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Impacts of ground vegetation management strategies in a kiwifruit orchard on the composition and functioning of the soil biota

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Abstract

In production horticulture, it is desirable that ground management strategies are selected in such a way as to ensure that there are adequate levels of soil biota present to carry out key ecosystem processes required for long-term crop growth. We established replicated field plots in a New Zealand kiwifruit orchard of each of five ground management treatments, i.e. maintenance of pasture, planting of a dwarf fescue mulch, sawdust application, cultivation and repeated use of herbicides, and then monitored the responses of components of the soil biota to these treatments over a 5-year period. Those treatments involving enhancement of basal resource inputs (pasture, fescue, sawdust) consistently supported higher levels of microbial biomass and activity than did the others. These effects were not consistently propagated through higher trophic levels of the decomposer food web, although populations of microbe-feeding and predacious nematodes did often differ significantly across treatments. This idiosyncratic response of decomposer food web components to treatments is believed to be due to the complex interplay of top-down and bottom-up forces in soil food webs. There were also important treatment effects on nematode community structure; ordination analysis revealed that the sawdust and cultivated plots supported different species assemblages to the pasture and fescue plots. Further, treatments supporting greater basal resource inputs tended to result in a higher diversity of nematodes; on average the Shannon–Weiner diversity index for the 0–5 cm depth layer was 2.80 and 2.64 for the fescue and pasture treatments, and only 2.32 and 2.45 for the cultivation and herbicide treatments. Populations of Collembola were also generally enhanced in plots with greater basal resource inputs. We utilised litterbag decomposition rates as a measure of the performance of ecosystem functioning carried out by the soil biota, and generally found that surface placed litter decomposition rates were greatest in those treatments supporting greater levels of basal resource inputs and microbial biomass (i.e. greatest for the mulched and fescue plots, least for the herbicide and cultivated plots), but were generally independent of higher trophic levels. Most of our results could be explained by the fact that treatments differed in the amounts of the basal resources that were likely to be present, rather than other components of agricultural intensification such as direct effects of cultivation-induced disturbance or herbicide toxicity. Finally, our study indicates that in order to gain a more complete picture of how agricultural intensification affects soil biota in the long-term requires experiments which simultaneously consider several trophic levels and several modes of intensification, and which run for several years.

Keywords: Agricultural intensification; Decomposition; Kiwifruit; Microbial biomass; Nematode; Soil food web

1. Introduction

An important issue in production horticulture is the selection of an appropriate approach for the management of orchard ground cover. Ground cover management is often required for reducing the levels of weeds likely to compete with the orchard crop, for managing potential pest and disease outbreaks, and for ensuring access of machinery into the orchard. Practices which are often adopted for managing ground cover include the use of fertilizers and herbicides, manipulation of residues and growth of green mulch species which out-compete weed species. Such approaches, which involve the enhancement of agricultural intensification (Triplett and Worsham, 1986; Springett et al., 1994; Giller et al., 1997) are aimed at increasing horticultural production in the short-term. However, maintenance of environmental quality is essential for the longer term performance of these systems (House et al., 1984; Altieri, 1991). In this light, it is desirable that ground cover management is performed in such a way as to ensure that there are adequate levels of soil biota to carry out key below-ground decomposition-related processes (Phillips, 1984; Andrén et al., 1990) because soil microbes and animals (and the processes

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that they regulate) are powerful regulators of plant nutrient acquisition and ultimately plant growth (Alphei et al., 1996; Laakso and Setälä, 1999).

Most forms of agricultural intensification involve alteration of disturbance regimes, manipulation of the quantity and quality of organic matter input, or the addition of synthetic compounds (Wardle et al., 1999a). Each of these three factors has been shown to influence elements of the decomposer biota. In particular, disturbance regimes such as those associated with tillage are well known to alter the structure of soil food webs (Hendrix et al., 1986; Beare et al., 1992) as well as the composition of biotic communities (Lagerlöf and Andrén, 1991; Frey et al., 1999), although the direction of these effects appears to be idiosyncratic and case specific (Wardle 1995). Manipulation of ground cover, either through the planting of green mulches or through heavy addition of residue, can profoundly influence the levels of soil biota, primarily through altering the quantities and nature of substrates which enter the below-ground system (Paoletti et al., 1991; Witter and Kanal, 1998; Lundquist et al. 1999). Addition of synthetic compounds such as herbicides can also influence the soil biota, but in the case of herbicides at least these effects appear to be mainly indirect and result primarily from soil organisms responding to herbicide-induced shifts in plant composition (Mahn and Kastner, 1985; Wardle, 1995; Kroos and Schaefer, 1998).

Despite the number of studies which have been conducted to investigate the effects of land management practices on soil biota, most have focused on only one component of agricultural intensification, and only on a specific group of organisms or processes. However, studies which compare a number of different components of intensification are essential for better understanding how management affects the decomposer subsystem because these components are often substituted for one another (Triplett and Worsham, 1986; Wardle, 1995). Further, integrated approaches for understanding how intensification of management practices affects soil biota, which simultaneously consider several groups of organisms or processes, are helpful for developing general principles of how management affects soil food webs and the processes that they regulate (Hendrix et al., 1986; Andrén et al., 1990; De Ruiter et al., 1993). In this paper, we report on a 5 year field experiment, conducted in an orchard planted with kiwifruit [*Actinidia deliciosa* (A. Chev)], in which we implemented different ground cover management strategies, each representing a different component of agricultural intensification, i.e. cultivation, herbicide use, and the use of living and dead mulches. We aimed to compare the effects of these strategies on different, trophically linked components of the soil 'micro-food web' (sensu Lavelle et al., 1993), i.e. microbes, nematodes and microarthropods, as well as the decomposition processes that they govern, so as to better understand the ways in which horticultural management may alter the composition and performance of the soil biota.

2. Methods

2.1. Study site and treatment details

The experiment was set up at the Rukuhia Experimental Research Station near Hamilton, New Zealand (37°45′S, 175°15′E). The soil present at the location is a Vitric hapludand (Horotiu sandy loam) with a sand:silt:clay ratio of 60:24:16. Climatic data for the site over the study period is given by Wardle et al. (1999b). The area upon which the plots were located was planted in 1987 with kiwifruit vines in rows 6 m apart with adjacent vines within each row being 4 m apart. Vines were trained to grow vertically for 2.5 m and then trained to grow horizontally so as to provide a closed canopy. Plots were set up in this orchard in July 1992; 25 plots were set up in a randomized block design with five replicate blocks of each of five treatments; each plot was 5×5 m and contained two kiwifruit vines. Prior to the plots being set up, the ground cover under the vines consisted of a pasture containing mainly perennial ryegrass (*Lolium perenne* L). The five treatments imposed were:

1. Pasture: this involved maintenance of the pasture that was present at the start of the experiment. It was mown (with clippings returned) every few weeks to maintain it at a height of approximately 4 cm.
2. Fescue: this involved spraying the plot with paraquat (applied as Gramoxone) at 1.2 kg ai/ha on 17 July 1992 and glufosinate-ammonium (applied as Buster) at 0.14 kg a.i./ha on 7 September 1992, to remove all ground vegetation. The plots were then scarified and planted with seeds of Cook dwarf tall fescue (*Festuca rubra* L.) on 16 September 1992. Broadleaf weeds emerging in these plots were then sprayed on 17 October 1992 with bentasone (applied as Basagran) at 1.44 kg ai/ha. After that time the fescue-developed into a mulch with sufficient density to suppress weed growth almost completely for the remainder of the experiment. The mulch was mown (with clippings returned) every 2–4 months to maintain its height at 8 cm.
3. Sawdust: untreated pine (*Pinus radiata* D. Don) sawdust was applied in a 10 cm thick mulch on each plot on 10 September 1992.
4. Herbicide: the ground was maintained in a relatively bare condition through the use of herbicides. Herbicide application consisted of spraying with simazine (applied as Gesatop) at 1 kg a.i./ha and glyphosate (applied as Roundup) at 1.8 kg a.i./ha; treatment was initiated on 16 September 1992 and thereafter each September and April, as well as at any other time during which weed problems developed.
5. Cultivation: a small rotary cultivator was used to manage weeds by shallow (5 cm depth) cultivation every few weeks during the peak of each growing season (i.e. late September–late February) (Wardle et al., 1999b).

All treatments were maintained until completion of the experiment on 16 July 1997.

2.2. Sampling

Soil samples were collected prior to the start of the experiment (8 September 1992) and approximately every six months thereafter (23 February 1993, 7 September 1993, 22 February 1994, 1 August 1994, 20 January 1995, 18 July 1995, 7 February 1996, 18 July 1996, 11 February 1997 and 16 July 1997). For each sampling except the baseline (8 September 1992) sampling, 15 5 cm diameter soil cores were taken from each plot, separated into 0–5 and 5–10 cm depth layers of mineral soil, and bulked within each layer for each plot. For the baseline sampling, ten randomly located areas, each 5×5 m, were located in the area to be used for the experiment (but avoiding those areas already sprayed for the fescue plots), and within each, 15 cores were sampled and processed exactly as for the subsequent samplings. Each soil sample collected at each sampling date was subsampled for various analyses (see below). Further, approximately at each date of soil sampling, ground vegetation biomass and surface residue levels were determined by placing three 0.3×0.3 m quadrats in each plot, removing all the weed and surface residue material, and determining the total mass of the material following oven drying (80°C, 72 h).

2.3. Soil sample analysis

A subsample of approximately half of each soil sample was sieved to 4 mm and the gravimetric soil moisture (80°C, 24 h) was determined on a 20 g (wet wt.) subsample. Soil chemical characteristics were made for each of the soil samples collected at the end of each 12-month period of the study (i.e. every second sampling). Soil C was determined through Dumas microelemental analysis; total N through Kjeldahl analysis and total P as described by Jackson (1958). Microbial activity and biomass determinations were made on sieved soil for all samples at all sampling dates, as described by Wardle et al. (1993b). Soil samples were adjusted to 55% moisture content (dry wt. basis), corresponding to −33 kPa, and the following measurements made:

1. Basal respiration, using 15 g (d.w.) subsamples, as described by Wardle et al. (1993b). Samples were placed in 169 ml airtight containers and kept at 22°C; the total CO_2–C released between 1 and 4 h in the headspace was measured by injecting 1 ml subsamples into an infra red gas analyser.
2. Substrate-induced respiration (SIR). This was determined as for basal respiration but with amendment of the subsample with 75 mg glucose at the beginning of the incubation period. This is based on approaches of Anderson and Domsch (1978); West and Sparling (1986) as used by Wardle et al. (1993b). The SIR values are assumed to be proportionally related to the glucose-responsive portion of the active microbial biomass. The ratio of basal respiration to SIR was used as a relative measure of the microbial metabolic quotient or qCO_2 (Anderson and Domsch, 1985) and is interpreted here as a measure of microbial inefficiency (Wardle and Ghani, 1995) because that carbon which is not used for growth or tissue maintenance is lost from the system as respired CO_2.
3. Inhibition of SIR by selective inhibitors. This was determined based on the approach of Anderson and Domsch (1975). Two subsamples were analysed as for (ii) above except that one of these was amended with streptomycin sulphate (50 mg) in addition to the glucose, while to the other actidione (75 mg) was added with the glucose. The level of inhibition of CO_2 release by streptomycin sulphate and by actidione relative to (ii) above was used as a relative measure of active bacterial biomass and of fungal biomass respectively (Wardle et al., 1993b).
4. Release of CO_2–C by fumigation. This was based on the approach of Jenkinson and Powlson (1976) as described by Wardle et al. (1993b). A subsample (15 g d. w. basis) was fumigated with chloroform, re-inoculated with 1.67 g (d.w.) soil from the same sample (so as to provide a 9:1 ratio of fumigated to non-fumigated soil) and incubated for 10 days at 22°C in 500 ml airtight containers each with a vial of 20 ml 1 M NaOH. Total CO_2–C released over 10 days in each container was assessed by titrating this against 0.5 M HCl. Non-fumigated 'controls' were not used (Voroney and Paul, 1984; Franzluebbers et al., 1999) because preliminary measurements revealed that meaningful determinations could only be obtained for this soil when non-fumigated control values were not considered (Wardle et al., 1993b).

An unsieved 250 ml subsample of each soil sample collected on 8 September 1992, 23 February 1993, 7 September 1993, 1 August 1994, 18 July 1995, 18 July 1996 and 16 July 1997 was used for soil nematode determinations. Nematodes were extracted from the subsample using a tray variant of the Baermann method (Southey, 1986). Total nematodes were counted under a stereomicroscope at 40× magnification and then killed and fixed by the addition of boiling double strength F.A. 4:1 (100 ml 40% formaldehyde: 10 ml glacial acetic acid: 390 ml distilled water). An average of 134 (typical range 91–221) specimens from each sample were identified to nominal genus or family level from temporary slides using up to 800× magnification; these taxa were then placed into trophic feeding groups as according to Yeates et al. (1993).

Mesofauna were extracted from a 30 g (d.w. basis) unsieved subsample of each sample collected at each sampling date, by placing the subsample in a modified Tullgren mesofaunal extractor (Merchant and Crossley, 1970; Crossley and Blair, 1991, as described by Wardle et al., 1993a); the extractor was normally run for 4 days and water was used as the collection medium. Mesofauna were

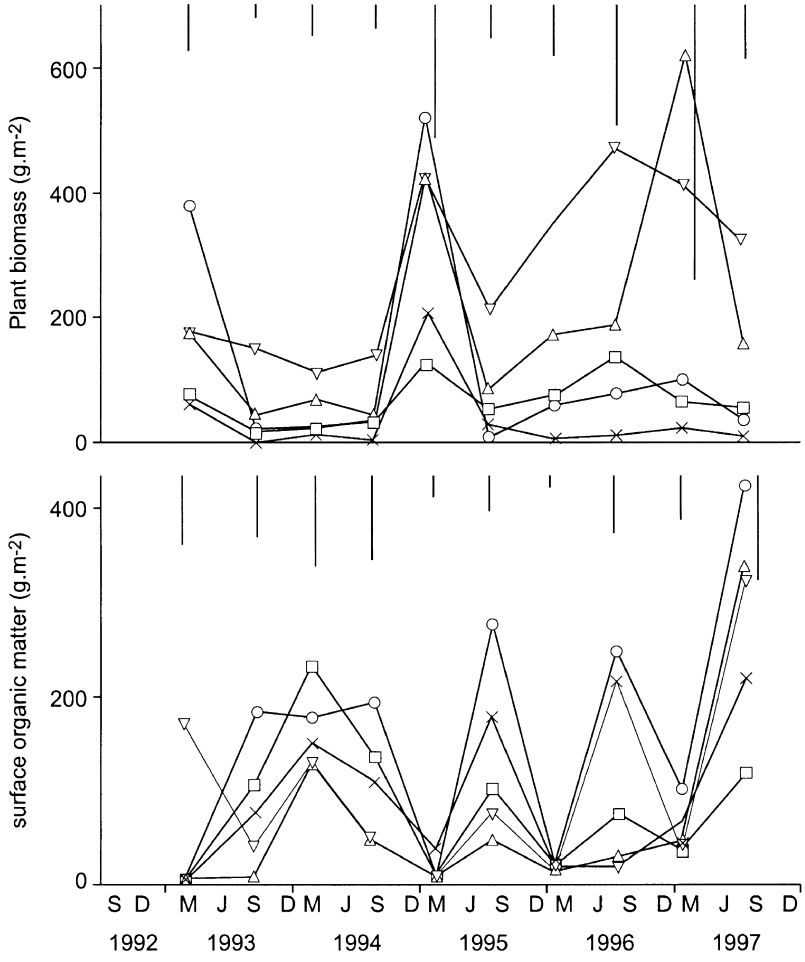

Fig. 1. Ground vegetation biomass and amount of surface dead organic matter in relation to ground vegetation management treatment. Vertical bars represent least significant difference at $P = 0.05$. Symbols: △, pasture; ▽, fescue mulch; ×, sawdust mulch; □, herbicide treatment; ○, cultivation treatment.

classified into the following groups: Collembola, Oribatid mites and non-Oribatid (mostly predatory) mites.

2.4. Litter decomposition

Litter decomposition was investigated in each plot during the 2nd and 5th years of the investigation by using a litter bag technique as described by Wardle et al. (1993b). At the beginning of each of both of these years (7 September 1993, 30 August 1996) eight litter bags were placed in each plot, i.e. four on the ground surface and four buried at 5 cm mineral soil depth. Each litter bag consisted of 3 g (d.w.) perennial ryegrass (*L. perenne*) leaf tissue placed in a 10×10 cm nylon mesh bag with 1×1 mm holes. For each of the 2 years of bag placement, one surface-placed and one buried litter bag was harvested from each plot on each of four separate occasions, i.e. approximately at 2, 4, 8 and 12 months after placement.

After collection, the adhering material on each bag was removed and the litter contained within each bag weighed. A weighed subsample of approximately one third of the tissue in each bag was then thoroughly rinsed with deionised water and oven dried (80°C, 24 h) to enable determination of the dry weight of the litter remaining; however when the wet weight of litter was below 200 mg the whole sample was used. The remainder of the sample was used for determination of basal respiration and SIR as described by Wardle et al. (1993b). Basal respiration was determined on a pre-weighed subsample by adjusting the moisture content to 200% (d.w. basis), placing it in a 169 ml airtight container and measuring CO_2–C evolution as described above. SIR was determined in the same way, but with amendment of the subsample with 10 mg glucose g^{-1} litter immediately prior to incubation.

3. Results

The ground management treatments had important effects on both total ground cover plant biomass and the levels of surface organic matter present on the ground (Fig. 1). Analysis of variance revealed that treatment effects were significant at $P = 0.05$ for all sampling times for plant biomass and for all but two times for surface organic matter.

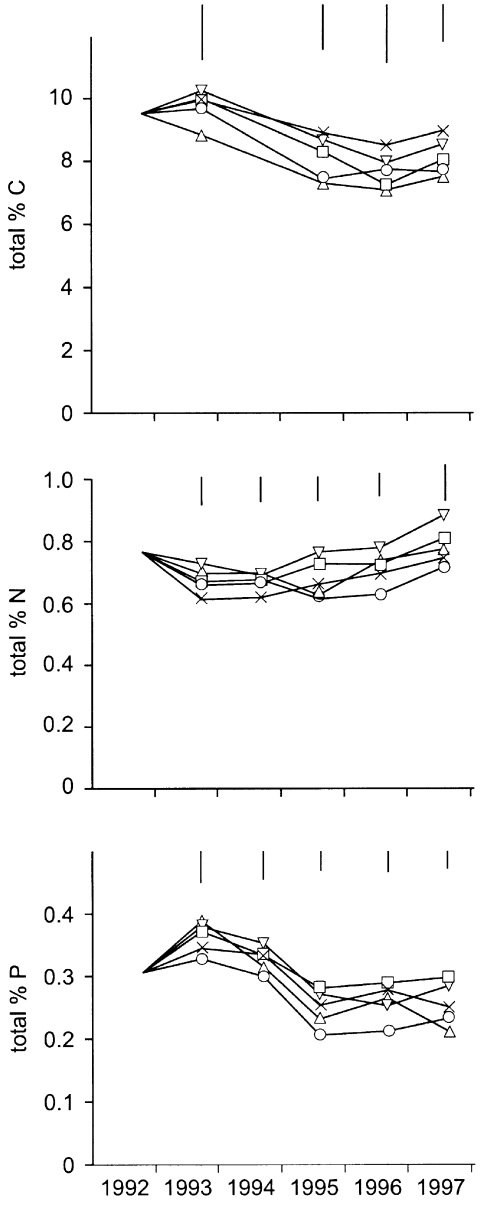

Fig. 2. Total C, N and P levels in the 0–5 cm soil depth layer, in relation to ground vegetation management treatment throughout the course of the experiment. Vertical bars represent least significant difference at $P = 0.05$. Symbols: △, pasture; ▽, fescue mulch; ×, sawdust mulch; □, herbicide treatment; ○, cultivation treatment.

The pasture and fescue treatments supported considerably larger amounts of vegetation than did the herbicide and sawdust treatments, especially from 1994 onwards. Rapid weed growth also resulted in high plant biomass levels in the cultivated plots in early 1993 and in early 1995. Surface organic matter levels fluctuated considerably with greatest levels frequently occurring in the cultivated plots and with the sawdust, fescue and herbicide treatments sometimes supporting significantly more surface residue levels than some of the other treatments.

The ground management treatments often had significant effects on C, N and P levels in the 0–5 cm soil depth layer; analysis of variance revealed that treatment effects on soil C were significant at $P = 0.05$ in 1995 and 1997; soil N in 1995 and 1996; and soil P in 1996 and 1997. However, the patterns of treatment responses differed for the different elements (Fig. 2). Soil C levels were greatest in the sawdust treatment from 1995 onwards, while for the last 2 years the lowest C levels occurred in the cultivated, pasture and herbicide treatments. From 1994 onwards soil N levels were greatest in the fescue treatment and least in the cultivated treatment. Total soil P levels were greatest in the fescue and herbicide plots and least in the cultivated and pasture plots.

The soil microbial properties were all responsive to treatments throughout much of the experiment, especially in the uppermost soil layer (Fig. 3). Analysis of variance revealed that treatment effects were significant at $P < 0.01$ for nearly all sampling dates in the 0–5 cm depth layer for SIR, fumigation CO_2–C flush, metabolic quotient, streptomycin inhibition and actidione inhibition. Effects of treatments on these variables were weaker, but still statistically significant at $P = 0.05$ for the vast majority of sampling dates, in the 5–10 cm layer. In the 0–5 cm layer, values of SIR (Fig. 3) and basal respiration (data not presented) were generally greatest in the fescue plots and least in the cultivated plots, and the pasture and sawdust plots generally supported greater values of SIR than did the herbicide plots. At 5–10 cm depth SIR was initially highest for the fescue plots, while later in the experiment the highest values were observed in the cultivated plots; herbicide-treated plots generally had the lowest SIR values throughout the experiment. The fumigation CO_2–C flush was consistently greater in the sawdust, pasture and fescue plots than in the cultivated and herbicide plots for the 0–5 cm depth layer, although for the 5–10 cm layer this trend was apparent at only some sampling dates. The microbial metabolic quotient or ratio of respiration to biomass (qCO_2, indicative of microbial inefficiency) was greatest in the sawdust plots throughout the experiment for the 0–5 cm layer, and for the first 2 years in the 5–10 cm layer. The other four treatments did not differ much, except that for the final 3 years the metabolic quotient for the cultivated treatment in the 5–10 cm depth layer was consistently less than for the other treatments. The magnitude of inhibition of SIR by streptomycin and actidione (indicative of relative values of active bacterial and fungal biomass) generally paralleled the values obtained by SIR (data not presented), but the ratio of bacteria to fungi varied significantly between treatments (Fig. 3). This was especially apparent for the 0–5 cm layer, in which the sawdust treatment supported the greatest ratio from 1993–1995, the cultivation treatment usually had the lowest ratio early in the experiment, and the herbicide treatment had the lowest ratio in early 1997.

Populations of nematodes in each of the six feeding groups showed significant treatment responses in the 0–5 cm depth layer for at least some sampling occasions (Fig. 4) although the effects were less apparent in the 5–10 cm depth layer (data not presented). Analysis of variance showed that

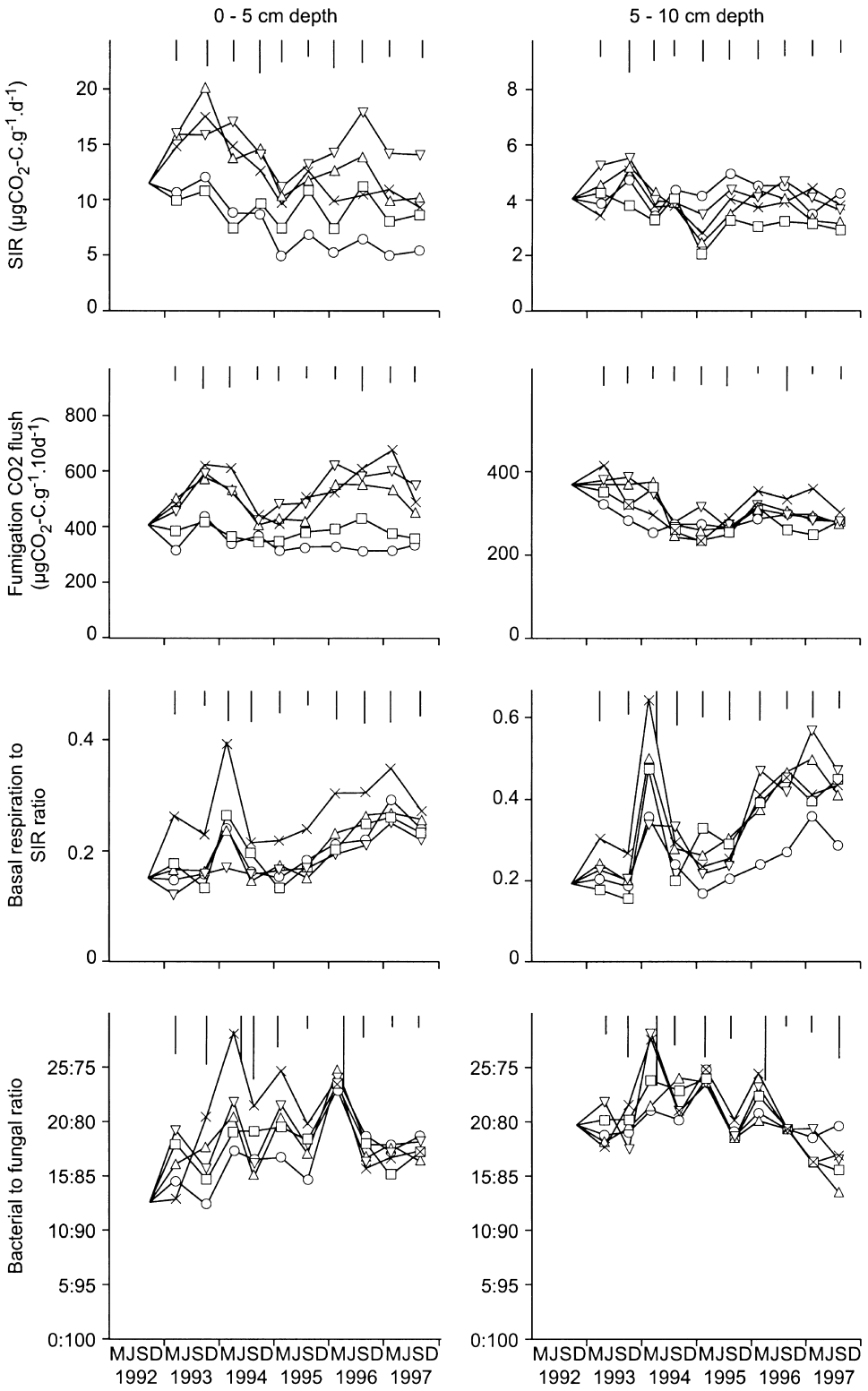

Fig. 3. Soil microbial properties in relation to ground vegetation management treatment throughout the course of the experiment. Vertical bars represent least significant difference at $P = 0.05$. SIR, substrate induced respiration. Symbols: △, pasture; ▽, fescue mulch; ×, sawdust mulch; □, herbicide treatment; ○, cultivation treatment.

in the 0–5 cm depth later bacterial feeding nematodes were significantly affected ($P = 0.05$) by treatment on four out of six sampling occasions, fungal feeders on three occasions, top predators on four occasions and plant pathogens on four occasions. Numbers of bacterial feeding nematodes were generally greatest in the cultivation and pasture treatments,

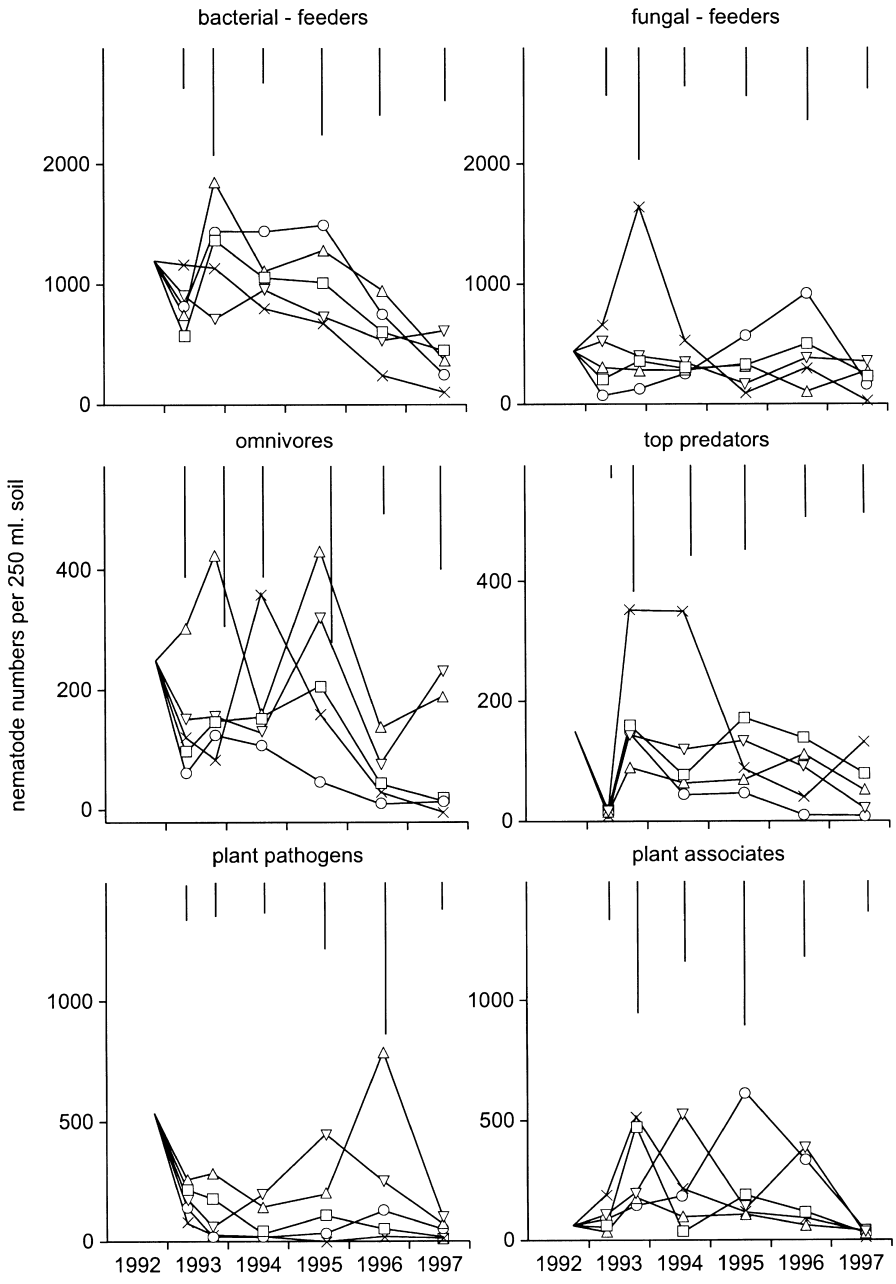

Fig. 4. Populations of soil nematodes in the 0–5 cm soil depth layer for each of six feeding groups in relation to ground vegetation management treatment throughout the course of the experiment. Vertical bars represent least significant difference at $P = 0.05$. Symbols: △, pasture; ▽, fescue mulch; ×, sawdust mulch; □, herbicide treatment; ○, cultivation treatment.

and from 1994 onwards were lowest in the sawdust treatment. Populations of fungal feeding nematodes were initially greatest in the mulch plots and later in the cultivation plots. For the majority of sampling occasions, numbers of omnivorous nematodes were greatest in the pasture plots and least in the cultivation plots. Top predatory nematode populations were greatest in the sawdust plots in 1993, 1994 and 1997, and in the herbicide plots in 1995 and 1996; lowest numbers were found in the cultivated plots from 1994 onwards. From 1994 onwards plant pathogen numbers were greatest in the pasture and fescue plots. Population dynamics of plant associated nematodes were less consistent and no general patterns of treatment effects emerged.

Populations of the most abundant nematode taxa were often related to treatment (Table 1); at the end of the experiment 11 of the 16 commonest taxa showed significant treatment responses ($P = 0.05$ as according to analysis of variance) in the 0–5 cm depth layer while five of the 16 taxa were affected by treatments in the 5–10 cm depth layer. For the 0–5 cm layer populations of *Aphelenchus* and *Helicotylenchus* were greatest in the pasture treatment; *Chronogaster*, Panagrolaimidae, Rhabditidae,

Table 1
Population densities of the most abundant nematode taxa (numbers per 250 ml soil) in relation to ground vegetation management treatment at the end of the experiment (16 July 1997)

Taxon and feeding group[a]	0–5 cm soil depth layer						5–10 cm soil depth layer					
	Pasture	Fescue	Sawdust	Herbicide	Cultivation	$LSD_{0.05}$[b]	Pasture	Fescue	Sawdust	Herbicide	Cultivation	$LSD_{0.05}$
Acrobeles (BF)	46	46	2	54	26	51	2	31	7	18	11	30
Anaplectus (BF)	9	15	0	1	0	16	0	0	0	0	0	–
Cephalobidae (BF)	129	96	74	113	101	114	78	100	36	126	86	75
Chronogaster (BF)	23	78	2	2	5	64	1	51	20	36	1	59
Panagrolaimidae (BF)	0	16	0	0	1	15	9	0	0	9	14	26
Plectus (BF)	31	13	9	19	8	30	3	0	3	0	5	8
Rhabditidae (BF)	179	355	30	274	128	321	81	284	262	309	114	442
Aphelenchus (FF)	8	0	0	0	0	8	0	0	0	0	2	2
Aphelenchoides (FF)	0	0	0	2	10	8	4	0	0	0	0	5
Leptonchidae (FF)	19	25	0	5	4	24	14	11	3	12	3	20
Aporcelaimidae (OM)	29	25	4	12	11	28	9	11	6	20	2	20
Chromadoridae (OM)	164	174	9	5	3	180	21	25	4	2	1	42
Mononchidae (PR)	69	18	134	83	19	89	25	13	7	18	32	24
Helicotylenchus (PF)	80	65	0	18	23	80	3	1	0	0	4	5
Pratylenchus (PF)	2	13	0	6	1	9	5	181	2	1	2	124
Tylenchus(PA)	7	4	2	8	14	11	40	17	12	69	15	68

[a] Feeding groups: BF, bacterial feeders; FF, fungal feeders; OM, omnivores; PR, top predators; PF, plant feeders; PA, plant associates
[b] $LSD_{0.05}$, least significant difference at $P = 0.05$.

Leptonchidae and *Pratylenchus* in the fescue treatment; Mononchidae in the sawdust treatment; *Acrobeles* in the herbicide treatment and *Aphelenchoides* and *Tylenchus* in the cultivation treatment. These differences in community composition were also apparent in ordination biplots summarizing the overall nematode compositional data at the end of the experiment (Fig. 5). For the 0–5 cm depth layer the sawdust and cultivated plots occupied generally different positions on the biplot than did the fescue and pasture plots, although these effects were not apparent for the 5–10 cm depth layer. Nematode community level responses to treatment effects were also apparent for diversity indices calculated from the nematode community data, at least for the 0–5 cm depth layer (Fig. 6). The pasture plots supported the greatest taxonomic diversity in 1993 while the fescue plots supported the highest diversity in 1994–1996. The cultivated plots supported the lowest diversity in 1993–1995 while the sawdust plots were the least diverse in 1997.

Collembola populations varied considerably during the experiment, but were significantly affected by treatments at $P = 0.05$ (as according to analysis of variance) for most sampling dates. Populations of collembola were often considerably greater in the pasture plots than in the other plots, especially in the 0–5 cm depth layer (Fig. 7). The fescue plots also supported more Collembola than did some of the other treatments. Collembola numbers in the cultivation, herbicide and sawdust plots were sometimes greater and sometimes less than that of some of the other treatments. In the 5–10 cm depth layer, treatment effects were generally weak, although in February 1993 and February 1994 the pasture plots supported considerably greater levels of Collembola than did the other plots, and to a lesser extent this was also true of the sawdust plots in August 1994. Populations of Oribatid and non-Oribatid mites were usually considerably less than those of Collembola, and were not consistently related to treatment (data not presented).

Litter decomposition patterns were clearly related to treatment for the surface-placed litter bags (Fig. 8); analysis of variance revealed that treatments significantly ($P = 0.05$) affected decomposition rates in each of the final three sampling dates for both years 2 and 5. Decomposition rates were significantly slower in the cultivated and herbicide plots than in the other plots in the 2nd year and to a lesser extent this was true in the 5th year. In the 5th year, litter decomposition rates were significantly faster in the fescue plots than in the other plots. Treatment effects on decomposition were less apparent with regard to the buried litter bags, although initial decomposition was greatest in the cultivated plots for both the 2nd and 5th years, and mass loss was generally least in the herbicide plots during the 2nd year. SIR values for the surface placed litter were least in the sawdust and cultivated plots in the 2nd year, but were greatest in the sawdust plots in the 5th year (Table 2). Values of SIR for buried litter only differed across treatments in the 2nd year, when SIR of litter in the sawdust plots were significantly greater than in the cultivated plots. Values for the ratio of basal respiration to SIR were only significantly related to treatment for the year 2 litter bags. For the surface litter, this ratio was greatest for the sawdust treatment and least for the herbicide and pasture treatments, while for the buried litter bags values were greatest for the cultivated plots and least for the sawdust and herbicide plots.

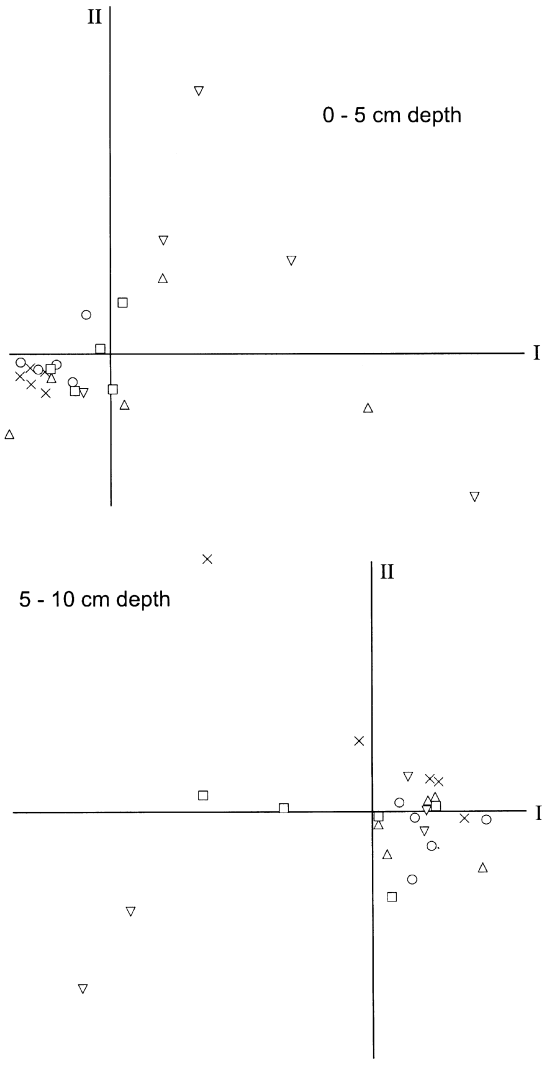

Fig. 5. Ordination biplot of field plots with regard to overall soil nematode community structure at the end of the experiment (16 July 1997) following principal components analysis. Symbols: △, pasture; ▽, fescue mulch; ×, sawdust mulch; □, herbicide treatment; ○, cultivation treatment.

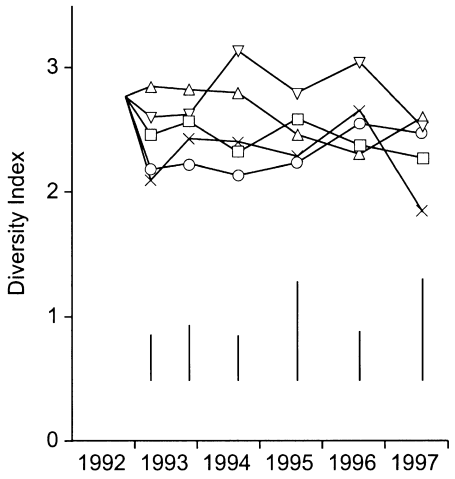

Fig. 6. Soil nematode community diversity (Shannon–Weiner index, H') in the 0–5 cm soil depth layer in relation to ground vegetation management treatment throughout the course of the experiment. Vertical bars represent least significant difference at $P = 0.05$. Symbols: △, pasture; ▽, fescue mulch; ×, sawdust mulch; □, herbicide treatment; ○, cultivation treatment.

4. Discussion

Our study involved the application of treatments which caused large variations in the amounts and quality of basal resources (organic matter) added to the decomposer subsystem. The pasture and fescue treatments involved maintaining high densities of herbaceous plants (mostly grasses) on the plots, which undoubtedly caused sustained inputs of litter and root residues and exudates. The sawdust treatment involved a one-off addition of a relatively recalcitrant source of C to the soil surface. In contrast, the cultivation and especially the herbicide plots usually had relatively little ground cover and no major sources of organic matter input over and above those derived from the kiwifruit vines. It is this variation of C input across treatments which was presumably largely responsible for driving the soil biota.

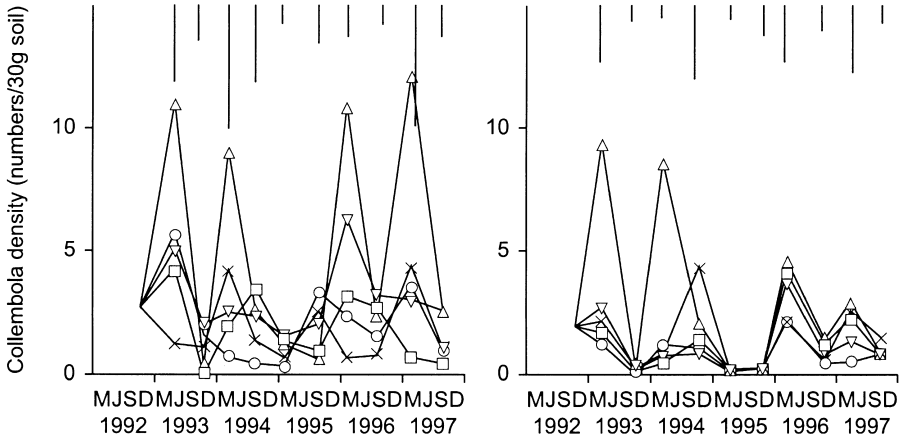

Fig. 7. Populations of soil Collembola in relation to ground vegetation management treatment throughout the course of the experiment. Vertical bars represent least significant difference at $P = 0.05$. Symbols: △, pasture; ▽, fescue mulch; ×, sawdust mulch; □, herbicide treatment; ○, cultivation treatment.

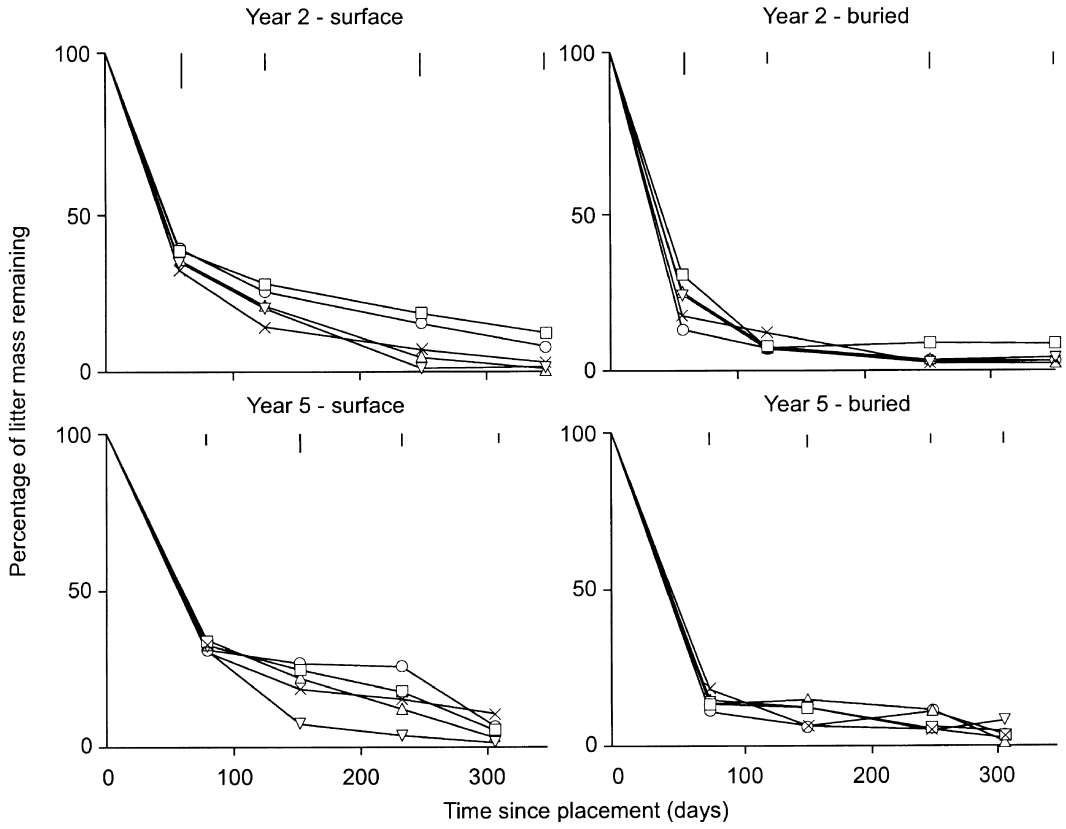

Fig. 8. Decomposition patterns of surface-placed and buried litter, placed in plots at the beginning of the 2nd and 5th years of the experiment, in relation to ground vegetation management treatment. Vertical bars represent least significant difference at $P = 0.05$. Symbols: △, pasture; ▽, fescue mulch; ×, sawdust mulch; □, herbicide treatment; ○, cultivation treatment.

Treatments with enhanced basal resource additions (i.e. those planted with grass species or amended with sawdust) consistently supported higher levels of microbial biomass than did the other treatments. This would suggest a 'bottom-up' control of the primary decomposer trophic level through resource availability (Vekemans et al., 1989; Jensen et al., 1997). However, these effects did not have consistent multi-trophic consequences and this can be demonstrated by considering two further trophic levels, i.e. microbe feeding nematodes, and top predatory nematodes (which feed upon microbe feeding nematodes). Equilibrium populations of those nematodes which feed on bacteria were often greatest in those plots with the lowest bacterial levels, especially those in the cultivation treatment. Further, the sawdust plots with high bacterial levels often supported the lowest levels of bacterial feeding nematodes. Fungal feeding nematodes were initially highest in the sawdust plots (which also supported high levels of fungi), but later in the experiment peaked in the microbially-depleted cultivated plots. Ambiguous results were found with regard to the top predatory

Table 2
Substrate-induced respiration (SIR) and the basal respiration to SIR ratio of litter bag contents after the first sampling (2–3 months) after placement in the field at the beginnings of years 2 and 5

Measurement	Stage of experiment	Placement	Treatment					$LSD_{0.05}$[a]
			Pasture	Fescue	Sawdust	Herbicide	Cultivated	
SIR ($\mu g\ CO_2$–C $g^{-1}\ h^{-1}$)	Year 2	Surface	588	597	458	586	494	70
		Buried	366	347	415	330	324	86
	Year 5	Surface	449	498	547	430	393	62
		Buried	455	502	429	444	446	107
Basal respiration to SIR ratio	Year 2	Surface	0.557	0.616	0.686	0.568	0.629	0.123
		Buried	0.415	0.465	0.404	0.353	0.516	0.105
	Year 5	Surface	0.472	0.501	0.450	0.469	0.492	0.061
		Buried	0.795	0.636	0.774	0.715	0.646	0.245

[a] Least significant difference at $P = 0.05$.

nematodes; sawdust addition often stimulated these nematodes, consistent with the effects of sawdust on microbes, but not the bacterial feeding nematodes representing the intermediate trophic level. Further, high numbers of top predators also occurred in the herbicide-treated plots, which involved both low levels of C input and low microbial biomass levels. In contrast, Collembola appeared to be at least partially regulated by basal resource levels (and thus bottom up control), often being most numerous in those plots containing grasses or sawdust.

Our results indicate that inducing changes in the amounts of resources entering the basal trophic level of the soil food web can exert important effects on higher trophic levels, but these do not necessarily work in the same direction across trophic levels. This appears to be because of the complex interplay of top-down (control by predation) and bottom-up (resource availability) forces in regulating components of the decomposer food web (Wardle and Yeates, 1993; De Ruiter et al., 1995) and is consistent with data showing that changes in basal resources can exert strong effects on lower trophic levels but rather more idiosyncratic (though often significant) effects on higher trophic levels (Mikola and Setälä, 1998; Wardle et al., 1999a).

In addition to varying the levels of basal resource inputs, we also included treatments which altered two other aspects of agricultural intensification, i.e. increased disturbance (cultivation) and the use of synthetic pesticides. Disturbance through cultivation caused reduction of the primary decomposer trophic level (microbes) and the top predatory nematodes, but often stimulated the microbe-feeding nematodes, relative to most of the other treatments. However, it is unclear as to whether this is a direct effect of cultivation (such as has been reported earlier, e.g. Hendrix et al., 1986; Yeates and Hughes, 1990; Angers et al., 1992) or an indirect effect of modified vegetation composition. However, the generally low levels of plant biomass, and the decline in soil N and P in this treatment relative to the other treatments, could have at least contributed to diminished levels of microbial biomass in these plots (see Angers et al., 1992). The use of herbicides did not have any effects on the soil food web over and above what could be expected in terms of reduced ground plant cover, and this is consistent with previous literature indicating that herbicide additions at realistic field concentrations exert mainly indirect effects on the soil biota (rather than direct toxicological effects) through modifying vegetation composition (Domsch et al., 1983; Wardle, 1995).

Further insights into effects of management practices on the soil biota can be gained by considering community-level responses. In the present study this was done for the nematode fauna. Different treatments clearly favoured different nematode taxa, and each of the five treatments supported the maximal nematode numbers for at least one taxon. Shifts in the composition of communities of nematodes are likely to be reflective of broad shifts in the composition of microflora, given that most nematodes are secondary consumers and feed upon microbes (Wasilewska, 1995; Wardle et al., 1999a). This suggests that alteration of basal resource levels are likely to have multitrophic consequences at the community level of resolution (Freckman and Ettema, 1993). Community-level patterns are also apparent with regard to the nematode diversity data, and those plots with grass cover often supported the most diverse assemblages of nematodes, possibly as a result of greater heterogeneity of resources added through the return of grass residues. Generally those treatments with low levels of ground-layer plants present also supported the lowest nematode diversity, a trend that is consistent with that shown by Watson et al. (1991) with regard to plant parasitic nematodes in kiwifruit orchards.

In assessing how agricultural management is likely to influence agricultural sustainability in the longer term, it is necessary to understand not just how management practices affect soil organisms, but also how these effects in turn influence the key ecosystem functions carried out by the soil biota. We used litter decomposition rates as our measure of below-ground ecosystem function, and assessed this both early in the experiment when treatment effects were likely to be diverging, and during the last year of the experiment. The clearest effects we found were for the surface-placed litter bags, and generally those treatments which supported lower levels of microbial biomass (i.e. the herbicide and cultivation treatments) also resulted in lower rates of decomposition; further, during the final year, the fescue plots supported the fastest rates of decomposition. This suggests that varying the level of basal resource inputs can also be important in determining those processes carried out by organisms comprising the soil food web. Curiously, decomposition rates were most consistently linked to the biomass and activity of the lowest decomposer trophic level (microflora) rather than to the levels of the higher level consumers. This supports previous findings that decomposition patterns can be independent of soil faunal dynamics (Andrén et al., 1995) and tend to be linked most closely to the performance of lower trophic levels in experimentally constructed food chains (Laakso and Setälä, 1999).

Our study provides clear evidence that different components of agricultural intensification differ tremendously in terms of their effects on the soil biota, as well as on a key ecosystem process (litter decomposition) regulated by the soil biota. It is apparent that those practices which result in greater addition of basal resources such as maintaining a vegetated ground cover (green mulch) or the addition of residues are likely to strongly stimulate the soil microflora and microbially-mediated processes. Manipulation of the levels of basal resources are likely to be more important in influencing the soil biota than are other components of agricultural intensification such as direct effects of cultivation or herbicide toxicity, at least in the system that we considered. Finally, our study indicates that in order to gain a more complete picture of how agricultural intensification affects soil biota in the long-term requires experiments which simultaneously consider several trophic

levels and several modes of intensification, and which run for several years.

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