes in arable soil under grass (*Festuca pratensis*) and barley (*Hordeum distichum*), *Biol. Fertil. Soils*, 3, 19–25, 1987.
- Sohlenius, B., Persson, H., and Magnusson, C., Distribution of root and soil nematodes in a young Scots pine stand in central Sweden, *Ecol. Bull.* (Stockholm), 25, 340–347, 1977.
- Sohlenius, B., Böstrom, S., and Sandor, A., Carbon and nitrogen budgets of nematodes in arable soil, *Biol. Fertil. Soils*, 6, 1–8, 1988.
- Trofymow, J.A. and Coleman, D.C., The role of bacterivorous and fungivorous nematodes in cellulose and chitin decomposition in the context of a root/rhizosphere/soil conceptual model, in Freckman, D.W., Ed., *Nematodes in Soil Ecosystems*, University of Texas, Austin, 1982, 117–138.
- United States Department of Agriculture, Report and recommendations on organic farming, U.S. Government Printing Office, Washington, D.C., 1980.
- USDA-SCS, Land resource regions and major resource areas of the United States, USDA-SCS Agriculture Handbook 296, U.S. Government Printing Office: Washington, D.C., 1981.
- Verhoef, H.A. and Brussard, L., Decomposition and nitrogen mineralization in natural and agro-ecosystems. The contribution of soil animals, *Biogeochemistry*, 11, 175–211, 1990.
- Vinciguerra, M.T., Role of nematodes in the biological processes of the soil, *Bull. Zool.*, 46, 363–374, 1979.
- Wasilewska, L., The structure and function of soil nematode communities in natural ecosystems and agrocenoses, *Pol. Ecol. Stud.*, 5, 97–145, 1979.
- Wasilewska, L., Impact of human activities on nematodes, in Charholm, C., and Bergström, L., Eds., *Ecology of Arable Land*, Kluwer Academic, Dordrecht, The Netherlands, 1989, 123–132.
- Wasilewska, L., The effect of age of meadows on succession and diversity in soil nematode communities, *Pedobiologia*, 38, 1–11, 1994.

- Wasilewska, L., Jakubczyk, H., and Paplinska, E., Production of *Aphelenchus avenae* Bastian (Nematoda) and reduction of mycelium of saprophytic fungi by them, *Pol. Ecol. Stud.*, 1, 61–73, 1975.
- Whitford, W.G., Freckman, D.W., Santos, P.F., Elkins, N.Z., and Parker, L.W., The role of nematodes in decomposition in desert ecosystems, in Freckman, D.W., Ed., *Nematodes in Soil Ecosystems*, University of Texas, Austin, 1982, 98–115.
- Yeates, G.W., How plants effect nematodes, *Adv. Ecol. Res.*, 17, 61–113, 1987a.
- Yeates, G.W., Significance of developmental stages in the co-existence of three species of Mononchoidea (Nematoda) in a pasture soil, *Biol. Fertil. Soils*, 5, 225–229, 1987b.
- Yeates, G.W., Modification and qualification of the nematode maturity index, *Pedobiologia*, 38, 97–101, 1994.
- Yeates, G.W. and Coleman, D.C., Nematodes in decomposition, in Freckman, D.W., Ed., *Nematodes in Soil Ecosystems*, University of Texas, Austin, 1982, 55–80.
- Yeates, G.W. and Wardle, D.A., Nematodes as predators and prey: relationships to biological control and soil processes, *Pedobiologia*, 40, 43–50, 1996.
- Yeates, G.W., Bongers, T., de Goede, R.G.M., Freckman, D.W., and Georgieva, S.S., Feeding habits in soil nematode families and genera: An outline for soil ecologists, *J. Nematol.*, 25, 315–331, 1993.