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# Structural and functional succession in the nematode fauna of a soil food web

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**Abstract**

Soil microplots were amended with organic materials of varying nature and complexity but providing similar amounts of carbon. Materials were either placed on the soil surface or incorporated. Unamended and mineral fertilizer control plots were established. Plots were maintained vegetation-free so that the food web activity was fueled by resident soil organic matter and the input material. Enrichment-opportunist bacterivore nematodes increased rapidly in response to low C/N plant materials and, to a lesser extent, to more complex materials. General-opportunist bacterivores increased in all plots, but at a slower rate. Fungivore nematodes also increased gradually in all plots but most rapidly in those amended with higher C/N and more complex materials. Indices derived from nematode faunal analysis suggested a constant rate of succession from enrichment-opportunist to general-opportunist bacterivore guilds across all treatments, probably mediated by bacterial abundance and differences in life course characteristics of the respective taxa. The rate of succession from bacterivore to fungivore nematodes was greatest in plots receiving high C/N materials. Succession to fungivory, presumably indicating a shift from bacterial to fungal decomposition channels, was slowest in those plots with a high level of organismal metabolic activity, as measured by soil respiration. The cumulative amounts of N mineralized in the plots were directly related to the enrichment index (EI), based on the abundance of opportunistic bacterial- and fungal-feeding nematodes. The amounts of mineralized N were inversely related to the slope of the channel index (CI), that is, the rate at which decomposition changed from bacterial to fungal. Maintenance of adequate soil fertility in systems driven by organic input may require maintenance of food web structure and function as indicated by high levels of enrichment-opportunist bacterivore nematodes. That will require frequent supply of labile organic sources. Allowing food web succession to guilds that indicate lower mineralization potential will result in lower levels of soil fertility.


*Keywords:* Decomposition; Mineralization; Succession; Nematodes; Soil food web

## 1. Introduction

Mainly through the response and function of organisms in the soil food web, organic matter amendments enhance soil structure, nutrient status, physical conditions, soil biological activity, crop production and generally contribute to soil health (Kang et al., 1981; Hungalle et al., 1986; Magdoff, 2001). Much is known, and there are many recent studies, on the rates of decomposition of various forms of organic material in different soils and under a range of environmental conditions (e.g. Rowell et al., 2001; Cobo et al., 2002; Leifeld et al., 2002; Zaccheo et al., 2002). Other studies attempt to couple rates of decomposition

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and other food web functions with biomass and activity of bacteria and fungi, and their higher trophic predators (e.g. Wasilewska et al., 1981; Seastedt, 1984; Bardgett and Cook, 1998; Mikola and Setala, 1998a; Laakso et al., 2000; Ekelund et al., 2002).

Depending on which primary decomposers predominate, the decomposition pathways or channels are described as bacterial (fast cycle) or fungal (slow cycle) (Coleman et al., 1983; Moore, 1994). The biomass and activity of bacteria and fungi in the soil may be limited by availability of carbon or mineral nutrients (e.g. Schmidt et al., 2000; Ruess et al., 2001) or by environmental extremes (e.g. Treonis et al., 2002). When the available organic pool, supplemented by mineral nutrients in the soil solution, no longer meets the growth and metabolic requirements of a particular guild of organisms, for example, the copiotrophic bacteria (Semenov et al., 1999), population increase in that guild is limited. In that case, succession to other guilds that are better adapted to utilize the available resources may occur. Such changes can be monitored by measure of food web function, for example, rates of decomposition and mineralization (Coleman and Crossley, 1996; Gunapala et al., 1998), or by evaluation of food web structure through direct or indirect assessment of abundance and biomass of the decomposer organism groups (Frostegård and Bååth, 1996; Semenov et al., 1999; Fu et al., 2000). We refer to changes through time in the abundance of organisms in the soil community that have different trophic roles as structural succession. The concurrent changes in food web function are referred to as functional succession. Where organism guilds are difficult to measure or require a variety of techniques, their present or recent abundance may be inferred from the abundance of indicator organisms that selectively feed on those guilds, although the potential for trophic cascade of fluxes must be considered. In the case of soil bacteria and fungi, fungivore and bacterivore nematodes are proving useful indicators (e.g. Ferris et al., 2001; Neher, 2001). Their abundance is presumed to mirror that of other important bacterivores (e.g. protozoa) and fungivores (microarthropods) and reflect the current or recent availability of their food. Fungal- and bacterial-feeding nematodes, and other organisms that graze on primary decomposers, accelerate the decomposition of soil organic matter and increase mineralization, thus releasing nutrients for plant growth (Trofymow et al., 1983; Ingham et al., 1985; Griffiths, 1986; Freckman, 1988; Verhoef and Brussaard, 1990; Ferris et al., 1996b, 1997, 1998; Chen and Ferris, 1999; Akhtar and Malik, 2000; Neher, 2001). The decomposition fate and products of organic materials in the soil depends on their nature and C/N ratios and on the time-course of decomposition (Magdoff et al., 1997; Akhtar and Malik, 2000; Rowell et al., 2001; Cobo et al., 2002). Nitrogen may become immobilized in microbial tissue when organic material has a C/N ratio >20:1 but mineralized in the form of $NH_4^+$ or $NO_3^-$ when the C/N ratio <20:1 (Jones, 1982). In the obverse, the predominance of various functional groups in the soil food web is driven by the nature and availability of the organic source. Fungal energy channels tend to predominate when the organic material is of high C/N ratio and/or is placed on the soil surface rather than incorporated; bacterial decomposition channels predominate when the organic material is of low C/N ratio and is incorporated into the soil (Hendrix et al., 1986; Holland and Coleman, 1987; Moore, 1994).

Nematode faunal analysis is evolving as a powerful bioindicator of the soil condition and of structural and functional attributes of the soil food web (Bongers and Ferris, 1999; Neher, 2001). Recent developments of such analyses include recognition of an enrichment trajectory and a structure trajectory. The latter measures the abundance of trophic linkages in the food web and the probability of regulatory effects on opportunist populations through exploitation and competition. The enrichment trajectory reflects supply-side characteristics of the food web and the increase in primary consumers of incoming organic material (Ferris et al., 2001). In the current study, we attempt to verify the effects of supply-side inputs on nematode abundance and food web function and to increase resolution of our understanding of the subsequent successional events.

Food webs become enriched when disturbance occurs and resources become available due to external input, organism mortality, turnover, or favorable shifts in the environment (Odum, 1985; Van Veen and Kuikeman, 1990). Enrichment is followed by heterotrophic succession whereby the predominance of organisms changes through time depending on trophic roles, life course dynamics, and prevailing environmental conditions. The mass of available C diminishes

with each trophic interchange. Enrichment stimulates a flush of microbial activity and opportunistic predators respond by exploiting the new resource. Some of the organismal responses to enrichment are ephemeral and can be detected only with intensive sampling (Nannipieri et al., 1990; Neher, 2001); others, including responses of certain guilds of nematodes, are more persistent and can be measured reliably (Ferris et al., 1996b; Bongers and Ferris, 1999).

The enrichment-opportunist bacterivore nematode guild includes species in the families Rhabditidae, Panagrolaimidae and Diplogasteridae (Bongers and Ferris, 1999; Ferris et al., 2001). They are classified as cp-1 organisms, characterized by short generation time, small eggs and high fecundity, in the colonizer–persister scale of Bongers (1990). They appear to feed continuously in enriched media and then form metabolically suppressed *dauerlarvae* as resources are diminished. As microbial blooms fade, enrichment-opportunist microbivores may be replaced by general opportunists with specialized morphological, physiological and behavioral adaptations for more deliberate feeding on less-available resources. The general-opportunist nematodes, classified as cp-2, are predominantly bacterial scavengers in the Cephalobidae and fungal-feeders in the Aphelenchidae, Aphelenchoididae and Anguinidae. Increased abundance of fungal-feeding opportunists occurs when the available organic pool is conducive to fungal decomposition as, for example, when complex organic material becomes available in the soil or when fungal activity is enhanced under conditions less favorable for bacterial decomposition (e.g. Eitminavičūtė et al., 1976; Wasilewska et al., 1981). In fact, nematodes in the general-opportunist guild commence to increase with the initial enrichment, but at a slower rate than the enrichment opportunists so that they become successionally predominant as the latter guild is declining (Bongers, 1990; Ferris et al., 1996b, 2001; Bongers and Bongers, 1998; Bongers and Ferris, 1999; Chen and Ferris, 2000). In this paper, we introduce a bacterivore index (BaI) as a measure of succession from enrichment-opportunist to general-opportunist bacterivore nematodes and as an indicator of the nature and abundance of the microbial biomass.

Indication of the relative flow of substrate along bacterial and fungal decomposition pathways is provided by the channel index (CI) (Ferris et al., 2001; Ruess and Ferris, 2002). The CI also provides a means of tracking succession between fungivore and bacterivore nematodes as organic resources are supplied and depleted in agricultural systems (Ruess and Ferris, 2002). Decomposition rates of readily degraded materials in bacterial pathways are expected to be faster than that in fungal pathways where materials may be more complex. Due to the similarity of C/N ratios of fungi and fungivore nematodes, mineralization rates in fungal channels should be slower than those in bacterial channels where there is greater difference between C/N ratios of predators and prey (Ingham et al., 1985; Ferris et al., 1997; Chen and Ferris, 1999; Okada and Ferris, 2001). Further, the redistribution of bacteria to new food sources by survival of passage through the nematode intestine is an important accelerator of decomposition processes (Wasilewska et al., 1981; Freckman, 1988) for which fungivore nematodes probably do not provide an equivalent function in the fungal channel.

The objectives of these studies were: (i) to assess the impact of organic sources on the enrichment index (EI) descriptor of the soil food web; (ii) to validate the notion that enrichment-opportunist bacterivores will be succeeded by general-opportunist bacterivores and fungivores as readily decomposable resources diminish; and (iii) to determine the relationship between components of the enrichment trajectory and the function of N mineralization.

## 2. Materials and methods

### *2.1. Field plot location, experimental design and plot management*

The experimental site was on the Student Farm at the University of California, Davis. The area had not been cropped for 2 years and was covered with four species: (1) *Claytoni preforia* (miner's lettuce, 90%); (2) *Conyza canadensis* (horse weed, 6%); (3) *Lamium* sp. (henbit, 3%); and (4) *Silybum marinum* (milk thistle, 1%). The last crop grown at the site was corn (*Zea mays*). The experimental design was a randomized complete block of 56 microplots in four replications. Microplots were 1 $m^2$ and separated from each other by 1 m on each side. In December 2000, the site was mowed close to the soil surface and organic material raked from the area. Remaining stubble was cleared

Table 1
Treatment definitions and their effects on stimulation of the food web as reflected in intercept values of the enrichment index (EI) relationship with physiological time in early March and by the aggregate enrichment index (AEI) after that date

| Input[a] | Amount (kg) | C content (g) | C/N | Placement[b] | EI intercept[c] | AEI (×1000) |
|---|---|---|---|---|---|---|
| Alfalfa | 0.9 | 287 | 10.6 | Surface | 78.0c | 73.8 |
| Alfalfa St. | 0.9 | 287 | 10.6 | Incorp. | 73.9c | 70.0 |
| Alfalfa | 0.9 | 287 | 10.6 | Incorp. | 66.5b | 62.4 |
| Alfalfa-wheat | 0.8 | 284 | 24.7 | Incorp. | 69.7b | 62.0 |
| Wheat straw | 0.7 | 282 | 75.9 | Incorp. | 71.6b | 61.8 |
| Wheat straw St. | 0.7 | 282 | 75.9 | Incorp. | 67.4b | 57.2 |
| Wheat straw | 0.7 | 282 | 75.9 | Surface | 63.7b | 56.1 |
| Compost-wheat | 2.5 | 335 | 20.5 | Incorp. | 66.9b | 55.2 |
| Compost St. | 6.0 | 442 | 10.6 | Incorp. | 58.5a | 53.0 |
| Compost | 6.0 | 442 | 10.6 | Incorp. | 56.4a | 51.7 |
| Compost | 6.0 | 442 | 10.6 | Surface | 59.3a | 49.7 |
| Control | 0 | 0 | 0 | Incorp. | 57.4a | 52.5 |
| Control | 0 | 0 | 0 | – | 52.0a | 46.2 |
| $(NH_4)_2SO_4$ | 0.2 | 0 | 0 | Incorp. | 52.8a | 47.9 |

Data are sorted by C/N ratio within each organic source.
[a] Materials followed by "St." were pasteurized by heating at 70 °C for 24 h before application.
[b] Incorp. indicates material incorporated into the soil.
[c] Intercept values followed by the same letter do not differ from each other ($P < 0.05$).

to soil level using a propane burner. After the clearing and burning of the top vegetation, six-core soil samples (2.5 cm diameter, 15 cm deep) were collected for baseline nematode and soil chemistry analysis.

There were four main amendment sources, three organic and one inorganic. The organic materials were wheat straw (C/N 75.9), alfalfa (C/N 10.6) and aged compost (C/N 10.6), while the inorganic was mineral fertilizer ($(NH_4)_2SO_4$, 21–0–0 NPK) (Table 1). The aged compost had been turned over several times and was mixed with a considerable amount of sand and soil. That resulted in a rather low C content per unit weight. Some of the organic materials were blended to provide intermediate C/N ratios. All organic materials were passed through a chipper–shredder and chopped into pieces no larger than 1 cm. The materials were then homogenized and blended, where appropriate, in a cement mixer. The amount of material applied to each plot was designed to provide a similar amount of C in each case. Dry weights were determined for each material by drying overnight at 100 °C. We determined the amount of alfalfa required to cover a 1 $m^2$ microplot to a depth of 2 cm and estimated relative amounts of other materials to be applied to supply approximately the same amount of C to each plot. Consequently, the total amount of material applied, and the amount of N, differed among treatments (Table 1).

Since mist chamber extraction of nematodes from the organic materials revealed small numbers of Aphelenchidae, Tylenchidae and Rhabditidae, a set of the amendment treatments was pasteurized by heating to 70 °C for 24 h to allow determination of whether any changes in nematode abundance were due to introductions with the organic material. The various combinations constituted 14 different treatments. On 19 December 2000, organic materials were applied to each plot, either spread on the surface or incorporated to 20 cm by two passes with a rototiller. The fertilizer treatment was incorporated. Control plots without amendments, undisturbed and rototilled, were also established. Actual amounts of C and N applied were determined after analysis of the inputs (Table 1).

Throughout the course of the experiment, plots were hand weeded as needed to keep them free of vegetation. By mid-May, winter rainfall had ended and the soil in the plots was becoming dry. An irrigation system was established with a sprinkler head at each plot delivering 0.8 l $min^{-1}$. Plots were watered as needed, at approximately 2-week intervals, delivering 48 l of water per plot each time.

### 2.2. Soil respiration

The rate of $CO_2$ emission from the soil was used as an indicator of soil respiration and of the level of biological activity. $CO_2$ emission rates were measured approximately weekly. Collection chambers 26 cm diameter and 15 cm high were cut from the bases of plastic buckets. A neoprene self-sealing flange was inserted into a hole drilled in the center of each chamber. Collection chambers were pushed into the soil surface of each plot to a depth of 2 cm and allowed to accumulate $CO_2$ for 2 h. Soil temperature and moisture conditions were recorded. Headspace $CO_2$ was measured by inserting a hypodermic needle attached to a 10 ml syringe through the flange. The syringe was filled and flushed 10 times before a 10 ml headspace sample was collected. The needle was sealed with a cap for transportation to the laboratory and determination of $CO_2$ concentration with an infrared gas analyzer. $CO_2$ concentrations were based on peaks determined from calibrated standards (Gunapala et al., 1998).

### 2.3. Soil sampling, processing and analyses

Six-core composite soil samples (2.5 cm diameter, 15 cm deep) were taken from each plot at 4-week intervals. Cores were collected randomly from the central portion of each plot and the holes closed with minimum soil disturbance. Soil samples were placed in an insulated box for transportation to the laboratory. In the laboratory, each soil sample was shaken through a 0.7 cm mesh screen and hand-mixed. The sample was divided into subsamples for nematode faunal analysis (200 $cm^3$), soil moisture (50 $cm^3$), soil N determination (50 $cm^3$) and phospholipid fatty acid (PLFA) analysis (25 $cm^3$). PLFA samples were stored frozen before submission for analysis.

Nematodes were extracted using a combination of decanting and sieving and Baermann funnel methods (Barker, 1985). Each soil sample was placed in a 1 l beaker and suspended in water by pouring it between two beakers ten times. The suspended material was passed through a 60 mesh (246 μm aperture) sieve into a 2 l beaker, leaving the settled particles behind. That residue was resuspended in water and the process repeated. The collected suspension was stirred, allowed to settle for 1 min, and nematodes were extracted from the suspension on a 400 mesh (38 μm aperture) sieve. The sieve was backwashed into a beaker and transferred to a Baermann funnel. Nematodes were collected after 48 h.

All nematodes in the sample were counted under a dissecting microscope. The sample was then centrifuged and the supernatant removed. The pellet was resuspended in about 0.25 ml water and spread on a microscope slide, covered with a cover slip, and sealed with fingernail polish. A minimum of 100 nematodes on each slide was identified to genus level. The actual abundance of each taxon was adjusted according to the total number of nematodes in the sample.

Soil moisture level in each sample was determined by weight loss after heating at 70 °C for 24 h. Soil nitrogen ($NO_2$–N and $NH_4$–N) was extracted by shaking for 1 h in 2 M KCl, centrifuging and collecting 25 ml of the supernatant. KCl extracts were submitted to the University of California Division of Agriculture and Natural Resources Analytical Laboratory for N determinations.

Given the number of treatments and sampling dates in this study, resources were not available for comprehensive PLFA analysis. Rather, samples taken in March and July from representative treatments were analyzed in an attempt to verify shifts from bacterial to fungal decomposition pathways. PLFAs were extracted from soil according to described methodology (Bossio and Scow, 1998; Chen et al., 2001) and measured by gas chromatography. The weights of individual PLFAs were measured as nanogram per gram dry soil. The biomass of bacteria was determined using the combined weights of fatty acids *iso*15:0, *anteiso*15:0, 15:0, *iso*16:0, 16:1ω5c, *iso*17:0, *anteiso*17:0, 17:0cy, 17:0 and 19:0cy. That of fungi was determined as the sum of 18:3ω7c, *anteiso*18:0 and 18:2ω6, 9c (Bossio and Scow, 1998; Bossio et al., 1998; Mikola and Setala, 1998b).

### 2.4. Other measurements

Soil temperature data for the experimental period were downloaded from a nearby California Irrigation Management Information System (CIMIS) site (UCIPM, 2001).

### 2.5. Data analysis

Nematode faunal analysis, based on a weighted matrix classification of life course traits and feeding habits (functional guilds *sensu* Bongers and Bongers, 1998), provides three qualitative measures of the soil food web (Ferris et al., 2001). In a *Basal* food, diminished by resource limitation or adverse environmental conditions, nematode guilds in the cp-2 class (Bongers, 1990) predominate, mainly bacterial scavengers in the Cephalobidae ($Ba_2$) and fungal-feeders in the Aphelenchidae and Aphelenchoididae ($Fu_2$). In a *structured* food web, there is a continuum of taxa in the cp classes 3–5. The higher the cp classification of the indicator guilds, the greater the number of trophic linkages and community interactions. Structure and basal indicator guilds are weighted based on the postulated degree of trophic connectance ($l$) in the food web in relation to species richness ($s$), that is, $l = \alpha s^2$ (Cohen, 1989). Initial assessments are that relative nematode taxonomic richness increases by about 0.5 with each increment in cp class number ($n$) and is 2.5 times greater in the most structured food webs than in basal food webs, so in structured food webs, $s^2 = 6.25$. To standardize to a maximum connectance value of 5.0, $\alpha$ is set at 0.8 and the weights ($k_s$) of guilds along the structure trajectory are calculated as $0.8(0.5n)^2$.

An *enriched* food web has abundant resources due to elevated microbial abundance and activity. Bacterial-feeding enrichment opportunists of the cp-1 class are enhanced; the $Ba_1$ guild includes the Rhabditidae, Panagrolaimidae and Diplogasteridae. Enrichment guild weights reflect responsiveness to available resources. The population increase rate of the $Ba_1$ is about four times as great as that of the basal $Ba_2$ guild, which has a weight ($k_b$) of 0.8 as calculated above; consequently, $Ba_1$ taxa are assigned a weight ($k_e$) of 3.2. The $Fu_2$ guild is an indicator of fungal enrichment; since it has similar reproductive potential to the $Ba_2$ guild, it has a $k_e$ of 0.8. Further details and rationale are provided in Ferris et al. (2001).

Two indices are calculated based on the weighted abundance of nematodes guilds representing structure ($s$), enrichment ($e$) and basal ($b$) characteristics. As an example, the $s$ component is calculated as $\sum k_s n_s$, where $k_s$ are structure indicator weights and $n_s$ are the abundance of nematodes in those guilds. The structure index (SI) is calculated as $100(s/(s+b))$ and the enrichment index as $100(e/(e+b))$. Enrichment is partitioned into bacterial and fungal channels through the channel index, based on the weighted abundance of fungal-feeders among the opportunistic nematode grazers on fungi and bacteria ($CI = 100(0.8Fu_2)/(3.2Ba_1 + 0.8Fu_2)$), where the coefficients are the $k_e$ enrichment weightings for the respective guilds (Ferris et al., 2001).

In the current study, we were also interested in the succession from more ephemeral enrichment-opportunist bacterivores to more stable, general-opportunist, species. Consequently, we constructed a bacterivore index as $100k_bBa_2/(k_eBa_1 + k_bBa_2)$, where $k_b$ and $k_e$ are the weights for the respective guilds (Ferris et al., 2001).

Data were subjected to regression analysis using the data analysis tools of Microsoft Excel 97 and to analysis of variance, when appropriate, by the GLM procedure of SAS version 6.12 (SAS Institute Inc., Cary, NC). Means were separated by Duncan's multiple range test. Differences in the effects of input materials and methods of application were tested by assigning the interactions of these effects as qualitative independent variables in the regression analysis (Neter et al., 1990).

## 3. Results

### 3.1. Nematode populations

During the course of these studies, 22 genera or larger groupings of nematodes, representing 16 families, were identified in samples from the plots (Table 2). Population levels of the various taxa varied across the plots at the commencement of the study in December 2000. During the first two sampling periods following the initial disturbances of plant removal and plot establishment, there was an increase in enrichment-opportunist bacterial-feeding nematodes in the upper 15 cm of soil in plots amended with labile, low C/N organic material (examples in Fig. 1). Rhabditidae and Aphelenchoididae generally increased in the spring and then declined where there were no additional organic resources or where the resources were labile. In plots that received organic matter input, there was a slow increase in general-opportunist

Table 2
Mean and range of nematode abundance across all plots and sampling periods for a control treatment (no additional organic material, no incorporation) and an alfalfa amendment (low C/N, incorporated) (see Table 1)

| Family | Genus | Guild[a] | Control | | Alfalfa | |
|---|---|---|---|---|---|---|
| | | | Mean[b] | Range | Mean[b] | Range |
| Panagrolaimidae | *Panagrolaimus* | b1 | 57 | 0–252 | 189 | 0–2113 |
| Rhabditidae | *Cruznema* | b1 | 23 | 0–138 | 97 | 0–1276 |
| Rhabditidae | *Mesorhabditis* | b1 | 38 | 0–390 | 100 | 0–1690 |
| Rhabditidae | *Rhabditidae* | b1 | 36 | 0–762 | 32 | 0–762 |
| Cephalobidae | *Acrobeles* | b2 | 9 | 0–77 | 10 | 0–130 |
| Cephalobidae | *Acrobeloides* | b2 | 578 | 0–1897 | 677 | 0–2710 |
| Cephalobidae | *Cephalobidae* | b2 | 12 | 0–128 | 12 | 0–128 |
| Cephalobidae | *Chiloplacus* | b2 | 6 | 0–86 | 13 | 0–154 |
| Cephalobidae | *Drilocephalobus* | b2 | 8 | 0–86 | 11 | 0–230 |
| Monhysteridae | *Monhystera* | b2 | 8 | 0–86 | 21 | 0–135 |
| Plectidae | *Plectus* | b2 | 90 | 0–984 | 70 | 0–984 |
| Prismatolaimidae | *Prismatolaimus* | b3 | 5 | 0–59 | 15 | 0–230 |
| Aphelenchidae | *Aphelenchus* | f2 | 220 | 0–1057 | 241 | 0–1382 |
| Aphelenchoididae | *Aphelenchoides* | f2 | 233 | 0–984 | 605 | 0–4685 |
| Mononchidae | *Mylonchulus* | c4 | 5 | 0–86 | 9 | 0–307 |
| Qudsianematidae | *Eudorylaimus* | c4 | 6 | 0–132 | 12 | 0–174 |
| Discolaimidae | *Discolaimus* | c5 | 63 | 0–556 | 96 | 0–998 |
| Thornenematidae | *Mesodorylaimus* | o5 | 15 | 0–62 | 47 | 0–538 |
| Tylenchidae | *Tylenchidae* | h2 | 335 | 39–2438 | 363 | 18–2438 |
| Tylenchulidae | *Paratylenchus* | h2 | 0 | 0–0 | 1 | 0–32 |
| Pratylenchidae | *Pratylenchus* | h3 | 2 | 0–26 | 3 | 0–33 |
| Longidoridae | *Xiphinema* | h5 | 5 | 0–58 | 23 | 0–579 |

[a] Guild designation is the composite of feeding habit and cp value: b, bacterivore; f, fungivore; c, carnivore (predator); o, omnivore; h, herbivore. Numbers following the letters indicate the cp classification of each taxon (see Bongers, 1990; Bongers and Bongers, 1998).
[b] Numbers per L soil, not corrected for extraction efficiency.

bacterivore and fungivore nematodes, for example, in the disturbed plots, Cephalobidae and Aphelenchidae increased throughout the experiment (Fig. 1).

The nematode populations responding to the organic inputs were those resident in the soil. Plots receiving pasteurized organic material did not behave differently from those receiving unpastuerized material (data not shown).

### 3.2. Soil biological activity

The slope of linear models fitted to the relationship between cumulative $CO_2$ evolution and physiological time was used as an estimator of the relative rate of soil respiration. The stimulation effect of plot establishment and input incorporation was evident from the relative soil respiration rate in relation to physiological time ($DD_0$: day-degrees above 0 °C) during the period that soil temperatures were below 10 °C (Table 3). Plant material significantly raised the rate of soil respiration above those of the compost and control plots, with alfalfa having the greatest effect. The main effect of low C/N compost was not different from that of the control. Incorporation did not significantly influence the rate of soil respiration during the winter season (Table 3).

After soil temperatures reached 10 °C, we used that temperature as the base for the physiological time scale ($DD_{10}$). Relative soil respiration rates were lowest in surface-applied materials, the mineral fertilizer treatment and the unamended controls. They were greatest is the incorporated alfalfa treatments followed by the intermediate C/N compost material, which was blended with wheat straw (Table 3). The main effect of alfalfa amendment was greater than other organic sources and the unamended controls. During the summer months, the main effect of incorporation elevated the relative respiration rates above that in

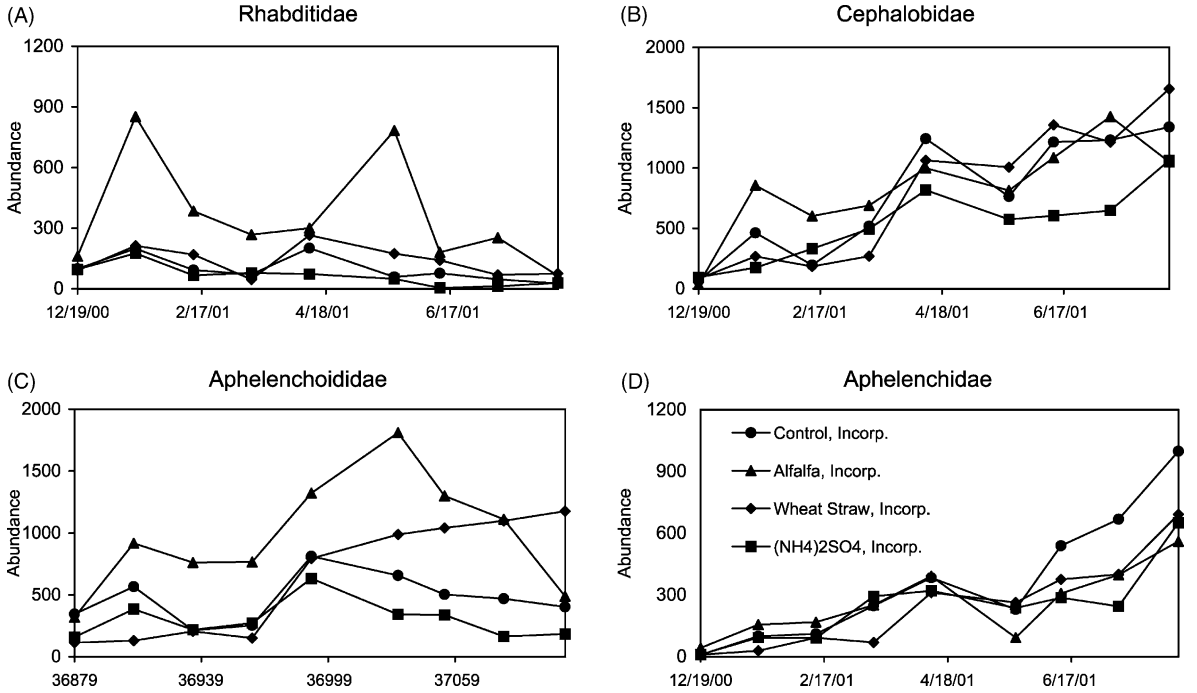


Fig. 1. Abundance of taxa representative of different functional guilds: (A) Rhabditidae ($Ba_1$ guild); (B) Cephalobidae ($Ba_2$ guild); (C) Aphelenchoididae ($Fu_2$ guild); and (D) Aphelenchidae ($Fu_2$ guild). Guild designations are derived from feeding habit (Ba, bacterivore; Fu, fungivore) and the Bongers (1990) colonizer–persistor (cp) designation. Nematode numbers are expressed per L soil.

Table 3
Effects of organic matter source and placement on relative soil respiration rates in winter (μg $CO_2$ $m^{-2}$ $h^{-1}$ $DD_0^{-1}$) and summer (μg $CO_2$ $m^{-2}$ $h^{-1}$ $DD_{10}^{-1}$)

| Input | C/N | Placement | Winter[a] | Summer[a] |
|---|---|---|---|---|
| Control | | Surface | 1441d | 1926d |
| Control | | Incorporated | 1565d | 2285bcd |
| $(NH_4)_2SO_4$ | | Incorporated | 1745cd | 2254bcd |
| Compost-wheat | 20.5 | Incorporated | 2611bc | 2653b |
| Compost | 10.6 | Surface | 1765cd | 2224bcd |
| Compost | 10.6 | Incorporated | 1969bcd | 2412bc |
| Wheat straw | 75.9 | Surface | 2731bc | 1996cd |
| Wheat straw | 75.9 | Incorporated | 2778b | 2336bcd |
| Alfalfa-wheat | 24.7 | Incorporated | 3753a | 2308bcd |
| Alfalfa | 10.6 | Surface | 4641a | 2141cd |
| Alfalfa | 10.6 | Incorporated | 3825a | 3042a |
| Main effects | | | | |
| Control | | | 1532r | 2043q |
| Compost | 10.6 | | 1915r | 2298q |
| Wheat | 75.9 | | 2809q | 2171q |
| Alfalfa | 10.6 | | 4213p | 2554p |
| | | Surface | 2681x | 2043y |
| | | Incorporated | 2681x | 2554x |

[a] Means (followed by letters within an alphabetic series) sharing the same letter do not differ significantly based on Duncan's multiple range test ($P < 0.05$). Means followed by letters in different alphabetic series are not comparable.

surface-applied treatments (Table 3). Incorporation of ammonium sulfate did not increase the relative rate of soil respiration above that of the incorporated control.

### 3.3. Soil chemistry

Total mineral N recovered from soil samples varied with the nature and C/N ratio of the organic material input. The total amount of N recovered from the $NH_4SO_4$ was almost three times that from the highest organic amendment treatment (Table 4). The greatest amount of mineral N recovered from an organic treatment was from the incorporated low C/N alfalfa. Less N was recovered from plots enriched with the high or intermediate C/N plant material (alfalfa-wheat blend), whether incorporated or not ($P < 0.05$). The main effect of organic source was higher for alfalfa than for any other organic input or for the unamended control. The main effect of incorporation on mineral N recovery over the whole sampling period was not significant. Interestingly, during the winter months, approximately half of the N recovered from plots amended with alfalfa, whether placed on the surface or incorporated, was in the $NH_4$–N form. Greater amounts of $NH_4$–N were recovered from those plots than for all treatments other than the mineral fertilizer. Although the aged compost treatments had levels of N equivalent to or higher than those applied in plant material (Table 1), most of it was in the $NO_3$–N form. There were no differences in mineral N recovery among aged compost treatments. Of all organic amendment treatments, cumulative N recovery from the soil was greater than the unamended control only in plots where low C/N material was incorporated (Table 4).

During both winter and summer periods, more mineral N was recovered from soil in plots amended with alfalfa, whether incorporated or not, than from the controls or from plots amended with any other organic source (Table 4).

Phospholipid fatty acids attributed to bacteria were greater in the incorporated alfalfa treatment than in the other treatments ($P < 0.05$). However, there were no differences in bacterial PLFAs between March and July (Fig. 2). Fungal PLFAs in March were greater in all amended treatments than those in the unamended control ($P < 0.05$). The treatments with wheat straw

Table 4
Total mineral N, and its $NH_4$–N and $NO_3$–N components ($\mu g\ N\ g^{-1}$ dry soil), recovered from plots during winter and summer periods for amendments applied to the soil surface or incorporated in December

| Material | C/N | Placement | Winter | | | Summer | | | Winter + summer |
|---|---|---|---|---|---|---|---|---|---|
| | | | $NH_4$–N | $NO_3$–N | Total N[a] | $NH_4$–N | $NO_3$–N | Total N[a] | Total N[a] |
| Control | | Surface | 0.17 | 1.15 | 1.31cd | 0.09 | 2.42 | 2.51b | 3.82cd |
| Control | | Incorporated | 0.11 | 0.74 | 0.85d | 0.10 | 1.78 | 1.88b | 2.73cd |
| $(NH_4)_2SO_4$ | | Incorporated | 7.99 | 2.60 | 10.59a | 2.91 | 8.49 | 11.40a | 21.99a |
| Compost-wheat | 20.5 | Incorporated | 0.15 | 0.70 | 0.85d | 0.11 | 2.05 | 2.16b | 3.01cd |
| Compost | 10.6 | Surface | 0.18 | 1.09 | 1.27cd | 0.11 | 2.19 | 2.30b | 3.57cd |
| Compost | 10.6 | Incorporated | 0.15 | 1.04 | 1.19cd | 0.10 | 1.87 | 1.97b | 3.16cd |
| Wheat | 75.9 | Surface | 0.12 | 0.57 | 0.69d | 0.09 | 2.42 | 2.50b | 3.20cd |
| Wheat | 75.9 | Incorporated | 0.14 | 0.43 | 0.57d | 0.11 | 1.58 | 1.68b | 2.26d |
| Alfalfa-wheat | 24.7 | Incorporated | 0.22 | 0.93 | 1.15cd | 0.10 | 2.21 | 2.31b | 3.46cd |
| Alfalfa | 10.6 | Surface | 1.29 | 1.24 | 2.53b | 0.13 | 2.99 | 3.12b | 5.65bc |
| Alfalfa | 10.6 | Incorporated | 1.54 | 2.07 | 3.61b | 0.12 | 3.51 | 3.63b | 7.24b |
| Main effects | | | | | | | | | |
| Control | | | | | 1.08qr | | | 2.19q | 3.27q |
| Compost | 10.6 | | | | 1.23q | | | 2.14q | 3.37q |
| Wheat | 75.9 | | | | 0.63r | | | 2.10q | 2.73q |
| Alfalfa | 10.6 | | | | 3.07p | | | 3.37p | 6.44p |
| | | Surface | | | 1.45x | | | 2.61x | 4.06x |
| | | Incorporated | | | 1.56x | | | 2.29x | 3.85x |

[a] Means (followed by letters within an alphabetic series) sharing the same letter do not differ significantly based on Duncan's multiple range test ($P < 0.05$). Means followed by letters in different alphabetic series are not comparable.

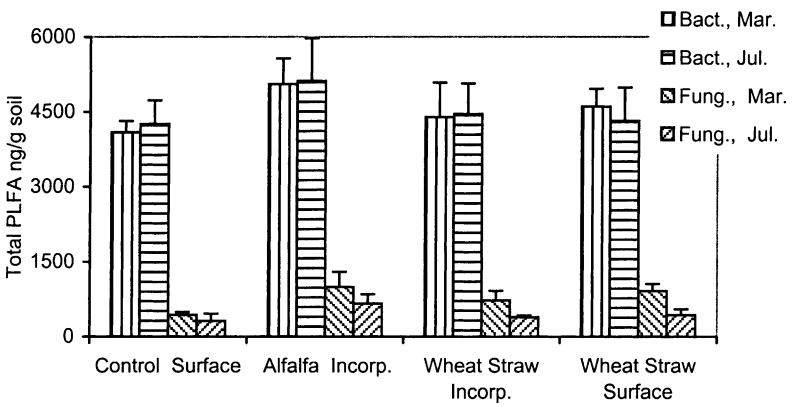


Fig. 2. Weights of phospholipid fatty acid (PLFA) markers of bacteria and fungi in March and July after stimulation of the soil food web by organic input in the previous December. Comparison of plots with plant materials placed on the surface and an unamended control. Bars represent 1S.D.

incorporated or placed on the surface did not differ from each other in fungal PLFAs. However, the incorporated alfalfa treatment had higher fungal PLFAs than the incorporated wheat straw ($P < 0.05$). Fungal PLFAs were lower in each treatment in July than in March (Fig. 2).

### 3.4. Nematode faunal indices

The EI in all plots increased following removal of old plant material, application of organic material and soil disturbance during incorporation. It declined linearly with the passage of physiological time ($DD_{10}$) (Fig. 3A–C). Since a higher EI is associated with greater bacterial abundance and activity (Ferris et al., 2001), we examined the magnitude of the EI for each input at 0 $DD_{10}$ (March 2001) and the rate of its decline in relation to the nature of the input. Intercept values of the linear relationships between EI and $DD_{10}$ (Fig. 3) were used as estimators of the magnitude of the EI at the beginning of the biologically active period for the nematode community. Since soil temperatures at 15 cm depth during December, January and February ranged between 5 and 9 °C, differences in the intercept values must reflect either differences among the plots at initiation of the experiment or increase in enrichment-opportunist nematodes during low-temperature soil conditions (Fig. 1). Intercept values for the relationship between the EI and $DD_{10}$ for all plots that received plant material inputs were greater than those for the disturbed and non-disturbed controls ($P < 0.05$). Composted materials and mineral fertilizer did not elevate the EI levels above those of the control plots (Table 1). There was no clear trend associated with the disturbance factor of incorporation. Although the highest EI was measured in plots with low C/N ratio materials placed on the soil surface, similarly high EI values were achieved with alfalfa that was defaunated by heating and then incorporated (Table 1).

For all treatments, there was a linear decline ($P < 0.01$) in the EI with progression of $DD_{10}$ but the slopes of the lines did not differ (Fig. 3A–C). Neither the disturbance of the soil nor the type of organic matter incorporated affected the EI decline rate. Differences among the EI regression lines were determined only by the magnitude of the intercept at 0 $DD_{10}$ (Table 1).

The product of the EI and $DD_{10}$, that is the area under the regression line between the two variables, provides an integral measure of the enrichment effect of organic matter input (Fig. 3). We define that product as the aggregate enrichment index (AEI). The rankings of AEI differ slightly from those of the intercept values alone as they also integrate the small differences in rates of EI decline in the various resource treatments. Highest AEI was achieved with low C/N alfalfa, followed by high C/N wheat straw and then compost. Plots with low and high C/N plant materials had significantly higher AEI values ($P < 0.05$) than compost or control plots. The affect of the latter on AEI was not different from the unamended control plots (Table 1).

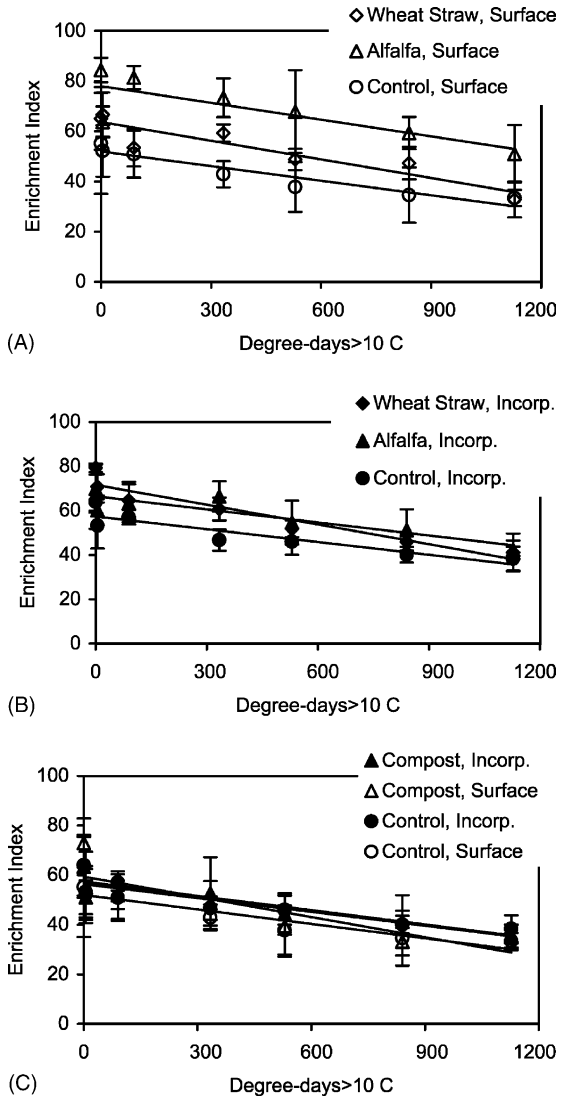


Fig. 3. Relationship between the enrichment index, derived from nematode faunal analysis, and physiological time between March and August after stimulation of the soil food web by organic input in the previous December: (A) comparison of plots with plant materials placed on the surface and unamended control; (B) comparison of plant materials incorporated and unamended control; and (C) comparison of aged compost, placed on the surface or incorporated, and unamended controls. Bars are ±1S.D.

### 3.5. Food web succession

Changes in the nematode fauna resulted in a positive, linear relationship between the channel index and physiological time for all input treatments, indicating succession from bacterial to fungal decomposition pathways (examples in Fig. 4A–C). The main effect of incorporation disturbance on the increase rate of the CI was not significant. Low C/N alfalfa did not alter the CI increase rate, but high C/N wheat straw increased it over the controls ($P < 0.05$) (Fig. 4A and B). The succession from bacterial to fungal decomposition was faster with high C/N than with low C/N plant material ($P < 0.001$) and faster with low C/N compost than with low C/N alfalfa ($P < 0.05$). Low C/N compost and high C/N wheat straw were not different in their effect on rate of succession from bacterial to fungal decomposition (Table 5). The rate of succession to fungivore predominance was not different between plots in which ammonium fertilizer had been applied and the no-input control plots (Fig. 4C).

Among the bacterivores, the rate of succession from enrichment opportunists to general opportunists, indicated by change in the BaI, was similar in all plots, regardless of original input (examples in Fig. 5A). Differences in the BaI through time were a function of the degree of stimulation of enrichment-opportunist bacterivores in response to the initial organic input. Their early abundance and subsequent rate of decline were greatest when readily degraded, N-rich substrates were incorporated in the soil. They were least when there was no organic input or with organic inputs of high C/N ratio (Fig. 5B). In fact, the rate of decline of the $Ba_1$ guild in relation to time did not differ from zero for wheat straw, while it declined significantly from elevated levels for the surface-applied and -incorporated alfalfa ($r^2 = 0.96$, $P < 0.01$ and $r^2 = 0.79$, $P < 0.05$, respectively).

## 4. Discussion

The theory underlying the expected responses of nematode functional guilds to soil enrichment, and the associated successional events in nematode faunal structure, emerges from the colonizer–persister categorizations of taxa and functional groups (Bongers, 1990; Bongers and Bongers, 1998). In that scheme, cp-1 taxa are enrichment-opportunist bacterial-feeding nematodes that respond rapidly to increase in microbial biomass. As bacterial resources decline, general-opportunist bacterivores (cp-2) replace the

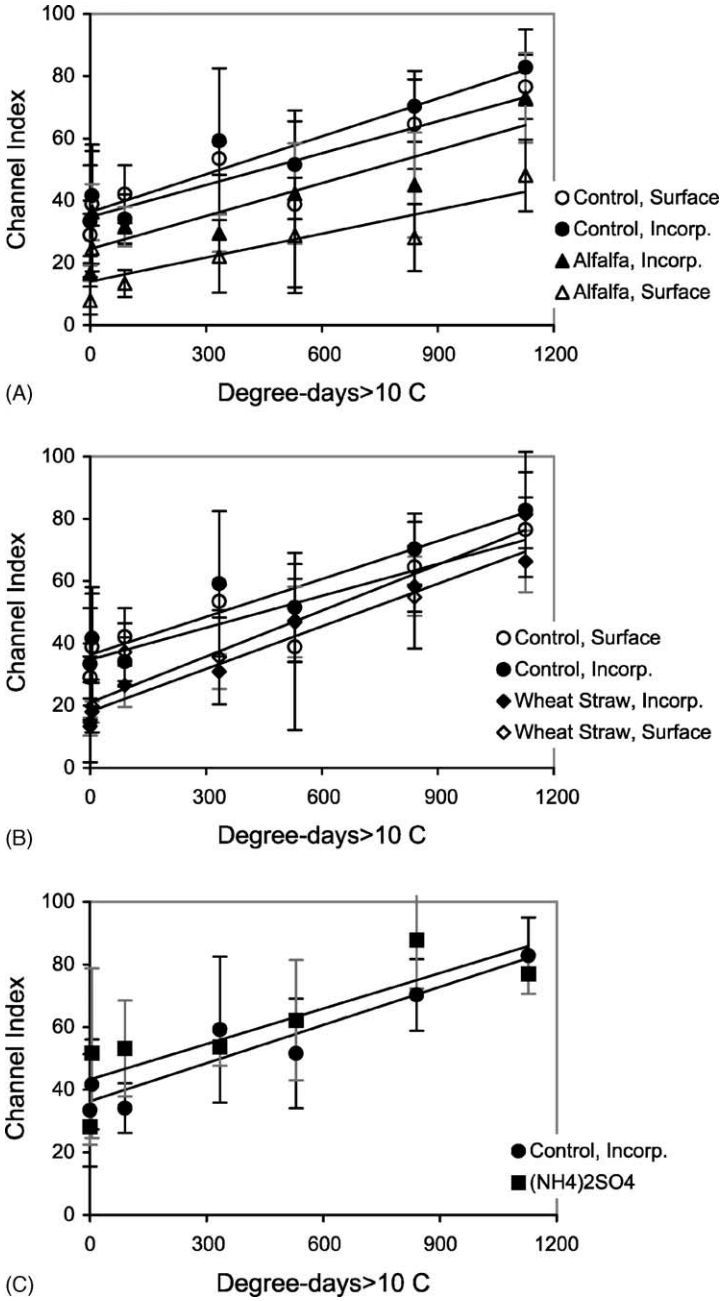


Fig. 4. Bacterivore to fungivore succession indicated by the relationship between the channel index, derived from nematode faunal analysis, and physiological time between March and August after stimulation of the soil food web by organic input in the previous December: (A) comparison of plots amended with alfalfa and unamended controls; (B) comparison of amended with wheat straw and unamended controls; and (C) comparison of mineral fertilizer and unamended control. Bars are ±1S.D.

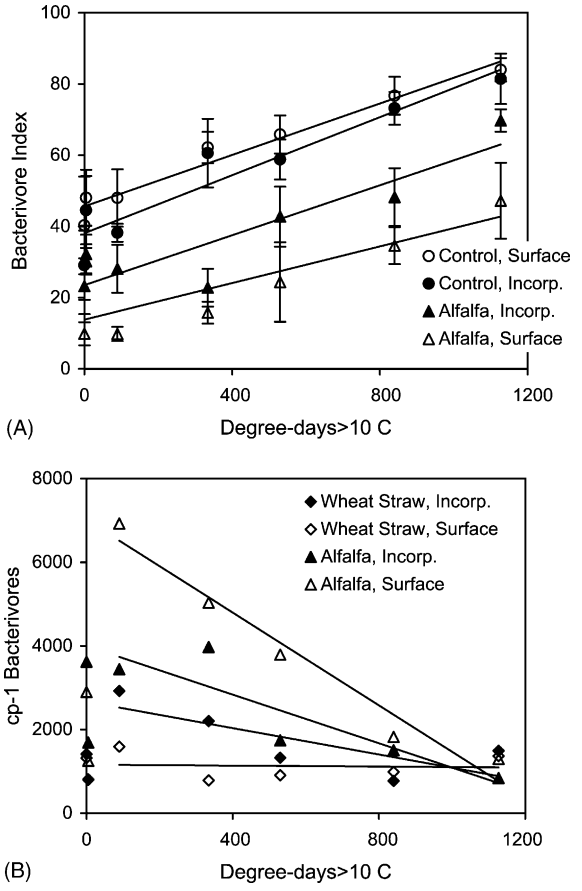


Fig. 5. Succession among bacterivore guilds and dynamics of the cp-1 bacterivore ($Ba_1$) guild (Bongers and Bongers, 1998) between March and August after stimulation of the soil food web by organic input in the previous December. Data for the plots amended only with mineral fertilizer are omitted. (A) Bacterivore succession indicated by the relationship between the bacterivore index, derived from nematode faunal analysis, and physiological time; comparison of plots amended with alfalfa and unamended controls. Bars are ±1S.D.; for all relationships, $P < 0.05$. (B) Comparison of relationship between the abundance of cp-1 guild bacterivores and physiological time for plots amended with alfalfa or wheat straw (for alfalfa, $P < 0.05$, high C/N relationships are n.s.). Nematode numbers are expressed per L soil.

enrichment-opportunist species (Bongers and Ferris, 1999). Also, as the decomposing organic source becomes more recalcitrant to bacterial decomposition, fungi become increasingly prevalent and the ratio of fungivore to bacterivore nematodes is expected to increase. The structure of the nematode fauna at a site has been used to develop indices that are indicative of food web structure and function for each guild of nematodes and, arguably for other organisms in similar functional guilds (Ferris et al., 2001).

### 4.1. Dynamics of the nematode fauna

Since this experiment was initiated in December, soil temperatures were <10 °C during the first two sampling periods following the initial disturbances of plant removal and plot establishment. In plots amended with labile, low C/N organic material, there was an increase in enrichment-opportunist bacterial-feeding nematodes (mainly Rhabditidae and Panagrolaimidae (Table 2)) and of fungal-feeding Aphelenchoididae (examples in Fig. 1), perhaps consistent with adaptation to lower temperature conditions for local populations of these nematodes (Ferris et al., 1996a; Okada and Ferris, 2001) and an initial flush of microbial activity. The cp-1 nematodes were less stimulated by more recalcitrant, high C/N, materials. Their populations declined as the labile organic material dissipated (Figs. 1 and 5B). They were succeeded by general opportunists of the Cephalobidae (Figs. 1 and 5A) with slower reproductive rates and longer life cycles (Ferris et al., 1996a, 2001; Venette and Ferris, 1997; Bongers and Ferris, 1999). The succession to cp-2 bacterivores (Fig. 6A) was not only due to cp-1 bacterivore decline (Fig. 5B) but also to concurrent, but slower, changes in generalist bacterivores and fungivores (Fig. 1). The abundance of these latter guilds varied through time with the nature of the input.

In previous studies on a similar soil about 1 km from this site, cp-1 nematodes increased when organic material was incorporated into the soil and remained at high levels through the summer months (Ferris et al., 1997). The difference in the studies was that the plots in the previous experiment were planted with tomatoes, so there was a continuous supply of labile organic materials in the rhizosphere through root exudation. We conclude that continued priming of the food web with root exudates or another source of readily decomposed organic source, perhaps liquid manures, is necessary to keep the cp-1 nematode population at high levels.

In all plots that received organic matter input, there was a slow increase in general-opportunist bacterivore and fungivore nematodes (mainly Cephalobidae and Aphelenchidae) which have longer lifecycles

Table 5
Pairwise comparisons of main effects of source and nature of organic material on the rate of succession from bacterial to fungal decomposition

| Comparison *A* vs. *B* | Difference in slope (*A* − *B*) | Difference 100(*A* − *B*)/*B* | Probability of difference (*P*) |
|---|---|---|---|
| Alfalfa vs. control | −0.0086 | −25.1 | n.s. |
| Wheat straw vs. control | 0.0151 | 44.1 | <0.05 |
| Compost vs. control | 0.0083 | 24.4 | n.s. |
| Wheat straw vs. alfalfa | 0.0236 | 92.3 | <0.01 |
| Compost vs. alfalfa | 0.0169 | 66.1 | <0.05 |
| Compost vs. wheat straw | −0.0067 | −13.6 | n.s. |

Data are slopes of the relationship between the channel index and physiological time for the inputs compared. Probabilities that the changes in slope differ from zero are indicated.

and lower fecundity than the enrichment opportunists (Ferris et al., 1996a; Okada and Ferris, 2001) (Fig. 1). A smaller increase in these nematodes also occurred in plots that did not receive organic input, presumably fueled by decaying roots of previous vegetation and stored soil organic matter.

We separated the soil respiration assessments into two datasets, one that measured cumulative soil respiration from the start of the experiment until soil temperatures reached 10 °C, which was when we deemed that major nematode activity commenced. That initial period represented the microbial stimulation effect associated with soil disturbance and access to new organic resources. The second phase was the spring and summer growth period from the time that soil temperatures reached 10 °C until the end of the experiment. In the current experiment, there was a sharp increase in the relative rate of soil respiration over the first 350 $DD_0$ (from mid-December to early March) in plots amended with alfalfa, suggesting stimulation of copiotrophic microbes by introduction of labile resources. During this period, there was no apparent effect of exposure of organisms to new resources as a result of soil disturbance (Table 3).

In this experiment, the applied organic matter did not always increase the relative rate of soil respiration during the spring and summer months, but incorporation of material had a significant effect. There were few differences among plant materials with different C/N ratios but, consistent with the nematode population data, greatest relative soil respiration rates were measured in plots in which low C/N alfalfa was incorporated into the soil (Table 3). A blend of wheat straw and compost increased soil respiration over that of the control plots, but alfalfa increased soil respiration to a greater extent than low C/N compost. We suspect that the readily decomposed C fraction of the aged compost had already been utilized during the composting process so that mainly recalcitrant organic materials remained. Incorporation of alfalfa enhanced soil respiration in comparison to placing it on the surface whereas the effect of incorporation was not significant with compost or wheat straw.

EI levels were stimulated above those of the control plots to the greatest extent by plant inputs in general and then by compost. As with soil respiration rates (Table 3), the EI was not elevated by addition of mineral fertilizer. Interestingly, the greatest AEI was achieved with low C/N on the soil surface. Since the amount of C added to organic amended plots was more or less standardized across organic sources (plant or compost), the AEI was related inversely to the C/N ratio of the material (Table 1). While that might suggest N limitation effects, it could also be determined by the nature and degradability of the available materials, alfalfa and wheat straw. As labile resources declined, the EI declined. In our previous studies, in which the food web was continuously primed by root exudates throughout the growing season, the abundance of cp-1 nematodes and the EI were maintained (Ferris et al., 1996b; Ruess and Ferris, 2002).

### *4.2. Drivers of succession among the nematode fauna*

Disturbance of soil usually results in an increase in microbial biomass. Such increases due to tillage are well-documented and are ascribed to incorporation of organic residues into soil, disruption of soil aggregates, exposure of organic matter to microbial colonization. These events are often associated with an increase in soil respiration and a net loss of carbon

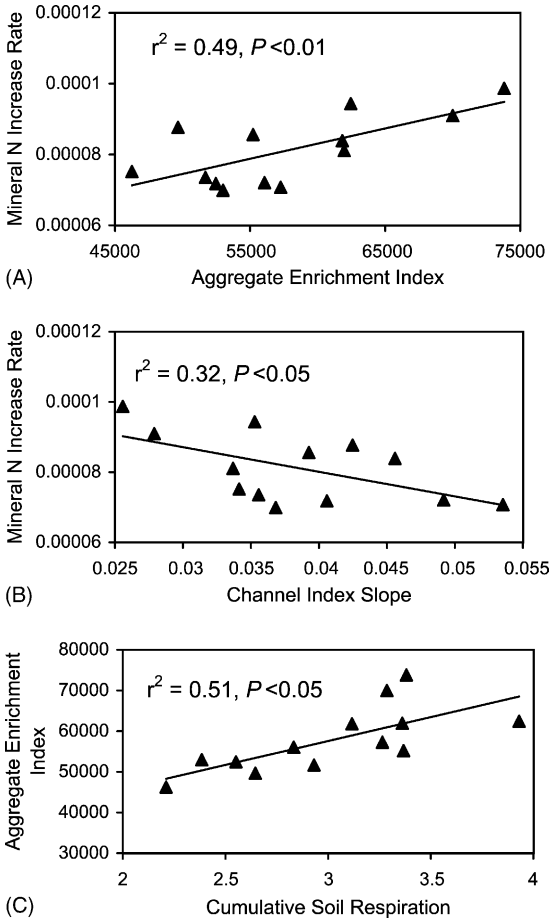


Fig. 6. Relationships between structure and function of the soil food web as indicated by nematode faunal analysis: (A) relative rate of N mineralization in relation to the aggregate enrichment index; (B) relative rate of N mineralization in relation to the rate of succession between bacterivores and fungivores as indicated by the rate of change of the channel index; and (C) relationship between the aggregate enrichment index and assessments of cumulative soil respiration.

from the soil (Van Veen and Kuikeman, 1990; Hendrix et al., 1998; Fu et al., 2000). Addition of readily decomposed organic materials, particularly those of high N content (low C/N), also fuel microbial biomass growth and a resultant increase in enrichment-opportunist nematodes (Ettema and Bongers, 1993; Ferris et al., 1996b).

Labile C compounds in most organic material are decomposed readily by copiotrophic bacteria. Their activity is accompanied by a concomitant flush of enrichment-opportunist nematodes. However, this flush will be brief unless the provision of labile C compounds is sustained, for example, by root exudation. The rate of change of the BaI indicates rates of succession from enrichment to general-opportunist bacterivore nematodes. Two of the factors that govern the succession are the rate at which labile resources are declining and the longer lifecycle and lower reproductive potential of the cp-2 nematodes. As a consequence, the BaI was lower across all sampling periods in the low C/N-amended plots than in the unamended control (Fig. 5A). It is useful to reflect that these indices have both a numerator and denominator and that an increase in the index does not necessarily indicate an increase in the numerator of the index. In this case, the index in the amended plots is low because the abundance of cp-1 nematodes was initially greater in those plots (Fig. 6B). The rates of succession among bacterivores (i.e. the slopes of the lines) were relatively constant in all treatments.

Where organic material is supplied to fallow field plots, we expect that the rate of succession to fungivory will be similar across a range of types of organic input, with differences in initial rates determined by the nature of the input. If the rate of succession is similar for the mineral fertilizer plots and unamended plots, that may indicate breakdown of old roots and residual organic sources in those plots. The rate of N mineralization should reflect community structure and activity. As succession occurs among nematode guilds, that should be reflected in the ecosystem function.

We expected that in treatments with limited readily decomposed material, the succession from bacterial to fungal decomposition would occur rapidly, resulting in a steep positive slope of the linear relationship between CI and time. Consistent with these expectations, and results from other studies (Ruess and Ferris, 2002), the succession from bacterial to fungal decomposition was accelerated by the addition of C in complex, less-labile forms. The rate of succession to fungivory was greater with high C/N wheat straw than with low and greater with aged compost than with low C/N alfalfa. It was greater in plots amended with wheat straw than in the control plots, which received no organic inputs and were predominated by generalist bacterivores (Fig. 5). The rate of succession to fungivore predominance was similar in plots receiving ammonium fertilizer and in the no-input control plots,

suggesting that the organisms were not N limited and that C was the rate-determining component in succession.

We expected to use the PLFA data to validate our assertions about changes in the nature of the organic substrate and consequent succession among functional guilds of nematodes. Rather than increasing, however, the weight of fungal PLFAs decreased with time. Also, there were higher amounts of fungal PLFA in the treatment receiving low C/N material than in those receiving high C/N material. These results were counterintuitive and contrary to the conventional wisdom of the effects of organic matter on soil organisms and on the time-course of decomposition. It is possible that taxa within the functional groups of decomposers indicated by the PLFA biomarkers differ in their importance and activity in decomposition so that estimates of total biomass do not reflect activity. Also, our PLFA determination period in July may represent a point in time when the fungal mass has been depleted by the high numbers of fungivores. We speculate that the differences in response to the treatment inputs of succession among bacterivores and succession from bacterivores to fungivores are related to the nature of the resources and life history characteristics that drive each nematode guild. In the case of bacterivores, the cp-1 and cp-2 guilds are utilizing the same resource, which itself is undergoing successional changes from copiotrophic to oligotrophic forms. In that case, nematode succession may reflect the life course duration and fecundity of the nematodes guilds. The succession to fungivores reflects a gradual shift in resource availability to two nematode guilds. The resources available to fungivores are greatest for those inputs with a greater abundance of complex carbon compounds, so population increases with those inputs.

### 4.3. The function of N mineralization

The rate of increase in cumulative mineral N through time was linearly related to the AEI ($r^2 = 0.49$, $P < 0.01$) (Fig. 6A). Here it is important to avoid inferring cause and effect. Although we know that bacterial-feeding nematodes do increase the rate of N mineralization in soils, it is quite likely that much of the mineralization is due to the primary decomposers. Since both N mineralization and nematode dynamics are a consequence of substrate dynamics as mediated by bacteria and fungi, the AEI provides a useful and measurable indicator of the state of these processes. Greater amounts of N are mineralized when a higher AEI is maintained through organic input manipulation. Those treatments that sustained higher levels of cp-1 bacterivores released N at a greater rate and presumably would sustain plant growth more readily. The more rapidly that decomposition switches to fungal pathways (higher values for the CI slope), the smaller the amount of N mineralized ($r^2 = 0.32$, $P < 0.05$) (Fig. 6B). With higher C/N ratio materials, or more recalcitrant materials (aged compost), where the succession rate was higher, the rate on mineral N release was lower (Table 4).

Treatment inputs that generated higher soil respiration generally resulted in an increased AEI, with a significant linear relationship between the two ($r^2 = 0.51$, $P < 0.01$) (Fig. 6C). The inputs that enhanced biological activity in the soil also enhanced AEI, which in turn was associated with a greater rate of mineral N release.

The rate of supply of N from decomposing organic material can be a growth- and yield-limiting constraint in organic and low-input production systems (Ferris et al., 1996b; Clark et al., 1999; Poudel et al., 2001). We believe that functional guilds of bacterivore and fungivore nematodes are indicators of other organisms with similar ecological function. Since the nematodes are readily measurable, they can be used to monitor the effects of soil management. For management of soil fertility in systems driven by organic input, it may not be sufficient to maintain or increase levels of bacterivore and fungivore nematodes. It may also be necessary to manage cp-1 nematodes selectively by frequent supply of labile inputs. In other words, it may be necessary to keep cp-1 nematode guild dynamics primed with continued or regular input rather than allowing succession to guilds that indicate lower mineralization potential and lower levels of soil fertility.

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