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Effects of long-term crop management on nematode trophic levels other than plant feeders disappear after 1 year of disruptive soil management

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Abstract

Nematode community analysis may provide a useful tool to quantify soil health. Nematode communities were monitored for 5 years during a 12-year period in the sustainable agriculture farming systems (SAFS) project at UC Davis, where conventional (CONV), low-input (LOW) and organic (ORG) management treatments were compared. After the completion of three 4-year crop rotation cycles, a uniform crop of oats was grown in 2001. The composition of the nematode genera was different from year to year, but there were significant management effects on genus composition in each year, with the CONV treatment being significantly different from the LOW and ORG treatments. Important contributors to the differences in genus composition among treatments were plant parasitic nematodes. Nematode community indices (enrichment (EI), basal (BI) and channel (CI) indices) of the CONV treatment differed from those of the ORG and LOW treatments in 1993, 1994, 1995 and 2000, but not in 2001. The difference in structure index (SI) among management treatments was significant in 1995 and 2000. EI and SI were generally lower, and BI and CI higher in CONV than in LOW and ORG treatments. There were significant crop effects on the community indices throughout the years. Even in 2001, there was a residual effect of the crop grown in 2000 on most nematode community indices. Differences in EI, BI and CI among crops were consistent, while those in SI were not. *Meloidogyne javanica* (Treub) Chitwood, juveniles added to various soil samples were reduced by 68% in soil where nematode trapping fungi had been added and which had low BI (12) and low CI (20) values. Soil from SAFS plots with a high BI (47) and high CI (70) after 1 year of oats and ploughing, suppressed root knot juveniles much less. There were significant negative correlations between BI and root knot nematode (RKN) suppression (−0.72) and between CI and RKN suppression (−0.74). Thus, BI and CI appeared to be most valuable as indicators for long-term effects of management on nematode suppression. However, BI and SI may be more suitable as general indicators for the health status of a soil, since CI can be high in highly disturbed agro-ecosystems as well as in undisturbed natural ecosystems. A high BI would indicate poor ecosystem health, while a high SI would indicate a well-regulated, healthy ecosystem. For agricultural soils the presence of large populations of plant parasitic nematodes forms an additional indication of poor ecosystem health, as natural regulation is limited in this case.

Keywords: Nematode community structure; Faunal analysis; Community indices; Organic management; Soil health; Suppressiveness

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1. Introduction

Healthy, thriving ecosystems are generally highly diverse with numerous taxa. These taxa form a complex food web of many trophic levels (Metting and Blaine, 1993). Soil ecosystems have food webs with a great variety of organisms, ranging from single celled bacteria, algae and protozoa, to multi-celled mites, earthworms, collembola and nematodes. Nematodes vary widely in life strategies and fulfill various functions in soil food webs (Bongers and Bongers, 1998). At the base, where decomposition takes place, there are fast-growing, fast-breeding, bacteria-feeding nematodes. At the top are slow growing, slow reproducing, predatory nematodes. The belief that there is a relationship between food web complexity and soil health has led to the use of taxonomic and functional diversity indices in attempts to characterize the health status of soils (Neher, 1999; Neher and Olson, 1999; Porazinska et al., 1999; Urzelai et al., 2000; Yeates and Bongers, 1999; van Bruggen and Semenov, 2000).

The structures of nematode and other soil communities are affected by natural and anthropogenic disturbances. In response to a disturbance, the nematode community becomes dominated by fast-growing, bacteria-feeding nematodes, and is then generally transformed to a more diverse community that includes slower-growing bacterivores and fungivores and, ultimately, predatory nematodes and omnivores (Ferris et al., 1996; Yeates et al., 1999; Fu et al., 2000). This evolution of complexity can be monitored by the maturity index (Bongers and Bongers, 1998; Neher, 1999; Yeates and Bongers, 1999). The maturity and diversity indices have been used successfully to distinguish well-functioning ecosystems from heavily disturbed or stressed systems, but more subtle differences among agro-ecosystems were not detected (Neher, 1999; Neher and Olson, 1999; Porazinska et al., 1999; Yeates and Bongers, 1999; Urzelai et al., 2000). An integration of trophic groupings and life strategies into functional guilds allowed definition of several indices that describe structure, function and condition of the food web relative to disturbance or stress (Bongers and Bongers, 1998). Ferris et al. (2001) distinguished the basal index (BI) as an indicator of a food web diminished by stress or limited nutrient resources, the structural index (SI) as a measure of the number of trophic layers and potential for regulation of opportunists (bacteria feeders and/or plant parasitic nematodes), and the enrichment index (EI) as a measure of resource availability. Also, they defined the channel index (CI) to distinguish fungi-based from bacteria-based food web structures. These indicators may also be useful to characterize soil quality or health (Ferris et al., 2001), but this has not been tested thoroughly.

A healthy soil is important for successful organic farming systems (van Bruggen, 1995; van Bruggen and Semenov, 2000). A healthy soil with a high SI could, for example, regulate or suppress plant parasitic nematode species. In soils in transition from conventional to organic management it may be desirable to manage the soil community so that regulatory functions are enhanced.

Changes in soil micro-organisms and fauna, and consequently in soil processes, after conversion from conventional to organic management, have been documented in several studies (van Bruggen, 1995). One of the most comprehensive studies has been the sustainable agriculture farming systems (SAFS) project at UC Davis, California (Clark et al., 1999). In this project, agronomic, ecological and economic aspects of irrigated cropping systems under conventional, low-input and organic management were compared in a Mediterranean climate. Three 4-year crop cycles were completed during the experiment. Positive, long-term effects on soil properties were documented for the low-input and organic treatments compared to the conventional treatments, including the accumulation of plant nutrients and soil organic carbon, greater soil biological activity, reduced root disease severity, and improved water infiltration (van Bruggen, 1995; Cavero et al., 1997; Clark et al., 1998, 1999; Poudel et al., 2001a). Populations of bacteria-feeding, fungi-feeding and plant-parasitic nematodes and nematode trapping fungi were also monitored (Scow et al., 1994; Ferris et al., 1996; Clark et al., 1998; Jaffee et al., 1998). However, the recent developments in nematode faunal indices have not been applied to nematode community data from the SAFS experiment.

Where differences in nematode community structure were described for farmers' fields with different management histories (Neher, 1999; Neher and Olson, 1999), it was not known whether these were primarily due to the farming system or due to the previous crops. The SAFS project offered a unique opportunity to separate concurrent and residual management effects (after a uniform crop at the end of the experiment) from previous crop effects on nematode community structure. It also offered the opportunity to relate nematode community structure to one indicator of soil health, namely RKN suppression.

The objectives for this study were to: (1) determine if there were concurrent and residual effects of management treatments and crops in the SAFS experiment on nematode community composition and indices, (2) determine if there was a relationship between nematode community indices and soil properties, and (3) assess the suppressiveness of soils from different management systems and cropping histories towards a representative plant-parasitic nematode species.

2. Materials and methods

2.1. Study site

The SAFS experiment was established in 1988 on an 11 ha site at the Agronomy Farm of the University of California at Davis (38°32′N, 121°47′W; 18 m elevation). The soil at the experimental site is classified partly as Reiff loam and partly as Yolo silt loam (Clark et al., 1998). The experiment had a split-plot design with four management treatments as main plots randomized in four blocks, and rotation crops as sub plots randomized in main plots. The sub plot size was about 0.13 ha.

Three of the four main treatments (farming systems) were included in the present study: conventional (CONV), low-input (LOW) and organic (ORG) management. All these treatments had a 4-year crop rotation in the following sequence: processing tomatoes (*Lycopersicon esculentum* L.), safflower (*Carthamus tinctorius* L.), corn (*Zea mays* L.), wheat (*Triticum vulgare* L.), and dry beans (*Phaseolus vulgaris* L.) in the same season as wheat. Instead of wheat and beans, a mixture of purple vetch (*Vicia benghalensis* L.) and oats (*Avena sativa* L.) was grown in the ORG and LOW treatments. Each entry in the rotation was represented every year. Management practices for these systems were described earlier (Clark et al., 1998, 1999). The greatest differences were in the use of winter cover crops (vetch and oats) in the LOW and ORG management systems and winter fallow in the CONV system. Soil fertility was supplemented by synthetic fertilizers in the CONV and LOW treatments but by composted poultry manure in the ORG treatment.

Three crop rotation cycles were completed between 1989 and 2000. In 2001, oats were planted on the entire SAFS field. No fertilizer was applied to the soil in this final year. The entire field was thoroughly ploughed after oats were harvested to prepare the site for a new study (the Irrigated Agriculture Conservation Tillage project).

2.2. Soil sampling

Thirty composite samples of 2.5 cm diameter soil cores to a depth of 30 cm were randomly taken from each plot after harvest of the summer crop in September of 1993 and 1994, August 1995 and 2000, and early December 2001. Samples were stored at 10 °C. During the 2001 sampling, soil moisture was high due to recent rainfall. Those samples were spread on paper and air-dried for 4 h before they could be processed further. All samples were passed through a screen of pore size 8 mm to break clods and remove rocks and large plant debris. The dry weight of each sample was measured by drying a small sub-sample for 24 h at 105 °C.

2.3. Nematode extraction, identification and community analysis

A sub-sample (300 g) was used for nematode extraction by elutriation and sugar-centrifugation (Ingham, 1994). The number of nematodes in each sample was estimated by counting half the sample under low magnification (50×). The rest of the sample was preserved using hot formaldehyde at a final concentration of 4%, and kept at 10 °C until identification. One hundred nematodes were identified to the genus level using the taxonomic keys provided in Bongers (1987). The nematodes were classified into functional groups to calculate four indices: enrichment (EI), basal (BI), structure (SI) and channel index (CI) (Ferris et al., 2001). The EI contains fast-growing, bacteria- and fungi-feeding nematodes with a colonizer-persister (c-p) value of 1 or 2 (Bongers, 1999). The BI contains bacteria-feeding and fungi-feeding nematodes with a c-p value of 2. The SI measures the slow growing and reproducing predatory and omnivore nematodes with c-p values of 3, 4 and 5. The CI is a comparison of the size of the fungal to bacterial feeding communities. The CI assesses the primary decomposition pathway of soil, a value of 100 being completely fungal and a value of 0 being completely bacterial.

2.4. Soil chemical analysis in 2001

To determine mineral N content, about 8 g of fresh soil was placed into a tube with 40 ml of 2 M KCl. The tubes were weighed before and after addition of soil so that the exact amount of soil (dry weight) could be calculated. The tubes were shaken for 1 h and centrifuged for 5 min at 5 g at room temperature (Bundy and Meisinger, 1994). Twenty milliliters of the supernatant was submitted to the University of California's Division of Agriculture and Natural Resources analytical laboratory for determination of $NO_3{}^{-}$–N and $NH_4{}^{+}$–N concentrations by automated flow injection and colorimetric analysis (Switala, 1993; Wendt, 1999). The total organic matter (OM) content was estimated by the loss on ignition method (Heiri et al., 2001).

2.5. Suppressiveness test

A test for nematode suppressiveness of the soil, developed from established protocols (Jaffee et al., 1998; Westphal and Becker, 2001), was applied to four plots of the CONV treatment and four plots of the ORG treatment. These plots had beans or corn as a crop in the year 2000. About 5 g fresh soil was added to eight tubes (height 1.6 cm, i.d. 2.0 cm), covered on the bottom by a fine net-cloth with openings 0.19 mm × 0.25 mm. Four of the tubes were heated for 2 h at 65 °C to pasteurise the soil. Many soil organisms were killed in this way but soil properties were largely unaffected. Distilled water was added to replenish the water that was lost during pasteurisation. As a positive control we included soil collected in January 2002 from micro-plots at UC Davis. This soil (beach sand) had been amended with endoparasitic and nematode-trapping fungi (Jaffee and Muldoon, 1997). Each tube was inoculated with 175 juveniles of *Meloidogyne javanica* (Treub) Chitwood and incubated for 6 days at 24 °C in the dark. After 6 days each tube was placed on a Baermann-funnel (Ingham, 1994) and extracted for 48 h after which the funnels were tapped to collect the root knot nematode juveniles.

2.6. Data analysis

Nematode community composition was compared among management treatments by contingency tables and χ^2 tests for all years. The five genera that contributed most to the differences between management treatments were compared among years. Populations of genera that were observed in most years and contributed significantly ($P < 0.05$) to the overall χ^2 value were analyzed by analysis of variance (ANOVA) to test treatment effects on individual genera.

To calculate the various nematode indices, all genera were assigned weights for EI, BI and SI according to their classification into functional groups (Ferris et al., 2001). For example, bacteria-feeding nematodes with a c-p value of 1 or 2 received a weight of 0.8 for BI only, while fungi-feeding nematodes with a c-p value of 2 received a weight of 0.8 for EI and BI. Bacteria-feeding nematodes with a c-p value of 3 received a weight of 3.2 for EI only. Plant-parasitic nematodes were omitted from the indices to eliminate host-status effects of the crop sequences. After assigning weights, the sum-products (called E, B, and S) were calculated from the assigned weights and numbers of individuals in all genera. The indices were calculated as follows:

$$\mathrm{EI} = 100 \times \frac{E}{B + E}$$

$$\mathrm{BI} = 100 \times \frac{B}{B + E + S}$$

$$\mathrm{SI} = 100 \times \frac{S}{B + S}$$

$$\mathrm{CI} = 100 \times \frac{E_\mathrm{f}}{E_\mathrm{b} + E_\mathrm{f}},$$

where E_f is E of fungi-feeding nematodes and E_b is E of bacteria-feeding nematodes (Ferris et al., 2001).

EI, BI, SI and CI were compared among management treatments and over time graphically. All data were tested for normality and subjected to log-transformation when needed. EI, BI, SI, CI, soil $NO_3{}^{-}$–N, $NH_4{}^{+}$–N, pH and organic matter contents were compared among (residual) management types and crops by a split-plot ANOVA for each year. Residuals of original or log-transformed data were all normally distributed. The Duncan multiple range test was used for separation of means by management type or crop when significant differences were detected ($P < 0.05$). In addition, Spearman ranked correlation coefficients were calculated between all variables to determine possible relationships.

Root knot suppression was calculated as the percentage reduction in root knot juveniles in untreated soil compared to pasteurized soil. Spearman ranked correlation coefficients were calculated to test if suppression was correlated with the nematode community indices.

All statistical analyses were carried out with the Statistical Analysis System (SAS Institute Inc., Box 8000, Cary, NC 27511–8000, USA), except for the χ^2 tests, which were done in Excel 97 (Microsoft Corp., One Microsoft Way, Redmond, WA 98052–6399).

3. Results

3.1. Management effects on nematode communities

The genus composition differed from year to year. Only a few genera were prominent throughout all of the years monitored. Nevertheless, the χ^2 tests showed that the genus composition was significantly affected by management treatment in all years, including the last year, after a uniform crop and extensive ploughing in 2001. The genera that contributed most to the χ^2 values are listed in Table 1. From 1994 onwards, *Pratylenchus* was the genus contributing most to the differences among management types. *Panagrolaimus*, *Mesorhabditis* (*Bursilla*), and *Tylenchorhynchus* were also major contributors to these differences (Table 1). *Pratylenchus* was consistently more numerous in CONV plots than in LOW and ORG plots in all years. *Tylenchorhynchus* was less numerous in CONV than in LOW or ORG plots from 1995 onwards. *Mesorhabditis*, *Cruznema*, *Panagrolaimus*, and Rhabditidae were always lower in CONV than in ORG and LOW, except in 2001 (Table 2). *Acrobeloides* was consistently higher in CONV than in ORG and LOW. Other genera showed no clear treatment effect.

Significant differences ($P < 0.001$) were found between farming systems in BI and CI in the years 1993, 1994, 1995, and 2000 (Fig. 1 and Table 3). EI differed significantly ($P < 0.05$) between farming systems in 1993, 1995 and 2000. Differences in SI were significant in 1995 and 2000. LOW and ORG farm management resulted in a higher EI than CONV (Table 3). The CONV management had a higher BI. The SI was highest in LOW and ORG farming systems (significant in 1995 and 2000). The CI was higher in CONV farming systems than in LOW and ORG. No residual farm management effects were found for any of the indices in the SAFS field in 2001. The SI was extremely low in all plots in 2001. In many samples, no structure-indicator (c-p, 3–5) nematodes were found at all. The CI was higher in 2001 than in any other year. Significant interactions between management effects and crop effects were sometimes observed in the earlier years, but not in 2000 and 2001.

Table 1
Contributions (CONTR) of the five most important genera to the total χ^2 for the frequency distribution of genera over management classes (CONV, LOW and ORG) in each of 5 years in the Sustainable Agriculture Farming Systems Project at UC Davis

Year	Total χ^2	d.f.	Genus 1	CONTR (%)	Genus 2	CONTR (%)	Genus 3	CONTR (%)	Genus 4	CONTR (%)	Genus 5	CONTR (%)
1993	557	34	Meso	18.0	Cruz	14.5	Panag	13.3	Rhab	10.8	Prat	9.7
1994	566	32	Prat	46.8	Panag	13.1	Meso	12.9	Meloid	8.7	Aph'choi	3.9
1995	564	62	Prat	37.8	Tylench	13.7	Meso	9.8	Panag	9.0	Eudor	3.4
2000	734	56	Prat	51.9	Diphth	10.4	Acrob	6.7	Meso	5.7	Tylench	3.1
2001	512	50	Prat	37.3	Tylench	15.8	Cephal	7.8	Aph'choi	7.6	Tylen	6.3

Acrob: *Acrobeloides*; Aph'choi: *Aphelenchoides*; Cephal: *Cephalobus*; Cruz: *Cruznema*; Diphth: *Diphtherophora*; Eudor: *Eudorylaimus*; Meloid: *Meloidogyne*; Meso: *Mesorhabditis* (*Bursilla*); Panag: *Panagrolaimus*; Prat: *Pratylenchus*; Rhab: Rhabditidae; Tylen: *Tylenchus*; Tylench: *Tylenchorhynchus*.

Table 2
Percentages of selected nematode genera of all nematodes that were present in organic, low-input, and conventional management treatments in 1993, 1994, 1995, 2000 and 2001

	Bacteria-feeding nematodes						Fungi-feeding nematode	Plant-parasitic nematodes	
	Treatment	Acrob	Meso	Cruz	Panag	Rhab	Aph	Prat	Tylench
1993	ORG	5.1 b	9.1 a	9.0 a	5.9 a	6.2 a	15.9 ab	9.2 b	0
	LOW	6.9 ab	11.6 a	12.1 a	6.2 a	3.7 ab	12.7 b	11.8 ab	0
	CONV	9.7 a	2.1 b	3.2 b	0.6 b	0.8 b	18.4 a	18.4 a	0
1994	ORG	9.9 a	8.1 a	4.1 a	7.4 a	1.8 a	17.1 ab	8.9 b	0
	LOW	7.0 a	6.2 a	5.9 a	2.7 b	0.9 a	21.0 a	10.1 b	0
	CONV	11.0 a	2.2 b	3.5 a	1.7 b	0.8 a	14.7 b	29.5 a	0
1995	ORG	5.2 b	7.9 a	5.0 a	6.7 a	1.6 a	8.2 a	6.0 b	9.8 a
	LOW	6.2 ab	5.5 a	6.3 a	4.2 ab	0.6 ab	8.5 a	8.0 b	7.4 a
	CONV	9.4 b	2.0 b	4.5 a	1.6 b	0.3 b	9.8 a	22.6 a	2.1 b
2000	ORG	22.4 a	6.0 a	4.7 a	3.8 a	1.3 a	19.0 a	3.4 b	3.3 a
	LOW	19.6 a	3.6 ab	6.2 a	3.4 a	0.3 a	19.5 a	7.5 b	2.2 ab
	CONV	19.3 a	1.6 b	3.0 a	1.4 a	0.4 a	14.5 a	26.2 a	0.9 b
2001	ORG	4.8 b	0	0	2.9 a	1.2 a	39.8 a	2.6 b	9.1 a
	LOW	4.1 b	0	0	2.1 a	1.2 a	40.4 a	3.8 b	8.8 a
	CONV	7.2 a	0	0	3.4 a	0.9 a	28.6 b	14.3 a	1.9 b

Numbers represent percentages of the genera present in the treatment in that particular year. Therefore, the genera cannot be added. Acrob: *Acrobeloides*; Meso: *Mesorhabditis* (*Bursilla*); Panag: *Panagrolaimus*; Rhab: Rhabditidae; Cruz: *Cruznema*; Aph: *Aphelenchus*; Prat: *Pratylenchus*; Tylench: *Tylenchorhynchus*. Different letters within a column and within an year indicate a significant effect of management treatment (ANOVA: Duncan test; $P < 0.05$).

Table 3
Effects of management treatment on nematode community indices (enrichment [EI], basal [BI], structure [SI], and channel [CI] indices) in the SAFS project at UC Davis, initiated in 1988

Year	Treatment	EI		BI		SI		CI	
		Mean	S.E	Mean	S.E	Mean	S.E	Mean	S.E
1993	ORG	76.9 a	2.9	20.5 b	2.5	35.2 a	4.5	22.6 b	4.4
	LOW	79.6 a	2.7	17.9 b	2.2	37.1 a	4.6	17.1 b	3.1
	CONV	52.1 b	2.9	42.8 a	2.4	18.4 a	2.3	53.1 a	5.5
1994	ORG	69.5 a	3.1	28.2 b	2.9	15.2 a	4.8	30.6 b	3.5
	LOW	66.6 a	2.5	30.7 b	2.2	18.6 a	3.2	38.5 ab	4.5
	CONV	58.7 a	2.8	39.1 a	2.9	11.5 a	3.6	45.1 a	5.0
1995	ORG	74.8 a	2.0	22.3 b	2.0	31.3 a	5.3	18.4 b	2.1
	LOW	70.9 a	2.1	24.7 b	1.7	32.5 a	5.1	21.2 b	2.4
	CONV	56.8 b	2.9	41.0 a	3.0	10.0 b	3.5	42.1 a	6.1
2000	ORG	62.1 a	3.8	30.0 b	2.7	37.8 b	3.6	30.9 b	5.0
	LOW	61.5 a	2.3	30.0 b	1.8	34.7 ab	5.4	33.1 b	3.5
	CONV	50.5 b	3.0	42.1 a	3.4	25.1 a	4.9	44.8 a	4.9
2001	ORG	46.1 a	1.4	51.6 a	1.4 a	7.5 a	1.6	75.5 a	3.4
	LOW	47.9 a	1.3	48.0 a	1.5 a	13.0 a	3.0	80.6 a	3.2
	CONV	45.8 a	2.4	51.3 a	2.2 a	8.7 a	2.4	75.0 a	5.0

Different letters within a column and within a year indicate a significant effect of management treatment (ANOVA: Duncan test; $P < 0.05$).

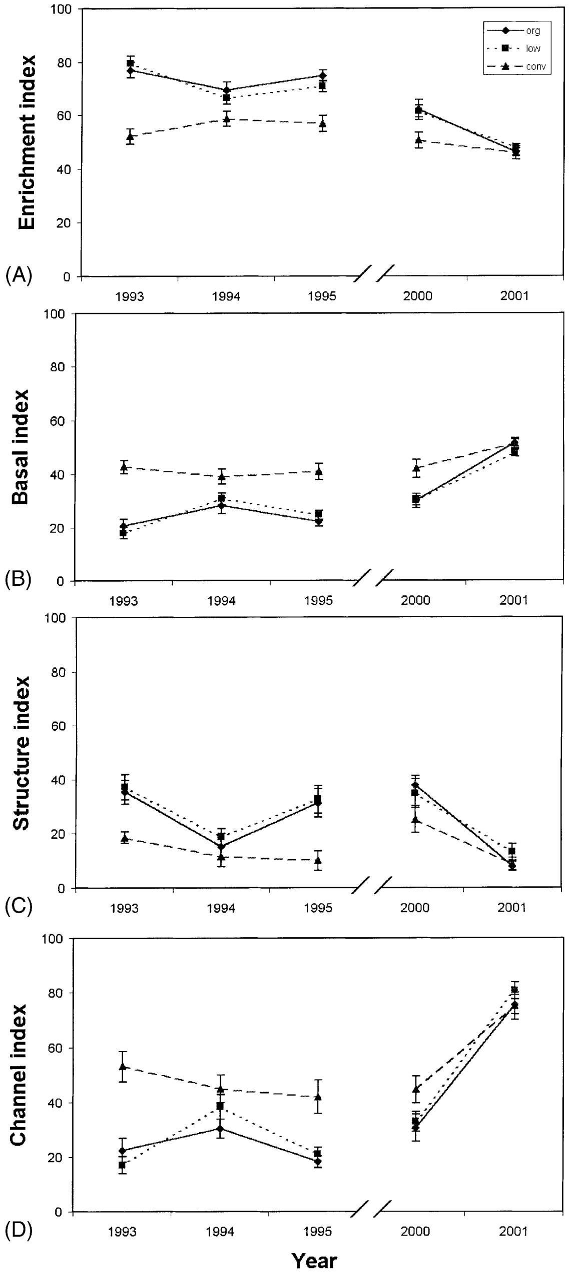

Fig. 1. Mean nematode community indices: enrichment index (A); basal index (B); structure index (C); and channel index (D), and S.E. over time in ORG, LOW and CONV plots with four rotation crops each year and four replications ($n = 16$). No samples were analyzed for nematode communities between 1995 and 2000.

3.2. *Crop effects on nematode communities*

Potential crop effects on individual genera were not tested. There were highly significant crop effects (generally, $P < 0.0001$) on all community structure indices in all years (1993–2000), except for BI in 1995. EI was always highest in tomato plots, and mostly lowest in bean or corn plots (Table 4). BI was generally highest in bean or corn plots. Differences in SI among crops were not consistent. CI was highest in bean and/or corn plots. After 1 year with a uniform crop in 2001, residual crop effects ($P < 0.01$) on EI, SI and CI were still detected from the crops planted in 2000 (Table 4). The nematode community in plots that were under corn had a higher EI and lower CI than in plots with other crops. Plots that were under beans had a higher SI than plots under other crops. No crop effects were observed for BI in 2001.

3.3. *Residual management and crop effects on soil properties*

In 2001, there were no residual effects of management on soil pH (Table 5). Total organic matter (OM content was higher in the ORG plots than in the CONV plots; LOW plots were intermediate in OM (Table 5). $NH_4{}^+$–N and $NO_3{}^-$–N were higher in the ORG than in the CONV and LOW management treatments.

There were no residual crop effects on soil pH and $NH_4{}^+$–N content in 2001 (Table 6). There were no interactions between management and crop effects, except for $NO_3{}^-$–N. Differences in $NO_3{}^-$–N content between crops were greater in CONV than in ORG or LOW treatments (interactions not shown). Extractable $NO_3{}^-$–N concentration was highest in plots that had beans and tomato in 2000, lower in safflower plots and lowest in corn plots. Plots that had tomato and corn as a crop in 2000 had a higher OM content in 2001 than plots that had beans and safflower as a crop.

3.4. *Correlations of nematode community indices with soil properties in 2001*

There were no significant correlations between community indices and OM, pH, or $NO_3{}^-$–N. $NH_4{}^+$–N was negatively correlated with the SI ($r = -0.34$; $P < 0.05$) and positively correlated

Table 4
Effects of crops on nematode community indices (enrichment [EI], basal [BI], structure [SI], and channel [CI] indices) in the SAFS project at UC Davis, initiated in 1988

Year	Crop	EI		BI		SI		CI	
		Mean	S.E	Mean	S.E	Mean	S.E	Mean	S.E
1993	Beans	62.2 b	1.4	33.2 a	1.5	27.1 ab	3.1	42.8 a	2.9
	Safflower	70.6 ab	6.3	26.1 b	5.7	38.3 a	6.3	28.9 b	7.9
	Tomato	75.2 a	3.7	22.9 b	3.5	26.2 b	6.2	19.6 b	3.4
	Corn	70.2 ab	6.0	26.1 b	4.9	29.4 ab	3.9	32.5 b	9.5
1994	Beans	57.3 c	3.2	37.1 a	3.7	28.2 a	5.6	47.5 a	5.3
	Safflower	69.4 ab	3.2	29.0 ab	2.8	13.4 ab	3.4	30.4 b	3.4
	Tomato	72.3 a	1.6	26.7 b	1.6	10.7 b	3.7	26.5 b	2.0
	Corn	60.6 bc	3.8	37.9 a	3.7	8.1 b	2.9	47.8 a	6.1
1995	Beans	63.0 b	1.9	30.3 a	2.0	35.7 a	5.0	30.7 a	3.0
	Safflower	69.7 ab	3.7	27.5 a	4.2	31.8 ab	8.1	22.7 b	3.9
	Tomato	72.6 a	2.4	26.3 a	2.3	11.1 b	3.2	17.3 b	2.4
	Corn	64.6 b	4.9	33.2 a	4.8	19.7 ab	4.9	38.2 a	8.6
2000	Beans	50.2 b	2.7	34.6 b	3.1	46.8 a	5.0	41.9 b	3.2
	Safflower	69.2 a	2.1	28.9 bc	2.1	18.3 b	3.6	18.3 d	2.2
	Tomato	66.4 a	2.8	26.8 c	2.0	41.4 a	3.7	28.6 c	4.1
	Corn	46.5 b	2.8	46.0 a	3.6	23.7 b	5.3	56.4 a	4.3
2001	Beans	44.8 b	2.8	48.8 a	2.8	19.5 a	3.0	76.7 ab	5.4
	Safflower	44.4 b	0.8	52.7 a	1.3	9.1 b	2.6	89.3 a	2.3
	Tomato	44.5 b	1.3	53.4 a	1.4	6.9 b	1.6	78.6 a	3.7
	Corn	52.8 a	1.8	46.4 a	1.7	3.5 b	1.5	63.6 b	3.0

Different letters within a column and within a year indicate a significant effect of the previous crop (ANOVA: Duncan test; $P < 0.05$). In 2001, the crop effect is a residual crop effect since the entire field was planted with oats in that year.

Table 5
Residual management effect on soil properties for soil sampled in the year 2001

Management	OM		pH		NH_4^+–N (μg/g dry soil)		NO_3^-–N (μg/g dry soil)	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
CONV	3.8 b	0.07	7.0 a	0.02	0.57 b	0.02	6.15 b	0.51
LOW	4.0 a	0.06	7.0 a	0.03	0.54 b	0.03	7.24 b	0.72
ORG	4.2 a	0.12	7.2 a	0.12	0.66 a	0.05	8.65 a	0.63

Different letters within a column indicate a residual effect of management (ANOVA: Duncan test; $P < 0.05$).

Table 6
Residual effect of the crop planted in 2000 on soil properties sampled in 2001

Crop planted in 2000	OM		pH		NH_4^+–N (μg/g dry soil)		NO_3^-–N (μg/g dry soil)	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Beans	3.8 b	0.09	7.0 a	0.03	0.54 a	0.03	8.56 a	0.65
Safflower	3.9 b	0.07	7.0 a	0.03	0.59 a	0.04	7.05 b	0.46
Tomato	4.1 a	0.06	7.0 a	0.03	0.62 a	0.05	8.86 a	0.85
Corn	4.2 a	0.17	7.1 a	0.16	0.61 a	0.05	4.93 c	0.52

Different letters within a column indicate a residual effect of the crop planted in 2000 (ANOVA: Duncan test; $P < 0.05$). NH_4^+–N and NO_3^-–N measured in mgN/kg dry soil.

with the BI ($r = 0.34$; $P < 0.05$). As expected from the construction of the indices, BI was negatively correlated with SI ($r = -0.45$, $P < 0.01$) and EI ($r = -0.89$, $P < 0.01$), and positively with CI ($r = 0.66$, $P < 0.01$). CI was negatively correlated with EI ($r = -0.75$; $P < 0.01$).

3.5. Soil suppressiveness towards *M. javanica*

The suppressiveness tests resulted in reproducible effects of individual soil samples on survival of *M. javanica* juveniles. Some bacteria-feeding nematodes (juveniles and adults) were observed in all pasteurized samples, but the numbers were very low compared to non-pasteurized soil. No other feeding types, native to the soil, were found. The bacteria-feeding nematodes had no noticeable effect on *M. javanica* juveniles.

There were significant differences ($P < 0.05$) between soil types and significant interactions ($P < 0.05$) between soil types and crops. Soil from the micro-plots amended with nematode-trapping fungi decreased the recovered *M. javanica* juveniles by 68.2 ± 15.5% compared to the pasteurized controls, while *M. javanica* juveniles were on average suppressed by 14.1 ± 11.1% in the SAFS soils. Although *M. javanica* juveniles were suppressed by 46.7 ± 11.0% in the organically managed soil that had been cropped with beans the year before sampling, the suppression compared with conventionally managed plots (4.1 ± 17.1%) or plots with corn (15.5 ± 8.8%) was not significant ($P = 0.07$ and 0.14, respectively). The percentage suppression was negatively correlated with BI ($r = -0.72$, $P < 0.05$) and also with CI ($r = -0.74$, $P < 0.05$), and positively, but not significantly with EI ($r = 0.51, 0.05 < P < 0.1$) and SI ($r = 0.55, 0.05 < P < 0.1$). Nevertheless, SI was very high (86.4 ± 0.3%) while CI was low (19.9 ± 8.1%) in the micro-plots, that showed the highest suppression. SI and CI were on average 10.4 ± 3.7% and 70.2 ± 5.2%, respectively, in the SAFS plots.

4. Discussion

In 1993, 4 years after conversion of the experimental plots to ORG and LOW management, the nematode community composition had undergone a major change from that in the CONV plots. After this initial change, the differences in nematode communities stabilized and were essentially the same until the end of the experiment in 2000. Bacteria-feeding nematodes were more prevalent in the ORG and LOW treatments than in the CONV treatment, as reported earlier (Scow et al., 1994; Ferris et al., 1996). This was attributed to the greater plant biomass turned under in the ORG and LOW treatments, where winter cover crops were grown, resulting in consistently higher microbial biomass levels in those plots (Scow et al., 1994; Ferris et al., 1996). In the current paper, we have shown that three of the four nematode community indices differed consistently for the ORG and LOW treatments compared to the CONV treatment. CONV management resulted in a lower EI than LOW and ORG management. This is comparable to results of Neher and Olson (1999) who found lower values for the nematode maturity index in an organic farming system than three conventional farming systems. CONV plots had no winter cover crops, resulting in a food web that was apparently less bacteria-dominated with a higher CI than in LOW and ORG plots. The relatively larger abundance of fungi-feeding nematodes, and the lower numbers of bacteria-feeders, in CONV resulted also in a higher BI. These results are contrary to the observation that fungal populations were greater in the ORG than in the CONV treatment of the SAFS experiment based on phospholipid fatty acid analysis (Bossio et al., 1998). However, some fungal-specific fatty acid markers are also found in plant membranes (Schutter et al., 2001). Thus, fatty acids that were considered to be of fungal origin could have been mainly of plant origin in this case, and our observations on a high BI and CI may indicate that the food web structure was probably fungi-dominated in CONV plots.

The SI was only different between management treatments in 1995 and 2000, being lower in the CONV than in the ORG and LOW management. In the other years there were trends in the same direction, but the differences were not significant. SI is primarily determined by omnivorous and predatory nematode populations, which are sensitive to disruption and need much more time to establish than the more rapidly growing fungi- and bacteria-feeding nematodes (Ferris et al., 2001). The SI values of disturbed annual agricultural systems, whether conventional or alternative, are characteristically low due to repeated tillage and other soil disturbance (H. Ferris, unpublished). All

SAFS plots were tilled annually, and the CONV plots were deep-ploughed once every 4 years to break up a hard pan that developed only in CONV plots. This last practice may have resulted in the lower SI in CONV plots.

After uniform management with an oat crop for 1 year, the differences in nematode community indices disappeared. The probable cause for the disappearance of the differences is twofold. Crops had a much greater effect on the nematode community than management type (this paper; Neher, 1999). After 1 year of a uniform crop of oats previous management effects were probably masked by the crop effect. The second reason for the uniformity in the nematode community is the heavy plowing after the harvest of oats. The drop in the SI (contains sensitive nematodes) and the rise in the CI (fungal feeders) in all plots demonstrated that the soil food web was severely disrupted. The relative abundance of fungi-feeding and bacteria-feeding nematodes has been suggested as a sensitive indicator (Yeates and Bongers, 1999), but the CI may be high and the EI low in impoverished conventional agro-ecosystems as well as non-disturbed natural ecosystems with a high nutrient turn-over rate (Yeates, 1996), rendering these indices less suitable as general indicators of soil health.

Only a few weak correlations were found between the nematode community indices and soil properties in 2001, particularly a negative correlation between NH_4–N and SI, and a positive correlation between $NH_4{}^+$–N and BI. These correlations suggest that fungi-feeding nematodes contributed considerably to NH_4 release several months after turning under oat residues. Previous SAFS studies demonstrated higher soil organic matter and mobile humic acid contents in the ORG plots, and higher water infiltration rates and water contents in the ORG and LOW plots than in the CONV plots (Poudel et al., 2001b). This resulted in a bacteria-dominated food web, a higher EI and lower BI and CI in ORG and LOW plots than in CONV plots from 1993 to 2000.

Although differences in nematode community indices disappeared, the composition of nematode genera was still different between management regimes. The plant parasitic nematode *Pratylenchus* was the largest contributor to the χ^2 in all years after 1993. This genus had already built up in conventional plots in 1992 (Scow et al., 1994; Clark et al., 1998), became a dominant genus in 1994, and remained more dominant in the conventional than in the other plots even after one year of uniform treatment. The most prevalent species was *P. thornei* (Sher and Allen), a parasite of oats, vetch and corn (Bongers, 1987; Ferris et al., 1996). However, it was probably suppressed by the higher microbial populations in the ORG and LOW plots (Scow et al., 1994), which may have stimulated nematode-feeding predators other than predatory nematodes (Jaffee et al., 1998). Another contributor to the differences between management types was the plant parasitic nematode *Tylenchorhynchus*, which became more prominent in ORG and LOW plots since 1995. Local species of *Tylenchorhynchus* have wide host ranges on grasses and legumes (McKenry and Roberts, 1985) used as cover crops in ORG and LOW management types. The predominant species in this region is *T. clarus* (Allen) which reproduces more effectively on its hosts during the relatively cool period when cover crops are grown (Edongali and Lownsbery, 1980).

One explanation for the insensitivity of the tested community indices for residual effects of management is that a large portion of the nematodes (plant parasitic) present in the community are not included in these indices (because of disturbing host effects). Bongers et al. (1997) suggested that inclusion of plant parasitic nematodes in the maturity index would make this index less sensitive to environmental changes, as the maturity index for plant parasites is sometimes inversely related to that for the rest of the nematode community. To detect long-term effects of management systems, we need an index that is less sensitive to temporary changes due to nutrient inputs. It may be worth testing whether inclusion of plant parasitic nematodes in the maturity index or SI could result in a more sensitive index to register long-term management effects in agro-ecosystems. This has also been suggested for diversity and maturity indices (Urzelai et al., 2000). However, the unique feature of SI is that only higher trophic levels are considered, so that this index should detect natural pest regulation. Apparently, this mechanism of natural regulation was not strong enough to suppress plant-parasitic nematodes in our and other agricultural soils (Ferris et al., 1996). *Pratylenchus* may have been suppressed by another mechanism in the LOW and ORG management treatments, considering that the frequent tillage operations would probably have prevented populations of omnivorous and predatory nematodes from building up to levels encountered in undisturbed ecosystems. This hypothesis is currently being tested in an experiment with an ORG no-till treatment in the SAFS experimental field.

Crop effects on all community indices were highly significant in almost all years (1993–2000). Differences in various indices among crops could be explained by the plant remains available for decomposition before soil samples were analyzed for nematode communities. For example, tomatoes always resulted in the highest EI, probably because fresh residues were turned under late in the season (just before soil sampling). In 2001, EI was highest after corn in 2000, probably due to the slow decomposition rate of corn residues. The BI and CI were generally highest in bean plots (after wheat or oats/vetch in the same season) and/or corn plots, possibly because the residues of the Gramineae are relatively fibrous and more easily decomposed by fungi. Neher (1999) also found that differences in crop species were more important than management types with respect to maturity and diversity indices.

One reason for the large crop effects compared to the management effects in our study is the split-plot design. The error term and associated degrees of freedom are much lower for management than for crop effects, as management effects were tested in main plots and crop effects in subplots. Thus, with a split-plot ANOVA, management effects on SI were detected in fewer years than with a regular ANOVA ignoring the split-plot design (data not presented). For a long-term experiment with primary interest in management effects, it would have been better to have management types in subplots.

The first suppressiveness tests with soil from micro-plots, previously managed to enhance suppressiveness, were reproducible and looked promising. The same test was, however, much more variable with the SAFS soil samples. This soil was generally not suppressive to RKN, except for soil from the organic bean plots; these plots were also exceptional in that they had a much higher SI than any other plots in 2001. The suppression levels were negatively correlated with BI and CI, and weakly positively correlated to EI and SI. Thus, potential reasons for nematode suppression might have been relatively high bacteria-dominated food webs or predatory nematode populations. This is supported by the positive correlation found between substrate-induced respiration and RKN suppression in 1995/96 (Jaffee et al., 1998). Nematode-trapping fungi could be partly responsible for the suppression of RKN in the microplots, which were infested with nematode-trapping fungi in the past, but there were also large populations of omnivorous nematodes in these plots. No differences were found in total populations of nematode-trapping fungi among the SAFS plots in 1995 (bean crop) and 1996 (tomato crop), but two genera were more numerous in the ORG than in the CONV plots (Jaffee et al., 1998). These could have contributed to suppression of Pratylenchus in the LOW and ORG plots as described in this paper.

5. Conclusions

This study demonstrates that the nematode community responds quickly (within a few years) to a change in farming system and remains similar as long as that system is maintained. The selected community indices reflected differences in nematode communities well as long as the management systems were kept intact, but were too insensitive to expose residual effects of management system one year after termination of the treatments. The χ^2 test was still able to detect large differences in nematode communities among management treatments at that time, but these differences were primarily caused by plant-parasitic nematodes. Differences in second and third trophic levels of nematode communities disappeared after a single year of uniform management. The need for good indicators for soil health is great but it is difficult to find a universal indicator for soil quality (Yeates and van der Meulen, 1996). Of the indices selected for this paper, BI and SI have most potential as indicators for unhealthy and healthy systems, respectively. SI is always higher in perennial crops and undisturbed natural systems than in annual cropping systems, even when these are managed organically (Ferris et al., 2001). Soil-borne plant diseases and pests, including nematodes, are frequently suppressed in organic farms (van Bruggen, 1995). It is therefore important to consider individual genera of plant parasitic nematodes as a negative factor when evaluating agricultural soil for its health status (van Bruggen and

Semenov, 2000) besides community indices like BI and SI.

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