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Effects of sod-cutting on the nematode community of a secondary forest of *Pinus sylvestris* L.

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Abstract Atmospheric S and N compounds accumulate in the surface layers of the forest soil environment, where they affect soil biota and nutrient availability for tree growth. In addition to measures to reduce the input of atmospheric deposition, removal of the ectorganic layers by sod-cutting may contribute to the recovery of the soil ecosystem. In this study, we examined the effects of sod-cutting on the nematode fauna of a Scots pine forest, 1 and 3 years after treatment. Sod-cutting reduced the total numbers of nematodes, nematode taxa, and Maturity Index. The first taxa that colonized the newly developing organic layers after sod-cutting had low colonizer-persister (c-p) values, and appeared to have originated from the tree canopy and mineral soil. Colonization, presumably from nearby untreated plots, was observed 3 years after the sod-cutting. The initial (after 1 year) nematode community of the new organic layer comprised hyphal-, bacterial-, and algal-feeding nematodes, whereas plant-feeders, predators, and omnivores were not detected. The composition of the nematode fauna in the ectorganic layers 15 and 39 months after sod-cutting was highly similar to that of the nematode fauna of the early stages of a primary succession of Scots pine forest in a reference area in the Netherlands. In the mineral soil only insect parasites were negatively affected by sod-cutting.

Key words Nematode community · Sod-cutting · Scots pine · Trophic structure · Canopy fauna · Maturity Index · Forest management

Introduction

Forests are among the terrestrial ecosystems that are exposed to the highest levels of atmospheric deposition of pollutants. Compared to other ecosystems they have a large receptive surface (Erisman and Heij 1991) and accumulate relatively high quantities of atmospheric S and N (van Breemen et al. 1982; Nihlgård 1985; Roelofs et al. 1985; Grennfelt and Hultberg 1986). In Europe, forest decline has been recognized as a significant problem (Zöttl and Hüttl 1991; Innes 1993) of high political interest (Nationaal Milieubeleidsplan 1990; Natuurbeleidsplan 1990; Heij et al. 1991). Measures to reduce the input of atmospheric pollutants are required to counteract the deterioration of forest ecosystems. The increased level of N compounds in soil has direct and/or indirect effects on soil microflora (Arnolds 1988, 1991) and fauna populations (van Straalen et al. 1988; Verhoef and Meintser 1991; De Goede and Dekker 1993; Hogervorst et al. 1993), causes an imbalance in the availability of nutrients for tree growth (Roelofs et al. 1985; Houdijk 1990; Innes 1993), and can seriously delay forest recovery (Klap and Schmidt 1992). Many of these compounds accumulate in the ectorganic horizon of the forest soil. Removal of this ectorganic horizon by sod-cutting may contribute to the recovery of the soil ecosystem (Klap and Schmidt 1991). Sod-cutting (i.e., removal of the litter, fermentation, and humus layers, and herb vegetation) in secondary Scots pine forests positively influenced numbers of ectomycorrhizal sporocarps and species (Baar and Kuyper 1993; Baar 1995).

In the present study, the effects of sod-cutting on soil nematode fauna were investigated. Changes in the composition of the nematode fauna of the ectorganic layer and mineral soil of a secondary Scots pine forest were studied 15 and 39 months after treatment. The following hypotheses were tested:

(1) Sod-cutting will result in significant shifts in the trophic compostion of the nematode community. Besides removal of the ectorganic layer, the herb vegetation and a major part of the rooting system of the Scots pine is also

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removed. This will result in reduced numbers of plant-feeding nematodes. The nematode fauna of the newly developing ectorganic layer will be dominated by hyphal-feeding nematodes, as the initial stages of decomposition of Scots pine needles are dominated by fungi (Kendrick and Burges 1962; Ponge 1991). Plant-feeding nematodes will be absent until the ectorganic layer is recolonized by herbs or Scots pine roots.

(2) The nematode fauna of the newly developing ectorganic layers in the sod-cut plots will initially consist of nematode taxa with a low c-p value (Bongers 1990). This nematode fauna will consist of taxa occurring in tree canopies, the mineral soil of the sod-cut plots, and/or the ectorganic layer of nearby control plots. Taxa restricted to the ectorganic layers of the control plots which do not occur in the tree canopy will colonize the sod-cut plots from the edges at a relatively low rate.

Materials and methods

Study area

The study site, a Scots pine (*Pinus sylvestris* L.) stand (52°49′N, 6°26′E) planted in 1924, is located in the nature reserve Dwingelderveld, about 4 km east of Dwingeloo, the Netherlands. It is a siliceous, mesic Typic Udipsamment (Soil Survey Staff 1975) with pH($CaCl_2$) in the ectorganic layer and 0–5 cm mineral soil of 2.9 and 3.7 respectively. In 1991, $CaCl_2$ soluble concentrations (μg/g) of total N, NH_4^+, NO_3^-, and P were, respectively 54.3, 30.2, 2.7, 7.3 in the ectorganic layer and 7.7, 3.1, 1.0, 0.2 in the 0–5 cm mineral layer (J. Baar, personal communication, 1994). Tree density was 30 per 1000 m^2, and the canopy cover was 5–10%. The herb vegetation cover of the control plots was 100%, consisting mainly of *Deschampsia flexuosa* (L.) Trin, *Hypnum cupressiforme* Hedw., *Pleurozium schreberi* (Brid.) Mitt., and *Brachythecium rutabulum* (Hedw.) Schmip., *Dryopteris dilatata* (Hoffm.) A. Gray, *Dryopteris carthusiana* (Vill.) H.P. Fuchs, *Corydalis claviculata* (L.), and *Pseudoscleropodium purum* (Hedw.) Fleisch. ex Broth. occurred in low numbers.

Within the stand, eight adjacent plots (20×20 m each) were established, four on each side of a forest path dividing the stand. In June 1990, the ectorganic layer (litter, fermentation, and humus horizons) and herb vegetation of four plots (two on each side of the forest path) were removed mechanically. The other plots were used as controls. The four plots at each side of the forest path formed a square in which the treatments were positioned diagonally.

Soil sampling and extraction of nematodes

On 16 September 1991 and 6 September 1993, 15 and 39 months after sod-cutting, respectively, the nematode fauna was sampled. From each plot two soil samples were collected with a shallow-profile sampler (internal surface area 36.5 cm^2; Wardenaar 1987), one from the centre and one at 1 m from the edge of the plot. The edge samples were collected in the area where the four plots met. The ectorganic layer of the control plots was divided into litter, fermentation, and humus horizons. The average thickness of these horizons was 1.8, 4.6, and 1.9 cm (n=8), respectively. The ectorganic layer of the sod-cut plots was composed of litter only. In 1991 this ectorganic layer of the sod-cut plots was sampled by hand from 225 cm^2. The mineral soil was sampled to a depth of 5 cm and 10 cm in 1991 and 1993, respectively.

Nematode extraction, counting, and processing followed de Goede and Dekker (1993). Nematodes were extracted from whole samples, and extractions were completed within 2 days of sampling.

Canopy samples

On 2 December 1993, weathered needles (dead, brown needles attached to twigs or unattached but resting on twigs or in tree axils) were collected by hand from the canopy (at ≥6 m above the ground) of eight Scots pine trees. Within each plot one tree was selected and from each tree one needle sample was collected in a plastic bag. On the day of sampling, nematodes were extracted using a modification of the cottonwool filter method (Schouten and Arp 1991). The needles were spread on a single cottonwool filter (Hygia Milac Sandwich discs of cotton/non-woven for manual milk filtration, Hartmann B.V. Nijmegen, diameter 220 mm), mounted in a supporting sieve, and placed in an extraction dish filled with 150 ml tap-water. After 24 and 72 h of extraction, the nematodes were identified and counted by inverted microscopy (magnification ×400).

Statistical analyses

The taxonomic classification and the classification of the genera into feeding groups followed Bongers (1988) and Yeates et al. (1993), respectively. The Maturity Index and Plant Parasite Index were calculated according to Bongers (1990). The c-p and plant-parasite (p-p) value distributions (de Goede et al. 1993a) in the nematode samples were calculated from the c-p scores of non-plant feeders and plant feeders, respectively, as given by Bongers (1990). Changes in generic abundance, feeding groups, and community indices due to sod-cutting were tested by univariate repeated measures analysis (SPSS/PC+V3.1; SPSS Inc., Chicago, Ill, USA) on log-transformed data. Only differences significant at $P \leq 0.05$ are discussed here. To avoid the chance effects of sod-cutting through testing individual items on taxa or indices lists, the Bonferroni adjustment of confidence limits (Snedecor and Cochran 1989) was applied. The overall probability for determining significant effects for a group of items on a list was set at $P<0.05$, resulting in a probability of significant effects for individual items on such lists of $P<0.05/N$, where N is the number of items on the list, lists may comprise taxa, trophic groups, c-p groups, or p-p groups.

Results

A total of 46 taxa was found in the course of the experiment. The following taxa were identified to species: Plant-feeders: *Rotylenchus robustus, Cephalenchus hexalineatus, Ecphyadophora* cf. *quadralata, Tylenchorhynchus microphasmis, Filenchus ditissimus, F. discrepans, F. helenae, Malenchus cognatus;* Algal-, lichen-, or moss-feeders: *Laimaphelenchus penardi;* Fungal-feeders: *Ditylenchus intermedius, D. myceliophagus, Aphelenchoides* 1 (female body length: 177–190 μm), *A.* cf. *saprophilus* A, *A.* cf. *saprophilus* B, *A. composticola, A. fragariae, Diphtherophora brevicollis, Tylolaimophorus typicus*; Bacterial-feeders: *Bunonema richtersi, B. reticulatum, Panagrolaimus subelongatus, P. paetzoldi, P. rigidus, Pristionchus lheritieri, Eumonhystera hungarica, Heterocephalobus elongatus, Acrobeloides nanus, Cervidellus serratus, Drilocephalobus moldavicus, Plecuts longicaudatus, P. acuminatus, P. parvus, P. geophilus, Wilsonema otophorum, Halicephalobus minutus, Teratocephalus tenuis, T. terrestris, Metateratocephalus crassidens, Prismatolaimus dolichurus, P. intermedius*; Animal predators: *Clarkus papillatus*; Unicellular eucaryote feeders: *Achromadora ruricola*; Insect parasites: *Steinernema bibionis, S. intermedius*; Omnivores: *Eudorylaimus carteri.*

The composition of the nematode fauna of one of the litter samples from the control plots deviated strongly from the others, and was therefore excluded from the analyses. It was highly dominated by two taxa belonging to c-p 1 (*Protorhabditis* 60% and *Pristionchus* 21%). The sample was collected under a herb vegetation composed of *B. rutabulum*, whereas all other samples were collected under D. *flexuosa*.

Effects of sod-cutting on the nematode fauna of the litter horizon

Fifteen months after sod-cutting, a new ectorganic layer (classified as litter) of approximately 0.5 cm had developed. The thickness of this layer increased to an average of 1.8 cm (n=8), 39 months after sod-cutting. On both sampling dates, the total number of nematodes (per dm^2) and the average number of taxa were reduced in the sod-cut plots (Table 1). *Eudorylaimus* and *Prodesmodora* were present in the litter horizon of the control plots, but were not detected 15 months after sod-cutting (Table 1). After 39 months, *Eudorylaimus* had colonized the ectorganic layer of the sod-cut plots. Densities of *Malenchus* and *Ditylenchus* were reduced 15 and 39 months after sod-cutting. In 1991, *Achromadora* was rare or absent in the litter horizons of both the control and sod-cut plots. However, in 1993 it reached high frequencies in the control plots, but was not detected in the sod-cut plots.

A significant increase after sod-cutting was found for *Laimaphelenchus*. *Laimaphelenchus* was not detected in the control plots, but was present 15 and 39 months after sod-cutting in four and two of the sod-cut plots, respectively.

The plant-feeding nematode community of the litter horizon of the control plots consisted almost exclusively of epidermal and root-hair feeding nematodes (Table 2). Sod-cutting reduced their numbers significantly, and almost eliminated them from the ectorganic layer. Total

Table 1 Nematode numbers (dm^{-2}) in the litter horizon of a secondary Scots pine forest 1 and 3 years after sod-cutting (*SC*) and in the control. *Sig.* Univariate repeated-measures analysis was used to determine significant differences between objects (control versus treatment, *a*), within objects (between years, *b*), and for the interaction treatment×year (*c*); Bonferroni adjustment of confidence limits was used with an overall confidence of P<0.05

Taxon	1991				1993				Sig.
	Control		SC		Control		SC		
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Achromadora	0	0	2	5	612	811	0	0	a, b, c
Arcrobeloides	14	37	0	0	0	0	60	147	
Aphelenchoides	872	905	394	277	2546	2503	3457	1862	
Aporcelaimellus	0	0	0	0	0	0	10	27	
Bunonema	31	38	0	0	644	566	402	627	
Cephalenchus	1	4	0	0	0	0	0	0	
Clarkus	219	351	0	0	55	111	0	0	
Deladenus	22	25	92	100	0	0	13	36	b
Ditylenchus	195	114	7	14	1440	1371	122	138	a, b
Drilocephalobus	4	12	0	0	0	0	0	0	
Eudorylaimus	186	198	0	0	293	219	234	194	a, b, c
Eumonhystera	0	0	1	4	128	217	10	27	
Filenchus	15	25	0	0	674	1654	6	18	
Halicephalobus	2	5	0	0	0	0	0	0	
Heterocephalobus	174	268	37	67	1944	2365	16	31	
Laimaphelenchus	0	0	386	226	0	0	29	35	a
Malenchus	365	458	1	2	775	795	0	0	a
Mesodorylaimus	121	251	0	0	427	652	0	0	
Metateratocephalus	27	37	0	0	775	390	647	1030	
Nototylenchus	118	333	0	0	0	0	35	73	
Panagrolaimus	0	0	10	15	447	546	434	634	b
Plectus	561	479	284	220	2675	1078	918	1139	
Prismatolaimus	6	12	3	6	8	22	10	28	
Pristionchus	0	0	0	0	42	111	0	0	
Prodesmodora	176	238	0	0	8	22	0	0	a
Protorhabditis	7	20	0	0	579	1311	3	9	
Teratocephalus	2	7	0	0	186	203	0	0	
Tylocephalus	0	0	0	0	13	35	0	0	
Tylolaimophorus	2	5	0	0	0	0	10	28	
Tylencholaimus	33	86	0	0	0	0	0	0	
Tylenchus	4	11	0	0	0	0	0	0	
Wilsonema	20	21	0	0	26	70	0	0	
Total number	3205	1545	1232	636	14550	7936	6486	3239	a, b
Number of taxa	11.9	1.6	6.9	0.6	12.7	1.1	8.5	2.7	a

Table 2 Trophic group, c-p and p-p distribution, Maturity Index (*MI*), and Plant Parasite Index (*PPI*) in the litter horizon (numbers dm^{-2} $horizon^{-1}$) and mineral soil (numbers dm^{-2} cm^{-1}), 1 and 3 years after sod-cutting (*SC*) and in the control (*C*). Plant-feeding nematodes: *c* semi-endoparasite, *d* ectoparasite, *e* epidermal and root-hair feeder. *Unicel. euc.* Unicellular eucaryote. For further explanations, see Table 1

	Litter					Mineral soil				
	1991		Sig.	1993		1991		Sig.	1993	
	C	SC		C	SC	C	SC		C	SC
Plant feeding c	0	0		0	0	57	6		54	10
Plant feeding d	1	0		0	0	82	11		105	30
Plant feeding e	380	1	a	1449	6	53	18	b	109	39
Plant feeding f	4	386	a	0	29	0	0		0	0
Plant feeding c–e	381	1	a	1449	6	192	36	b	269	79
Hyphal feeding	1242	494	b	3986	3637	134	75	b	194	162
Bacterial feeding	1052	346	b	7531	2560	198	188	b	570	398
Animal predation	219	0		55	0	0	0		0	0
Unicel. euc. feeder	0	2	a, b c	612	0	0	0		0	0
Insect parasitic	0	0		0	0	13	0	c	17	8
Omnivorous	307	0	a, b, c	721	244	19	3		6	52
c-p 1	38	11	b	1840	849	5	1		7	17
c-p 2	1986	1201	b	8644	4651	250	230	b	595	457
c-p 3	241	16	a, b	1644	726	77	31	b	162	85
c-p 4	438	0	a, b, c	349	234	8	3		3	52
c-p 5	121	0		427	10	11	<1		3	1
p-p 2	382	1	a	1449	6	55	18	b	116	39
p-p 3	0	0		0	0	107	16		142	40
p-p 4	0	0		0	0	30	1		11	0
MI	2.54	2.00	a, c	2.21	2.10	2.30	2.15	c	2.22	2.40
PPI	2.00	2.00		2.00	2.00	2.74	2.38		2.63	2.57

numbers of fungal-feeding nematodes in the sod-cut plots did not differ significantly from those found in the control plots. On both sampling dates, the fungal-feeding nematodes were the most abundant trophic group in the ectorganic layer of the sod-cut plots. These observations on plant-feeding and hyphal-feeding nematodes in the newly developing ectorganic layer after sod-cutting are consistent with hypothesis 1. Although present in the control plots, no predatory and omnivorous nematodes were detected 15 months after the sod-cutting. Two years later, i.e., 39 months after the sod-cutting, omnivorous nematodes had colonized the litter, but predatory nematodes were still not detected. Algal-feeding nematodes increased significantly after sod-cutting.

The Maturity Index decreased after sod-cutting (Table 2). This decrease was significant after 15 months and was the result of a significantly increased proportion of c-p 2 and decreased proportion of c-p 3–4 (c-p 2 in control and treatment comprised 69 and 97%, respectively; p=0.02). Moreover, sod-cutting resulted in a significantly decreased absolute abundance of c-p 3, while taxa belonging to c-p 4 and c-p 5 were not detected (Table 2). Two years later, the nematode fauna of the ectorganic layer comprised taxa belonging to all five c-p groups and no significant differences were detected between the c-p distributions of the control and sod-cut plots. Nevertheless, c-p 3 still occurred in lower absolute numbers.

The plant-feeding nematodes in the litter horizons all belonged to p-p 2, and were decreased in abundance after the sod-cutting (Table 2).

Effects of sod-cutting on the nematode fauna of the mineral soil

Sod-cutting had a negative effect on the total number (per dm^2 per cm) of nematodes in the mineral soil, and reduced the average number of taxa per sample (Table 3). The effects of sod-cutting on individual taxa were not statistically significant.

The hypothesis that sod-cutting decreases the number of plant-feeding nematodes in the mineral soil could not be confirmed. In the sod-cut plots on both sampling dates the total abundance of plant-feeding nematodes was reduced; this decrease, however, was not statistically significant (P=0.022; Table 2). Also, no significant effects of sod-cutting were detected on the absolute abundances of bacterial- and fungal-feeding nematodes. Insect-parasitic nematodes (i.e., *Steinernema*) were significantly affected by sod-cutting. They were not detected 15 months after sod-cutting, but they were present 2 years later.

The effect of sod-cutting on the Maturity Index depended on the time of sampling after treatment; 15 months after the sod-cutting this index was reduced. However, 2 years later the Maturity Index of the sod-cut plots had increased and was significantly higher than in the control (Table 2). This increase was mainly the result of an increased abundance of c-p 4.

Table 3 Nematode numbers ($dm^{-2}\,cm^{-1}$) in the mineral soil of a secondary Scots pine forest 1 and 3 years after sod-cutting (*SC*) and in the control. For further explanations, see Table 1

Taxon	1991				1993				Sig.
	Control		SC		Control		SC		
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Acrobeloides	83	52	28	43	197	101	211	223	
Aphelenchoides	81	70	50	55	168	122	122	153	
Aporcelaimellus	9	16	<1	1	3	5	1	4	
Bunonema	0	0	0	0	0	0	3	5	
Cephalenchus	2	5	0	0	6	16	0	0	
Cephalobus	1	2	0	0	0	0	0	0	
Cervidellus	21	39	11	25	137	106	40	52	
Deladenus	1	2	<1	1	0	0	0	0	
Diphtherophora	0	0	4	10	0	0	5	8	
Ditylenchus	27	45	11	12	0	0	0	0	
Domorganus	4	12	0	0	14	25	0	0	
Drilocephalobus	6	8	2	6	0	0	1	2	
Ecphyadophora	0	0	0	0	1	3	0	0	
Eudorylaimus	8	9	2	5	3	6	51	49	
Eumonhystera	0	0	0	0	5	10	7	8	
Filenchus	49	78	18	26	108	119	39	40	
Halicephalobus	0	0	0	0	13	26	5	9	
Heterocephalobus	<1	1	1	2	0	0	3	4	
Malenchus	4	10	<1	1	2	5	0	0	
Mesodorylaimus	2	5	0	0	0	0	0	0	
Metateratocephalus	5	8	1	2	30	21	22	14	
Panagrolaimus	0	0	1	2	0	0	1	2	
Plectus	19	23	122	104	40	39	34	24	b
Prismatolaimus	18	14	6	8	80	46	30	24	
Prodesmodora	0	0	<1	<1	0	0	0	0	
Protorhabditis	5	11	0	0	2	5	8	17	
Pseudhalenchus	<1	1	0	0	0	0	0	0	
Rotylenchus	57	101	6	11	54	61	10	22	
Steinernema	13	10	0	0	17	28	8	17	
Teratocephalus	14	48	<1	1	6	8	1	2	
Trichodoridae	30	55	1	3	11	16	0	0	
Tylencholaimus	0	0	1	2	0	0	1	3	
Tylenchorhynchus	50	47	10	17	88	79	30	25	
Tylolaimophorus	25	42	9	23	26	32	22	34	
Wilsonema	12	15	3	5	39	35	29	33	
Total numbers	555	349	301	177	1059	334	699	425	a, b
Number of taxa	15.8	2.5	11.6	3.0	13.5	1.4	13.5	3.2	a

Nematode fauna of the tree canopy

Nine nematode taxa were collected from the needles of Scots pine canopies (Table 4). The most abundant taxa were *Laimaphelenchus, Panagrolaimus*, and *Aphelenchoides*, with relative abundances of 46, 33, and 15%, respectively. Only fungal- and bacterial-feeding nematode taxa were detected (three and six taxa, respectively). The fungal-feeding nematodes comprised 62% of the nematode community. The nematode taxa belonged to the c-p classes 1 (n=3) and 2 (n=6), which made up 34.4 and 65.6% of the nematode community, respectively. The nematode community of the Scots pine needles had a low average Maturity Index of 1.66 (SD 0.231, n=8).

Table 4 Proportion and frequency of nematode taxa of weathered needles collected from the canopy of eight Scots pine trees (*dw* dry weight)

Taxon	Mean	SD	Frequency
Laimaphelenchus	46.32	17.54	8
Panagrolaimus	33.25	22.80	8
Aphelenchoides	15.31	24.59	6
Deladenus	0.71	1.46	3
Acrobeloides	1.14	2.52	2
Plectus	0.91	1.89	2
Eumonhystera	0.78	1.84	2
Heterocephalobus	0.66	1.86	1
Prodesmodora	0.08	0.22	1
Indeterminate	0.75	1.44	3
Total number (g^{-1} dw)	38.6	21.94	

Table 5 Frequency of nematode taxa in the mineral soil and organic horizons of a secondary Scots pine forest, 1 and 3 years after sod-cutting (*SC*) and in the control. *A* c-p or p-p value, *B* trophic group, *1c-e* plant feeding, *1f* algal, lichen, and moss feeding, *2* hyphal feeding, *3* bacterial feeding, *5* animal predation, *6* unicellular eucaryote feeding, *7* insect parasitic, *8* omnivorous, *E* plot edge, *M* plot centre. For further explanations, see Table 2

Taxon	A	B	Mineral soil				Humus		Fermentation		Litter					
			Control		SC		Control		Control		Control		SC			
			91	93	91	93	91	93	91	93	91	93	91		93	
													E	M	E	M
n			8	8	8	8	8	8	8	8	8	7	4	4	4	4
Taxa not detected in mineral soil of control plots																
Laimaphelenchus	2	1f	–	–	–	–	–	–	–	–	–	–	4	4	1	3
Tylenchus	2	1f	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Diphtherophora	3	2	–	–	1	2	–	–	–	–	–	–	–	–	–	–
Nototylenchus	2	2	–	–	–	–	–	–	2	–	1	–	–	–	1	1
Tylencholaimus	4	2	–	–	3	1	1	–	1	–	2	–	–	–	–	–
Acrobeles	2	3	–	–	–	–	1	–	2	–	–	–	–	–	–	–
Bunonema	1	3	–	–	–	2	5	3	6	5	4	7	–	–	3	1
Panagrolaimus	1	3	–	–	3	1	–	–	–	–	–	5	2	2	3	4
Pristionchus	1	3	–	–	–	–	–	–	–	2	–	1	–	–	–	–
Prodesmodora	3	3	–	–	1	–	–	–	–	–	6	1	–	–	–	–
Clarkus	4	5	–	–	–	–	–	–	3	1	5	2	–	–	–	–
Achromadora	3	6	–	–	–	–	–	1	–	2	–	6	–	1	–	–
Taxa present in mineral soil of control plots																
Rotylenchus	3	1c	6	8	3	3	–	2	–	–	–	–	–	–	–	–
Cephalenchus	2	1d	2	1	–	–	–	1	1	–	1	–	–	–	–	–
Ecphyadophora	2	1d	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Tylenchorhynchus	3	1d	7	8	5	6	1	–	1	–	–	–	–	–	–	–
Trichodoridae	4	1d	5	3	1	–	2	–	–	–	–	–	–	–	–	–
Filenchus	2	1e	7	7	6	6	8	7	8	8	3	3	–	–	–	1
Malenchus	2	1e	1	1	1	–	6	1	8	8	7	7	–	1	–	–
Aphelenchoides	2	2	8	8	8	7	8	8	7	8	7	7	4	4	4	4
Deladenus	2	2	1	–	1	–	3	–	2	–	4	–	4	4	–	1
Ditylenchus	2	2	6	–	7	–	7	4	7	8	8	7	1	1	2	4
Pseudhalenchus	2	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Tylolaimophorus	3	2	6	5	4	3	8	6	6	3	1	–	–	–	1	–
Acrobeloides	2	3	8	8	7	8	8	8	8	8	2	–	–	–	1	2
Cephalobus	2	3	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Cervidellus	2	3	4	8	4	6	1	–	1	–	–	–	–	–	–	–
Domorganus	3	3	1	3	–	–	–	5	–	2	–	–	–	–	–	–
Drilocephalobus	2	3	3	–	1	1	3	–	1	–	1	–	–	–	–	–
Eucephalobus	2	3	–	–	–	–	–	–	1	–	–	–	–	–	–	–
Eumonhystera	1	3	–	2	–	5	–	7	–	3	–	3	–	1	1	–
Halicephalobus	2	3	–	2	–	2	3	7	–	5	1	–	–	–	–	–
Heterocephalobus	2	3	1	–	4	3	4	1	5	4	6	4	3	3	1	1
Metateratocephalus	3	3	4	6	2	7	6	8	8	6	4	7	–	–	2	3
Plectus	2	3	7	7	8	8	8	8	8	8	7	7	4	4	4	4
Prismatolaimus	3	3	8	8	7	6	8	8	8	5	2	1	1	1	–	1
Protorhabditis	1	3	2	2	–	2	2	4	3	6	1	3	–	–	–	1
Teratocephalus	3	3	4	3	1	1	3	3	5	6	1	5	–	–	–	–
Tylocephalus	2	3	–	–	–	–	–	–	–	–	–	1	–	–	–	–
Wilsonema	2	3	6	6	4	6	8	8	8	7	5	1	–	–	–	–
Steinernema	–	7	7	4	–	2	4	3	–	2	–	–	–	–	–	–
Aporcelaimellus	5	8	5	2	1	1	2	–	1	–	–	–	–	–	1	–
Mesodorylaimus	5	8	1	–	–	–	1	–	1	–	2	3	–	–	–	–
Eudorylaimus	4	8	6	2	2	7	6	3	7	7	8	6	–	–	3	3

Colonization of the new ectorganic layer

The colonization of the new formed ectorganic layer of the sod-cut plots may take place from the tree canopy, the mineral soil, or from outside the plots. Table 5 presents the frequency of occurrence of the nematode taxa in the control and sod-cut plots per soil horizon. When occurring in the ectorganic layer of the sod-cut plots, populations that were not detected in the mineral soil of the control plots (*Laimaphelenchus, Nothotylenchus, Panagrolaimus, Bunonema,* and *Achromadora*) must have originated from populations present in tree canopy or outside the plots. *Laimaphelenchus* (c-p 2) and *Panagrolaimus* (c-p 1) probably originated from the tree canopy as they occurred on the needles collected in the tree canopy, were found with equal frequency in the centre and edge samples from the sod-cut plots 15 months after sod-cutting, and were not detected in the litter horizon of the control plots 15 months after sod-cutting. Similarly, the populations of *Deladenus* (c-p 2) and *Heterocephalobus* (c-p 2) could also have originated from the tree canopy, but from each taxon one specimen was also found in the samples taken from the mineral soil of the control plots (n=16 samples). In contrast, *Bunonema* (c-p 1) most probably colonized the sod-cut plots from the adjacent plots, as *Bunonema* was not found on the needles from tree canopy, was first detected only after 39 months in the sod-cut plots, and was found most frequently in the edge samples. *Clarkus* (c-p 4) and *Prodesmodora* (c-p 3) two taxa which also must have colonized the sod-cut plots from adjacent plots, were still not found in the newly established ectorganic layer of the sod-cut plots 39 months after treatment. They were both common in the litter horizon but were not present in the mineral soil of the control plots or in the tree canopy.

Eight taxa (*Aphelenchoides, Plectus, Ditylenchus, Filenchus, Wilsonema, Teratocephalus, Metateratocephalus,* and *Eudorylaimus*) were common in both the litter horizon and mineral soil of the control plots. The results indicate that they colonized the newly developing ectorganic layer at different rates, but their colonization route is not clear. Fifteen months after the sod-cutting, *Aphelenchoides* (c-p 2) and *Plectus* (c-p 2) occurred with similar frequencies to the litter horizons of the control plots, *Ditylenchus* (c-p 2) was found with a significantly lower frequency in the sod-cut plots (χ^2-test, $P<0.05$), whereas *Filenchus* (p-p 2), *Wilsonema* (c-p 2), *Teratocephalus* (c-p 3), *Metateratocephalus* (c-p 3), and *Eudorylaimus* (c-p 4) were not found in the ectorganic layers of the sod-cut plots. In contrast to *Eudorylaimus, Metateratocephalus*, and *Filenchus*, 2 years later *Wilsonema* and *Teratocephalus* were still not present.

Fifteen months after the sod-cutting, at least 44% of the taxa with c-p 1–2 that were found in the litter horizons of both the control and sod-cut plots had colonized the newly developing ectorganic layer of the treatments, whereas this held for only 18% of the c-p 3–5 taxa (Table 6). Two years later these figues had increased to 67 and 45%, respectively.

These results are consistent with hypothesis 2 of an initially high proportion of nematode taxa with a low c-p value in the newly developing ectorganic layers, and a relatively low colonization rate of taxa from nearby control plots.

Table 6 Proportion of non-plant-feeding taxa that was detected in the litter horizon of the sod-cut plots tabulated by c-p group and year of treatment. *Values* represent the percentage of the total number of non-plant-feeding taxa detected in the litter horizons of the control and sod-cut plots

c-p group	Year		*n*
	1991	1993	
1	40	80	5
2	46	62	13
3	29	43	7
4	0	50	2
5	0	50	2

Discussion

Effects of sod-cutting on trophic group composition

Sod-cutting resulted in a significant decrease in plant-feeding nematodes. They almost disappeared from the ectorganic layer and showed decreased (not statistically significant) abundances in the mineral soil, indicating decreased food availability. The newly established ectorganic layer of the sod-cut plots was devoid of plant roots because sod-cutting also removed the complete herb vegetation; 1 year after sod-cutting the plots had been colonized by seedlings of *Calluna vulgaris* and *Rumex acetosella* (J. Baar, personal communication, 1994), but these patches were avoided when collecting the nematode samples. As a consequence of this, the only living roots in the mineral soil after sod-cutting belonged to *Pinus sylvestris*. Of the plant-parasitic nematodes which were common in the mineral soil, *Filenchus* sp., *Tylenchorhynchus microphasmis* and *Rotylenchus robustus* survived the sod-cutting. The latter two species are ectoparasites of various woody and herbaceous plants (Fortuner 1991; Zoon et al. 1993) and probably survived on Scots pine roots. The trophic status of the species within the genus *Filenchus* is less clear. Although they are generally classified as root/fungal feeders, the most recent trophic classification (Yeates et al. 1993) listed *Filenchus* as feeding on root epidermal cells and root hairs. Their survival in the mineral soil and their absence in the newly developing ectorganic layer until 3 years after sod-cutting in the present study is in agreement with the observations of De Goede et al. (1993c), who found them associated with plant roots.

In the newly developing ectorganic layer, hyphal-feeding nematodes comprised the most abundant trophic group, indicating the importance of the fungal energy channel in the early stages of decomposition (Kendrick and Burges 1962; Twinn 1974; Ponge 1991; De Goede et al. 1993c). Three years after the sod-cutting, hyphal-feeding nematodes still showed the highest relative abundance. Although for practical reasons, the new ectorganic layer of the sod-cut plots after 39 months was called litter, a major part of this layer should have been classified as fermentation layer. In the fermentation layer of the control plots bacterial- and plant-feeding nematodes significantly ($P<0.001$) outnumbered the hyphal-feeders; these observations are in agreement with trophic group distributions found in other Scots pine forests of a similar age (de Goede et al. 1993c). However, in the latter study the fermentation layer of relatively young primary Scots pine forest (25–30 years old) contained 41% hyphal-feeders, 37% bacterial-feeders, and 22% plant-feeders. First, this relatively high abundance of hyphal-feeding nematodes in the 39-month-old ectorganic layer of the sod-cut plots could have been the result of an increased density of extramatrical ectomycorrhizal mycelium in the ectorganic layer. Sporocarp production of ectomycorrhizal fungi was strongly increased after the sod-cutting (J. Baar, personal communication, 1994). Second, the strongly reduced abundance of plant roots, and thus the rhizosphere, could have resulted in a relatively low abundance of bacterial-feeding nematodes (Parmelee et al. 1993). Finally, with sod-cutting, a major part of the accumulated N pool was removed from the soil compartment. This was followed by the development of a new ectorganic layer composed of leaf litter with a relatively high C:N ratio, creating conditions favouring fungi over bacteria (Swift et al. 1979; Paul and Clark 1989).

Effects of sod-cutting on the nematode community

Removing the ectorganic layer from the forest floor is a forestry practice which can contribute to the recovery of forest ecosystems on dry, nutrient-poor soils exposed to elevated levels of N due to atmospheric deposition (Klap and Schmidt 1992). Sod-cutting reduced the N concentrations in the soil of the stand, indicating a partial return to relatively nutrient-poor soils (Baar 1995). Moreover, 3.5 years after sod-cutting, no differences in N, P, Ca, and Mg concentrations in 0.5-year-old needles and tree vitality were detected (Baar 1995). However, sod-cutting inevitably disturbs the soil ecosystem. Soil biota restricted to the ectorganic layer are eliminated from the ecosystem, whereas soil biota in the mineral soil are confronted with changes in microclimate, nutrient supply, and food availability. Disturbance to the nematode community of the mineral soil, expressed by a decrease in species richness and the Maturity Index, was evident 15 months after the sod-cutting. Nematode taxa with a high c-p value (c-p≥3; persisters or K-strategists sensu latu) decreased in abundance, whereas c-p group 2 (opportunists) was not affected, so that the proportion of the latter was increased. Similar patterns of change in c-p value distribution were also found following acidification, chemical pollution, and heavy metal contamination (de Goede et al. 1993a). Three years after the sod-cutting the Maturity Index of the mineral soil had increased from 2.15 to 2.40 and was even higher than the index of the control plots (2.22), indicating recovery (de Goede et al. 1993a).

Colonization of the sod-cut plots

Although in practice it is not feasible to determine whether any taxon is absent in a treatment (Wright and Coleman 1993), taxa were assumed to be absent when they were not detected in any of the samples from a particular date (i.e., after the examination of more than 800 speciments).

Nematode colonization and succession in natural habitats or disturbed soils can be described by changes in the c-p value group distribution (de Goede et al. 1993a, b; Ettema and Bongers 1993). Under food-rich conditions the first stages of succession are characterized by a dominance of taxa belonging to c-p 1 (enrichment opportunisits), subsequently followed by taxa belonging to c-p 2 and c-p 3–5. When food availability is low, not c-p 1 but c-p 2 will become the first dominant group of taxa, followed by an increase in taxa belonging to the higher c-p groups. Fifteen months after sod-cutting, the nematode community of the litter horizon was highly dominated by c-p 2 taxa. A similar dominance of c-p 2 taxa was found in the nematode community of the litter horizons in a primary succession of Scots pine forests (de Goede et al. 1993b). However, de Goede et al. (1993b) found that in the litter horizon of the first forested stages of Scots pine forest succession, and occasionally in the older stages, the enrichment opportunist *Panagrolaimus* reached high relative abundances. A similar pattern could have occurred following sod-cutting as *Panagrolaimus* was a dominant taxon on needles in the tree canopy and was present in the ectorganic layer. As the first sampling was 15 months after sod-cutting the initial colonization pattern of the ectorganic layer remains unknown.

Although Cobb (1915) mentioned the occurrence of free-living nematodes in trees, little is known about the status of non-herbivorous canopy fauna in the succession of soil fauna populations during litter decomposition. The majority of taxa found in the ectorganic layer 15 months after the sod-cutting also occurred on needles collected in the tree canopy. The data for *Laimaphelenchus, Panagrolaimus, Deladenus* and *Heterocephalobus* indicate that their litter populations could have originated from the tree canopy. However, with the development of the soil fauna community in this new ectorganic layer 2 years later, *Laimaphelenchus, Deladenus*, and *Heterocephalobus* occurred less frequently and their abundances showed decreasing trends. These results indicate that the nematode fauna of a new ectorganic layer initially depends on tree canopy populations. Subsequently, with the development of the ectorganic layer such canopy species can sustain their populations only near the surface of this layer, in the litter horizon (de Goede et al. 1993c).

Sod-cutting as a forestry practice

To assess the status of the nematode fauna in the newly developing ectorganic layers 15 and 39 months after sod-cutting, a comparison was made with the nematode fauna of two early stages of a primary succession of Scots pine forest in the relatively undisturbed drift sand area Hulshorsterzand, the Netherlands (de Goede et al. 1993c). After 15 months the nematode fauna of the ectorganic layer in the sod-cut plots showed highest similarity with the nematode fauna of the ectorganic layer under 3- to 5-year-old Scots pine trees at Hulshorsterzand: six of the eight nematode taxa that were detected in the organic layer under these 3- to 5-year-old trees also occurred in the newly developing ectorganic layer of the sod-cut plots (Table 7). The ectorganic layer under the 25- to 30-year-old trees at Hulshorsterzand comprised five taxa that were not de-

Table 7 Number of nematode taxa in ectorganic layers of sod-cut plots (*SC*) 15 and 39 months after treatment compared to the taxa present in the ectorganic layer of 3- to 5- (stage 1) and 25- to 30- (stage 2) year-old Scots pine forests in the relatively undisturbed drift sand area Hulshorsterzand, the Netherlands (de Goede et al. 1993c)

Taxa present in:	Months after sod-cutting	
	15	39
Stage 1 and SC plots	6	6
Only stage 1	2	2
Only SC plots	5	11
Stage 2 and SC plots	5	10
Only stage 2	5	0
Only SC plots	6	7

tected 15 months after sod-cutting. The distribution of four of these taxa was restricted to the fermentation layers. However, 2 years later, i.e., 39 months after sod-cutting, the nematode fauna of the newly developing ectorganic layer (comprising litter and fermentation material) showed the highest similarity with the nematode fauna of the ectorganic layer under the 25- to 30-year-old Scots pine trees: all taxa present at Hulshorsterzand also occurred in the newly developing ectorganic layer of the sod-cut plots. Thus, after sod-cutting the development of the nematode fauna in the ectorganic layers showed a resemblance to that of the nematode fauna in the organic soil profile during a natural primary succession of Scots pine forest. In contrast, the nematode taxa occurring in the ectorganic layers 15 or 39 months after sod-cutting, but not detected respectively under the 3- to 5- and 25- to 30-year-old Scots pine trees in Hulshorsterzand (nine taxa in total), indicated that this nematode fauna differed from that of the natural primary succession. Seven of these taxa had populations in the mineral soil and/or tree canopy, and thus emphasize the influence of the successional stage of the sod-cut forest (here a >67-year-old secondary Scots pine forest) on the composition of the nematode fauna of the newly developing ectorganic layer. These taxa, however, comprised only an average 3.6–5.1% of the total number of nematodes (per dm^2) in both years.

In parallel with findings on the numbers of species and sporocarps of ectomycorrhizal fungi (Baar and Kuyper 1993; Baar 1995), sod-cutting in secondary forests can eventually have positive effects on nematode species diversity. However, Sohlenius and Wasilewska (1984) concluded from the results of their forest fertilization and irrigation study that nematode colonization from nearby locations appears to be a relatively slow process. Also, in reports on forest liming experiments, no mention has been made of the establishment of populations of new nematode species (Hyvönen and Huhta 1989; Ratajczak et al. 1989; Hyvönen and Persson 1990; de Goede and Dekker 1993). Eleven more nematode species were found in the ≤90-year-old primary Scots pine forests in Hulshorsterzand (de Goede et al. 1993b, c) than in the present study. Whether these potential colonizer species will establish populations after sod-cutting will not only be time-dependent, but will also depend on environmental conditions and on the distance to source populations.

Conclusions

We conclude that sod-cutting resulted in a disturbance to the nematode fauna of the mineral soil as indicated by a decreased Maturity Index, total abundance of nematodes, number of taxa, and insect-parasitic nematodes. The average total abundance of plant-feeding nematodes also decreased, but this decrease was not statistically significant. Three years after sod-cutting, an increased Maturity Index indicated recovery.

One year after the sod-cutting, the nematode fauna of the newly developing ectorganic layer initially comprised taxa with low c-p values (1–3), belonging to hyphal-, bacterial-, and algal-feeding trophic groups, originating from the tree canopy, mineral soil and, to a lesser extent, from nearby control plots. Three years after the sod-cutting, taxa belonging to the higher c-p groups (4–5) were detected, and omnivores also. Animal predators and plant-feeders were not detected or occurred in very low numbers, respectively. The composition of the nematode fauna in the ectorganic layers 15 and 39 months after sod-cutting showed high similarity to the nematode fauna of the early stages of a primary succession of Scots pine forest in a reference area.

Nematode species restricted to the ectorganic layers are eliminated from the ecosystem by sod-cutting. Re-establishment of their populations after sod-cutting appears to be a relatively slow process, which is probably strongly dependent on the environmental conditions in the new ectorganic layer and the distance to source populations. The same holds true for new, colonizing species. Analyses of the nematode fauna of the reference area showed the occurrence of 11 such potential colonizer species.

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