Ecological Applications, 12(2), 2002, pp. 565–575

DISTINGUISHING SENSITIVITY OF FREE-LIVING SOIL NEMATODE GENERA TO PHYSICAL AND CHEMICAL DISTURBANCES

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Abstract. During the past 50 yr, ecological and agricultural scientists have pursued an integrated definition and metric of soil quality. In the past 20 yr, considerable attention has been paid to nematodes, demonstrating that these ubiquitous members of the soil community reflect change in ecological structure and function of soils in ways more predictable and efficient than for other soil flora or fauna. With the help of multivariate analysis, we studied the application of free-living nematode communities as model indicators of physical and chemical disturbance of agricultural soil. We used canonical correspondence analysis (CCA) and partial CCA to segregate effects of tillage and chemical/nutrient treatments. With the results of CCA, we assigned relative direct and indirect tillage sensitivity and chemical/nutrient sensitivity ratings to soil genera found in two test data sets, each containing three matrices: (1) sites by species or genera, (2) sites by soil properties, and (3) sites by management practices. Of 46 total genera, the ones most sensitive to direct effects of tillage include *Aphelenchoides*, *Eucephalobus*, *Eudorylaimus*, *Heterocephalobus*, and *Wilsonema* compared to the tolerant genera *Achromadora*, *Anatonchus*, *Cephalobus*, *Chiloplacus*, *Clarkus*, *Epidorylaimus*, *Mylonchulus*, *Plectus*, and *Tylencholaimellus*. Some genera are more sensitive to indirect than direct effects of tillage: these include *Achromadora*, *Cephalobus*, *Microdorylaimus*, *Monhystera*, *Panagrolaimus*, and *Prionchulus*. With the exception of *Discolaimus* and *Prismatolaimus*, genera sensitive to chemical/nutrient treatments differ from those sensitive to tillage treatments including *Alaimus*, *Cylindrolaimus*, *Mesorhabditis*, *Odontolaimus*, and *Protorhabditis*. Likewise, genera uniquely sensitive to indirect but not direct effects of chemical/nutrient treatments are *Aphelenchus*, *Aporcelaimellus*, and *Diplogaster*. *Eudorylaimus* and *Eumonhsytera* are sensitive to indirect effects of both tillage and chemical/nutrient treatments. Our results suggest that physical and chemical/nutrient disturbances can alter populations of nematode genera differently, and that indirect effects of management are greater than direct effects. This methodology aids in distinguishing nematode genera that have distinctive responses to agricultural management practices from those that are ambiguous. This knowledge is useful for both interpretation and enhancement of free-living nematode community indices.

Key words: bioindicator; conventional-till agriculture; environmental monitoring; index for biotic integrity (IBI); keystone species; maturity index; no-till agriculture; ordination; organic agriculture; perennial crops; soil quality.

INTRODUCTION

During the past 50 yr, ecological and agricultural scientists have pursued an integrated definition and metric of soil quality (e.g., Howard 1947, Brussaard et al. 1997, Debruyn 1997). In the past 20 yr, considerable attention has been paid to nematodes, demonstrating that these ubiquitous members of the soil community reflect change in ecological structure and function of soils in ways more predictable and efficient than for other soil flora or fauna. These studies provide a foundation from which measures of nematode communities may be used as indicators of soil quality in agricultural ecosystems. Enhancement of indicator performance will be possible as resolution of identification of free-living nematodes improves from trophic groups to genera and species (Bernard 1992, Ferris et al. 1996, 1997, Yeates and van der Meulen 1996), life history characteristics of nematode species and genera are tested empirically rather than inferred from morphology (Yeates et al. 1993*a*), and indices are refined (Porazinska et al. 1998, 1999) and calibrated (Anas et al. 1995).

Criteria of successful ecological indicators are provided by Neher et al. (1995) and a conceptual framework for monitoring and assessment of agricultural lands by Hess et al. (2000) and Hellkamp et al. (2000). Three key characteristics of nematodes to meet these criteria are established. First, nematode community composition affects soil function in ways that are relevant to agricultural production and sustainability. Relative abundances of nematode trophic groups affect nutrient cycling in decomposition and primary pro-

Manuscript received 25 October 2000; revised 27 June 2001; accepted 29 June 2001.

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duction pathways (Yeates and Coleman 1982, Anderson et al. 1983, Ingham et al. 1985, Verhoef and Brussaard 1990, Beare et al. 1992, Wardle et al. 1995*b,* Setälä et al. 1998). Second, examples of temporal and spatial dynamics of free-living nematode community succession are documented (de Goede et al. 1993, Ettema et al. 1998). The Maturity Index (Bongers 1990) has been used effectively to detect successional change in nematode communities and relate these changes to anthropogenic disturbance. Community successional status is known to proceed rapidly within the initial weeks following severe disturbance (Yeates et al. 1991, Ettema and Bongers 1993, Wardle et al. 1995*b*) and to move downward in the soil profile (Brussaard 1998). Third, successful methodologies of sampling, feeding type classification, analysis, and interpretation are better known for nematodes than other soil microfauna (Yeates et al. 1993*a*, Elliott 1994, Neher et al. 1998).

Environmental forces impact nematode community structure in two important ways. First, natural abiotic variables such as soil texture (Elliott 1994) and pH (de Goede 1993, Korthals et al. 1996*a*) affect nematode community composition more than moisture (Neher et al. 1999). Second, land management practices such as cultivation (Neher and Campbell 1994), mineral fertilizers (Beare 1997), and toxic substances such as pesticides (Yeates et al. 1991, Ettema and Bongers 1993), heavy metals (Weiss and Larink 1991, Korthals et al. 1996*a, b,* 1998), or petroleum products (Blakely 1999) affect nematode community composition.

The goal of the present study is to increase understanding of specific ways in which environmental factors within human management regimes alter nematode community composition. Most published studies represent controlled plot or laboratory experiments. Monitoring and assessment of soil at the national or regional scale involves samples from production farm fields in which multiple types of disturbance plus large natural environmental variation are confounded. Links between management and community composition in such data are tangled and complex (Fiscus 1997). The objective of this study was to differentiate mechanisms involved in predicting nematode community composition. We focused on free-living nematode genera because of their role in decomposition and nutrient cycling. The first hypothesis tested was that effects of tillage practices (physical disturbance) and fertilizer/pesticide applications (chemical/nutrient disturbance) could be detected separately. Following the inspiration of Bongers (1990) and Yeates (1994), we estimated the relative sensitivities of nematode taxa (in this case, genera) to anthropogenically driven environmental variables. Second, we tested the prediction that management practices influence nematode communities either directly from impact of human activity or indirectly through changes in the soil environment. We introduce a method for calculating direct and indirect tillage and chemical/nutrient sensitivity ratings for free-living nematode genera.

METHODS

Data selection

Preliminary analyses of several nematode and soil-environment data were performed to explore potential metrics of soil quality. An initial approach was to adapt the index of biotic integrity (IBI) (Kerans and Karr 1994) for use as a measure of disturbance to soil nematode communities. This type of index is based on the concept that 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). Data were used that characterized nematode communities and compared the effects of the following practices on these communities: annual and perennial cropping systems (Yeates and Bird 1994) and chemical applications (McQuaid and Olson 1998). Preliminary results suggested that metrics similar to those used in IBI for fish and invertebrates (e.g., proportional abundances of trophic groups including both free-living and plant-parasitic nematodes) were not responsive clearly or consistently to management treatments. However, results from these analyses (Table 1) exposed a distinctive response of metrics to physical practices, such as tillage, compared to chemical/nutrient treatments. Tillage is a major management difference in perennial and annual cropping systems. Based on these observations, tillage and chemical effects of agricultural management were chosen as two distinct types of disturbance.

Sensitivity ratings

Two data sets were analyzed in detail to develop tillage and chemical/nutrient sensitivity ratings for free-living soil nematode genera. One data set came from a study that compared nematode communities and 11 chemical/physical properties in soils of conventional-till (n = 2 fields), no-till for 0–3 yr (n = 9 fields), and no-till for >3 yr (n = 5 fields) sampled in September 1994 in the Piedmont region of North Carolina. Crops at these sites were tobacco (*Nicotiana tobaccum*), corn–wheat (*Zea mays* L.–*Triticum aestivum* L.) rotation, corn–soybean (*Glycine max* (L.) Merr. rotation, or continuous corn (McQuaid and Olson 1998). The second data set compared four chemical/nutrient applications [manure (n = 32 experimental plots), fertilizer (n = 32 experimental plots), fertilizer plus herbicide (n = 32 experimental plots), and fertilizer plus herbicide and insecticide (n = 8 experimental plots)] across four crops [corn, oats (*Avena sativa* L.), soybeans, and sorghum (*Sorghum bicolor* (L.) Moench)] in southeastern Nebraska. Although treatments had been established since 1975, nematode communities were sampled only in September 1993 (Neher and Olson 1999).

TABLE 1. Initial tests of nematode community attributes.

Attribute	North Carolina tillage‡	Annual/ Perennial§	Nebraska chemical‖	North Carolina organic/conv.¶
Tillage sensitive				
Taxon richness, genera	NT > CT†	P > A***		
Taxon richness, family	NT > CT†	P > A*		
Percentage intolerant#		P > A***		
Omnivore abundance	NT > CT†	P > A†		
Percentage endoparasites		A > P***		
Fungal feeders : bacterial feeders		P > A***	H > F***	
Percentage in two most abundant taxa		A > P†		
Chemical/nutrient sensitive				
Total abundance			M > F*	O > C*
Percentage bacterial feeders		P > A***		C > O***
Percentage fungal feeders		P > A*	H > F*	C > O*
Percentage microbial grazers††			H > F†	C > O***
Percentage plant parasites			F > H*	O > C***
Percentage ectoparasites			F > M†	
Percentage predators				O > C†

† $P < 0.1$; * $P < 0.05$; *** $P < 0.001$.

‡ NT = no-till, CT = conventional till (McQuaid and Olson 1998).

§ Tillage occurred in annual (A) but not perennial (P) crops (Yeates and Bird 1994).

‖ Applications of M = manure, F = fertilizer, H = fertilizer plus herbicide (Neher and Olson 1999).

¶ O = organic, C = conventional agricultural practices (Neher 1999).

Freeliving and plant-parasitic nematodes with CP5 classification according to Bongers (1990).

†† Sum of bacterial, fungal, and unicellular eukaryote feeders.

Sensitivity ratings of nematode genera to direct effects of management practices were calculated using canonical correspondence analysis (CCA) with CANOCO software Version 4 (ter Braak 1990). Ordination of sites and genera for each data set was performed separately such that management factors (tillage and chemical/nutrient applications) were included with those environmental variables thought to be most influential in structuring nematode populations, i.e., soil moisture, texture, and pH (de Goede 1993). Environmental class variables (i.e., manure, fertilizer, herbicide, insecticide, crop, tillage type, and replicate block) were coded as nominal 0 or 1 variables. Nematode abundances were transformed as $\ln(x + 1)$ to normalize data prior to application of CCA, as is typical for many analyses of nematode population counts (Neher et al. 1995). Rare species were not down-weighted because they may represent taxa sensitive to disturbance or, otherwise, play key roles in soil function.

Indirect effects were defined as changes in nematode abundance due to secondary, physical, or chemical effects of a management practice. For example, an indirect effect may be a nematode community response associated with decreased organic carbon, which was decreased primarily by cultivation. Decreased organic carbon would be a direct effect, and the secondary community or population response of nematodes would be an indirect effect. Responses of nematode populations to indirect effects were estimated using partial CCA (ter Braak 1988) ordinations. Known physical and chemical impacts of agricultural practices were regressed first on covariables for which it is desirable to have the effects "partialed out," i.e., crop and site variation due to natural causes. Known impacts were included for changes in pH, total carbon, and bulk density (Scott et al. 1994, Robertson et al. 1993). The rationale was that after regression on natural or "uninteresting" covariables, the community-structuring role of physical and chemical variables that remained was due mostly to management practices. The location of genera in the ordination bi-plot was considered to represent a measure of relative sensitivity to anthropogenic changes in physical and chemical soil properties. No attempts were made to correct observations of nematode abundances for regional or natural variation in soil physical and chemical properties.

In CCA bi-plots, each vector for an environmental variable defines an axis, and site or genus scores can be projected onto that axis (Jongman et al. 1995). An indication of relative importance of a vector is its length; the angle indicates correlation with other vectors and CCA axes. Eigenvalues for CCA axes indicate the importance of the axes in explaining relationships in the genera–environment data matrices. Sensitivity ratings were assigned on a scale from 1 to 3, with 1 representing the least sensitive and 3 the most sensitive. Sensitivity ratings were estimated by the relative influence of direct and indirect management impacts on populations of genera using quadrants of the CCA diagrams. For direct effect sensitivities, a genus that had a CCA score in the same quadrant as the manure or no-till treatments were rated 3 or sensitive to direct effects. Conversely, a genus that scored in the same quadrant as pesticide, herbicide, or conventional-till treatments was rated 1 or insensitive. Sensitivity ratings to direct effects were based on the assumption that

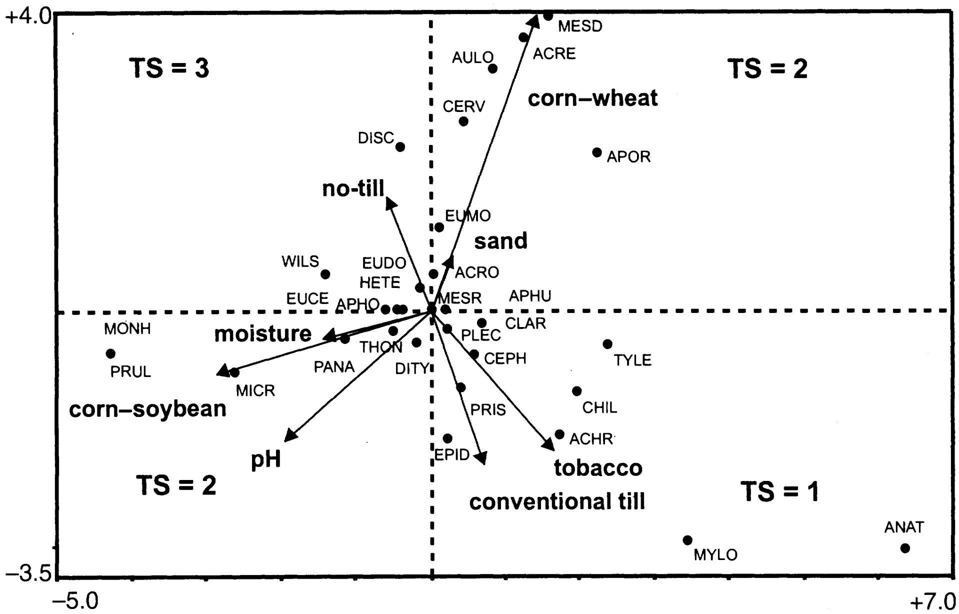

FIG. 1. Canonical correspondence analysis (CCA) bi-plot of direct tillage effects on nematode genera in a North Carolina tillage study (McQuaid and Olson 1998). Management practices including tillage (conventional and no-till), crops (corn and wheat rotation, corn and soybean rotation, and tobacco), sand, pH, and moisture are illustrated as vectors. Points represent relative sensitivity of nematode genera to tillage (TS), rated on a scale of 1–3 with 1 = least to 3 = most sensitive. Sensitivity is inversely proportional to population size in association with a specific disturbance type. Eigenvalues (lambda) are 0.205, 0.177, 0.112, and 0.110 for the x-, y-, third, and fourth axes, respectively. See Table 2 for nematode genus abbreviations.

manure and no-till were less disruptive to nematode communities than pesticides, herbicides, or conventional tillage. For indirect effect sensitivities, genera that had a CCA score in the same quadrant as a pH vector would be rated 3 or sensitive to indirect impacts as mediated by soil chemical properties, because pH values and organic carbon content are assumed to be correlated negatively with disturbance. Conversely, a genus that scored in the same quadrant as a vector for a soil property assumed to be correlated positively with disturbance, such as sodium, bulk density, or nitrate, was rated 1 or insensitive to indirect impacts, and so forth. Genera that fell in a quadrant with no direct or indirect environmental variables other than crop or natural variation, or in a quadrant with conflicting environmental vectors, were rated 2 and assumed to have intermediate sensitivity. The rating system was based on the assumption that abundant populations occur when a genus is tolerant or insensitive to a specific disturbance and populations decline if sensitive.

Validation of the ratings

To test the sensitivity ratings, independent data from the Kellogg Biological Station Long-Term Ecological Research site near East Hickory, Michigan, USA (Freckman and Ettema 1993) were employed. These data contained samples from eight positions on a gradient of human intervention from successional, never-tilled (SN) to conventional agriculture (CT). Samples sizes (n = 6 replicate experimental plots) were equal except for SN, where n = 4 replicate experimental plots. From these data were calculated a weighted mean frequency ($W = \Sigma[(s_i \times f_i)/n]$) of tillage sensitivity (TS) and chemical sensitivity (CS) for both direct and indirect ratings, where s represents TS or CS ratings, f represents the abundances for each genus, and n represents the total abundance. Genera were not the same in the three test data sets. Sensitivity ratings were tested only for genera present in Freckman and Ettema (1993) data.

RESULTS

Based on CCA ordinations of genera present in the North Carolina tillage study sites, direct (Fig. 1) and indirect (Fig. 2) TS ratings were assigned to each nematode genus. Vectors, representing environmental variables, of indirect TS ratings were relatively short, suggesting that nematode abundances are more correlated with sand and cropping regime, thus leaving little variation in the residuals to be explained by pH, bulk density, and organic carbon. CCA ordinations of genera present in the Nebraska chemical/nutrient treatment plots were used to assign direct (Fig. 3) and indirect (Fig. 4) CS ratings to each nematode genus. Results of all TS and CS ratings are listed by genus (Table 2). Of 46 total genera, six were sensitive to direct tillage, 15 to indirect tillage, and seven each to direct and indirect chemical/nutrient amendments. *Aphelenchoides*, *Discolaimus*, *Eucephalobus*, *Eudorylaimus*, *Heterocephalobus*, and *Wilsonema* were sensitive to direct till-

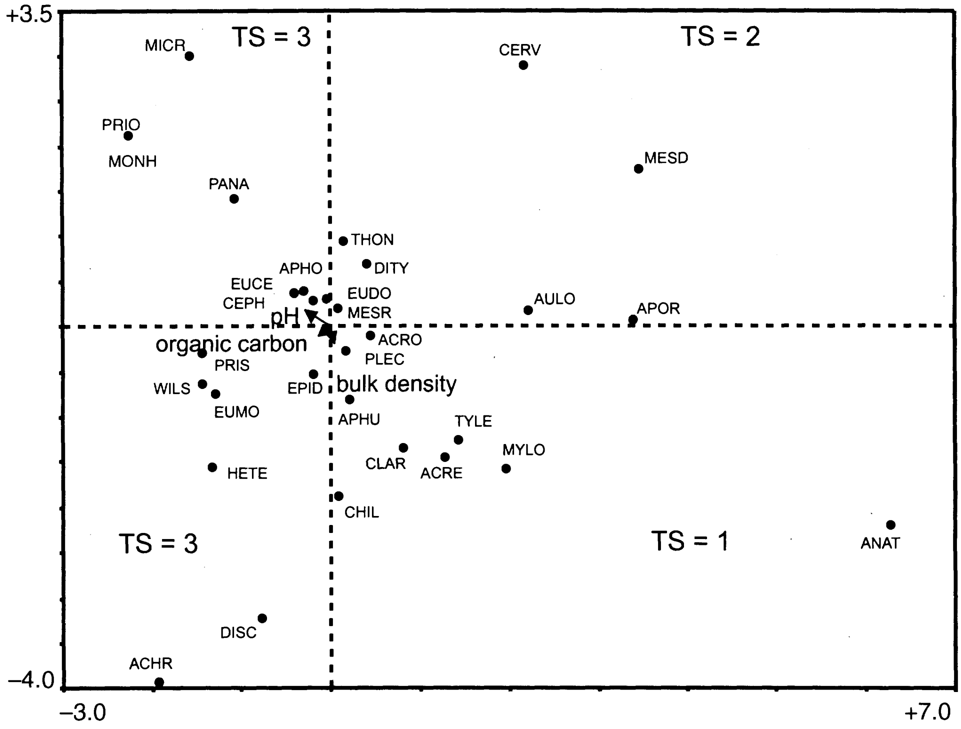

FIG. 2. Canonical correspondence analysis (CCA) bi-plot of indirect tillage effects on nematode genera in a North Carolina tillage study (McQuaid and Olson 1998). Bulk density, organic carbon content, and pH are illustrated as vectors with crop and sand content as covariables. Symbols and definitions are as in Fig. 1. Eigenvalues (lambda) are 0.151, 0.110, 0.058, and 0.175 for the *x*-, *y*-, third, and fourth axes, respectively. See Table 2 for nematode genus abbreviations.

age. In contrast, *Achromadora*, *Anatonchus*, *Cephalobus*, *Chiloplacus*, *Clarkus*, *Epidorylaimus*, *Mylonchulus*, *Plectus*, *Prismatolaimus*, and *Tylencholaimellus* were not sensitive to direct tillage (Table 2). Some genera were more sensitive to indirect than direct effects of tillage, including *Achromadora*, *Cephalobus*, *Epidorylaimus*, *Eumonhystera*, *Microdorylaimus*, *Monhystera*, *Panagrolaimus*, *Prionchulus*, and *Prismatolaimus*. Sensitivity responses to direct effects of chemical/nutrient treatments were most pronounced in the genera *Alaimus*, *Cylindrolaimus*, *Discolaimus*, *Mesorhabditis*, *Odontolaimus*, *Prismatolaimus*, and *Protorhabditis*. Genera more sensitive to indirect than direct effects of chemical/nutrient treatments were *Aphelenchus*, *Aporcelaimellus*, *Diplogaster*, *Eudorylaimus*, and *Eumonhsytera*.

The colonizer–persister (CP) scale values (Bongers 1990) and modified CP values on a 1–3 scale (de Goede 1993) are included for comparison. The original CP1–5 scale rates nematode genera least sensitive to disturbance with a value of 1, and genera most sensitive to disturbance with a value of 5. The modified CP scale of de Goede (1993) matches the original CP scale for values of 1 and 2, but de Goede's value 3 combines the original CP values 3, 4, and 5. Inconsistency between CP values and sensitivity ratings occurred for many genera. Opposite of what one might anticipate based on their CP value of 4, *Anatonchus*, *Clarkus*, *Epidorylaimus*, *Mylonchulus*, and *Tylencholaimellus* were relatively tolerant to cultivation; and *Aporcelaimus*, *Clarkus*, *Enchodelus*, *Microdorylaimus*, *Mylonchulus*, and *Tylencholaimellus* were relatively tolerant to chemical/nutrient amendments. In contrast, one would anticipate genera with CP values of 1 or 2 to tolerate tillage and/or chemical/nutrient treatments but *Aphelenchoides*, *Heterocephalobus*, *Wilsonema*, *Cephalobus*, *Eucephalobus*, *Eumonhystera*, *Monhystera*, and *Panagrolaimus* were sensitive to cultivation; and *Aphelenchus*, *Diplogaster*, *Eumonystera*, *Mesorhabditis* and *Protorhabditis* were sensitive to nutrient/chemical enrichment. Based upon the TS and CS ratings (Table 2), a weighted mean frequency of tillage and chemical sensitivity was validated on independent data (Fig. 5). Indirect tillage and chemical sensitivities showed clear responses to the gradient of increasing human intervention; however, the weighted mean frequency of direct sensitivities show a less obvious relationship to this gradient (Fig. 5). The indirect TS weighted mean frequency decreased with increasing human intervention, while the indirect CS weighted mean frequency increased.

DISCUSSION

Currently, environmental monitoring programs, strategies, conceptual frameworks, and methodologies have been evaluated at national levels in recent years

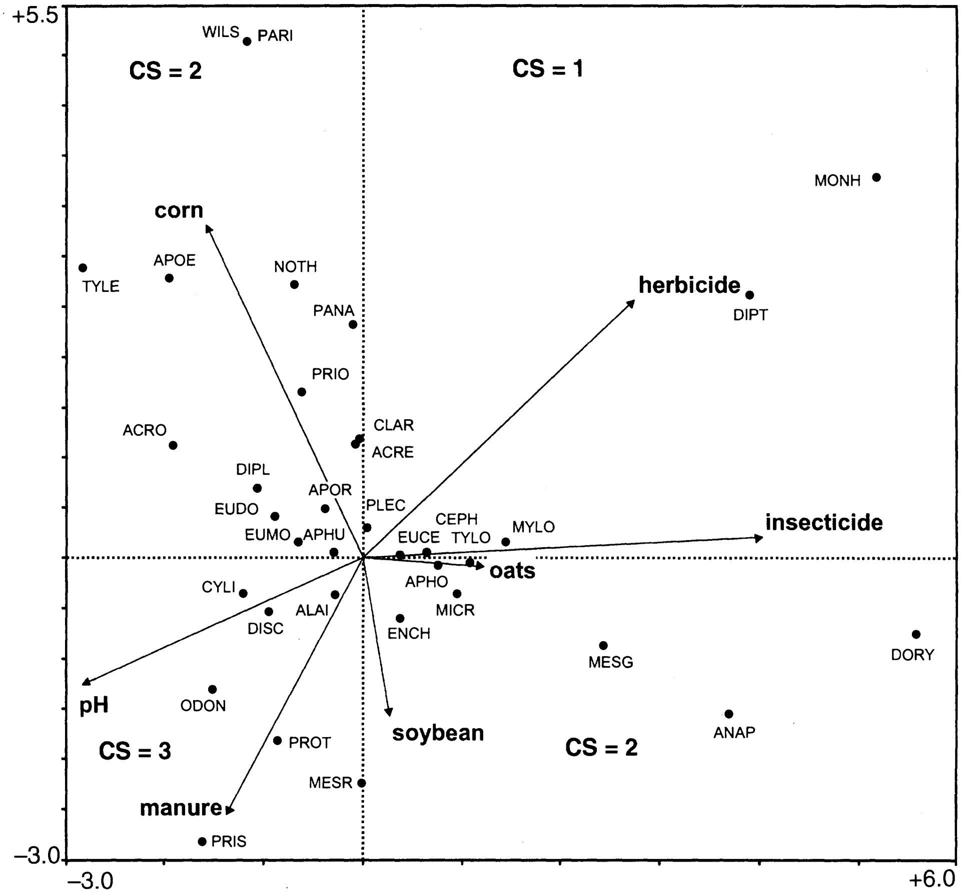

FIG. 3. Canonical correspondence analysis (CCA) bi-plot of direct chemical/nutrient effects in a Nebraska long-term study (Neher and Olson 1999) on nematode genera. Management practices including manure applications ("manure"), mineral fertilizer and herbicides ("herbicide"), a mixture of herbicides, mineral fertilizers, and insecticides ("insecticide"), pH, and crops (corn, soybean, and oats) are illustrated as vectors. Symbols and definitions are as in Fig. 1. Eigenvalues (lambda) are 0.203, 0.159, 0.118, and 0.097 for the *x*-, *y*-, third, and fourth axes, respectively. See Table 2 for nematode genus abbreviations.

(e.g., Olsen et al. 1997). Monitoring of a nation's cropland is a priority in the United States government as demonstrated by the planned inclusion of cropland, along with forests and coastal/marine systems, in initial U.S. environmental health reports (Kaiser 1997, Heinz Center 2001). The largest agricultural conservation effort, the USDA's Environmental Quality Incentives Program in the 1996 Farm Bill, had no provision for assessing the impacts of this important program on agroecosystem condition or quality (USDA 1997). The approach and method presented may benefit such efforts.

Ordination based on multivariate canonical correspondence analysis (CCA) was useful for organizing and analyzing three complex data sets used in this study; such data are similar to those used in regional monitoring and assessment studies. CCA is a direct gradient analysis technique that assumes unimodal responses of species (genera in this study) to environmental gradients, and produces ordinations that attempt to detect the main pattern in genera and environment matrices (Jongman et al. 1995). Environmental variables constrain the ordination, i.e., site scores are restricted to be a linear combination of the environmental variables. Partial CCA holds promise for providing a means to filter out background variation due to crops or differences among geographic sites (ter Braak 1988).

Initial sensitivity ratings support both hypotheses proposed. First, tillage and chemical/nutrient applications affect some nematode genera in opposite ways. For example, abundances of *Eucephalobus* increase with chemical/nutrient treatment but decrease with tillage treatment. *Prismatolaimus* populations are reverse. Tillage and chemical/nutrient sensitivity represent two types of management practices, the former creating a disturbance, interrupting successional maturity, and the later serving an enrichment capacity. Often, management practices confound these types of disturbance. For example, soils may be cultivated followed by applications of mineral fertilizer and herbicides. In management practices that combine these two opposing impacts, it is difficult to link an indicator based on nem-

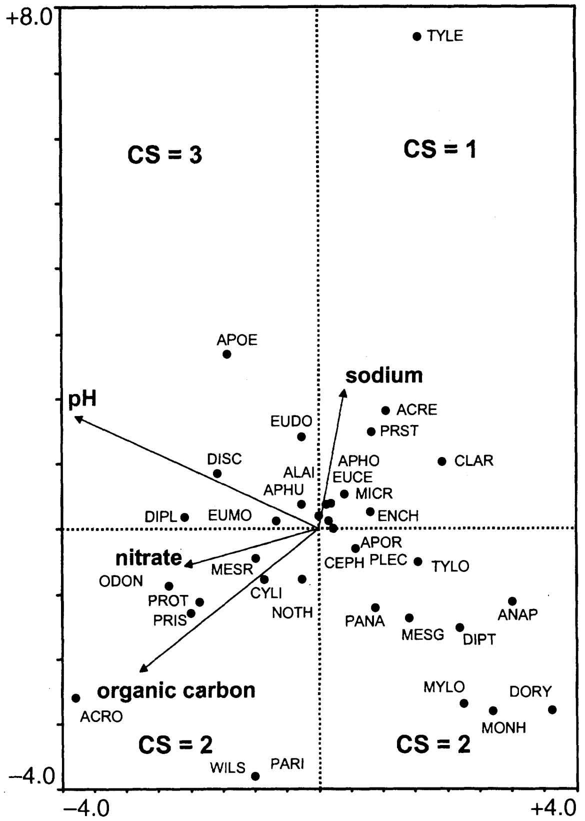

FIG. 4. Canonical correspondence analysis (CCA) bi-plot of indirect chemical/nutrient effects in a Nebraska long-term study (Neher and Olson 1999) on nematode genera. Extractable sodium, organic carbon content, available nitrate, and pH are illustrated as vectors with crop and replicate block as covariables. Symbols and definitions are as in Fig. 1. Eigenvalues (lambda) are 0.164, 0.099, 0.084, and 0.045 for the *x*-, *y*-, third, and fourth axes, respectively. See Table 2 for nematode genus abbreviations.

atode community structure directly to changes in ecological function. Second, the weighted mean frequency of direct sensitivities was negligible compared to the clear response of indirect sensitivities for both tillage and chemical/nutrient applications. Both physical and chemical aspects of agricultural management practices have both direct and indirect effects on nematode communities. Greater sensitivity to indirect than direct effects suggests that nematode communities are more responsive to secondary impacts of management mediated by the soil environment than they are to impacts of tillage or chemical/nutrient practices exclusively. Perhaps, these results can be explained by nematodes having a longer evolutionary history of exposure to soil properties such as pH, organic carbon, and bulk density than to tillage or chemical applications. Based on this study, we recommend that nematode community indicators for environmental monitoring purposes be interpreted differently for response to direct and indirect tillage (TS) and chemical sensitivity (CS).

Some genera noted in our study to be sensitive to tillage and/or chemical/nutrient applications support previous findings. For example, cultivation is associated with abundant populations of *Aphelenchus* (Wardle et al. 1995*a*) and small populations of Dorylaimidae and *Eucephalobus* (López-Fando and Bello 1995, McSorley 1997). Under conditions of nutrient/chemical enrichment, populations of *Aphelenchoides*, *Cephalobus*, *Diphtherophora*, and *Plectus* increase, and *Aphelenchus*, *Aporcelaimellus*, and *Eudorylaimus* decrease. In contrast to previous reports, we observed Anatonchidae (*Anatonchus*) and Mononchidae (*Mylonchulus*) were tolerant instead of sensitive to tillage and Rhabditidae (*Parisitorhabditis* and *Protorhabditis*) populations were intermediately sensitive rather than tolerant of chemical/nutrient enrichment (Wardle et al. 1995*a*, Ferris et al. 1996, Yeates and van der Meulen 1996, Yeates et al. 1997, Wasilewska 1998, Porazinska et al. 1999, Villenave et al. 2001).

Although this study identifies nematode genera that are sensitive to tillage and/or chemical applications, further research is warranted that test the effects of tillage and chemical applications individually or combined to verify proposed sensitivity ratings. Our results could be made more robust by testing the following conditions. First, differences in nematode community composition, abundances, and successional maturities between states of North Carolina and Nebraska (Neher et al. 1998) could be considered in developing TS and CS ratings. We also did not attempt to correct nematode abundances for regional variation. Verification of TS and CS ratings on other agricultural data would allow comparison to these results and refinement of ratings for each genus. Second, spatial variability within agricultural fields could be incorporated (Robertson and Freckman 1995, Neher et al. 1995). Third, determination of consistency of sensitivity to tillage or chemical/nutrient factors through time is necessary. When testing temporal patterns, asynchrony of peak values of soil environmental attributes and nematode abundances should be considered (Wardle et al. 1995*a*, Yeates et al. 1993*b*).

Trade-offs of cost and reliability (Neher and Campbell 1996) are critical for continued refinement of monitoring and sampling designs. However, nematode community indices would be more feasible logistically and more cost effective for use in environmental monitoring programs by reducing the number of genera that need to be enumerated and identified. This could be achieved by narrowing indices to include only sensitive or tolerant genera or species while eliminating ambiguous ones. We propose three criteria for selecting genera for inclusion in indices of soil quality: (1) consistency in sensitivity to both direct and indirect forms of a disturbance type, (2) consistency in sensitivity to both physical and chemical/nutrient types of disturbance, and/or (3) opposite types of responses to physical than chemical/nutrient disturbance. Examples of genera meeting these respective criteria are *Alaimus*, *Anaton-*

TABLE 2. Tillage and chemical sensitivity ratings for free-living nematode genera found in the North Carolina pilot tillage study (McQuaid and Olson 1998) and Neher and Olson (1999).

Genus	Tillage		Chemical/nutrient		Maturity index values		Genus code
	Direct	Indirect	Direct	Indirect	CP1–5	CP1–3	
Achromadora	1	3	…†	…	3	3	ACHR
Acrobeles	2	1	2	1	2	2	ACRE
Acrobeloides	2	1	2	2	2	2	ACRO
Alaimus‖	…	…	3	3	4	3	ALAI
Anaplectus	…	…	2	2	2	2	ANAP
Anatonchus‡,‖	1	1	…	…	4	3	ANAT
Aphelenchoides‡,#	3	3	2	1	2	2	APHO
Aphelenchus‡	2	1	2	3	2	2	APHU
Aporcelaimellus	…	…	2	3	5	5	APOE
Aporcelaimus‡	2	2	2	1	5	3	APOR
Aulolaimus	2	2	…	…	3	3	AULO
Cephalobus‡,¶	1	3	1	2	2	2	CEPH
Cervidellus	2	2	…	…	2	2	CERV
Chiloplacus‖	1	1	…	…	2	2	CHIL
Clarkus‡,¶	1	1	2	1	4	3	CLAR
Cylindrolaimus	…	…	3	2	3	3	CYLI
Diplogaster‡	…	…	2	3	1	1	DIPL
Diphtherophora‖	…	…	1	2	3	3	DIPT
Discolaimus§	3	3	3	3	5	3	DISC
Ditylenchus	2	2	…	…	2	2	DITY
Dorylaimidae‡	…	…	2	2	4	3	DORY
Enchodelus‡	…	…	2	1	4	3	ENCH
Epidorylaimus‡	1	3	…	…	4	3	EPID
Eucephalobus‡,#	3	3	1	1	2	2	EUCE
Eudorylaimus¶	3	3	2	3	4	3	EUDO
Eumonhystera‡	2	3	2	3	1	1	EUMO
Heterocephalobus‡,‖	3	3	…	…	2	2	HETE
Mesodiplogaster	…	…	2	2	1	1	MESD
Mesodorylaimus	2	2	…	…	5	3	MESG
Mesorhabditis‡	2	2	3	2	1	1	MESR
Microdorylaimus‡	2	3	2	1	4	3	MICR
Monhystera‡,#	2	3	1	2	1	1	MONH
Mylonchulus‡,§	1	1	1	2	4	3	MYLO
Nothotylenchus	…	…	2	2	2	2	NOTH
Odontolaimus	…	…	3	2	3	3	ODON
Panagrolaimus‡	2	3	2	2	1	1	PANA
Parasitorhabditis	…	…	2	2	1	1	PARI
Plectus§	1	1	1	1	2	2	PLEC
Prionchulus	2	3	…	…	4	3	PRUL
Pristionchus	…	…	2	1	1	1	PRST
Prismatolaimus	1	3	3	2	3	3	PRIS
Protorhabditis‡	…	…	3	2	1	1	PROT
Thonus	2	2	…	…	4	3	THON
Tylencholaimellus‡,¶	1	1	2	1	4	3	TYLE
Tylencholaimus‡	…	…	2	2	4	3	TYLO
Wilsonema‡,#	3	3	2	2	2	2	WILS

Notes: Sensitivity ratings are assigned based on CCA (Figs. 1 and 3) and partial CCA (Figs. 2 and 4) bi-plots. Each quadrant of each biplot was rated 1, 2, or 3 based on relative influence of direct or indirect tillage or chemical/nutrient variables: 1 = least sensitive to 3 = most sensitive. Maturity Index values are based on either Bongers' (1990) colonizer–persister (CP1–5) scale, in which scores range from 1 (least sensitive) to 5 (most sensitive), or the CP1–3 modified scale as per CP triangles (de Goede 1993).

† Not present.

‡ Inconsistency between CP1–5 value and sensitivity rating(s).

§ Genus recommended as general indicator of disturbance.

‖ Genus has consistent sensitivity rating to both direct and indirect forms of a disturbance type.

¶ Genus has consistent sensitivity rating to both tillage and chemical/nutrient treatments.

Genus has opposite sensitivity rating for tillage than for chemical/nutrient treatments.

chus, *Chiloplacus*, and *Heterocephalobus* (criterion 1); *Clarkus*, *Eudorylaimus*, and *Tylencholaimellus* (criterion 2); and *Aphelenchoides*, *Eucephalobus*, and *Wilsonema* (criterion 3). Based on our results, we recommend *Discolaimus*, *Mylonchulus*, and *Plectus* as indicators of general disturbance because they meet both criteria 1 and 2. Sensitivity of *Discolaimus* and tolerance of *Plectus* are consistent with their CP values of 5 and 2, respectively. In contrast, *Mylonchulus* was abundant under both cultivation and enrichment conditions, opposite of its CP value of 4.

The TS and CS ratings derived in this study provide different information than the CP scales of Bongers (1990) and de Goede (1993). For example, while most

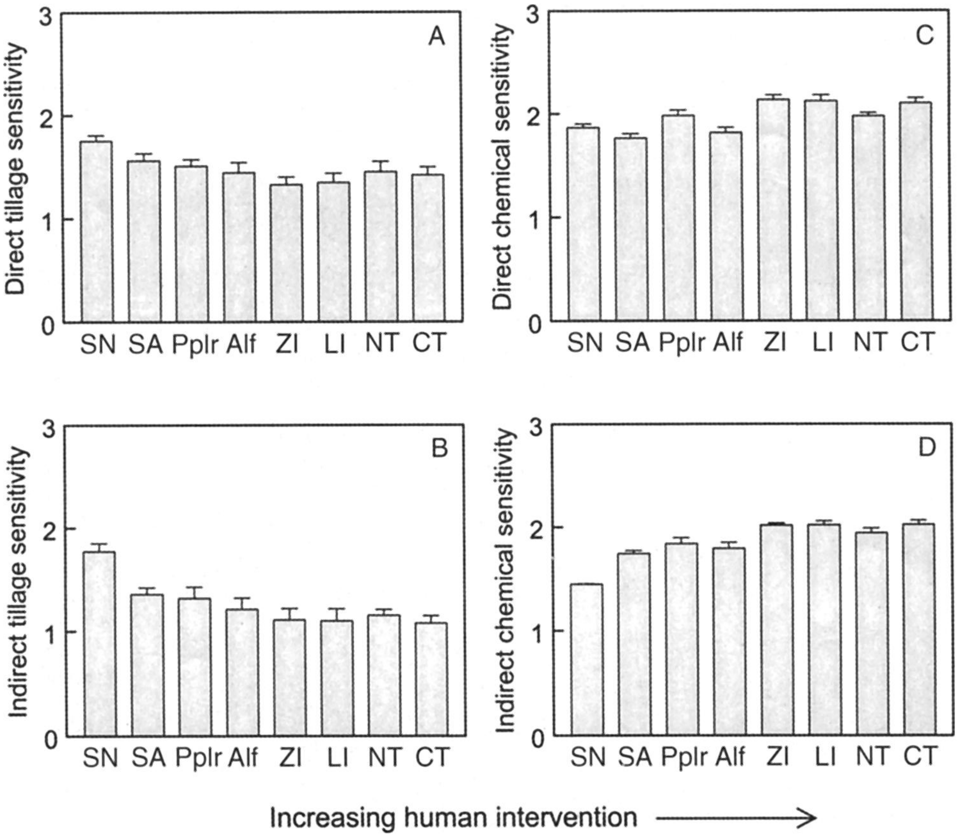

FIG. 5. Weighted mean frequencies and standard errors of (A, C) direct and (B, D) indirect nematode sensitivities to (A, B) tillage and (C, D) chemical/nutrient additions. Treatment abbreviations: SN = successional, never tilled; SA = successional, abandoned; Pplr = poplar (*Populus euramericana*); Alf = alfalfa (*Medicago sativa* L.); ZI = zero input; LI = low input; NT = no-till; CT = conventional till. Data are used by permission (Freckman and Ettema 1993).

predaceous genera are rated 4 or 5 on the Bongers' (1990) CP scale, several are rated 2 or even 1 on the TS and CS scales. Further analysis is warranted to compare more directly the TS and CS ratings to the CP scale for each genus. It is possible that agricultural management practices that include both tillage and chemical/nutrient amendments not only disturb nematode communities but also enrich them. For example, predatory genera may benefit from increased abundance of opportunist-genera prey despite being disturbed by physical alterations, resulting in ratings that differ from the CP scale. Our results support previous requests for re-evaluation of certain CP value assignments (Porazinska et al. 1999, Korthals et al. 1996). We suggest that the CCA method aids in distinguishing nematode genera that have distinctive responses to agricultural management practices from those that are ambiguous. This knowledge is useful for both interpretation and refinement of free-living nematode community indices.

ACKNOWLEDGMENTS

We dedicate this manuscript to our deceased mentor, colleague, and friend, C. Lee Campbell. We thank A. F. Bird, Christien H. Ettema, Diana Freckman Wall, Betty McQuaid, Gail Olson, Richard K. Olson, and Gregor Yeates, who provided empirical data for this study. No criticism of original methods of analysis or conclusions drawn by the authors is intended. This work was supported by funding from the U.S. Environmental Protection Agency through interagency agreement DW12934170 to the United States Department of Agriculture and through Specific Cooperative Agreement 58-6645-2-016 between the USDA Agricultural Research Service and the North Carolina Agricultural Research Service.

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