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Soil management to enhance bacterivore and fungivore nematode populations and their nitrogen mineralisation function

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Abstract

We tested the hypotheses that management of the soil food web in the fall would enhance grazing on bacteria and fungi by microbivorous nematodes in the spring, consequently increasing N availability in cover-crop driven organic and low-input farming systems. The food web was manipulated by irrigating the dry soil of late summer and/or providing carbon sources. By creating conditions conducive for biological activity, we increased the abundance of bacterivore and fungivore nematodes in the fall and the following spring. Greater biological activity in the soil enhanced concentrations of mineral N available to the subsequent summer tomato crop. Mineral N concentration in the spring was associated with abundance of bacterivore nematodes, and with the corresponding Enrichment Index (EI) provided by nematode community analysis. Because environmental conditions that favour increase of bacterivore nematodes probably also favour other microbial grazers, including protozoa, the abundance of bacterivore nematodes may be an indicator of overall grazing activity and N mineralisation rates from soil fauna. Decomposition pathways in the spring, inferred from nematode bioindicators, were dominated by bacteria in plots that had been irrigated the previous fall while fungi were more prevalent in those that had not. The responses of omnivore and predator nematodes to our treatments were not consistent and there was no evidence that regulation of opportunist species by predators would be enhanced by the management practices imposed.

Keywords: Decomposition; Management; Mineralisation; Nematodes; Soil food web; Succession

1. Introduction

In most agricultural systems of developed countries, N and other plant nutrients are supplied as mineral fertilisers prior to planting or early in the growing season. Since the needs of the crop must be met for the entire growing season, the amount applied exceeds plant requirements at the time of application. Excessive N may have adverse effects on plants and soil organisms or may be lost through leaching or denitrification (Poudel et al., 2001c; Joyce et al., 2002; Mosier et al., 2002). In agricultural systems (e.g. organic and low-input) that rely on incorporated crop residues, cover crops and composted manures for plant nutrients, the availability of N and other minerals at any point in time is a function of rates of decomposition and mineralisation, driven by soil microbes and mediated by other soil organisms (Laakso et al., 2000). In such systems, maintenance of adequate soil fertility at important crop growth stages may be a challenge and deficiencies can

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arise (Russell, 1957; Magdoff et al., 1997; Delgado et al., 2001; Poudel et al., 2001b; Weinert et al., 2002). For example, in a long-term sustainable agriculture farming systems (SAFS) project in Davis, CA (Temple et al., 1994; Poudel et al., 2001a), concentrations of mineral N in soils managed with organic and low-input farming practices were consistently lower than in soils managed with conventional practices, particularly during vegetative growth and fruit set of tomato (*Lycopersicon esculentum* L.), the highest value crop in the rotation. Plants in the organic system sometimes displayed symptoms of N deficiency early in the growing season (Scow et al., 1994; Ferris et al., 1996; Clark et al., 1999).

A primary function of microbial grazers in soil food webs is to enhance mineralisation of plant nutrients that are immobilised in the component organisms of detrital food webs (Anderson et al., 1981; Ingham et al., 1985; Hunt et al., 1987; Griffiths, 1994; Moore, 1994; Ferris et al., 1998; Chen and Ferris, 1999; Coleman and Hendrix, 2000). Hunt et al. (1987) estimated that bacterial grazers (protozoa and bacterivore nematodes) contributed 83% of the N mineralised by fauna, which was 64% of that mineralised by microbes. Their model suggests that fauna mineralise N at a rate equivalent to 14 times their biomass each year, whereas bacteria mineralise 0.6 and fungi 0.51 of their biomass N per year. In laboratory microcosm experiments, bacterivore nematodes enhanced N mineralisation by 1.2–5.8 ng N nematode^{-1} day^{-1} and fungivore nematodes by 1.8–3.3 ng N nematode^{-1} day^{-1} depending on the suitability of fungal hosts (Ferris et al., 1998; Chen and Ferris, 1999; Okada and Ferris, 2001).

These results, coupled with our field observations, fostered two primary hypotheses: enhanced N mineralisation rates in soil are associated with greater densities of microbial-feeding nematodes; and, population levels of bacterivore and fungivore nematodes become constrained by environmental conditions and resource availability. The inference from these hypotheses was that removing constraints to nematode population growth should enhance N mineralisation rates.

Recent studies on the use and management of cover crops in agricultural systems have been directed towards conservation of resources, improvement of soil quality, minimising pest effects, improving soil fertility in minimum input systems, and reducing weed competition in minimum tillage systems (Caamal-Maldonado et al., 2001; Delgado et al., 2001; Herrero et al., 2001; Ross et al., 2001; Shrestha et al., 2002). In the current study, we examine the effects of cover crops and irrigation on nematodes that are beneficial in soil mineral cycling. We report the results of field experiments, conducted over 3 years, to: (a) test the effect of late summer/fall cultural and cropping practices on abundance of bacterivore and fungivore nematodes; (b) determine abundance and activity of those nematodes the following spring; (c) determine the relationship between mineral N availability and nematode abundance, and coincidentally the utility of bacterivore and fungivore nematode populations as indicators of soil fertility; and (d) determine the effect of enhanced N availability through soil food web activity on growth and yield of transplanted tomatoes.

2. Materials and methods

2.1. Experimental site and design

The SAFS project is located on the Agronomy Farm of the University of California, Davis. The soils are classified as a Reiff loam (coarse-loamy, mixed, non-acid, thermic Mollic Xerofluvents) and a Yolo silt loam (fine-silty, mixed, non-acid, thermic Mollic Xerofluvents). Soil textural analysis is, on average, 35% sand, 46% silt, and 19% clay at 0–30 cm depth (Temple et al., 1994; Poudel et al., 2001a). Our experiments were located in a 3 ha companion area of the SAFS site where management strategies are tested before implementation in the main experiment. In each year, plots were either three or four beds wide and 10 m long, with a 2 m buffer between plots in the same row. Plots were arranged in randomised complete block designs with four replications. Border rows separated neighbouring treatments. Weeds in the plots were spot treated periodically with glyphosate herbicide. Plots were furrow-irrigated in accordance with the experimental design. In the spring of each year, following fall and winter management practices, tomatoes (cv. Brigade) were transplanted into each plot. No mineral fertiliser was applied and the plots were irrigated as needed during the summer growing season. Tomatoes were hand-harvested from two 3 m sections of each plot in August and weighed for yield determination.

2.2. Treatment details

The experiments were conducted over 3 years. Treatments changed slightly each year to address different yet related aspects of the objectives.

In Experiment 1 (1995–1996), treatments were designed to test the addition of organic C to increase soil microbial activity, to determine the effects on soil food web activity of cover crops planted either in the late summer or the late fall, and to determine the effects of adjusting soil moisture using irrigation. Experimental factors included (a) incorporation of a C source (barley straw at 4.5 t ha^{-1} on 17 August) (+O) versus no organic amendment (−O); (b) summer cover crop planted late August (+S), winter cover crop planted in November (+W), no cover crop (−S, −W); (c) irrigation sufficient to meet the needs of the summer cover crop (+I) versus no irrigation (−I) during the late summer and fall. The summer cover crop was a four seed mix: "Maximum Organic Builder", Lohse Mill. Inc., Artois, CA (40% cayuse oats, *Avena sativa*; 30% bell beans, *Vicia faba*; 20% magnus field peas, *Pisum arvense*; 10% common vetch, *Vicia sativa*). The winter cover crop was common vetch. Both summer and winter cover crops were allowed to grow until spring, which created substantial differences in biomass above ground (and probably below ground) among treatments. In an attempt to isolate the effects of the fall management and to avoid having them masked by different amounts of incorporated organic material, all cover-cropped plots were mowed in the spring and the aboveground growth was removed. To approximately equalise the organic source for the food web in each plot, a vetch/oats herbage mixture was distributed across all plots and incorporated 2 weeks prior to planting the tomato crop.

In Experiment 2 (1996–1997), the cover crop treatments were modified because, in the first experiment, the attempt to equalise material incorporated into each plot as fuel for the soil food web probably did not resolve differences in below-ground biomass. Also, in Experiment 1 there was some evidence of reduced N availability in the spring, from immobilisation due to excess C, in summer cover-cropped plots. Consequently, in 1996–1997, the summer cover crop was mowed and raked off during the first week of November, and all cover crop plots were sown with vetch for winter growth. Our intent was to provide uniform amounts and quality of organic material in the spring in all cover-cropped treatments. The treatments were designed to test the effects of summer and winter cover crops, and the effects of irrigation. Specific factors and levels were: (a) summer cover crop planted mid-September (+S); (b) winter cover crop planted mid-November (+W), no summer cover crop (−S), no winter cover crop (−W) (the summer and winter cover crops were the same as those used in Experiment 1); and (c) irrigation (+I) versus no irrigation (−I) in the late summer and fall.

In Experiment 3 (1997–1998), the primary focus was to test the effects of varying the frequency of irrigation during the warm soil conditions of late summer/early fall on nematode population levels and community structure, and on N mineralisation activity in the spring. The experiment was established following a safflower (*Carthamus tinctorius*) crop that did not receive fertiliser and which should have depleted available soil N. The treatments tested the effects of a summer cover crop followed by a winter cover crop (+S+W), a summer cover crop continued through the winter (+S + S), a winter cover crop alone (−S + W), or no cover crop (−S−W). Cover crops were the same as for previous years. Superimposed on these treatments were levels (frequency) of fall irrigation: no irrigation (−I) (not used with the summer cover crop treatments), irrigation sufficient to meet needs of the summer cover crop (+I), and irrigation every 2 weeks (+I2), approximately double the frequency of the +I treatment.

2.3. Soil sampling and data collection

Soil samples were composites of 16 cores (2.5 cm diameter) per plot taken to a depth of 30 cm mid-way between plants in the middle plant row(s), or distributed through the central region of each plot when plants were absent. Samples were collected in plastic bags and immediately placed in an insulated box for transportation to the laboratory. Soil cores were manually disintegrated; the soil was passed through a coarse sieve (5 mm aperture), hand-mixed and subsampled.

In Experiment 1, samples for soil N (NO_3^- and NH_4^+) analysis (Bundy and Meisinger, 1994) were taken weekly for 7 weeks, then at 11 and 14 weeks, after organic matter incorporation. Samples for basal soil respiration and substrate-induced respiration

(Gunapala et al., 1998) were processed at 1, 4 and 7 weeks after organic matter incorporation in the spring. Samples for phospholipid fatty acid (PLFA) analysis of the soil microbial community (Bossio and Scow, 1998) were taken in October, 1 week prior to establishing the winter cover crop in November, then 3 weeks before and 1 week after cover crop incorporation in the spring. Samples for nematode faunal analysis (Ferris et al., 2001) were taken on four occasions during the late summer, fall and winter, starting with establishment of the experiment in late August, and at weeks 1, 4, 7, 11, 14 and 18 after cover crop incorporation in the spring.

In subsequent experiments, nematode faunal analyses and soil N determinations were conducted less frequently than during the first year. In year 2, plots were sampled in early spring, 6 weeks prior to cover crop incorporation, at incorporation, and 3 weeks after incorporation. In year 3, plots were sampled in September to establish baseline levels of populations, in the spring, and then 4 weeks after cover crop incorporation and at the end of the tomato-growing season.

2.4. Analytical techniques

2.4.1. Nematodes

Soil samples were hand-mixed and 350 ml subsamples processed by elutriation and centrifugation (Byrd et al., 1976; Barker, 1985). All nematodes in a sample were counted, then the sample was centrifuged, the supernatant removed and the nematodes suspended in a small volume of water. That volume was spread on a 50 mm × 75 mm microscope slide and covered with a 45 mm × 50 mm coverslip. The first 200 nematodes encountered in the sample were identified to genus, or species where possible, at 100× or 400× magnification. Relative abundance of each taxon was calculated from the proportion of that taxon among the identified nematodes. Abundance was expressed as the number of nematodes in each taxon l^{-1} soil and was not corrected for extraction efficiency.

2.4.2. Soil nitrogen

Soil NO_3^- and NH_4^+ status was determined by KCl extraction. Forty ml of 2 M KCl was pipetted into conical centrifuge tubes. Tubes with KCl solution were capped and weighed. About 10 g soil was placed in each tube and tubes were weighed again to determine the weight of soil. Tubes were shaken for 1 h to displace bound NH_4^+, centrifuged, and 12 ml of the supernatant was pipetted into a scintillation vial and the vial capped (Bundy and Meisinger, 1994). The University of California's Division of Agriculture and Natural Resources Analytical Laboratory conducted nitrogen assays. Soil moisture content of each sample was determined by weight loss of a subsample after drying for 48 h at 80 °C. The soil moisture data were used to adjust the N amounts for each sample to μg N g^{-1} oven-dried soil.

2.4.3. PLFA

Subsamples of 150 ml soil from each sample were frozen for PLFA analysis. Samples from selected plots were processed for assessment of fungal and bacterial fatty acid markers. 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 ng g^{-1} dry soil. Total weight of PLFAs was used as a measure of total microbial biomass. 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 (Frostegård and Bååth, 1996; Bossio and Scow, 1998; Mikola and Setala, 1998).

2.4.4. Soil respiration

Soil respiration was determined by amending soil subsamples with either nutrient broth (basal respiration) or nutrient broth plus glucose (substrate-induced respiration). The difference in head-space CO_2 between the subsamples was determined by infrared gas analyser after 2 h of incubation (Smith et al., 1985; Gunapala et al., 1998). This technique provides a measure of the activity of the soil microbial biomass.

2.4.5. Nematode faunal analyses

Nematode faunal analyses were performed as indicators of food web structure, status, functionality, and resource availability (Ferris et al., 2001; Ferris and Matute, 2003). Two indices are calculated based on abundance of nematodes, weighted relative to their indicator importance ($k_{e,b,s}$), in guilds representing enrichment, basal and structure components of the

food web. The Enrichment Index (EI) is calculated as $100(e/(e+b))$, where e is the abundance of individuals in guilds in the enrichment component weighted by their respective k_e values and b is the abundance of individuals in the basal component weighted by their k_b values. The EI provides an indicator of resources available to the soil food web and the response of primary decomposers to those resources. The Structure Index (SI) is calculated as $SI = 100(s/(s+b))$, where s is the abundance of individuals in the structure component weighted by their k_s values. A higher SI value results from the presence of omnivore and predator nematodes; it suggests a food web with more trophic linkages. The two indices allow graphic representation of the condition of the food web (Ferris et al., 2001).

Decomposition of organic matter may proceed through different pathways or channels in the soil food web. At one extreme, materials of high cellulose and lignin content and high C-to-N ratio are decomposed through fungal-dominated "slow" pathways; at the other extreme, moist, N-rich tissues are decomposed through bacterial-dominated "fast" pathways (Coleman et al., 1983; Wardle and Yeates, 1993; Moore, 1994). The Channel Index (CI) is calculated as $100(k_{Fu_2}Fu_2)/(k_{Ba_1}Ba_1 + k_{Fu_2}Fu_2)$ where the coefficients are the enrichment weightings for the Fu_2 fungivore guild and Ba_1 enrichment-opportunist bacterivore guild. A high CI indicates that fungal decomposition pathways predominate while a low CI suggests that bacterial decomposition are more important (Ferris et al., 2001).

2.4.6. Statistical analyses

To test the hypothesis that populations of target nematode taxa could be increased by soil food web management in the fall (hypothesis 1), we calculated the change in nematode populations in Experiment 1 between the initial sampling in August or September (Pi) and that in November (Pf) as Pf/Pi. The ratios measured the effect on the nematode community of soil food web enrichment and removal of environmental constraints. The enrichment effect was determined for nematode taxa grouped as functional guilds—Ba_1 enrichment-opportunist bacterivores in the cp1 class, $Ba_{2,3}$ general-opportunist bacterivores in the cp2 and 3 classes, Fu_2 enrichment and general-opportunist fungivores in the cp2 class, and $Om_{3,5}$ omnivores in cp classes 3–5 (Table 2) (Bongers, 1990; Bongers and Bongers, 1998; Ferris et al., 2001).

To test the hypothesis that nematode populations will be at high levels in the spring following conducive fall management practices (hypothesis 2), each year we subjected spring (April) population densities of the same functional guilds to analysis of variance and means separation.

Each year, the experimental designs for these studies were incomplete factorials with some combinations of factors omitted because they were biologically or agronomically impractical. That restricted the statistical analysis to testing differences between treatment combinations and examination of main effects. Since, for example, a summer cover crop could only be grown with irrigation, the interaction of summer cover crop and irrigation could not be tested. Data on crop yields, soil N, nematode abundance and nematode functional guild indices were subjected to analysis of variance according to the GLM procedure of SAS version 6.12 (SAS Institute Inc., Cary, NC). Means were separated by Duncan's Multiple Range Test with $\log_{10}$ transformation where necessary to stabilise variance. For convenience of data handling, regression analyses of crop yields with soil N levels and of soil N levels with nematode index values were performed using the data analysis tools of Microsoft Excel 97.

3. Results

3.1. Nematode faunal structure

During Experiment 1, nematodes were identified in 320 soil samples (10 treatments, four replications and eight sampling dates). The nematodes were representatives of 41 genera (Table 1). Of the six genera in the Ba_1 guild, *Cruznema*, *Mesorhabditis* and *Panagrolaimus* predominated over the course of the experiment. *Cephalobus*, *Chiloplacus* and *Acrobeloides* were predominant among the nine genera in the general-opportunist $Ba_{2,3}$ guilds while *Aphelenchus* and *Aphelenchoides* were the most prevalent of the four genera of the Fu_2 fungivore guild. *Eudorylaimus*, *Aporcelaimus* and *Discolaimus* predominated among the eight genera designated as omnivores; nematodes designated as predators were found infrequently. Herbivore guilds ($H_{2,5}$) were predominantly

Table 1
Mean abundance per (l^{-1} of soil) of each identified taxon across all treatments, replications and sampling dates for Experiment 1

Genus	Guild	Mean	S.D.	Maximum
Cruznema	Ba_1	2295.8	2718.5	13074.7
Mesorhabditis	Ba_1	1607.2	2533.8	16090.9
Panagrolaimus	Ba_1	962.7	1255.9	10443.4
Rhabditis	Ba_1	202.1	394.4	2887.5
Monhystera	Ba_1	18.0	65.7	438.3
Diploscapter	Ba_1	14.2	175.9	3093.4
Cephalobus	Ba_2	1822.5	2078.5	18626.0
Chiloplacus	Ba_2	548.2	711.5	6328.1
Acrobeloides	Ba_2	451.9	962.6	12031.3
Heterocephalobus	Ba_2	144.8	255.9	1518.5
Acrobeles	Ba_2	56.6	145.3	1087.6
Cervidellus	Ba_2	13.3	46.3	320.8
Wilsonema	Ba_2	9.1	40.6	350.9
Eucephalobus	Ba_2	7.6	40.0	516.0
Plectus	Ba_2	3.0	39.3	687.5
Prismatolaimus	Ba_3	170.0	288.8	2105.3
Seinura	Ca_2	12.7	67.0	629.3
Aphelenchus	Fu_2	5181.4	3986.2	21848.5
Aphelenchoides	Fu_2	1474.5	1758.6	13666.8
Ditylenchus	Fu_2	234.0	368.1	2583.4
Aprutides	Fu_2	1.7	16.1	207.7
Eudorylaimus	Om_4	325.5	477.5	2500.0
Tylencholaimus	Om_4	9.6	57.1	638.6
Dorylaimus	Om_4	5.7	31.8	320.8
Mononchus	Om_4	0.3	6.2	111.1
Aporcelaimus	Om_5	106.6	205.9	1582.0
Discolaimus	Om_5	30.2	100.5	905.7
Mesodorylaimus	Om_5	0.7	7.8	108.3
Prodorylaimus	Om_5	0.2	4.1	73.7
Tylenchus	H_2	1893.0	1491.5	7952.8
Pratylenchus	H_2	946.3	1047.0	5670.0
Filenchus	H_2	56.3	231.9	2272.6
Paratylenchus	H_2	16.7	143.0	1955.9
Psilenchus	H_2	0.1	1.7	30.6
Tylenchorhynchus	H_3	1149.6	1192.1	6278.3
Meloidogyne	H_3	245.8	579.3	3881.7
Helicotylenchus	H_3	2.7	24.7	357.1
Rotylenchus	H_3	0.2	4.0	71.3
Trichodorus	H_4	0.6	7.2	101.4
Xiphinema	H_5	6.5	44.6	435.0
Longidorus	H_5	0.4	6.3	112.5

Data are based on 320 observations for each taxon. In each case, the lowest number in a sample was zero. Functional guild classifications are represented by designated feeding habit (b: bacterivore, f: fungivore, c: predator (carnivore), o: omnivore, h: plant feeder (herbivore). Suffix numbers are cp values (Bongers, 1990) for the taxa).

represented by *Tylenchus*, *Tylenchorhynchus*, *Pratylenchus* and *Meloidogyne* juveniles. In all trophic categories, taxa in lower cp classes were generally more abundant than those in higher cp classes. The same taxa were represented in the soil samples taken during Experiments 2 and 3 (data not shown).

3.2. Nematode response to fall management

We determined the change in the population levels of various functional groups between 30 August 1995 (Pi) and 9 November 1995 (Pf) in Experiment 1. Since winter cover crops were not established during this period, data for those plots were combined with data for plots that were never cover-cropped.

Enrichment-opportunist (Ba_1) nematodes responded positively ($Pf/Pi > 1$) to the main effect of barley straw addition (+O) during the August to November period but did not respond to the main effects of a summer cover crop or irrigation (Table 2). Abundance of general-opportunist bacterivore ($Ba_{2,3}$) nematodes increased with the main effects of barley straw, irrigation, and a summer cover crop. Fungivore (Fu_2) and herbivore ($H_{2,5}$) guilds increased in abundance with irrigation. The presence of a summer cover crop increased herbivore nematodes.

Of the individual treatment combinations, the greatest augmentative effect on the Ba_1 guild was through the combination of straw, a summer cover crop and irrigation. The Ba_1 guild was least abundant in a treatment without straw addition or irrigation. The $Ba_{2,3}$ guilds increased least during the fall in plots that were not irrigated and had no cover crop. The enrichment effect on the Fu_2 guild was greatest in treatments that were irrigated and least in those not irrigated, whether or not straw was added or a cover crop grown. Herbivore nematodes increased most when there was an irrigated summer cover crop but their numbers were relatively unchanged ($Pf/Pi \pm 1$) when soil was irrigated but cover crops were not grown. They declined in the absence of an irrigated cover crop ($Pf/Pi < 1$). Omnivore nematodes occurred in low numbers and were very patchy in their distribution; there was no significant enrichment effect of any treatment on the $Om_{3,5}$ guilds.

3.3. Nematode abundance in the spring

Each year, 1 month after cover crop incorporation in the spring, bacterivore nematodes were more abundant, or trended that way, in plots that had either a summer or winter cover crop than in plots without

Table 2
Experiment 1

Treatment[a]	Enrichment Effect (Pf/Pi)[b]					Ci[c]	Ei[c]	SI[c]	Cum-N[d]	Yield (t ha^{-1})
	Ba_1	$Ba_{2,3}$	Fu_2	$Om_{3,5}$	$H_{2,5}$					
− O − C − I	0.39 b	0.74 c	0.47 c	2.33	0.54 b	27 a	69 e	10 ab	74 ab	76 ab
+ O − C − I	1.44 ab	0.81 c	0.74 bc	1.21	0.51 b	21 ab	73 cde	10 ab	62 abc	73 ab
− O − C + I	1.24 ab	1.58 ab	1.29 a	4.49	1.01 a	29 a	70 de	6 b	81 ab	80 a
+ O − C + I	1.40 ab	2.37 a	1.34 a	0.94	1.10 a	20 abc	76 cde	12 ab	87 a	83 a
− O + S + I	0.68 b	1.21 bc	1.17 ab	13.65	1.51 a	12 bcd	80 abc	17 ab	72 ab	73 ab
+ O + S + I	3.95 a	2.97 a	1.25 a	11.64	1.63 a	9 d	86 a	24 a	82 ab	78 ab
− O + W − I						18 bcd	75 cde	12 ab	58 bc	78 ab
+ O + W − I						15 bcd	79 abcd	11 ab	42 c	65 b
− O + W + I						11 cd	84 ab	12 ab	80 ab	87 a
+ O + W + I						17 bcd	78 abcde	5 b	83 ab	83 a
Main effect of barley straw addition										
−O	0.69 n	1.10 n	0.84	4.31	0.85	19	76	11	73	78
+O	1.74 m	1.62 m	1.05	1.72	0.88	16	79	12	71	76
Main effect of cover crop										
−C	1.00	1.22 y	0.88	1.86	0.74 y	24 x	72 y	10 y	76	78
+S	1.63	1.89 x	1.21	12.60	1.57 x	11 y	83 x	21 x	77	76
+W						15 y	79 x	10 y	66	78
Main effect of fall irrigation										
−I	0.75	0.77 q	0.59 q	1.68	0.53 q	20	74 q	11	59 q	72 q
+I	1.42	1.92 p	1.28 p	3.76	1.20 p	16	79 p	13	81 p	81 p

Nematode community analyses and soil mineral N concentrations in the spring, and yields of the summer tomato crop, following fall and winter management practices, 1995–1996.

[a] +O: incorporation of barley straw at 4.5 t ha^{-1}, −C: no late summer (fall) or winter cover crop, +S: late summer (fall) cover crop, +W: winter cover crop, +I: fall irrigation.

[b] Enrichment effect calculations are based on November 9 (Pf) and August 30 (Pi) population levels.

[c] Channel, Enrichment and Structure indices.

[d] Cumulative soil mineral N concentration over six sampling dates in April and May 1996. For each data block (combined treatment means or main effects of individual factors), numbers in a column not followed by a letter, or followed by the same letter, do not differ significantly ($P < 0.05$) according to Duncan's Multiple Range Test.

a cover crop (Fig. 1). Lowest numbers of bacterivores in the spring occurred in plots with the agronomically unlikely treatment of fall irrigation without a cover crop (Fig. 1A and B). Fungivore nematodes responded variably to the cover crop and irrigation treatments in different years. Either they were more abundant in straw-amended plots without cover crops or fall irrigation (Fig. 1A) or they were positively influenced by cover crops (Fig. 1B) or there was no measurable response to the treatments (Fig. 1C). As a trend, plots irrigated twice during the fall generally had greater numbers of bacterivore nematodes; those cover-cropped during the winter months had greater numbers than those not cover-cropped (Fig. 1C). Populations of plant-feeding nematodes were increased by growth of an irrigated summer cover crop (data not shown). Omnivores were variable and in rather low abundance in all treatments. (Table 2).

3.4. Faunal profile analyses

Soil food web enrichment in the spring, as indicated by the EI, was variously influenced by the fall and winter treatments. In Experiment 1 (Table 2), the food web was most enriched when a summer or winter cover crop was grown and there was fall irrigation (markers "1", Fig. 2). For simplicity of display, the straw and non-straw treatment pairs were averaged and treatments that received both cover crops and irrigation were averaged. The food web was less enriched when there was no cover crop, regardless of fall irrigation (Table 2; markers "2", Fig. 2). Across all treatments,

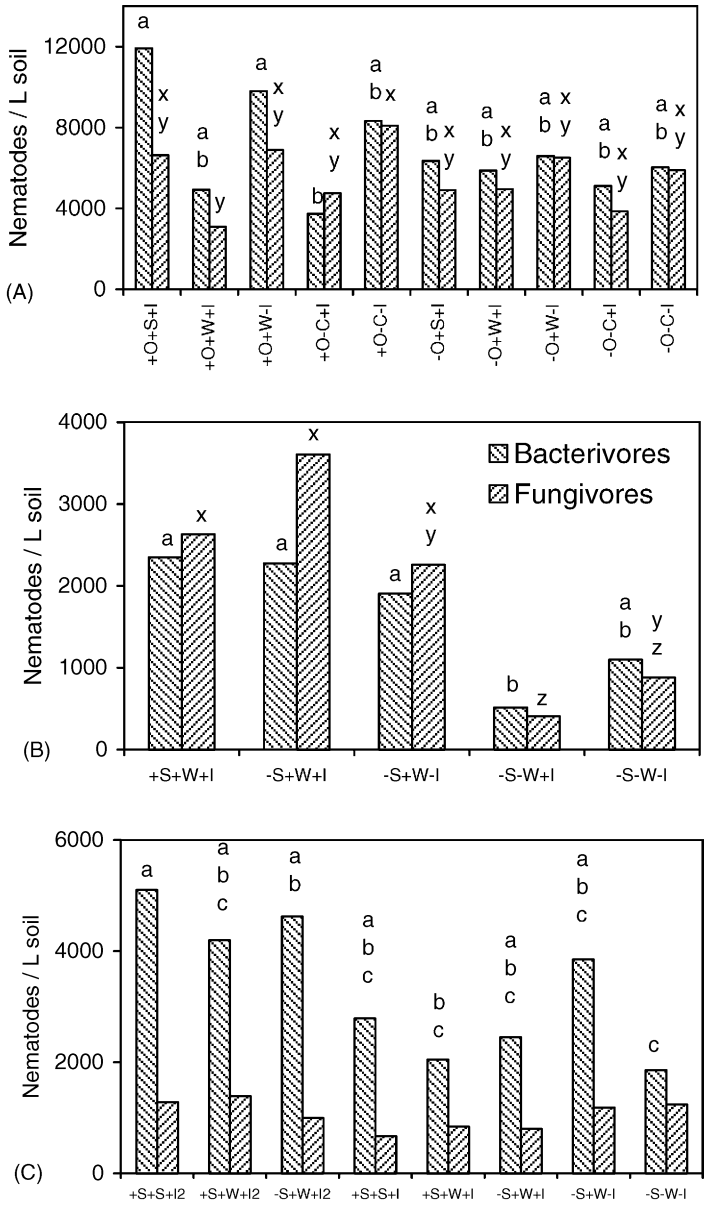

Fig. 1. Abundance of bacterivore and fungivore nematodes in the spring following irrigation and cover crop treatments in the fall and winter. (A) Experiment 1 (1995/1996). (B) Experiment 2 (1996/1997). (C) Experiment 3 (1997/1998).

the main effects of summer cover crop and irrigation significantly increased the EI over the no cover crop and non-irrigated treatments, respectively (Table 2).

There were no differences in the EI in the spring among treatments in Experiment 2 (Table 3), however, faunal analysis suggested that food web enrichment was greatest in those treatments with either summer or winter cover crop, and irrigated the previous fall (markers “3”, Fig. 2). The food web was less enriched when there was no irrigation to activate the organisms during the conducive conditions of the late summer (markers “4”, Fig. 2), and least enriched when no cover

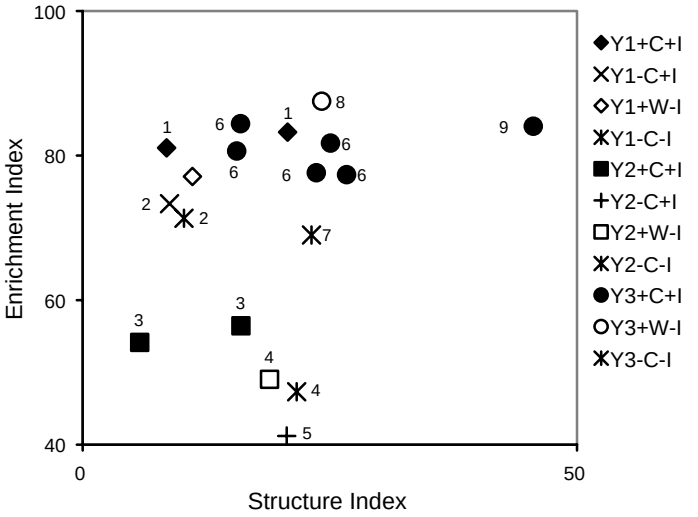

Fig. 2. Faunal profiles in various treatment combinations of cover crop and fall irrigation experiments. The Enrichment Index and Structure Index of various treatments is portrayed at the time of planting of the summer tomato crop in years 1, 2 and 3. Profiles mapped at higher positions on the graph represent a more enriched condition of the food web, while those mapped further right indicate a more structured food web. Treatment codes: Y1, Y2, Y3 = years (experiments) 1, 2, 3; +C = plots in which either summer or winter cover crops, or both, were grown and irrigation was supplied; −C = plots in which there was no cover crop; +W = a winter cover crop grown with seasonal rain and no irrigation; +I = fall irrigation supplied; −I = no fall irrigation. Numbers associated with markers are referred to in the text.

crop was grown (marker “5”, Fig. 2). In Experiment 3, the EI was affected positively by growth of a cover crop during the winter but there was little additional benefit derived from a summer cover crop. Despite the increase in total bacterivores, there was no effect of fall irrigation frequency on the EI where a cover crop had been grown (Table 4). Initial soil profile analysis in Experiment 3 (data not shown) indicated that the food web of the site was already rather enriched prior to application of the treatments. To simplify portrayal of the faunal analysis, data were averaged for similar cover crop treatments across the two irrigation regimes. Faunal analysis suggested that the cover crops enhanced enrichment (markers “6”, Fig. 2) over no cover crop (marker “7”, Fig. 2) and generally with one obvious exception (marker “8”, Fig. 2), irrigation in the fall resulted in greater enrichment.

There were no differences across fall management treatments in the magnitude of the CI of the food web in the spring in Experiment 2 (Table 3) but it was greatest in plots that did not have a cover crop in Experiment 1. The main effect of cover crop absence increased the CI over the cover-cropped treatments in both Experiment 1 (Table 2) and Experiment 3 (Table 4).

In Experiment 1, the food web SI was greatest in irrigated plots that had both summer and winter cover crops and least in plots that received fall irrigation and only a winter cover crop. The main effect elevating the SI was the irrigated summer cover crop (Table 2). While there were no treatment effects on the SI in Experiment 2, the index was greater in a treatment with highest irrigation frequency and plant growth throughout the fall and winter than in a similar treatment with less frequent irrigation in Experiment 3 (Table 4; marker “9”, Fig. 2). The total biomass of nematodes in enrichment indicator guilds in treatments receiving irrigation every 2 weeks was approximately double that in the equivalent cover crop treatments with less frequent irrigation (data not shown).

3.5. Phospholipid fatty acids

The total amount of PLFAs is an indicator of the mass of microbial cell membranes, a measure of total microbial biomass (Bossio and Scow, 1998). In

Table 3
Experiment 2

Treatment[a]	Ci[b]	Ei[b]	SI[b]	9 May N[c]	Yield (t ha^{-1})
− S − W − I	64	47	22	16 b	94 b
− S − W + I	76	41	21	15 b	94 b
− S + W − I	66	49	19	22 b	92 b
− S + W + I	59	54	6	35 a	110 a
+S + W + I	50	56	16	37 a	108 a
Main effect of late summer (fall) cover crop					
−S	66	47	18	21 y	96 y
+S	50	56	16	37 x	108 x
Main effect of winter cover crop					
−W	68	45	21	16 q	94 q
+W	58	53	14	31 p	103 p
Main effect of fall irrigation					
−I	65	48	21	18 n	94 n
+I	61	51	14	19 m	103 m

Nematode community analyses and soil mineral N concentrations in the spring, and yields of the summer tomato crop, following fall and winter management practices, 1996–1997.

[a] +S: late summer (fall) cover crop, +W: winter cover crop, +I: fall irrigation.

[b] Channel, Enrichment and Structure indices (measured May 9).

[c] Soil mineral N concentration measured on 9 May 1997. For each data block (combined treatment means or main effects of individual factors), numbers in a column not followed by a letter, or followed by the same letter, do not differ significantly ($P < 0.05$) according to Duncan's Multiple Range Test.

Table 4
Experiment 3

Treatment[a]	Ci[b]	Ei[b]	SI[b]	20 May N[c]	Yield (t ha^{-1})
− S − W − I	26 a	69 b	38 ab	7 c	40 ab
− S + W − I	10 b	87 a	36 ab	12 b	49 a
− S + W + I	13 b	78 ab	37 ab	11 b	43 ab
− S + W + I2	9 b	84 a	26 b	17 a	43 ab
+S + W + I	16 b	77 ab	41 ab	3 d	31 b
+S + W + I2	13 b	84 a	61 a	6 cd	40 ab
+S + S + I	10 b	81 a	25 b	5 cd	34 b
+S + S + I2	11 b	82 a	41 ab	5 cd	29 b
Main effect of late summer (fall) cover crop					
−S	12	81	22	12 x	45 x
+S	14	81	28	5 y	34 y
Main effect of winter cover crop					
−W	26 p	69 q	23	7 q	40
+W	12 q	83 p	27	10 p	43
+S	11 q	81 p	20	5 q	31
Main effect of fall irrigation					
−I	16	81	24	11 m	47 m
+I	13	79	22	7 n	36 n
+I2	11	83	29	9 m	38 n

Nematode community analyses and soil mineral N concentrations in the spring, and yields of the summer tomato crop, following fall and winter management practices, 1997–1998.

[a] +S: late summer (fall) cover crop, +W: winter cover crop, +I: fall irrigation as needed, +I2: fall irrigation every 2 weeks.

[b] Channel, Enrichment and Structure indices.

[c] Soil mineral N concentration measured on 20 May 1998. For each data block (combined treatment means or main effects of individual factors), numbers in a column not followed by a letter, or followed by the same letter, do not differ significantly ($P < 0.05$) according to Duncan's Multiple Range Test.

Experiment 1, amounts of total PLFA in the irrigated +S and −S plots were similar, but were greater than those in the non-irrigated plots, both in October and November (Fig. 3A). Non-irrigated −S or −W plots had consistently lower total values during the fall and spring. Interestingly, total PLFA value in the +S treatment in April was less than in the non-irrigated +W treatment. That difference did not correspond with any of the nematode indices. However, available mineral N concentrations were greatest in treatments with smallest total PLFA levels in April (compare N levels of −O + S + I and +O + S + I with −O + W − I and +O + W − I in Table 2). Data in Fig. 3A for October and November were pooled across treatments destined to become +W and −W because the sampling period was before the winter cover crop was established.

There were few differences among the ratios of PLFA markers of bacterial and fungal activity for the various treatments in October and November. By April, those treatments that had not received a cover crop, or had not been irrigated the previous fall, had higher fungal-to-bacterial PLFA ratios (data not shown).

3.6. Soil respiration

In Experiment 1, we used basal soil respiration, i.e. not induced by substrate addition, averaged over three sampling dates in April and May as a measure of spring microbial activity in the soils (Fig. 3B). Differences between treatments were not significant.

3.7. Mineral nitrogen

In Experiment 1, the main effect of fall irrigation significantly enhanced soil mineral N in the spring.

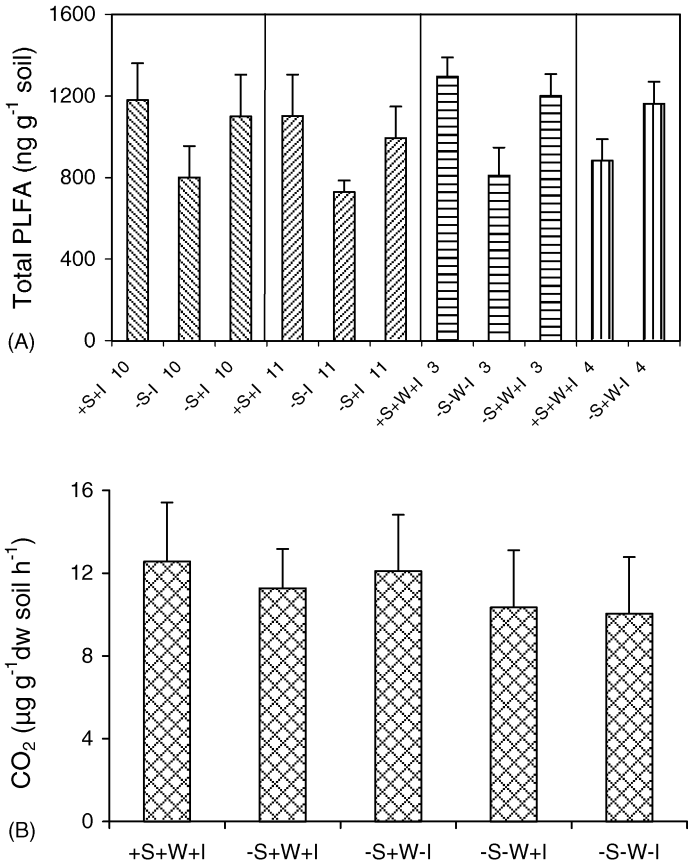

Fig. 3. Structure and activity of the soil food web. (A) Total phospholipid fatty acids, an indicator of microbial biomass extracted from samples taken from selected treatments during and after application of fall and winter management practices (year 1, 1995/1996). +S or −S = presence or absence of a summer cover crop; +W or −W = presence or absence of a winter cover crop; +I or −I = fall irrigation supplied or not supplied; 10, 11, 3, 4 = month of sampling—October, November, March or April. Some of the plots included in the averages for months 10 and 11 received a winter cover crop (+W) planted in late November. (B) Basal soil respiration averaged over three sampling dates in April and May, 1996 (year 1) as an indicator of soil microbial activity.

Mineral N concentrations were particularly low when a winter cover crop was grown without irrigation during the previous fall (Table 2). In Experiment 2, soil mineral N in the spring was greatest in plots that received winter cover crops and fall irrigation the previous year (Table 3). In Experiment 3, there was significantly more N in the spring in treatments with a winter cover crop that did not follow a summer cover than in those with an irrigated summer cover crop (Table 4).

In Experiment 1, there were no apparent relationships between abundance of any nematode trophic group and mineral N measured on the same date. However, a lag effect of the EI on mineral N was evidenced by a strong relationship between N on 28 May and EI on 16 May ($r^2 = 0.81$, $P < 0.01$) (Fig. 4B). The relationship between EI on 28 May and N on other dates was much weaker ($r^2 = 0.16$ with N on 6 May and 0.21 on 13 May). Mineral N concentration in May also was related positively to the EI in Experiment 2 ($r^2 = 0.87$, $P < 0.05$, Fig. 5B).

In both Experiments 1 and 2, there were strong negative relationships between the CI and available mineral N in May ($r^2 = 0.54$, $P < 0.05$; Fig. 4C and $r^2 = 0.76$, $P < 0.05$; Fig. 5C).

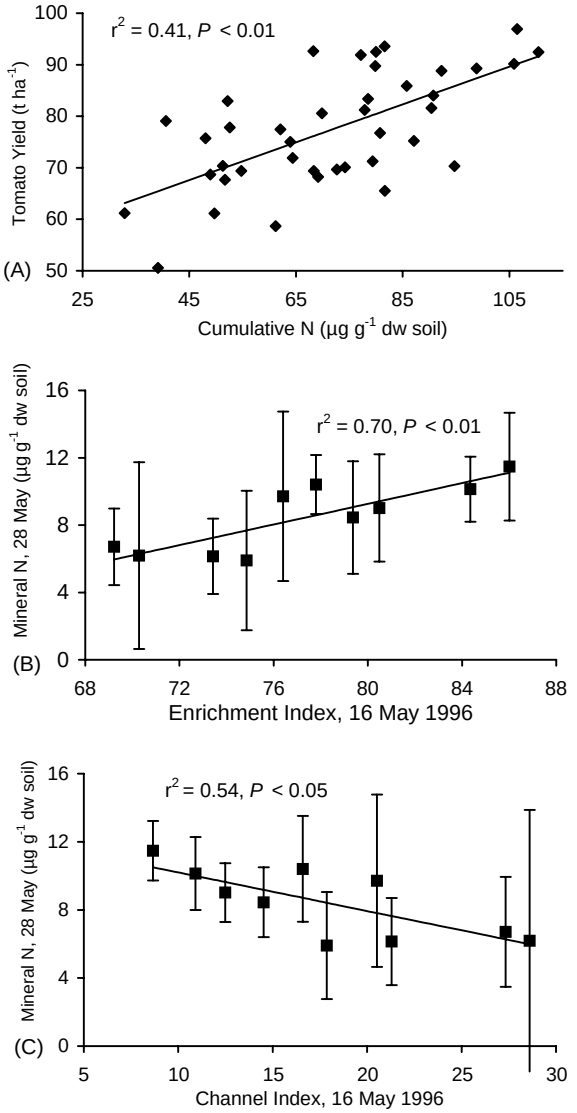

Fig. 4. Crop yield and spring soil mineral N concentrations in relation to indices derived from nematode faunal analysis in the spring in Experiment 1 (1995/1996). (A) Tomato yield in August 1996, in relation to cumulative soil N measurements over five sampling dates in April and May, prior to planting (year 1); $y = 22.8 + 0.164x$. (B) and (C) Soil N concentrations on 28 May 1996 in relation to indices derived from nematode faunal assessment 12 days previously. (B) Enrichment Index; $y = -15.3 + 0.307x$. (C) Channel Index; $y = 12.5 - 0.227x$.

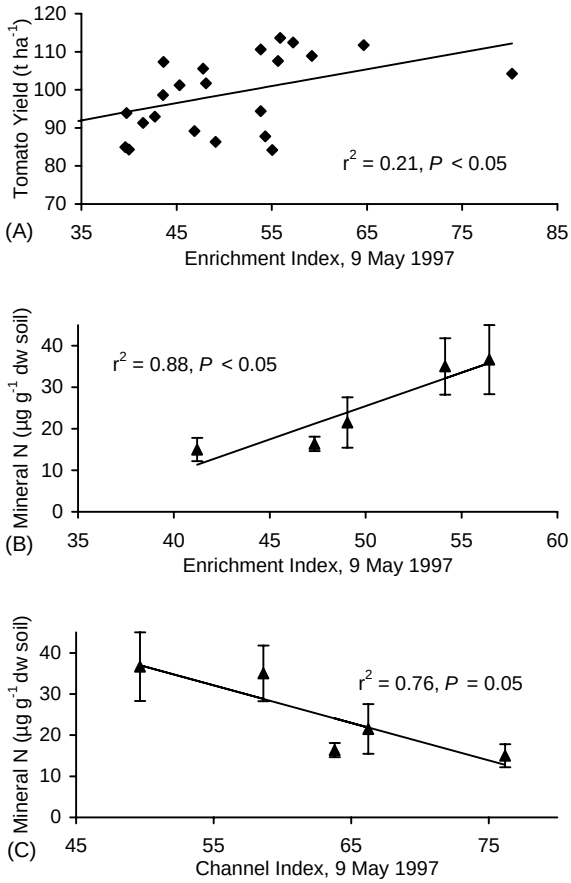

Fig. 5. Crop yield and spring soil mineral N concentrations in relation to indices derived from nematode faunal analysis in the spring in Experiment 2 (1996/1997). (A) Relationship between crop yield and the Enrichment Index (EI); $y = 76.5 + 0.445x$. (B) Relationship between spring mineral N concentrations in the soil and the EI; $y = -55.0 + 1.6x$. A higher value of the EI indicates recent enrichment with readily-decomposed organic material. (C) Relationship between spring mineral N concentrations in the soil and the Channel Index (CI); $y = 82.4 - 0.914x$. A higher value of the CI indicates proportionally greater fungal rather than bacterial decomposition.

3.8. Summer crop yields

In Experiment 1, the main effect of fall irrigation was to increase tomato yields. Yield trends were greater in plots receiving irrigation in the fall, whether or not a winter cover crop had been grown (Table 2). There was a clear relationship between cumulative mineral N measured over six dates in the spring and the subsequent crop yield (Fig. 4A). Treatment combinations that generated highest mineral N concentrations also generated the highest crop yields (Table 2). The main effects on tomato yield of a cover crop

(summer or winter) or addition of high C organic material in the late summer of the previous year were not significant (Table 2).

Tomato yields in Experiment 2 were greater in plots that had a winter cover crop and had been irrigated in the fall. The main effects of a winter cover crop, fall irrigation and a summer cover crop all contributed to significant increases in yield (Table 3). The main effects of summer cover crop, winter cover crop and fall irrigation all enhanced mineral N in May (Table 3). Tomato yield was correlated with soil mineral N and with the EI measured in early May ($r^2 = 0.32$, $P < 0.05$, Fig. 5A). Treatment combinations that generated greatest mineral N concentrations also generated the greatest crop yields (Table 3).

In Experiment 3, tomato yields were generally suppressed after an irrigated summer cover crop (Table 4). In general, the treatment combinations that produced lowest mineral N concentrations also produced lowest tomato yields (Table 4). There was a significant relationship between yield and total soil N at the end of May ($r^2 = 0.3$, $P < 0.01$, Fig. 6A). EI values in all plots were very high by 20 May and did not provide a sufficient range to reveal influences on total N or eventual yield (Fig. 6B).

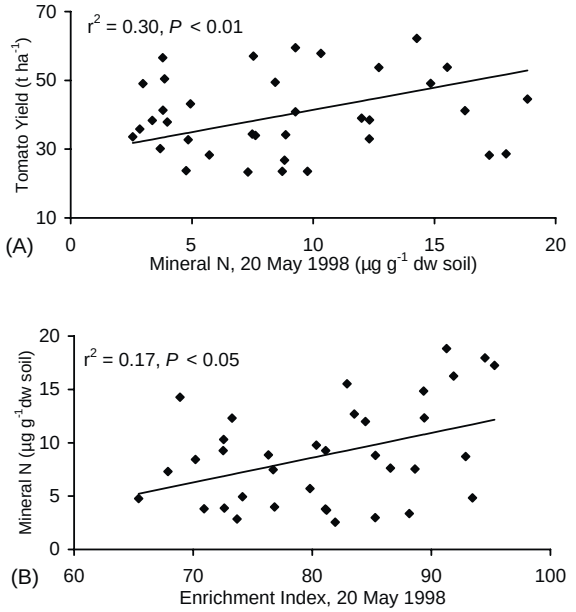

Fig. 6. Crop yield, soil mineral N concentrations in the spring and the Enrichment Index (derived from nematode faunal analysis in the spring) in Experiment 3 (1997/1998). (A) Relationship between crop yield and the soil mineral N concentrations in the spring; $y = 12.7 + 0.578x$. (B) Relationship between spring mineral N concentrations in the soil and the EI; a higher value of the EI indicates recent enrichment with readily-decomposed organic material; $y = -10.0 + 0.232x$.

4. Discussion

Some of the most intensive and productive agricultural systems in the world occur in Mediterranean climates with high summer temperatures and seasonal rainfall. Where the cropping season does not coincide with the rainfall period, the systems are particularly productive when supplied with irrigation, as in the agricultural systems of California, the Mediterranean, and Australia. California's Sacramento Valley is representative of such production systems. In this region, the winter rain period (average 47 cm precipitation annually) extends from November to March. Summer crops are planted when winter rainfall ceases and the soil becomes sufficiently dry to allow tillage without undue compaction. The average monthly minimum temperature in April is 9 °C and average monthly maximum in July is 32 °C. The summer crops are irrigated as needed throughout the growth cycle and are followed by an extended dry fallow period until the commencement of the wet season. During this dry period, average monthly maximum temperatures are 32, 29, and 24 °C in August, September and October, respectively.

Under the dry fallow conditions following harvest of a summer crop, bacterivore and fungivore nematodes decline in abundance due to lack of soil moisture and, perhaps, food. The decline was more evident in bacterivores than fungivores in the present experiments. When rainfall occurs in November, the soil temperature is too low to support their feeding and reproduction. Consequently, bacterivore and fungivore nematodes are in low abundance the following spring when organic material from winter-grown cover crops is incorporated into the soil in low-input and organic systems (Ferris et al., 1996).

The fall irrigation and cover crop manipulations in these studies undoubtedly affect many components of the soil food web. Enhanced N mineralisation in the spring was not only the product of the activities of bacterivore and fungivore nematodes. However, based

on the comparative estimates of Hunt et al. (1987) and our previous studies (Ferris et al., 1998), nematodes appear to be major contributors. We believe that nematode responses to food web management also provide useful markers of the responses of other organisms with similar feeding activities (Ferris et al., 2001). Although it is well documented that pulses in mineral N may follow the irrigation of dry soil (e.g. Sparling and Ross, 1988; Lundquist et al., 1999), mineralisation by microbes following fall irrigation is probably offset by the considerable leaching of N that occurs during winter months at our field site (Poudel et al., 2001c).

We conclude that the activities of organisms in the soil food web contribute substantially to the increased levels of mineral N measured in the spring.

4.1. Treatment effects on the soil food web

The faunal profile is a graphic representation of the effect of management practices or other perturbations on the structure and enrichment components of the food web, based on the relative weighted abundance of nematode guilds (Ferris et al., 2001). The inference of greater structure is that there are more links in the food web, more organismal interactions, greater functional redundancy and, potentially, more stability of function. The position of all data points in the faunal profiles of these experiments (Fig. 2) is consistent with our experience for disturbed annual agricultural systems; i.e. enriched but with little structure (Ferris et al., 2001; Ferris and Matute, 2003).

We conclude that conditions conducive for activity of the soil food web can be created through irrigation in the late summer in winter-rainfall Mediterranean climates. Growing a cover crop during the late summer irrigated period will generally further enhance activity in the soil food web. The cover crop also has the potential benefits of improving soil structure, fixing N, adding organic matter to the soil to fuel the food web, reducing leaching, improving winter-rainfall storage and, providing weed suppression through competition. If soil C is low when acceleration of food web activity is initiated, addition of organic material is probably beneficial. It may be unnecessary to add additional C to fuel the food web if residues remain from previous crops. The growth of a winter cover crop is beneficial for many of the same reasons as those for the summer cover crop. From a practical standpoint, rather than growing two separate cover crops, the summer cover crop probably should be established as a species mixture of grains and legumes that will go through a successional process spanning the late summer and winter.

4.2. Nematode function in food webs

Both bacterivore and fungivore nematodes mineralise N in soil (Ingham et al., 1985; Ferris et al., 1998; Chen and Ferris, 1999). Contributions of bacterivore nematodes on a per capita basis are greater than those of fungivore nematodes, and populations of some bacterivore nematodes are more opportunistic in response to resource enrichment than others. Ecophysiological attributes of different nematode guilds affect the magnitude of their contribution to the mineral N pool (Ferris et al., 1996, 1998; Bongers and Bongers, 1998; Bongers and Ferris, 1999). Bacterivores of the Ba_1 guild, enrichment opportunists, were most responsive to increase in their food source. In particular, *Mesorhabditis* (*Bursilla*) *labiata* (family Rhabditidae) dominated the bacterivore nematode community early in the growing season in previous studies (Ferris et al., 1996). Because the thermal adaptations and temporal dynamics of bacterivore and fungivore nematodes lead to a succession of species predominance (Ferris et al., 1996; Venette and Ferris, 1997), soil management to enhance abundance and activity of these functional guilds as a whole, rather than targeting individual species, should provide sustained N mineralisation during the growing season. Such practices will simultaneously enhance activity and abundance of the larger community of microbial grazers.

Decomposition pathways under the major treatments in Experiment 1 were not discernibly differentiated by the CI through November but differences were evident by the late winter and early spring (March and April) (Fig. 7). Treatment combinations that had not been irrigated the previous fall, or had not received a cover crop, had higher CI values and their decomposition pathways appeared to be more fungal-dominated. That was substantiated by fungal-to-bacterial PLFA ratios as indicators.

Under the warm, dry soil conditions of these annual cropping systems, the component of the soil nematode community that functions in decomposition pathways has a dominant fraction of fungal-feeding

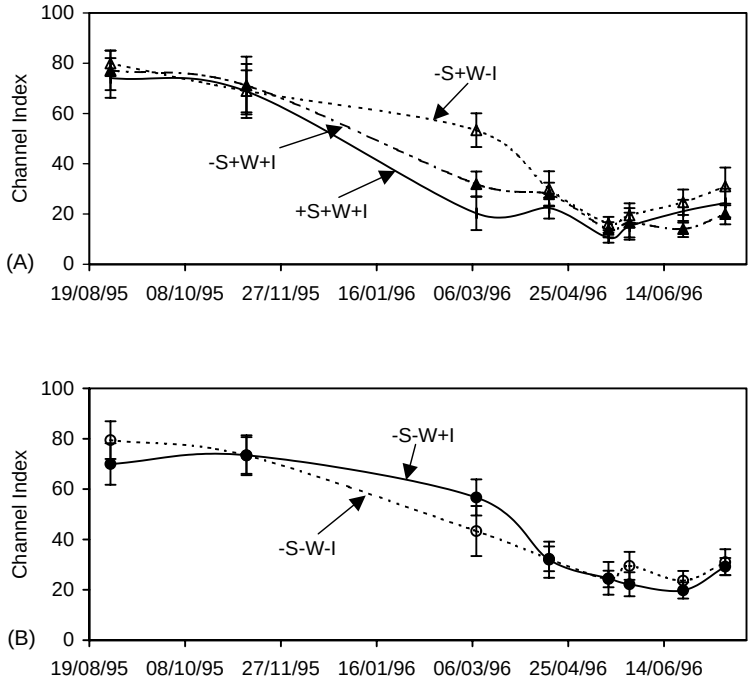

Fig. 7. Temporal dynamics of the Channel Index (CI), the relative predominance of fungal and bacterial decomposition pathways as indicated by nematode faunal analysis, in Experiment 1 (A) CI progression for treatments with cover crops (+S = summercover crop, +W = winter cover crop, +I = fall irrigation, −I = no fall irrigation). (B) CI progression for treatments without cover crops (−S − W: no cover crop).

forms (Ferris et al., 1996). When we modified the environment so that it was more conducive to the bacterial decomposition pathway, there was an increase in bacterial feeders although fungal feeders (and inferred fungal decomposition) remained at appreciable levels. We would anticipate similar results in other winter-rainfall Mediterranean climates.

We conclude that fall management practices can enhance numbers of bacterivore and fungivore nematodes. While fungivore nematodes may make a smaller direct contribution to N mineralisation, they are an indicator that fungal decomposition of recalcitrant organic matter is in process, and they also contribute to the pool of immobilised soil N. The bacterivores include enrichment opportunists and general opportunists. Both are important and collectively they contribute to the release of N immobilised in the microbial biomass until at least the middle of the growing season.

Nematodes are useful bioindicators of other organisms and trophic species that fulfil similar functional roles in the food web. We hypothesise that if the bioindicator species are abundant, the whole of the functional group that they represent (e.g. protozoa and other microbivores) is also active and abundant. The response of omnivore and predator nematodes to late summer and fall management was inconsistent in these highly-disturbed annual agriculture systems. The potential for top down regulation of opportunist species by predators was not reliably amplified by any of the management practices.

4.3. Management implications

In general, maintaining the soil food web in a biologically-active state during the warm period of the early fall enhanced N availability for the vegetative growth of the subsequent summer crop. The USDA Natural Resource Conservation Service defines our experimental site as a class I soil. N was never severely limited at this site during the several years of these experiments. In addition, prior to the experiments,

the soil had been managed under "low-input" farming system procedures that included annual growth of cover crops and minimal use of fertilisers and pesticides. We surmise that primary consumers in decomposer and herbivore channels of the soil food web were well represented in this annually-cropped agricultural system. When N was marginally limiting in some treatment combinations, the relationships between soil N concentrations in the spring, yield of the subsequent summer crop, and managed activity of the soil food web the previous fall, were evident.

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