

Dynamics of nematode communities in tomatoes grown in conventional and organic farming systems, and their impact on soil fertility

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Abstract

Nematode communities were monitored intensively through a tomato (*Lycopersicon esculentum* L.) growing season in plots managed by conventional and organic farming practices. The temporal dynamics of individual species of bacterial-feeding nematodes differed and suggested differing importance of species in their contribution to N-mineralization in the organically managed soil. Species with r-selected, colonizer characteristics were most responsive to incorporation of organic matter and the subsequent increase of microbial biomass. Bacterial-feeding nematode populations were lowest early in the growing season, when tomato plants exhibited symptoms of nitrogen deficiency. We hypothesize that increasing abundance, biomass and activity of these nematodes in the spring by organic matter incorporation at the end of the previous crop would reduce the observed nitrogen stress. Fungal-feeding nematodes were more abundant in the conventional than the organic plots during periods of organic matter decomposition, possibly related to the higher carbon:nitrogen ratios of the crop residues incorporated into the conventional soils than of the manures and leguminous cover crops incorporated into the organic soils. Predaceous and omnivore nematode populations were low in both farming systems, and plant-parasitic nematode species reflected the crop sequences in rotations used in each system.

Keywords: Bacterial-feeding nematodes; Soil fertility; Nematode community dynamics; Nematode abundance and biomass

1. Introduction

In a continuing, long-term experiment comparing conventional, low-input and organic farming systems, a major management concern is the maintenance of adequate soil fertility at key crop-growth periods in the organic and low-input systems (Scow et al., 1994; Temple et al., 1994a,b). Nitrogen is supplied through crop residues, incorporated cover crops and manures in the low-input and organic farming systems. In the

conventional farming system, it is applied to the soil as inorganic fertilizer (Table 1) (Temple, 1993). During 1993, the total amount of nitrogen supplied was somewhat greater in the organic than in the conventional system, but large amounts of carbon were included in the material required to achieve those levels in the organic plots (Table 1). In effect, the organic plots were carbon-rich and the conventional plots were carbon-starved as interpreted on the basis of microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), and measures of microbial activity (Scow et al., 1994; Gunapala and Scow, 1996).

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Table 1
Sources and amounts (kg ha^{-1}) of nitrogen in tomato plots under two farming systems in 1993 (Temple, 1993)

	Conventional	Organic
Previous crop residue	39	42
Mineral fertilizer	141	–
Cover crop	–	120
Organic fertilizer	–	3
Manure	–	67
Total N	180	232
C:N ratio	7.3	34.8

Nematodes play a significant role in decomposition of soil organic matter, mineralization of plant nutrients and nutrient cycling (Ingham et al., 1985; Hunt et al., 1987; Griffiths, 1990). Many of the nematodes in biologically active and productive soils are not herbivores but are bacterial- and fungal-feeding species. Primary decomposition of organic matter is accomplished by bacteria and fungi, which are grazed upon by Protista, microbivorous nematodes and other organisms. As bacterial-feeding nematodes are purported to have a higher carbon:nitrogen (C:N) ratio ($\pm 10:1$) than their substrate ($\pm 5:1$), considerable N-mineralization is associated with their metabolic activity (Anderson et al., 1981). In consuming sufficient bacteria to provide carbon for their body structure and respiration, nematodes assimilate more nitrogen than necessary. The excess nitrogen is excreted as ammonia (Rogers, 1969; Lee and Atkinson, 1977). Even if the reported C:N ratios of nematodes are incorrect and their body composition is closer to that of bacteria, as suggested by analyses of Persson (1983), the nitrogen consumed with carbon that is used in respiration (perhaps 40% of the food intake (Marchant and Nicholas, 1974)), will be in excess of structural needs and will be excreted. However, microbivorous nematodes exhibit a wide range of metabolic rates and behavioral attributes. The contribution of individual species to nitrogen cycling and soil fertility may vary considerably.

Several studies suggest that the diversity, species composition, and activity levels of nematode populations may be useful and readily measured indicators of environmental quality. Nematodes are proving useful indicators of pollution levels in aquatic and soil systems, and in industrial toxicology (Van Kessel et al., 1989; Vranken et al., 1991). In soil systems, Bongers

(1990) has developed a maturity index, based on species composition and abundance of the nematode community, which recognizes a continuum from colonizer to persister life-history characteristics. The maturity index provides an indicator of ecological disturbance and is used as a tool to assess the suitability of reference sites for environmental monitoring (Neher and Campbell, 1994). It has also been tested as a basis for an ecological classification of soil (De Goede and Bongers, 1994).

The objectives of this study were: to monitor the presence and abundance of species of bacterial-feeding, fungal-feeding, omnivore–predator and plant-parasitic nematodes in soils managed under conventional and organic farming systems; to evaluate the temporal relationships between soil fertility, soil microbial biomass and population levels of bacterial-feeding nematodes as influenced by farming systems; to determine whether the presence or abundance of any of the nematode species, or the indices thereof, constitutes an indicator of soil fertility.

2. Materials and methods

During 1993, soil samples were taken from tomato (*Lycopersicon esculentum* L.) plots under 4 year rotations in conventional and organic farming systems in the Sustainable Agriculture Farming Systems (SAFS) project at Davis in California's Sacramento Valley. The SAFS project is located on an 11.3 ha site of Class I Yolo silty loam soil. Samples were taken from tomato plots in conventional 2 year and low-input farming systems less frequently. Samples were taken at approximately 3 week intervals from the beginning of April, following incorporation of the winter cover crop in the organic and low-input systems, and fertilizer application in the conventional plots, to the termination of the tomato crop in September. Samples were composites of 30 cores (2.5 cm diameter) of soil taken to a depth of 15 cm in the 0.135 ha plots. In this paper, three time scales are used to allow portrayal of events through time. They are: Julian date, to indicate number of days between events, where 1 January 1993 is Day 1; calendar date, for easy reference to season and sampling times; physiological time, calculated as degree-days of soil temperature at 15 cm (base 10°C), for consideration of nematode population events (Table 2).

Table 2

Calendar dates, Julian date and elapsed degree-days (base 10°C soil temperature) at which soil samples were removed for microbial and nematode analysis in 1993

Calendar date	Julian date	Degree-days (base 10°C)
5 April	95	153.8
26 April	116	266.5
10 May	130	387.4
24 May	144	534.2
4 June	155	656.1
21 June	172	868.5
2 July	183	1032.6
19 July	200	1282.9
9 August	221	1614.2
17 August	229	1725.8

Each sample was mixed thoroughly, passed through a 4 mm sieve and subdivided for soil nitrate, microbial and nematode assays. Soil nitrate assays were conducted by the University of California's Division of Agriculture and Natural Resources Analytical Laboratory. Microbial biomass was measured as MBC and MBN (Gunapala and Scow, 1996). Microbial activity was measured by potentially mineralizable nitrogen (PMN), arginine ammonification, and substrate-induced respiration (Gunapala and Scow, 1996). Samples for nematode assay were hand-mixed and 400 cm³ subsamples processed by elutriation and sugar-centrifugation (Byrd et al., 1976).

2.1. Nematode species composition, abundance, trophic groupings and diversity

All nematodes in each sample were counted, then the first 200 nematodes encountered in the sample were identified to genus, or species where possible, by picking out individuals and examining them under a compound microscope at 400× magnification. The abundance of each taxon in the sample was calculated from the proportion of that taxon among the identified nematodes. Abundance was expressed as the number of nematodes in each taxon per liter of soil and was not corrected for extraction efficiency. For all nematodes and for each nematode trophic group (Yeates, 1971; Yeates et al., 1993), three indices of species diversity were calculated to indicate the effective number of species present (Hill, 1973). N_0 was determined as the total number of species, N_1 as the number of abundant

species, and N_2 the number of very abundant species (Ludwig and Reynolds, 1988). N_1 was calculated as $e^{H'}$, where $H' = -\sum [p_i(\ln p_i)]$, the Shannon–Wiener index (Shannon and Weaver, 1949) with p_i the proportion of each of the i taxa present. N_2 was calculated as $1/\lambda$, where $\lambda = \sum (p_i)^2$, Simpson's index (Simpson, 1949). Additionally, Bongers' Maturity Index (Bongers, 1990) was calculated for all nematode species present in the samples, and within each nematode trophic group, as $\sum p_i c_i$, where c_i is a rating for taxon i on a pre-specified 'colonizer ↔ persister' scale. Bongers' Maturity Index measures the stability and disturbance level of an ecosystem based on the type and abundance of nematodes present.

2.2. Biomass and related indices for bacterial-feeding nematodes

As nematodes of different stage and species differ in size, we calculated biomass of bacterial-feeding nematodes as an indicator of potential nematode feeding pressure on the bacterial community, and as an indicator of the bacterial resource requirement to support that component of the nematode community. Biomass was calculated by the following steps:

(1) we divided the life cycle of each nematode species into four separable life stages beyond the egg stage: first- and second-stage juveniles, third-stage juveniles, fourth-stage juveniles, and adults. Eggs were not recovered by our extraction process and were not considered in the calculations. Based on the average time spent in each of the life stages (t_i , where $i = 1-4$) for each nematode species (Ferris et al., 1995), we calculated the relative probability of an individual being in a life stage as a proportion of the total life span of that species (T). A refinement to this approach is to recognize that age-specific survivorship values differ and to base the probability of presence as a function of relative time in the life stage and relative survivorship. In the absence of information on survivorship in field soils, we assumed equal survivorship of all life stages.

(2) The extraction efficiency of our elutriation–centrifugation process, which involves sieving of nematodes from a water suspension using a 400 mesh (38 μm aperture) sieve, was estimated for each nematode life stage as a linear function of the median length of individuals in that life stage (Ferris et al., 1995). We assumed that the extraction efficiency of the adults of

the largest nematodes (*Cruzema tripartitum*, median length of adults 1460 μm) was 80% and calculated extraction efficiency as $0.8L/1460$, where L is the median length of each stage.

(3) The number of nematodes of each species, calculated from the proportion of each species among the identified nematodes, was partitioned into the number of individuals in each life stage by multiplying by the probability of that life stage being present and dividing by the extraction efficiency for that life stage. The sum of the estimated numbers of each life stage multiplied by their respective extraction efficiencies provided the estimated abundance of that species.

(4) The biomass of each life stage of each species was calculated as the mean weight for that life stage multiplied by the estimated number of individuals of that life stage present in the population. The sum of the calculated biomasses for the four life stages represents the total biomass for that species, and the sum of the biomasses for all species of bacterial-feeding nematodes represents the total biomass for that trophic group.

(5) In recognition that rates of nematode metabolism and development are temperature-dependent, we expressed changes in nematode biomass on a physiological time basis for instructive interpretation of temporal events (Table 2).

To determine whether food availability was a constraint in population increase of bacterial-feeding nematodes, we made the assumption that larger nematodes consume more food than smaller nematodes to meet maintenance and growth requirements. Consequently, we divided biomass of bacterial-feeding nematodes on each sampling date by the abundance of their food as measured by MBC. That allowed determination of changes in biomass per unit of food availability.

3. Results

3.1. Soil fertility, microbial biomass and bacterial-feeding nematodes

During 1993, the available nitrate in the soil solution differed during the growing season in the conventional and organic tomato plots (Fig. 1(A)). In the conventional system there was abundant soil nitrate detected in soil samples between April and mid-June, resulting

from preplant and sidedress applications of inorganic fertilizer. Those levels were probably in excess of plant needs, but available during key growth periods for the tomato plants (Fig. 1(C)). In the organic plots, the level of extractable soil nitrate was very low at tomato planting and remained low throughout the growing season. It was below the norms for conventional agriculture and, under those criteria, the soil would be diagnosed as nitrogen deficient for tomato production. Plants exhibited nitrogen stress in the organic tomatoes during the early part of the growing season (Scow et al., 1994). However, crop yields in the two systems were comparable in 1993.

Soil fertility, microbial and nematode assays in the conventional 2 year system were similar to those in the conventional 4 year system and are not reported. Those in the low-input system were similar to the organic system in terms of soil fertility, and intermediate between conventional and organic systems for microbial and nematode data. Owing to the infrequency of their measurement they are also not reported.

Microbial biomass, measured as MBC, was significantly higher in the organic farming system than the conventional system throughout the tomato growing season (Fig. 1(B); Gunapala and Scow, 1995). Following cover crop incorporation in the organic farming system, MBC increased until the end of June. After mid-summer, MBC decreased and declined to levels comparable with those in the conventional plots by the end of the growing season. In the conventional plots, MBC remained relatively constant throughout the growing season.

Total numbers of bacterial-feeding nematodes were similar in conventional and organic farming systems at the time of tomato planting ($P=0.29$). It was more than 30 days after cover crop incorporation before the bacterial-feeding nematodes in the organic plots became more abundant than those in the conventional system ($P=0.06$) (Fig. 1(D)). Bacterial-feeding nematode numbers in the conventional system remained low throughout the growing season, whereas those in the organic system declined from their high levels following decrease in microbial biomass at mid-summer. By the end of the growing season, the numbers in the two farming systems were not significantly different ($P=0.51$).

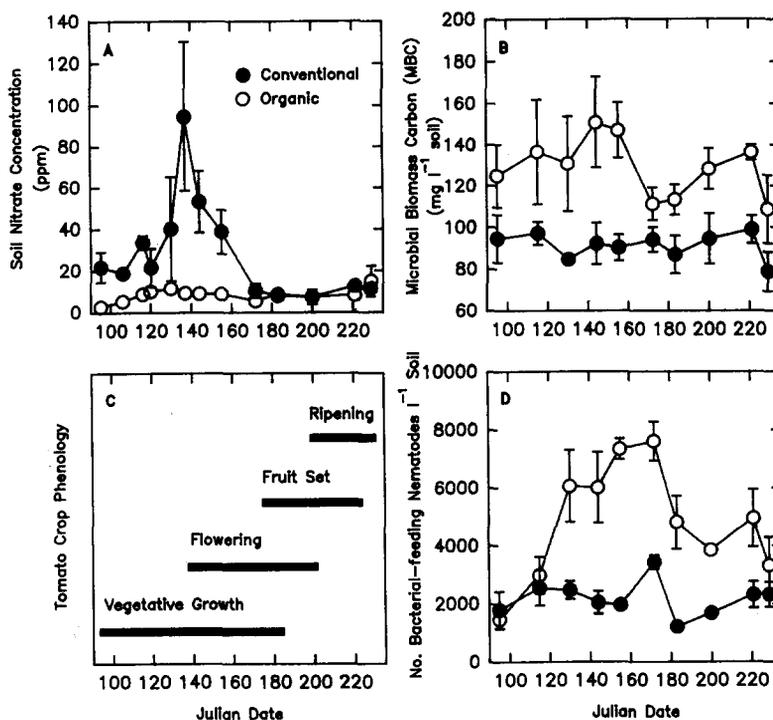


Fig. 1. Relationship of 1993 soil nitrate availability, microbial biomass and bacterial-feeding nematode abundance in soils under organic and conventional farming systems to tomato crop phenology. Data are means and standard errors across four replicates. (A) Extractable soil nitrate concentration (from Temple (1993)). (B) Tomato crop phenology (adapted from Flint (1985)). (C) Microbial biomass expressed as microbial biomass-carbon (from Gunapala and Scow (1996)). (D) Abundance of bacterial-feeding nematodes.

3.2. Nematode species composition, abundance and trophic groupings

There were more nematode species of all trophic groups present in the conventional than in the organic plots for the first 6 weeks of the tomato growing season following incorporation of lana vetch (*Vicia dasycarpa* Ten.) in the organic plots ($P=0.03$ at Day 130), although the differences were not statistically significant on all sampling dates. By mid-summer, however, the number of nematode species detected in the two farming systems were indistinguishable ($P=0.64$ at Day 172) (Fig. 2(A)). That pattern was influenced most strongly by the species of bacterial-feeding nematodes, as the numbers of plant-parasitic and omnivore-predator species were similar in both farming systems (Figs. 2(B), 2(C) and 2(D)), and the number of fungal-feeding species did not change through time.

The average number of nematodes of all trophic groups was higher in the conventional plots than in the organic at the beginning of the tomato growing season,

although again the differences were not statistically significant on all sampling dates. By 6 weeks into the season, the total number of nematodes was greater in the organic system, and remained that way until near the end of the growing season (Fig. 3(A)). The dynamics early in the growing season were influenced most strongly by the greater number of plant-parasitic species in the conventional system (Fig. 3(C); Lanini et al., 1994). Later in the season, the dynamics were influenced by the increase in bacterial feeders in the organic system (Fig. 1(D)). The number of fungal-feeding nematodes was marginally higher in the conventional than the organic system during the first 6 weeks of the growing season, but indistinguishable thereafter (Fig. 3(B)). Two species of nematodes in these soils represent groups whose feeding habits are not well defined, but include omnivores and predators on nematodes and other soil organisms. Numbers of omnivore-predator individuals were low and variable in both farming systems. They were lowest at planting

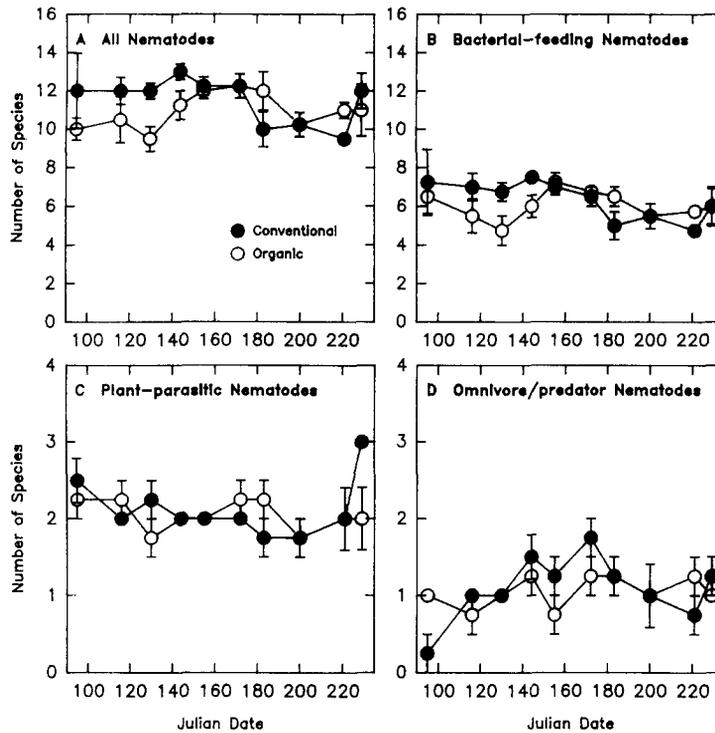


Fig. 2. Total number of nematode species, and number of species in each of three trophic groups in tomato plots under organic and conventional farming systems. Data are means and standard errors across four replicates. Number of species of: (A) all nematodes; (B) bacterial-feeding nematodes; (C) plant-parasitic nematodes; (D) omnivore–predator nematodes.

in the conventional system (Fig. 3(D)) although prey was abundant at that time (Fig. 3(A)).

Eleven taxa of bacterial-feeding nematodes, all in the order Rhabditida, were monitored during the course of this intensive sampling study. Those identified routinely to species were *Acrobeloides bodenheimeri* Thorne, *A. buetschlii* Steiner and Bührer, and *A. tricornis* Thorne (all family Cephalobidae). Those identified routinely to genus include: *Acrobeles* sp., *Cephalobus* sp. and *Chiloplacus* sp. (all family Cephalobidae); *Bursilla* sp., *Cruznama* sp., *Diploscapter* sp. and *Rhabditis* sp. (all family Rhabditidae); *Panagrolaimus* sp. (family Panagrolaimidae). Representatives selected from these genera were identified as the following species: *Bursilla labiata* Andrassy, *Cruznama tripartitum* Zullini and *Rhabditis cucumeris* Andrassy, *Cephalobus persegnis* Bastian, and *Panagrolaimus detritophagus* Fuchs. Voucher specimens of many of these species were deposited in the University of California Davis Nematode Collection with the following

accession numbers: *Acrobeloides bodenheimeri*—UCDNC 2908 and 2909; *A. buetschlii*—UCDNC 3030; *Bursilla labiata*—UCDNC 3028 and 3029; *Cephalobus persegnis*—UCDNC 3031; *Cruznama tripartitum*—UCDNC 2910 and 2911; *Panagrolaimus detritophagus*—UCDNC 3034; *Rhabditis cucumeris*—UCDNC 3033.

Different taxa of bacterial-feeding nematodes predominated at different times during the growing season. In the organic plots, *Panagrolaimus* sp. and *Rhabditis* sp. were most abundant in the top 15 cm of soil early in the tomato growing season and within about 20 days of organic matter incorporation. *Bursilla* sp. became numerically predominant by the end of June in the organic plots, and remained at high population levels until the end of the tomato growing season. *Chiloplacus* sp. were more numerous in the conventional than the organic plots until near the end of the growing season (Fig. 4(A)).

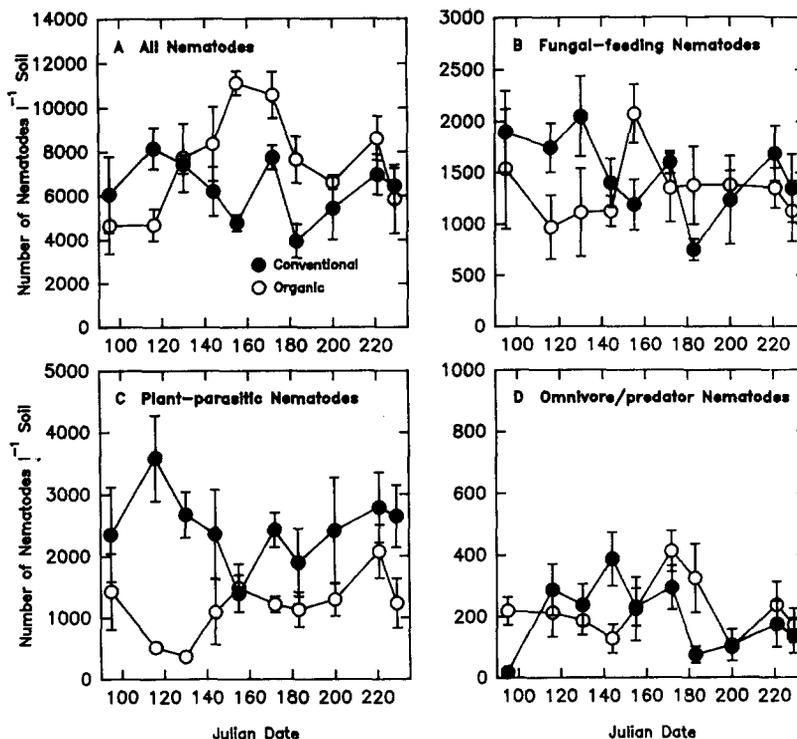


Fig. 3. Abundance of all nematodes, and abundance of nematodes in each of three trophic groups in tomato plots under organic and conventional farming systems. Data are means and standard errors across four replicates and are not corrected for efficiency of the extraction method. Average abundance of: (A) all nematodes; (B) fungal-feeding nematodes; (C) plant-parasitic nematodes; (D) omnivore-predator nematodes.

Two species of nematodes in the soil samples, both in the order Tylenchida, were categorized as fungal-feeders: *Aphelenchoides* sp. (family Aphelenchoididae) and *Aphelenchus avenae* Bastian (family Aphelenchidae). Both species were consistently present throughout the tomato growing season in both farming systems (Fig. 5(A)), although with a slightly greater abundance early in the conventional system, as already noted. The omnivore-predator nematodes included *Prismatolaimus* sp. (order Monhysterida, family Monhysteridae) and *Eudorylaimus* sp. (order Dorylaimida, family Dorylaimidae). *Prismatolaimus* sp. may be a non-selective feeder (Yeates et al., 1993) but was included in the group owing to the presence of teeth in the stoma. Other nematodes in the family Dorylaimidae were encountered occasionally and included in this grouping as omnivores. Although *Eudorylaimus* sp. was not detected in the conventional plots in early April, it was present in similar low numbers in the top 15 cm of soil as in the organic plots thereafter. *Pris-*

matolaimus sp. was detected only sporadically in both farming systems (Fig. 5(C)).

Seven species of plant-parasitic nematodes were found over the first 4 years of the SAFS project. On most sampling dates the plant-parasitic nematodes were identified only to genus, and the species characterization was inferred from identification of individuals at various points in time. Genera and species encountered (all in the order Tylenchida unless otherwise indicated) include *Meloidogyne incognita* Chitwood (family Heteroderidae), *Paratylenchus* sp. (family Tylenchulidae), *Pratylenchus thornei* Sher and Allen (family Pratylenchidae), *Rotylenchus* sp. (family Hoplolaimidae), *Tylenchorhynchus* sp. (family Belonolaimidae), *Tylenchus davainei* Bastian (family Tylenchidae), and *Xiphinema americanum* Cobb (order Dorylaimida, family Longidoridae). Of these, the feeding habits of *T. davainei* are uncertain. In fact, this nematode may also feed on fungi and/or algae, although we have not succeeded in culturing it

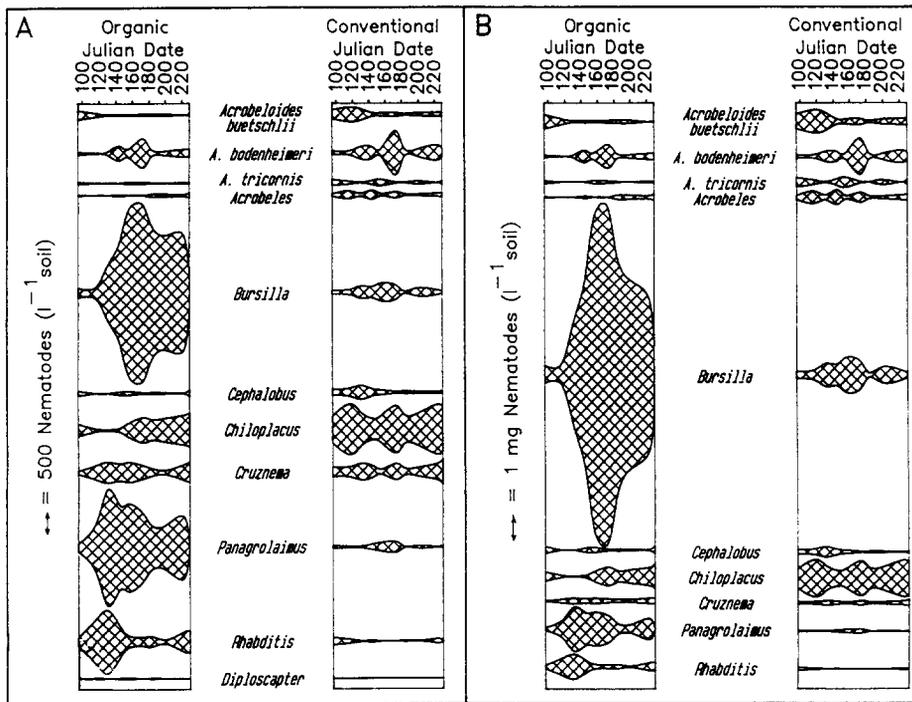


Fig. 4. Temporal abundance (A) and biomass (B) of individual taxa of bacterial-feeding nematodes in tomato plots under organic and conventional farming systems. Data are averaged across four replicates. Abundance data are not corrected for efficiency of the extraction method; biomass data are corrected for estimated extraction efficiency of nematodes in each taxon.

on the fungus *Rhizoctonia* sp. in the laboratory (see Yeates et al., 1993). Numbers of *M. incognita*, *Paratylenchus* sp. and *X. americanum* were at extremely low levels in the top 15 cm of soil in tomato plots under both farming systems throughout the monitoring period. *Pratylenchus thornei* was about twice as abundant in the conventional plots throughout the season, as was *T. davainei* (Fig. 5(B)).

3.3. Diversity indices across and within trophic groupings

The transformed Simpson's diversity index showed only subtle differences from the transformed Shannon-Weiner index (N_2 and N_1 of Hill (1973), respectively). They were almost identical for the plant-parasitic and omnivore-predator trophic groups, whereas for all nematodes and the bacterial-feeders there were two fewer very abundant species (N_2) than abundant species (N_1). Consequently, only the N_1 data are presented (Fig. 6). By 6 weeks after vetch incorporation (Day

130), the number of abundant species across all trophic groups was greater, and remained greater until after mid-season (Day 183), in the conventional than the organic plots (Fig. 6(A)). At the beginning and end of the growing season, the number of abundant species across all trophic groups was not significantly greater in the organic plots, and probably remained that way during the cover crop period of the autumn and winter months.

The number of abundant species in the bacterial-feeding nematode community was greater in the conventionally farmed plots than in the organic plots through most of the growing season ($P=0.03$ at Day 130) (Fig. 6(B)). That reflected the temporal predominance of individual opportunistic species in the organic plots in response to the incorporation of organic matter and the subsequent flush of bacteria (Fig. 4(A)). As we only recorded two species of both fungal-feeding (data not shown) and omnivore-predator nematodes (Fig. 6(D)), the numbers of abundant species were not different in the two farming systems.

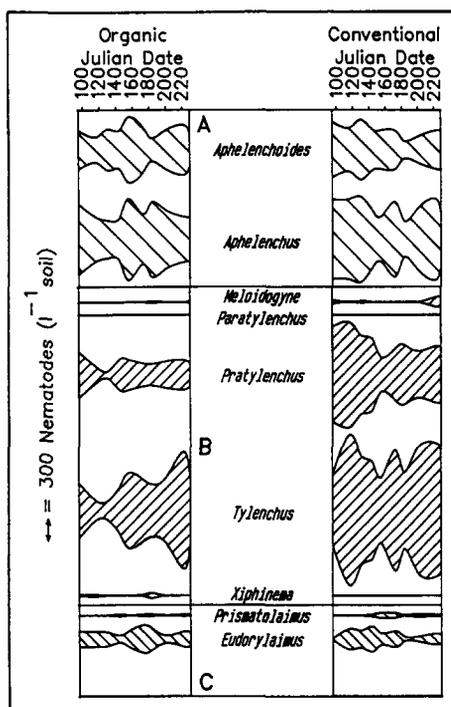


Fig. 5. Temporal abundance of individual taxa of fungal-feeding nematodes (A), plant-parasitic nematodes (B) and omnivore-predator nematodes (C) in tomato plots under organic and conventional farming systems. Data are averaged across four replicates and are not corrected for efficiency of the extraction method.

There also was no clear pattern of differences in numbers of abundant species in the plant-parasitic nematode community between the two farming systems (Fig. 6(C)).

After incorporation of vetch at the beginning of the growing season, Bongers' Maturity Index suggested a higher level of maturity, that is a trend towards persister (K-selected) species, across all nematode species and trophic groups in the conventional than in the organic farming system. Conversely, there was a preponderance of opportunistic colonizer species in the organic system (Fig. 7(A)). As with other indices, the data are strongly influenced by the diversity among the bacterial-feeding nematode species in the two farming systems (Fig. 7(B)). Actually, the maturity indices for the bacterial-feeding nematodes are based on only two maturity groups. Nematodes in the families Rhabditiidae (*Bursilla* sp., *Cruzinema* sp. and *Rhabditis* sp.) and Panagrolaimidae (*Panagrolaimus* sp.) predominated in the organic system (Fig. 4(A)). These nematodes

are all in Maturity Group 1, the most opportunistic colonizers (Bongers, 1990). In the conventional system, nematodes in the family Cephalobidae (*Acrobeloides* spp., *Acrobelus* sp., *Cephalobus* sp. and *Chiloplacus* sp.) were more abundant. These nematodes are all in Maturity Group 2 and are slightly less dynamic in their colonizing capabilities (Bongers, 1990).

There were no differences in Bongers' Maturity Index between farming systems for the fungal-feeding nematodes (data not shown), as both species present are in the same maturity group. Of the two omnivore-predator species, *Pristionchus* sp. is in Maturity Group 3 and *Eudorylaimus* sp. in Maturity Group 4. Bongers' Maturity Index was variable depending on whether one or both species were detected and on the number of replications of each farming system in which they occurred (Fig. 7(C)). Most plant-parasitic species are in Maturity Group 3. Bongers' Maturity Index data for plant parasites are not presented, as these nematodes are strongly influenced by host status of the current and previous crop, and application of the analysis is considered less appropriate (Bongers, 1990).

3.4. Biomass

The calculated absolute biomass of individual species of bacterial-feeding nematodes revealed a different pattern in their temporal predominance from that indicated by numerical abundance uncorrected for extraction efficiencies (Figs. 4(A) and 4(B)). *Bursilla labiata*, a small nematode abundant for much of the growing season in the organic farming system, had a maximum calculated biomass of 13.9 mg l⁻¹ soil on 21 June at mid-season, many times larger than that of any other bacterial-feeding nematode in either farming system (Figs. 4(A) and 4(B)). Larger nematodes, for which extraction efficiency is greater, were relatively less predominant when considered on a biomass basis.

Total biomass of the bacterial-feeding nematode community is illustrated in relation to approximate tomato crop phenology (Figs. 1(C) and 8(A)). The biomass differed slightly in trajectory from that of total numbers of individuals in the trophic group (Fig. 1(D)), reflecting differences in temporal predominance of different species in each farming system (Fig. 4(A)). Maximum biomass in both farming systems occurred at the 21 June sampling (868 DD) when it

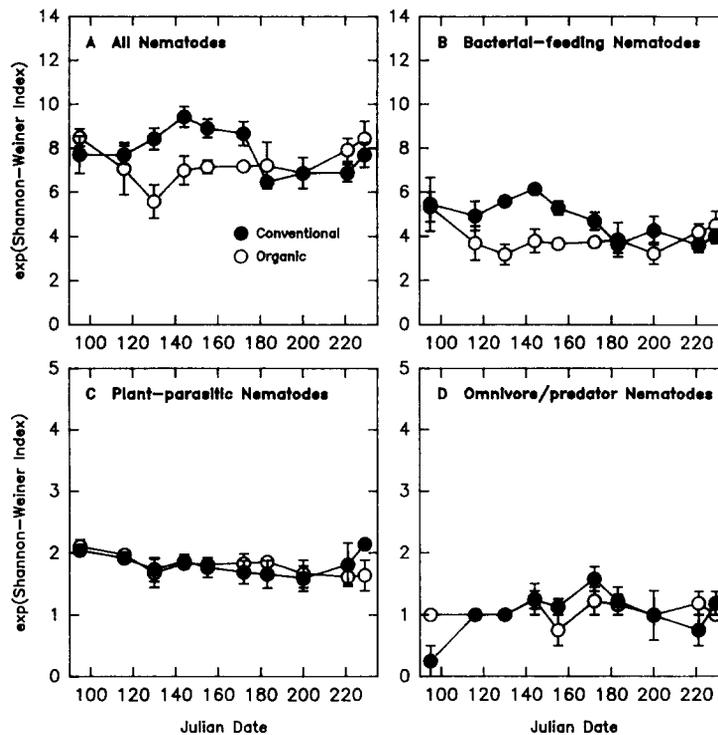


Fig. 6. Effective number of abundant nematodes, as indicated by the transformed Shannon–Weiner Index (Shannon and Weaver, 1949; Hill, 1973), of all nematodes and of the community in each of three trophic groups in tomato plots under organic and conventional farming systems. Data are means and standard errors across four replicates. Effective number of abundant nematodes for: (A) all nematodes; (B) bacterial-feeding nematodes; (C) plant-parasitic nematodes; (D) omnivore–predator nematodes.

was 3.25 times greater in the organic (17.4 mg l^{-1} soil) than in the conventional (5.4 mg l^{-1} soil) system. At that date, the total number of bacterial-feeding nematodes counted in the organic system was only 2.25 times greater than in the conventional system. Although nematode numbers and biomass were similar at the time of tomato planting in both farming systems, both measures had become significantly greater in the organic system by 10 May, and remained that way throughout the growing season.

Biomass per unit of MBC during the first half of the growing season increased in the organic farming system, indicating that food availability was not a limiting constraint during that period (Fig. 8(B)). After the mid-summer decline in MBC (Fig. 1(B)) there was a decline in biomass per unit of MBC. In the conventional farming system the biomass per unit of MBC remained relatively constant throughout the growing season.

4. Discussion

Although population densities of bacterial-feeding nematodes at the beginning of April (Day 95) were similar in the conventional and organic plots, consistent with our field inventory studies (Lanini et al., 1994; Scow et al., 1994), individual species did not increase opportunistically in the conventional system as in the organic system. In the conventional systems, the organic matter incorporated into the soil was crop residue of high carbon content. The manure and leguminous cover crops incorporated into the low-input and organic plots have lower C:N ratios than the crop residues. The complex, high C:N ratio, organic materials in the conventional plots probably select for fungal—rather than bacterial-dominated decomposition pathways (e.g. Beare et al., 1992). This may explain the greater numbers of fungal-feeding nematodes in those plots early in the growing season. Similar observations have been made in the spring in other conventional and

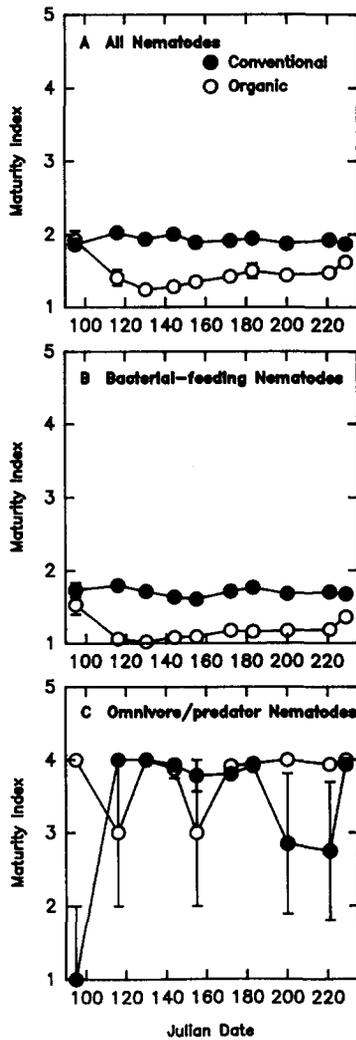


Fig. 7. Environmental disturbance, as indicated by Bongers' Maturity Index (Bongers, 1990), calculated for all nematodes (A) and for the bacterial-feeding (B) and omnivore–predator (C) nematode community in tomato plots under organic and conventional farming systems. Data are means and standard errors across four replicates.

organic farming system comparisons (Freckman and Ettema, 1993) and in differentiating between perennial and annual cropping systems (Neher and Campbell, 1994).

Predaceous and omnivorous nematodes, at least in the top 15 cm of soil, were probably below levels that would have any impact on regulation of populations of other nematodes. Predaceous nematodes are considered susceptible to environmental disturbance, as reflected by the placement of the species detected in

these studies in Maturity Groups 3 and 4 (Bongers, 1990). In a survey in Oregon, for example, predaceous nematodes were common in undisturbed hedgerows around agricultural fields, but were rare within the field (Jensen and Mulvey, 1968). They may be susceptible to herbicides and other pesticides applied to the conventionally farmed soil, and to the application of inorganic fertilizers (Wasilewska, 1989).

The abundance of each plant-parasitic nematode species is determined by the host status of each crop in the respective rotation, and the population survival and reproductive strategies of the individual species. Thus the detection of a species in soil samples from the organic or conventional tomato plots does not necessarily imply that tomatoes are a host for that species (Lanini et al., 1994). We are not surprised by the low number of plant-parasitic nematodes in the top 15 cm of soil. Many of these nematodes feed at or near root tips, which are usually below the upper layers of soil. *Xiphinema americanum* is reported to feed on corn (*Zea mays* L.) roots (Brodie et al., 1969), but host

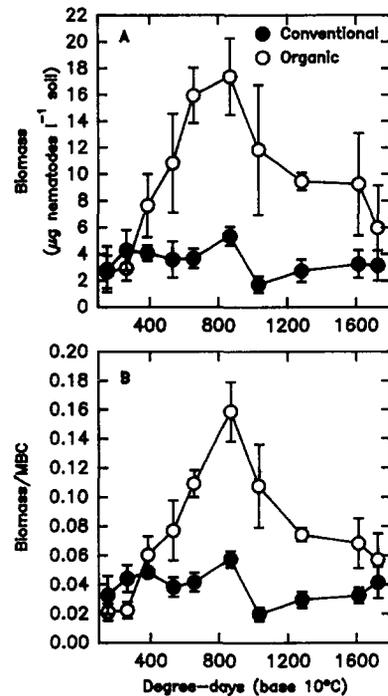


Fig. 8. Biomass (A), and biomass per unit of bacterial food substrate (B), of all species of bacterial-feeding nematodes in tomato plots under organic and conventional farming systems. Data are means and standard errors across four replicates.

range studies have not been done for the other crops in these farming systems. It is probably not hosted by tomato. *Pratylenchus thornei* is a migratory endoparasite for which oats (*Avena sativa* L.), vetch and corn are hosts (Larson, 1953, Van Gundy et al., 1974). Again, tomatoes are probably not hosts for this nematode, so it may be surviving within root pieces from previous crops. Although the tomato cultivars used in these rotations contain the Mi gene and are resistant to root-knot nematodes, the bean (*Phaseolus vulgaris* L.) varieties are good hosts (Omweaga et al., 1990). Corn is often reported as a host to populations of *Meloidogyne incognita* (e.g. Baldwin and Barker, 1970). Species of *Paratylenchus* usually have a wide host range, and that nematode is probably able to feed on several crops in the rotation although it does not appear to reach high levels. *Tylenchus davainei* may also be a fungal-feeder or an even broader generalist (Yeates et al., 1993); its host status on higher plants has not been tested. Interestingly, its dynamics are similar to those of the fungal-feeding species, *Aphelenchoides* sp. and *Aphelenchus avenae*.

Although the subject of ecological debate, the notion that diversity is an indicator of stability may provide some insights into the condition and resilience of component function in soil systems. The calculation of diversity indices and their transformations for all nematodes across all trophic groups is probably less useful than when there is some direct or subtle interaction among the species, as would be the case if the assemblage represented a true community. Soil nematodes represent a taxonomic, not an ecological, grouping and directly dependent relationships are absent among species in different trophic groups. Further, species in different trophic groups may not be spatially proximate; some aggregated around decomposing organic matter and others at root tips (Ferris, 1993). Possible linkages between trophic groups would be through the activities of predator and omnivore nematodes, but their numbers were very low in these studies. Transformed diversity indices within a trophic group are of greatest interest, as they reflect effective numbers of species at various levels of abundance and the degree of redundancy of common function in the system. They are more likely to be true indicators of stability within a feeding category or of a function than indices constructed from unrelated organisms across trophic and functional levels. Interestingly, at any point in time there was less

redundancy in common function among the bacterial-feeding nematodes of the organic farming system, perhaps suggesting that their impact on N-mineralization could be perturbed by small disturbances.

Bongers' Maturity Index applied to bacterial-feeding nematodes suggested that the abundance of individuals in Maturity Group 1 (families Rhabditidae, Panagrolaimidae, Diplogasteridae and others) may be indicators of a biologically active soil with enhanced rates of N-mineralization. These nematodes may have similar metabolic rates to species in the Cephalobidae (Ferris et al., 1995), but their population dynamics allow them to become more abundant in a shorter period of time. A large biomass of bacterial-feeding nematodes will mineralize more nitrogen than a smaller biomass with similar metabolic rates. We infer that at this field site, the 13.9 mg l⁻¹ soil of *Bursilla labiata* biomass, of a total bacterial-feeding nematode biomass of 17.4 mg l⁻¹ soil in the organic system, indicate that this nematode is the most significant contributor to N-mineralization. We conclude that correction for extraction efficiency and calculation of biomass are important components of the determination of relative contribution of various species.

We note that sampling at various times before, during and after the growing season provides very different pictures of the abundance and biomass of bacterial-feeding nematodes. In timing sampling to detect maximum abundance and biomass, it is important to recognize the probable lag period behind the increase of the bacterial food source that reflects the population dynamics of individual nematode species.

Clearly, bacterial-feeding nematodes are more abundant, represent greater biomass, and consume greater numbers of bacteria about 1 month after tomatoes are planted in the organic farming system than in the conventional farming system (Figs. 1(C), 1(D), 4(A), 4(B), 8(A) and 8(B)). Soil nitrate levels in the organic system throughout the growing season, and especially early, were low (Fig. 1(A)). They were never as great as in the conventional system, particularly at key periods of nitrogen demand during vegetative growth and fruit set (Fig. 1(C)). Plants in the organic system displayed symptoms of nitrogen deficiency early in the growing season (Scow et al., 1994). If bacterial-feeding nematodes are important contributors to N-mineralization, that contribution is minimal during the first month of the growing season but may

be more important during fruit set (Figs. 1(C), 1(D) and 8(A)). It seems desirable to increase their abundance and activity in N-mineralization early in the growing season in organic plots to meet the needs of young seedlings. That may require altering community structure by introducing actively feeding nematodes, or changing cultural operations to influence the abundance, biomass and activity of bacterial-feeding nematodes, early in the growing season.

One measure of constraints on development of bacterial-feeding nematode communities is the availability of their food. Bacterial abundance, as indicated by MBC, was greater in the organic than the conventional system throughout the growing season, despite a mid-season decline (Fig. 1(B); Gunapala and Scow, 1995). Biomass per unit of MBC during the first half of the growing season increased in the organic farming system (Fig. 8(B)). Apparently, bacterial abundance was not a limiting constraint to increase in nematode biomass during that period, although it may have become limiting after mid-season (Fig. 8(B)). After the mid-summer decline in MBC (Fig. 1(B)) there was a decline in biomass per unit of MBC. That suggested that the bacterial-feeding nematode community was then greater than the carrying capacity of the environment and declined correspondingly. Bacterial abundance may be the limiting factor in nematode biomass increase in the conventional system, however, although that is not of practical importance as nitrogen is supplied to the plants as inorganic fertilizer. The biomass per unit of MBC remained relatively constant throughout the growing season, suggesting that the two measures were in dynamic equilibrium and that food supply was a constraint in nematode population and biomass increase in that system. We conclude that bacterial abundance is not the factor that limits the number or biomass of bacterial-feeding nematodes present in the organic farming system at the time of tomato planting.

As metabolic rates of bacterial-feeding nematodes from this field site are at extremely low levels at the soil temperatures experienced during the winter months (Ferris et al., 1995), and cumulative physiological time increases slowly early in the growing season (Figs. 1(D) and 8(A)), it appears that an appropriate strategy may be to maximize nematode abundance at the end of the previous growing season. At that time their food abundance may be a limiting factor (Figs. 1(B) and 8(B)), although biological activity may also be limited

by abiotic factors such as cessation of irrigation prior to harvest. A manure application at termination of the previous summer crop in the organic farming system, followed by irrigation, may enhance bacterial abundance in the autumn and so increase nematode abundance. If overwinter survival is primarily mediated by abiotic (non density-dependent factors), a greater abundance of nematodes in the autumn should result in a greater abundance in the spring. That would enhance the potential contribution of bacterial-feeding nematodes to N-mineralization during a critical plant growth period in the first month of the next summer crop.

Under current practices, bacterial-feeding nematodes do not increase in the rhizosphere of the winter cover-crop because it is planted too late and/or sown and left to germinate with winter rain. Soil temperatures by that time are below a level conducive to rapid reproduction of the nematodes. We hypothesize that early (mid-September) germination of the cover crop, requiring an irrigation for the dry soil, would promote biological activity and nematode increase in the warm soils until about mid-October.

5. Conclusions

The abundance and biomass of individual species of bacterial-feeding nematodes varied through the tomato growing season. We infer that the contribution of the individual species to soil fertility through N-mineralization differed with their temporal dynamics. Species in Maturity Group 1 (Bongers, 1990) were most responsive to increase in their food source and, in particular, *Bursilla labiata* (family Rhabditidae) dominated the bacterial-feeding nematode community, both in abundance and biomass, for much of the growing season. We hypothesize that increasing the abundance, biomass and activity of Maturity Group 1 bacterial-feeding nematodes in the spring by organic matter incorporation at the end of the previous crop would reduce the observed nitrogen stress in organic tomatoes early in the growing season. We suggest that an abundance of Maturity Group 1 bacterial-feeding nematodes at the time of planting indicates a biologically active soil in which the nitrogen provided by incorporation of organic material will not remain bound in the microbial biomass but will be mineralized through the grazing activities of the nematodes. Differences in abundance

of fungal-feeding nematodes between conventional and organic plots suggest the decomposition of higher C:N ratio organic sources through fungal-dominated pathways in the conventional plots. The dynamics of the plant-parasitic nematode species reflected the crop sequences in rotations used in each system. Predaceous nematode populations were low in both farming systems and may have had little impact on other nematode populations in the top 15 cm of soil.

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