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Linking above- and below-ground biodiversity: abundance and trophic complexity in soil as a response to experimental plant communities on abandoned arable land

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Summary

1. This study investigates the effects of experimental plant communities on different trophic levels in the soil food web of abandoned arable land.
2. In April 1996, a biodiversity experiment commenced using a continuation of agricultural crop rotation (CCR), spontaneous succession with naturally colonizing plant species (NC) and late-successional plant species sown in low-diversity (LD, four plant species) and high-diversity (HD, 15 plant species) communities. The nematode community was used as an indicator of the influence of the experimental plant communities on different trophic levels in the soil food web.
3. The nematode abundance in the experimental plant communities differed from that of the continued crop rotation, but there were hardly any differences between the natural, the low-diversity and the high-diversity plant communities.
4. The abundant plant-feeding nematodes and the somewhat less abundant bacterivorous nematodes were stimulated most by the sowing treatments. Fungivorous nematodes were stimulated less, while the numbers of omnivorous and carnivorous nematodes did not change significantly.
5. The diversity of the nematode community did not change over 2 years.
6. It is concluded that experimental plant communities have either small short-term effects or a delayed impact on the soil food web compared with the effect they have on above-ground invertebrate community development.

Key-words: Nematodes, old-field succession, restoration, set-aside, soil food web

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Introduction

One of the more widely applied measures to counteract the rapid loss of species diversity and conserve the remaining diversity is to convert former agricultural land into more natural ecosystems. Due to the long-term influence of cultivation, vegetation development on abandoned arable land is known to be constrained by high soil fertility, disrupted fungal networks (Swift & Anderson 1993), depleted seed banks and limited propagule dispersal (Lepš & Rejmánek 1991; Burch 1996; Bekker, Bakker & Thompson 1997; Thompson, Bakker & Bekker 1997; Bakker & Berendse 1999). In studies on the relationship between plant species diversity and productivity (Naeem *et al.* 1994; Tilman, Wedin & Knops 1996; Hector *et al.* 1999), species diversity, abundance and complexity of arthropod communities were positively correlated to the number of plant species present (Siemann *et al.* 1998; Mulder *et al.* 1999; Koricheva *et al.* 2000). However, little is known of the possible consequences of plant community development for the species diversity and abundance of soil-living organisms (Hooper *et al.* 2000).

In order to obtain a better understanding of both the mechanisms driving vegetation development and plant species diversity and of the feedback on soil diversity on former arable land (old-field succession), an international research project (changing land usage, enhancement of biodiversity and ecosystem development, CLUE) was initiated in 1996. The main objective of CLUE was to examine whether manipulations of the vegetation composition at the start of land abandonment change the rate and direction of secondary

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succession and ecosystem development, both above- and below-ground (Van der Putten *et al*. 2000). One of the goals of CLUE was to investigate if (and how) plant species diversity and the characteristics of the plant species present affect abundance and diversity in the soil community.

So far, examples of (cor)relations between above- and below-ground biodiversity are confusing, demonstrating that they can be positive, negative or non-existent (Hooper *et al*. 2000). One of the reasons for this inconsistency may be the variety of mechanisms by which vegetation can affect the composition and diversity of the soil community and vice versa (Bardgett, Wardle & Yeates 1998; Hooper *et al*. 2000). Most examples originate from studies on symbiotic associations of plants and soil organisms, such as mycorrhizae and *Rhizobium* (Grime *et al*. 1987; Gange, Brown & Farmer 1990; Bever 1994; Van der Heijden *et al*. 1998). However, this leaves the question of how the majority of the soil community – non-symbiotic soil organisms – responds to species diversity in the plant community. Most of the diversity in soil will be indirectly linked to vegetation characteristics such as litter type, root exudates and carbon input. These may lead to a greater variety of food resources supporting a more diverse soil community (Anderson 1994; Lavelle *et al*. 1995; Bardgett, Wardle & Yeates 1998; Hooper *et al*. 2000). Another mechanism is via changes in environmental conditions – for instance vegetation influencing the microclimate, which may in turn affect the composition of the soil community (Coleman *et al*. 1991; Sulkava & Huhta 1998). Finally, there are obligate plant feeders, parasites, pathogens and their antagonists that may also depend on the plant species present.

An initial CLUE study on soil microbial communities in 2-year-old experimental plant communities on abandoned arable land showed no significant effect on net N-mineralization, short-term nitrification, respiration and arginine ammonification (Mal *et al*. 2000). This was despite considerable differences in plant species composition and average productivity (Lepš *et al*. 2000; Van der Putten *et al*. 2000). Along a productivity gradient in an old field, Broughton & Gross (2000) found similar patterns of plant productivity and microbial productivity, but they could not exclude covariance of different resources of which one may affect plants and another the soil microbes. The microbial communities along the gradient showed variation in composition (determined by fatty acid methyl ester profiles), but this was not correlated to plant productivity or diversity (Broughton & Gross 2000). Wardle *et al*. (1999) also found little evidence of the effect of plant community composition on the soil community. Experimental removal of plant species groups from 20 cm diameter plots in a pasture showed most pronounced effects on root herbivores, predominantly when all plants were removed.

The aim of the present study was to determine if, and at what level in the food web, short-term experimentally imposed differences in the composition of the plant community on abandoned arable land lead to changes in the soil community. Consumer organisms (nematodes) were used as an indirect measure of response. The phylum nematoda contains a variety of species with diverse life cycles and feeding types (Bongers 1990; Swift & Anderson 1993), making them extremely suitable as indicators (Bongers & Ferris 1999). There are strong trophic linkages between nematodes and other (often more difficult to study) components of the soil food web, such as bacteria and fungi (Freckman & Ettema 1993; Moore & De Ruiter 1993). Because of their position in the soil food web, herbivorous nematodes will show the most immediate response to changes in the plant community. Bacterivorous and fungivorous nematodes will respond secondarily to changes in the plant community, because changed inputs of detritus will act first on the microbial community (De Ruiter, Neutel & Moore 1995). Nevertheless, if changes in the microbial community appear, the short life cycle of many opportunistic bacterivorous nematodes may result in immediate changes in their community as well. Omnivorous and carnivorous nematodes are assumed to show the most delayed responses to changes in plant community composition due to their higher hierarchical position in the food web.

The main hypothesis of the present study was that the diversity and number of consumers (nematodes) will depend on their hierarchical position in the food web. It was expected that plant feeding and fast-reproducing bacterivorous nematodes would be most responsive to differences in plant diversity and plant productivity. In order to assess the effects of different land abandonment options, the effects of the sown, later-successional plant species on consumer diversity and abundance were compared with those of spontaneously establishing early successional plant species (mostly weed species germinating from the seed bank). In order to determine the effect of land abandonment, nematode community development in sown and naturally colonized plots was compared with that in plots where agricultural practice continued.

Materials and methods

SITE DESCRIPTION

The experimental site (Mossel, 52°04′ N, 05°45′ E) is located at Planken Wambuis, west of National Park Hoge Veluwe, The Netherlands. The site has been used as arable land since 1920. For the past 30 years, the area (55 ha) has been used for conventional agriculture, with a crop rotation of silage maize, potatoes, sugar beets, oats and ryegrass. In autumn 1995, the last crop (maize) was harvested, after which a Dutch nature conservation organization (Natuurmonumenten) obtained the site with the aim of restoring it to extensively grazed grassland.

Table 1. Soil characteristics (0–15 cm depth) of the experimental site

Characteristic	
Organic matter (%)	4·5
Texture < 2 μm (%)	3·4
Texture < 63 μm (%)	17
Texture > 63 μm (%)	80
$CaCO_3$ (%)	0·15
pH (KCl)	5·81
Conductivity (ms m^{-1})	7·26
Total N (mg kg^{-1})	1330
Total P (mg kg^{-1})	1127
Olsen P (mg kg^{-1})	110
0·01 M $CaCl_2$ extraction	
P (mg kg^{-1})	5·1
Na (mg kg^{-1})	8·2
K (mg kg^{-1})	75
Mg (mg kg^{-1})	63

EXPERIMENTAL DESIGN

In April 1996, the experimental field (50×100 m^2) was treated with a cultivator and soil samples were collected from the top 15 cm layer (1600 cores of 3 cm diameter, giving a total of 160 kg fresh soil). The chemical analyses were performed within a global testing programme for analytical laboratories according to Novozamsky *et al.* (1984). The soil characteristics are presented in Table 1. The soil can be characterized as a loamy sand with a relatively high proportion of soil particles larger than 63 μm, slightly acid and with relatively high total amounts of nutrients. The experimental treatments were organized in a randomized block design with five blocks as replicates. Within each block, there were four plots of 10×10 m^2, separated by 2 m border rows. Four treatments were installed: continued crop rotation (CCR, a continuation of monocultures of *Hordeum vulgare* and *Fagopyrum esculentum* in 1996 and 1997, respectively); natural colonization by spontaneously establishing plants, mostly arable weeds present in the seedbank (naturally colonizing plant species, NC); and the introduction of a low (four) or high (15) plant species diversity treatment by sowing mixtures of later-successional grasses, legumes and other dicots (LD and HD, respectively). The plant species used for the LD and HD treatments are characteristic for later successional stages in the area (Table 2). Each of the replicates of the LD treatment were sown with a different combination of two grasses, one legume and another forb, to avoid studying species effects instead of effects of diversity, as discussed by Huston (1997). All HD plots were sown with the same combination of 15 plant species (five grass species, five legumes and five species of other forbs). The seed batches used for establishing the low- and high-diversity mixtures consisted of the same total number of seeds per m^2 (grasses, 2500; legumes, 500; other forbs, 500). Only one species with heavy seeds (*Vicia cracca* L.) was downscaled to 100 seeds per m^2, to avoid it becoming dominant. The seeds were mixed with sand to facilitate equal sowing. After sowing, the plots were harrowed to bury the seeds into the surface layer. The CCR plots also received 300 kg ha^{-1} fertilizer (20% N as NH_4NO_3 and 14% P_2O_5) and 5000 L ha^{-1} dried cow manure pellets every spring. Since the experimental site was situated in an area with high natural grazing pressure (horses, deer and wild boar), a fence was erected to exclude these large herbivores. The border rows between the plots were mown and cultivated regularly. Every year at peak standing biomass (July–August), the vegetation was recorded at 12 permanent 1 m^2 subplots within each 10×10 m^2 replicate plot and the above-ground biomass was determined by clipping 225 cm^2 adjacent to each of the subplots. At the end of each growing season, the above-ground vegetation of all plots was mown and removed. For more details on the experimental design, see Van der Putten *et al.* (2000).

Table 2. Plant species used for the sowing experiments

Grasses	Legumes	Forbs
Phleum pratense L.	*Trifolium arvense* L.	*Tanacetum vulgare* L.
Poa pratensis L.	*Trifolium pratense* L.	*Hypericum perforatum* L.
Agrostis capillaris L.	*Trifolium dubium* L.	*Linaria vulgaris* L.
Anthoxanthum odoratum L.	*Lotus corniculatus* L.	*Hypochaeris radicata* L.
Festuca rubra L.	*Vicia cracca* L.	*Plantago lanceolata* L.

NEMATODE SAMPLING

Soil samples were taken twice each year (April and September), starting in 1996. In each 10×10 m^2 plot, 24 cores (diameter 17 mm) were taken in a regular pattern from the top 10 cm and mixed. After mixing the 24 cores, one subsample of 100 g was used for analysing soil water content and another subsample of 100 g was used to extract nematodes. The soil water content was determined by drying at 105 °C until constant weight. Nematodes were extracted by a modified Oostenbrink elutriator (Oostenbrink 1960). The total number of nematodes was counted and expressed per 100 g dry soil. Nematodes were heat-killed and fixed in 4% formalin, after which a minimum of 150 nematodes were identified at 400–1000 × according to Bongers (1988) and allocated to feeding groups according to Yeates *et al.* (1993).

STATISTICAL ANALYSIS

The complete dataset was analysed by analysis of variance (ANOVA) to test for main treatment effects. If necessary, logarithmic transformations were applied to meet assumptions of normality and homogeneity of variances. Tukey's multiple range test was employed to test for differences among treatments. Furthermore, the data were subjected to redundancy analysis (RDA), performed on square-root-transformed data with blocks taken into account as covariates, using the CANOCO for Windows program (Microcomputer Power 113, Ithaca, NY, USA) (Ter Braak & Smilauer 1998).

Table 3. Vegetation characteristics in 1996 and 1997: total number of plant species, number of non-sown plant species and above-ground biomass (means ± SE), $n = 5$

	Total number of plant species		Number of non-sown plant species		Above-ground biomass (gm^{-2})	
Treatment	1996	1997	1996	1997	1996	1997
NC	12·7 (± 2·0)	11·8 (± 2·3)	12·7 (± 2·0)	11·6 (± 2·3)	259 (± 15)	393 (± 25)
LD	15·9 (± 2·0)	9·9 (± 3·4)	12·3 (± 2·2)	5·6 (± 3·4)	347 (± 25)	649 (± 35)
HD	21·9 (± 2·0)	13·3 (± 2·0)	10·9 (± 1·7)	2·0 (± 1·3)	335 (± 18)	912 (± 30)

Since the CCR was sown with a commercial agricultural crop and kept free from weeds, there were no measurements on the number of plant species.

Results

VEGETATION DEVELOPMENT

From 1996 to 1997, in all treatments except CCR (which was kept free from weeds), the dominance of perennial plant species, total cover and associated above-ground biomass production increased (Table 3). The NC plots were characterized by a number of naturally colonizing weedy species, such as *Erigeron canadensis* L., *Vicia sativa* L., *Cirsium arvense* L., *Rumex acetosella* L. and *Myosotis arvense* L., which became strongly suppressed in the LD and HD plots. On average, this suppression was most effective in the HD treatment, since it was more dependent on the specific mixture of plant species in the LD plots. Therefore, the vegetation treatments NC, LD and HD resulted in three distinct plant communities, both in species composition and in diversity.

DIFFERENCES BETWEEN THE NEMATODE COMMUNITIES

During the first 2 years of the experiment, more than 30 different nematode taxa were identified. The total number of nematodes ranged from 2000 to 6500 per 100 g dry soil and clearly indicated that, irrespective of treatment, there was a sharp increase from April 1996 until September 1996, after which the total numbers declined again (Fig. 1). Plant parasitic nematodes were the most dominant trophic group and showed the most sensitive response to the experimental treatments (Tables 4 & 5). The ectoparasitic *Paratylenchus* (Fig. 2) and the endoparasitic *Pratylenchus* were mainly responsible for these results, since they made up 70–90% of the plant-feeding nematode population. Final numbers were significantly lower in the CCR plots than in the LD and HD plots. The main difference between the CCR and the NC, LD and HD treatments was that *Paratylenchus* numbers remained high (±80%) in the latter three treatments. *Paratylenchus* was slightly less dominant (±60%) in the CCR plots, while both *Pratylenchus* (±20%) and *Tylenchorhynchus* (±15%) were more abundant. During the first 2 years, differences between densities among the plant parasitic nematodes found in NC, LD and HD were smaller than when these three treatments were compared to CCR (Tables 4 & 5).

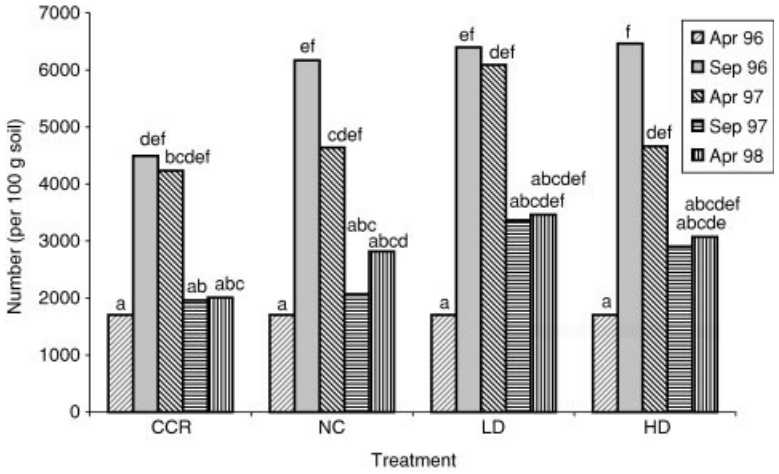

Fig. 1. Mean total number of nematodes per 100 g dry soil in the experimental treatments CCR, NC, LD and HD from September 1996 to April 1998. Means with the same letters were not significantly different according to a least significant difference (LSD) test ($P < 0·05$).

Nematode taxa belonging to the other trophic groups (bacterial feeding, hyphal feeding, carnivorous and omnivorous nematodes) were less abundant than the plant-feeding nematodes, and their numbers showed less changes in time as well as between the different treatments (Tables 4 & 5). However, some specific genera did reflect a sensitive response to the vegetation manipulations. The bacterial feeding *Acrobeloides* and *Acrobeles* showed trends similar to those found for the dominant plant-feeding nematodes *Paratylenchus* and *Pratylenchus* (i.e. a strong increase at first followed by a decline). During the experiment, the number of individuals belonging to some genera, such as *Plectus* and *Diphterophora* (Fig. 3), increased significantly in the NC, LD and HD treatments compared with the CCR plots. However, plant community manipulation had no significant effects at the abandoned plots.

The redundancy analysis also indicated significant differences in the nematode communities between the treatments. The nematode communities were far more different at the start of the experiment and in the CCR plots than in the other three treatments (NC, LD and HD) (Fig. 4). There was no significant difference between the nematode communities of the LD or HD treatments. The first two ordination axes together explained 17% of the total variability. Only the 15 nematode taxa

Table 4. Nematode community (number per 100 g dry soil) at the start (April 1996) and in CCR and NC plots from September 1996 to April 1998

	Start Apr. 96	CCR Sept. 96	CCR Apr. 97	CCR Sept. 97	CCR Apr. 98	NC Sept. 96	NC Apr. 97	NC Sept. 97	NC Apr. 98
Plant feeding									
Ecphyadophora	0	0	0	9	5	0	0	0	6
Pratylenchus	165	826	460	59	90	491	229	96	95
Tylenchidae	71	60	130	69	112	132	103	74	50
Tylenchorhynchus	82	334	343	184	210	267	106	87	120
Total*	820	2332	1733	901	767	4549	2989	1340	1315
Bacterial feeding									
Acrobeles	75	265	149	116	77	227	165	104	194
Acrobeloides	54	587	285	49	43	237	121	38	121
Cephalobus	17	50	55	26	48	18	67	9	12
Cervidellus	0	7	0	0	0	0	5	0	0
Chiloplacus	4	13	15	7	14	26	3	4	5
Eucephalobus	66	234	286	122	82	126	88	17	91
Heterocephalobus	86	130	250	80	147	98	181	36	81
Panagrolaimus	2	20	8	54	18	0	6	16	5
Plectus	66	105	296	135	139	50	117	55	207
Prismatolaimus	2	18	83	19	40	41	153	12	52
Rhabditidae	271	249	489	178	278	328	288	127	144
Teratocephalidae	9	31	22	17	18	70	20	16	19
Wilsonema	0	0	0	7	3	7	0	0	3
Total	652	1710	1975	818	926	1235	1227	440	951
Hyphal feeding									
Aphelenchus	18	267	353	108	136	150	207	61	170
Pseudhalenchus	50	29	24	49	3	36	12	13	5
Total	69	307	397	159	148	198	252	188	318
Omni-carnivores									
Mononchidae	2	5	5	2	18	20	4	8	22
Dorylaimidae	144	130	125	81	149	166	165	92	212
Total	146	135	130	83	167	186	169	100	234

*Data for total number of nematodes, *Paratylenchus* and *Diphterophora* are shown in figures.

Table 5. Nematode community (number per 100 g dry soil) in LD and HD

	LD Sept. 96	LD Apr. 97	LD Sept. 97	LD Apr. 98	HD Sept. 96	HD Apr. 97	HD Sept. 97	HD Apr. 98	ANOVA analyses		
									Treatment	Time	Interaction
Plant feeding											
Ecphyadophora	0	0	8	3	0	7	3	5			
Pratylenchus	268	171	104	41	285	81	30	19	***	***	
Tylenchidae	194	134	88	67	72	47	110	44			
Tylenchorhynchus	480	254	276	358	328	257	199	279	***	**	
Total	4758	3405	2071	2150	4668	3093	1595	1659	***	***	
Bacterial feeding											
Acrobeles	234	196	134	97	282	257	166	132	**		
Acrobeloides	184	186	62	71	291	205	70	74	***		
Cephalobus	37	82	16	26	8	45	13	14			
Cervidellus	0	0	0	0	0	0	0	0			
Chiloplacus	15	3	2	9	22	17	0	22			
Eucephalobus	148	125	82	74	143	42	36	59	**	**	**
Heterocephalobus	113	684	87	80	55	66	87	75			
Panagrolaimus	15	0	20	8	8	11	36	33	*	**	
Plectus	94	105	123	140	77	128	180	194			
Prismatolaimus	18	89	34	30	39	81	19	46	***		
Rhabditidae	300	339	203	171	333	337	195	232	*	***	
Teratocephalidae	61	55	37	50	29	17	40	40			
Wilsonema	0	0	0	0	0	6	12	5			
Total	1219	2104	831	769	1288	1228	859	944			
Hyphal feeding											
Aphelenchus	212	360	187	162	235	241	174	218	***		
Pseudhalenchus	54	98	32	40	72	0	70	43	*		
Total	296	458	306	304	313	251	316	319			
Omni-carnivores											
Mononchidae	0	3	5	12	5	11	4	0			
Dorylaimidae	125	119	148	228	188	76	130	151			
Total	125	122	154	240	193	88	134	151			

Asterisks indicate significant effects of treatment, time or their interaction: *$0{\cdot}05 > P > 0{\cdot}01$; **$0{\cdot}01 > P > 0{\cdot}001$; ***$P < 0{\cdot}001$.

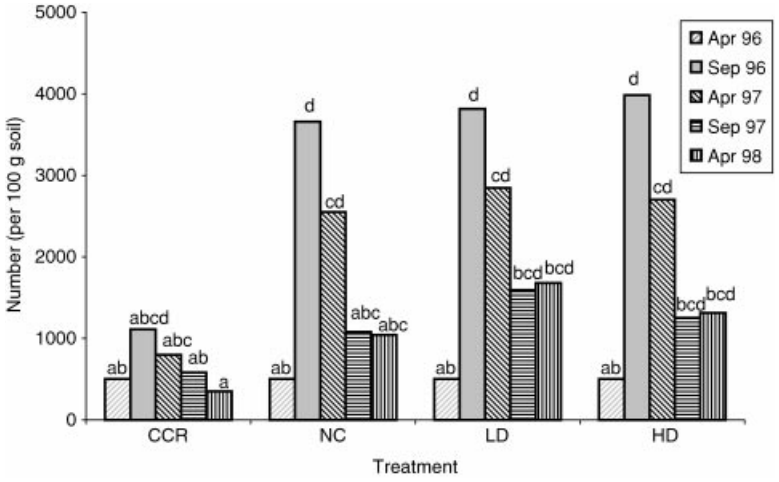

Fig. 2. Abundance of *Paratylenchus* (number per 100 g dry soil) in the experimental treatments CCR, NC, LD and HD from September 1996 to April 1998. Means with the same letters were not significantly different according to a LSD test ($P < 0{\cdot}05$).

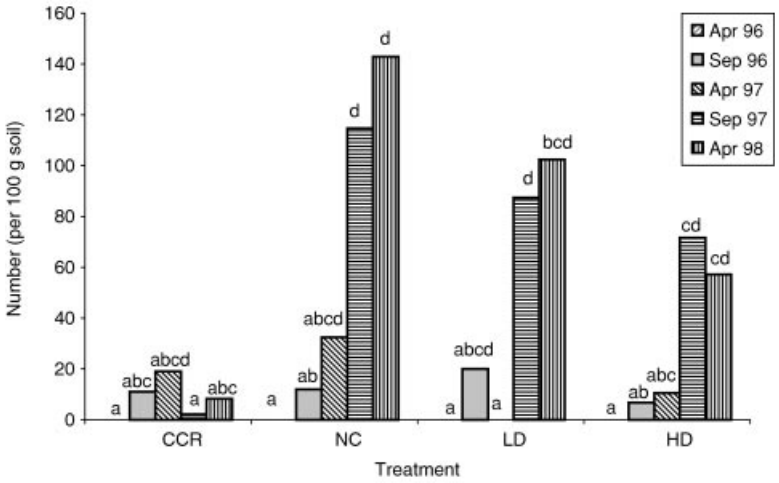

Fig. 3. Abundance of *Diphterophora* (number per 100 g dry soil) in the experimental treatments CCR, NC, LD and HD from September 1996 to April 1998. Means with the same letters were not significantly different according to a LSD test ($P < 0{\cdot}05$).

with the strongest relation to the treatments are shown. The abundancy of *Pratylenchus*, Rhabditidae, *Eucephalobus* and Cephalobidae was distinctly higher at the start and in the CCR treatment than in the NC, LD and HD treatments. As compared with the start and the CCR treatment, the NC, LD and HD nematode communities were mainly characterized by high densities of *Paratylenchus* (plant-feeding) and *Diphterophoridae* (hyphal feeding).

Discussion

At the start of the diversity experiment, the nematode community of the abandoned arable land was dominated by a few genera of plant-feeding nematodes and, to a lesser extent, by some genera of bacterial feeding nematodes, which is usual for agricultural land (Wasilewska 1979; Freckman & Ettema 1993; Lavelle *et al.* 1995; Wardle & Lavelle 1997; Boag & Yeates 1998). Plant-feeding nematodes, which are linked more directly to

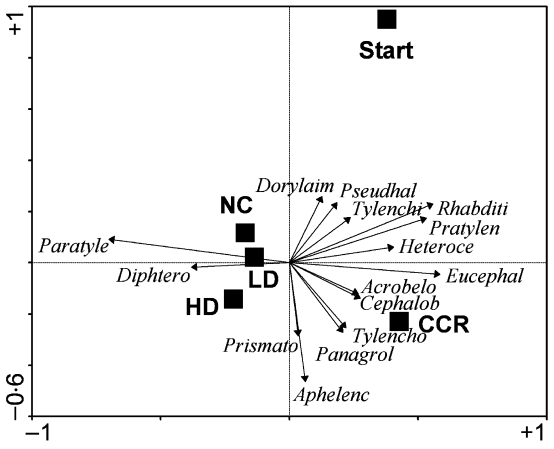

Fig. 4. Ordination diagram from RDA displaying the difference in species composition of nematode community between the start of the experiment and the treatments CCR, NC, LD and HD. First and second ordination axes are displayed. Paratyle = *Paratylenchus*; Rhabditi = Rhabditidae; Pratylen = *Pratylenchus*; Eucephal = *Eucephalobus*; Cephalob = *Cephalobus*; Prismato = *Prismatolaimus*; Tylencho = *Tylenchorhynchus*; Diphtero = Diptherophoridae; Acrobelo = *Acrobeloides*; Dorylaim = Dorylaimidae; Pseudhal = *Pseudhalenchus*; Tylenchi = Tylenchidae; Heteroce = *Heterocephalobus*; Panagrol = *Panagrolaimus*; Aphelenc = *Aphelenchus*.

vegetation than other feeding groups of nematodes, reflected the rapid changes in the (manipulated) vegetation much more strongly than species from other functional groups. The prolonged growing season in the abandoned plots (as compared with the summer barley crop) and the appearance of many different natural plant species might have stimulated resource availability (Rossner 1979). These factors might explain the strong response of root-feeding nematodes, also observed in set-aside land (Boag 1992).

During the following 1·5 years, the manipulated plant communities diverged, with HD plots having very few weedy species and a high biomass, whereas NC plots had the lowest biomass (Lepš *et al.* 2000). In LD plots, the biomass and contribution of weedy species to the plant community depended on the composition of the plant community (Van der Putten *et al.* 2000). Despite the enhancement of plant biomass with time and the differences among the experimental plant communities, population densities of the plant-feeding species decreased. The increase of perennial plants and the subsequent development of deeper root systems in combination with the ageing of the roots may have contributed to resource limitation for the plant-feeding nematodes (Mattson 1980).

Although the nematode community composition and diversity consistently indicated significant differences between CCR and the other three treatments, there were hardly any significant differences between the NC, LD and HD plant communities. This is in contrast to studies on above-ground arthropods by Siemann (1998), Siemann *et al.* (1998) and Koricheva *et al.* (2000), who showed quick responses of above-ground insects to plant diversity treatment. However, insect communities

in recently sown plots can still differ strongly from those in longer-existing vegetation (Mortimer, Van der Putten & Brown 1999). Our data show that there is a lag time in the response of the soil food web to plant diversity treatments as compared with the above-ground food web. Whether or not such a lag time may also occur after experimental and selective removal of plant species, as performed by Wardle *et al*. (1999), cannot be predicted from the present data.

The unresponsiveness of the bacterial feeding and hyphal feeding nematodes parallel soil microbial processes (net N mineralization, short-term nitrification, respiration and arginine ammonification), microbial biomass C and N (fumigation–incubation) and colony-forming units of the major microbial groups in the same experimental field (Malý *et al*. 2000). Lower trophic levels in soil food webs are strongly bottom-up controlled (De Ruiter, Neutel & Moore 1995). The yearly mowing of the experimental plots will slow down eventual microbial shifts, because the input of organic matter in the soil comes mainly from the decomposition of roots, which can be a very slow process (Mohr *et al*. 1998). In experimental plant diversity plots in Switzerland, plant community composition did affect some soil processes. These effects were mainly due to larger differences in plant diversity treatments (including one- and 32-species mixtures) and the role of legumes in some treatments (Spehn *et al*. 2000). Indeed, some specific plant species have strong effects on soil biological properties (Bardgett *et al*. 1999b).

The poor dispersal and colonization abilities of soil organisms such as nematodes (Ricklefs & Schluter 1993) may explain their unresponsiveness compared with above-ground insects. In natural chronosequences, colonization may take several decades (Yeates 1987; De Goede & Bongers 1994; Wasilewska 1997) – even longer in the case of abandoned land surrounded by completely different biotopes. Correlations between plant diversity and soil insects have been reported (Murdoch, Evans & Peterson 1972; Southwood, Brown & Reader 1979; Lawton 1983; Strong, Lawton & Southwood 1984) due to these insects' ability to get dispersed during their above-ground life stages (Mortimer, Van der Putten & Brown 1999).

It is still questionable how tightly linked plant species diversity and soil nematode diversity are. In a latitudinal comparison of mature systems, nematode diversity did not increase towards the equator, unlike plants and many other organisms (Boag & Yeates 1998). Species groups above or below ground could follow different trends of diversity, even though their ecological linkages are close. Apparently, plant traits are more important than plant diversity in determining the abundance and activity in soil *per se* (Bardgett, Wardle & Yeates 1998; Bardgett *et al*. 1999a; Wardle *et al*. 1999). Long-term studies on the development of the soil community of biodiversity plots are needed to assess when the microbial shift from a bacteria-dominated to a fungus-dominated soil community occurs, how the higher trophic levels respond and how this is affected by plant treatments and plant successional development.

The results from this study have important implications for nature restoration strategies. Firstly, short-term changes in the nematode community seem much more dependent on the history of crop rotation and associated management practices than on changes in (experimental) plant communities. The previous years of conventional agriculture will therefore affect the start of nature restoration. Secondly, since plant parasites can become dominant after land abandonment, initial vegetation development might be affected by herbivorous nematodes in a way similar to that demonstrated for soil insects by Brown & Gange (1992). Finally, the colonization of newly created nature reserves is a problem not only for many plant species (Bakker & Berendse 1999) but also for nematode species and perhaps many other soil inhabitants. Nature restoration strategies should therefore include methods on how to restore soil communities.

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