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Fluctuations of nematode populations in pine forest soil. Influence by clear-cutting

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Summary – The dynamics of nematode populations following clear-cutting of a pine forest stand in central Sweden were recorded during two periods : 1-5 years and 14-19 years after the cutting. The effects of slash removal were included in the study. The fluctuations in animal abundance were great during the first period and several species increased in numbers especially in plots with slash. During the second period most taxa occurred in lower abundance in the cut area than in a forested reference stand. The rates of increase or decrease of various species and genera were compared to a classification of nematodes (c-p scale) used for calculation of the maturity index (MI), which is used to indicate soil disturbances. It was concluded that clear-cutting is a kind of disturbance which promote nematode species that tolerate harsh climatic conditions. Several genera and species that generally increase after other types of disturbances such as forest fertilization decreased in the cut area. This gives a type of response of MI in the cut area, which does not correspond to model predictions.

Résumé – ***Fluctuations des populations de nématodes dans un sol de forêt de pins. Influence des coupes claires*** – La dynamique des populations de nématodes après coupes claires dans une forêt de pins du centre de la Suède a été suivie pendant deux périodes : de 1 à 5 ans et de 14 à 19 ans après la coupe. Les effets de l'enlèvement des abattis ont été pris en compte dans cette étude. Les fluctuations de l'abondance animale sont importantes pendant la première période et plusieurs espèces croissent en nombre, notamment dans les endroits sous abattis. Au cours de la seconde période, de nombreux taxons sont présents en abondance moindre dans les zones de coupe que dans une zone boisée de référence. Les taux de croissance ou de décroissance des différentes espèces et genres ont été comparés à un classement des nématodes (échelle c-p) utilisé pour le calcul de l'indice de maturité (IM), lequel est en usage pour indiquer les perturbations du sol. Il en est conclu que la coupe claire constitue une sorte de perturbation qui favorise les espèces tolérant des conditions climatiques rudes. Plusieurs espèces et genres dont les populations croissent après d'autres sortes de perturbations – telle la fertilisation de la forêt – décroissent au contraire à la suite de coupes claires. Cela conduit dans les coupes claires à un type de réaction de l'IM ne correspondant pas aux prédictions du modèle.

Key-words : Clear cutting, maturity index, nematode populations, slash removal.

Studies of nematode populations in pine forest soils indicate that particular species may be very sensitive to disturbances of various types (Bassus, 1968; Sohlenius & Wasilewska, 1984; de Goede & Dekker, 1993; Hyvönen, 1994; Yeates, 1995). However, the details of population dynamics of nematodes after the disturbance of forest soil during normal forest management are little studied.

The rate and intensity in response of nematode populations to a particular disturbance may differ greatly between species. It can also be difficult to determine whether observed changes in animal numbers are due to a disturbance as such or are due to " natural " variations in abundance or to an insufficient sampling programme.

When humus material from pine forest soils is brought into the laboratory for incubation experiments the nematode populations are likely to change rather dramatically (Sohlenius, 1985, 1993; Hyvönen & Huhta, 1989). Some species increase and others decrease in numbers. There are certain species which generally increase in numbers in a broad spectrum of incubation conditions, others increase only under specific conditions whereas the increase of yet others appear to be rather unpredictable. These observations indicate that the nematode fauna in pine forest soil is a rather labile component of the soil community.

An increase in population density may be a result of increased amounts of food, reduced predation and competition, and of more benign edaphic and climatic conditions for the particular species. A decrease may, on the other hand, be caused by reduced food availability, increased predation and competition, or other unsuitable biotic and abiotic conditions.

Detailed studies of temporal changes after a disturbance in laboratory and field experiments may give information on potential population growth rates and ecological requirements of various species. Comparisons with the fluctuations of other soil parameters and groups of organisms may yield some information on the role of particular nematode populations in the soil food web. Such information may be of a purely scientific interest but an applied aspect would be to reveal if and in what

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way nematode faunal changes can be used to indicate soil ecological changes.

In this study the changes in nematode numbers after a clear-cutting were followed by yearly samplings during two periods. The first took place during the initial 5 years after the cutting and the second after 14 to 19 years. The effects of slash removal were included. The effect on total numbers of nematodes, tardigrades and rotifers during the first years after the clear-cutting has been described by Sohlenius (1982) and studies on other soil organisms from this site have been published earlier (Bååth, 1980; Lundgren, 1982; Lundkvist, 1983).

Since the variation in nematode abundance from year to year appeared to be rather erratic even in an uncut stand (Sohlenius, 1979) it was considered desirable to follow the dynamics of the nematode fauna by using an uncut stand as a reference site.

Differences in the patterns of reaction to disturbance of nematode genera have been used by Bongers (1990) in a model to calculate a " maturity index " (MI) for nematode faunas. This index has been calculated in several studies to demonstrate how soil conditions can be indicated by the composition of the nematode fauna (Freckman & Ettema, 1993; de Goede & Dekker, 1993; Yeates & Bird, 1994; Neher *et al.*, 1995). A low MI should indicate that the soil is disturbed and a high MI value that the soil is more " mature ". In this paper the rate of increase in population densities of various nematode taxa after a clear-cutting was recorded. The results were then compared with the classification by Bongers. Thus, this paper focuses on details of population dynamics whereas forthcoming papers will put more emphasis on community ecological aspects.

Materials and methods

Site description

The research site, Ivantjärnsheden (Ih), is situated at Jädraås (60° 49'N, 16°30'E; altitude 185 m above sea level), in central Sweden. In the area the long-term annual mean temperature is 3.8 °C and the annual mean precipitation is 607 mm. Snow cover lasts approximately 5 months (December to April).

The area is a Scots pine forest (*Pinus sylvestris* L.) on glacifluvial sediment. The ground vegetation is of a dry dwarf shrub type (*Calluna vulgaris* [L.]. Hull, *Vaccinium vitis-idae* L., *Cladonia* spp. and feather mosses [e.g. *Hylocomium* sp.]). It was the main research area of the Swedish Coniferous Forest Project during the period of 1973-1980 (Persson, 1980).

This investigation was undertaken in two stands (Ih0 and IhV) about 120 year-old at the beginning of the investigation. The stands were 500 m apart. IhV was used as a forested reference stand and Ih0 was clear-cut in late winter 1976. The Ih0 site was divided into twelve plots each measuring 30 × 30 m. The slash (cutting wastes) was removed after felling on six of these plots while double amounts of slash were put on the other six plots. The litter and humus layers were not manipulated.

Due to the harsh climate in the area (Axelsson & Bråkenhjelm, 1980), the development of field layer vegetation and the growth of young Scots pine trees (planted in 1983 and 1985) were very slow. In recent years (1989-1994) clones of heather, *Calluna vulgaris,* have started to grow in patches over the area. Pine trees have established themselves but the trees are small and most of the soil surface is rather exposed. Soil samples were taken both inside the *Calluna* clones and in the area between them which was dominated by various species of lichens. In this study only samples taken from non-*Calluna* areas are considered.

Sampling and extraction

The sites were sampled in two periods, viz. 1976-1980 (1 to 5 years after the cutting) and 1989-1991 (14 to 16 years after the cutting). An additional sampling was done in 1994 (19 years after the cutting). The sites were sampled in September each year. Six duplicate samples were taken from plots with slash (Ih0+), from plots without slash (Ih0–), and from IhV. On each sampling occasion the samples were taken close to where the previous samples were taken. During the first period of the study the sampling was coordinated with samplings of microorganisms and other soil fauna groups.

The samples were taken with a steel corer (diameter 2.3 cm) to a depth of 10 cm below the border between the litter and humus layers. The animals were extracted with a modified Baermann method (Sohlenius, 1979). Each core was divided into three parts viz. litter (S) layer, humus (FH) layer and mineral (min) soil. Total abundance of nematodes, rotifers and tardigrades in the litter layer (S) and mineral soil (min) was estimated in suspension from one core from each sampling place (i.e. 6/treatment). From the humus layer (FH) the two cores from each sampling place were extracted (i.e., 12/treatment). For analysis of fauna structure the suspensions were pooled according to a scheme described previously (Sohlenius, 1979, 1982).

Faunal analysis

The abundance of various taxa was followed and their pattern of variation was analysed. For the whole period maximum and minimum values were recorded, and the year after the cutting when they were obtained was noted. If the taxa had disappeared or were absent during several years, it was not possible to give the time for occurrence of a minimum value; as in all such studies zero value indicates that the population may have dropped below the level of detection rather than be locally extinct. The coefficient of variation CV (standard deviation/mean value) was calculated (Tables 2-5). In Tables 2-5, those taxa which increased or decreased by more than two times the maximum values of the control forest and which had a density of at least 10/g dry weight in the litter- and humus-layers, or 1/g dry weight in the mineral soil in any of the treatments, are denoted by + or –, respectively. These taxa are considered as strong increasers or decreasers. Those which reached maximum values during the first or second year after the cutting are considered as rapid increasers (Ri in Table 6); those reaching maximum values in 3 to 5 years are called slow increasers (Si) and those which reached their peak abundance in 14 to 19 years after the cutting are considered as late increasers (Li). The rapid increasers in this study should agree with species having a low c-p values and those which increased late should have a high c-p value. Colonizers (c) and persisters (p) are extremes on a scale (c-p scale) from 1 to 5, respectively, according to Bongers (1990).

The fauna was classified into semitaxonomic feeding groups (S/F-groups) viz. Tylenchida obligate root feeders; Tylenchida (Including Aphelenchida) facultative fungal feeders; Rhabditida bacterial feeders; Adenophorea bacterial feeders, and Dorylaimida omnivores/predators and fungal feeders according to Sohlenius and Sandor (1989) (see Tables 3-5).

Mean values of abundance for 1977-1979 (period I) and 1989-1991 (period II) were calculated (Table 1, Fig. 3).

Results

Fluctuations of semitaxonomic feedings groups

Both in IhV and in Ih0+ and Ih0- the annual mean values of abundance of semitaxonomic feeding groups (S/F-groups) fluctuated considerably (Fig. 1, Tables 1-2). However, the pattern of fluctuation differed between the forest and the cut area especially in the litter and humus layers. The mean abundance increased during the first years after cutting especially in plots with cutting wastes (Ih0+). Generally Adenophorea bacterial feeders and Dorylaimida increased more markedly than Tylenchida and Rhabditida and, especially in the humus layer, higher numbers were found in Ih0+ than in IhV and Ih0– (Table 1). In the humus layer the peak abundance was reached during the first or second year in all groups except Dorylaimida; Dorylaimida reached peak abundances 3 to 4 years after the cutting (Fig. 1, Table 2). For Dorylaimida there was a very pronounced increase in abundance towards the end of the investigation in the mineral soil of the cut plots (Fig. 1, Table 2), which depended on one particular species, *Tylencholaimus mirabilis* (Table 5).

After the peak abundances during period I, most groups settled at a lower abundance with little variation

Table 1. *Mean abundance of semitaxonomic feeding groups of nematodes (S/F-groups) from pine forest soil.*

S/F group	PERIOD I (1977-1979)			PERIOD II (1989-1991)		
	IhV	Ih0,+	Ih0,–	IhV	Ih0,+	Ih0,–
Litter layer						
Tylenchida ORF	0	0	0	0	0.3	0
Tylenchida FFF	227	214	53.3 –	258	47.7 –	68.9 –
Rhabditida BF	78.2	60.1	9.8 –	138	5.3 –	26.8 –
Adenophorea BF	439	362	135 –	529	48.8 –	111 –
Dorylaimida	63.1	57	19.7 –	146	7.9 –	5.5 –
Total Nematoda	807	693	218 –	1071	110 –	213 –
Humus layer						
Tylenchida ORF	0	0	0	0	0	0
Tylenchida FFF	266	146	65.4 –	171	26.3 –	49.4 –
Rhabditida BF	80.7	49.2	35.2 –	113	15.8 –	12.3 –
Adenophorea BF	168	339	188	145	43.9 –	41.4 –
Dorylaimida	75.4	172 +	58.8	53.2	16.3 –	30.6 –
Total Nematoda	590	706	347	486	103 –	134 –
Mineral soil						
Tylenchida ORF	0	0	0.03	0.1	0	0.07
Tylenchida FFF	3.6	6.2	3.3	5.1	1.9 –	6.4
Rhabditida BF	3.8	9.7 +	4.4	8.6	4.8	4.9
Adenophorea BF	4	10.8 +	6.6	4.5	4	4.5
Dorylaimida	2.7	1.8	0.8 –	2.4	5.4 +	6.2 +
Total Nematoda	14	28.5 +	15.2	21.5	16.5	22

ORF = obligatory root feeders; FFF = facultative fungal feeders; BF = bacterial feeders; IhV = uncut stand; Ih0 + = cut area with slash; Ih0 – = cut area without slash. Figures show number/g soil dry weight. + and – show differences of at least two times the values of the reference stand (IhV).

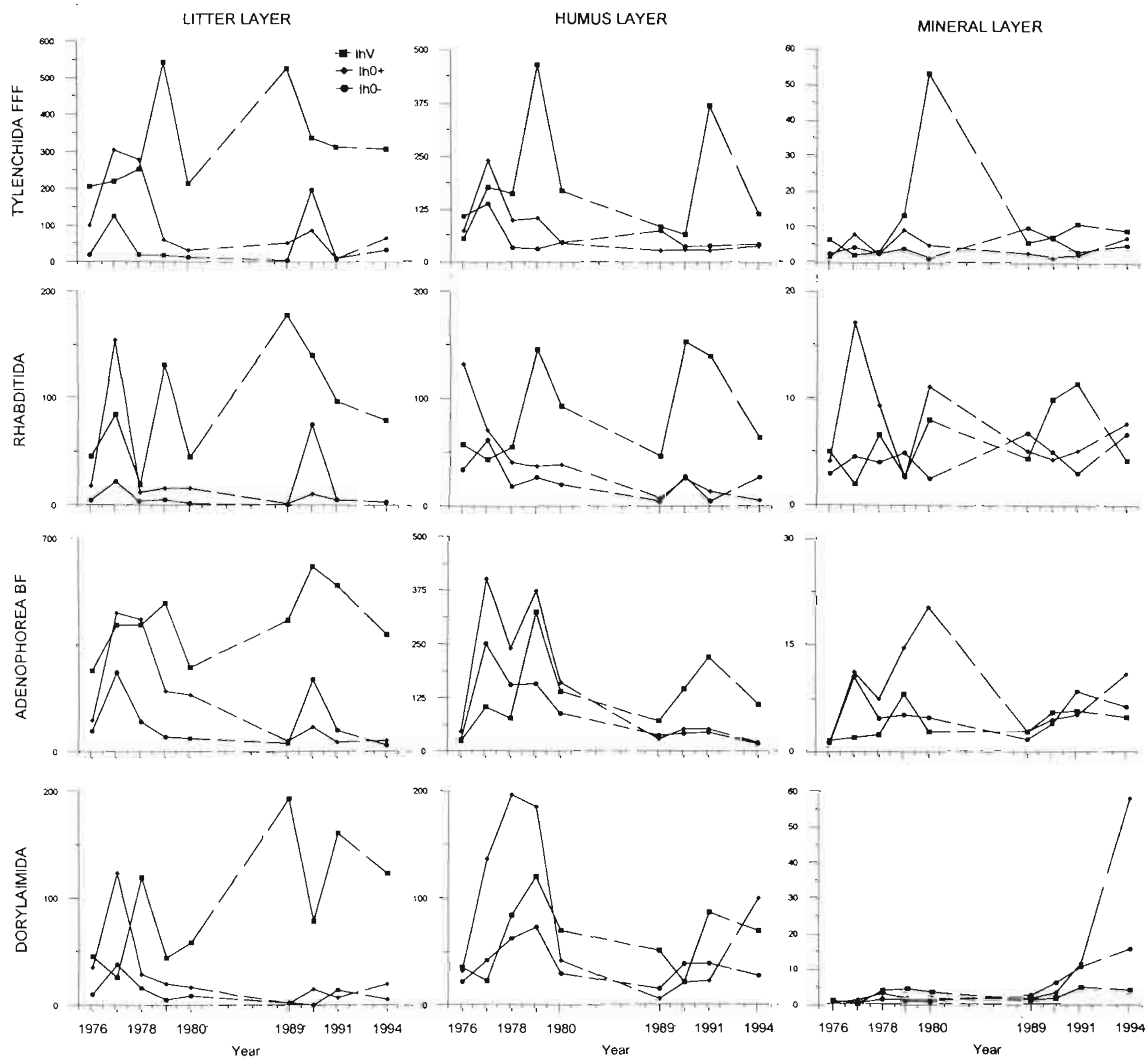

Fig. 1. Fluctuations in mean abundance of nematodes belonging to Tylenchida facultative fungal feeders (FFF), Rhabditida, Adenophorea bacterial feeders (BF) and Dorylaimida omnivore/predators and fungivores in various soil layers. ■ = uncut stand; ♦ = cut stand with cutting wastes; ● = cut stand without cutting wastes. No/gdw = number per gram soil dry weight.

between years during period II. Especially in litter and humus layers the values for the cut area were much below the control forest during period II (Table 1). One exception is Dorylaimida in the humus layer where no clear differences were seen during the second period (Fig. 1). The differences in abundances between Ih0+ and Ih0- were generally large during the first period, but during the second period this difference had disappeared or was rather reversed (Tables 1, 2).

The variability (CV) of the various groups and total nematode numbers was the highest in Ih0+ (reaching 2.1) whereas in IhV and Ih0- it was lower (reaching 1.6 and 1.8, respectively) and did not differ much (Table 2).

Dynamics of various taxa

In the cut area several taxa fluctuated markedly in numbers throughout the study period. However, in the

Table 2. *Maximum (Max) and minimum (Min) abundance of semitaxonomic feeding groups (S/F-groups) in soil samples taken in a cut (Ih0) and an uncut (IhV) pine forest soil up to 19 years after a clear-cutting.*

S/F group	TREATMENTS								
	IhV			Ih0 +			Ih0 –		
	Max	Min	CV	Max	Min	CV	Max	Min	CV
Litter layer									
Tylenchida ORF	0	0	0	0.9 (15)*	0	3	0	0	0
Tylenchida FFF	543 (4)*	204 (1)*	0.4	304 (2)	7.3 (16)*	1	196 (15)*–	2.8 (14)*	1.4
Rhabditida BF	177 (14)	19 (3)	0.6	154 (2)	1.3 (14)	1.9	75 (15)–	0.2 (14)	1.8
Adenophorea BF	608 (15)	263 (1)	0.3	455 (2)	31 (16)	1	259 (2)–	20 (19)	0.9
Dorylaimida	193 (14)	26 (2)	0.6	123 (2)	1.4 (14)	1.2	38 (2)–	0 (15)	1
Total Nematoda	1218 (19)	481 (1)	0.3	1035 (2)	51 (16)	1	509 (15)–	32 (14)	1.6
Humus layer									
Tylenchida ORF	0	0	0	0.1 (19)	0	3	0	0	0
Tylenchida FFF	463 (4)	53 (1)	0.7	239 (2)	26 (14)	0.9	137 (2)	29 (4)	0.7
Rhabditida BF	153 (15)	43 (14)	0.5	131 (1)	5 (19)	1	61 (2)	5 (14)	0.7
Adenophorea BF	323 (4)	24 (1)	0.6	401 (2)	21 (19)	1	251 (2)	17 (19)	0.9
Dorylaimida	120 (4)	22 (2)	0.5	196 (3)	6 (14)	0.9	73 (4)	15 (14)	0.5
Total Nematoda	1050 (4)	169 (1)	0.6	847 (2)	67 (14)	0.8	490 (2)–	112 (19)	0.6
Mineral soil									
Tylenchida ORF	0.5 (19)	0	1.6	0	0	0	0.2 (16)	0	1.5
Tylenchida FFF	53 (5)	1.8 (2)	1.3	9 (4)–	1 (1)	0.7	9.7 (14)–	1.2 (5)	0.6
Rhabditida BF	11 (16)	1.9 (2)	0.5	17 (2)	2.6 (4)	0.6	6.8 (14)	2.5 (5)	0.4
Adenophorea BF	8 (4)	1.4 (1)	0.6	20 (5)+	1.1 (1)	0.7	10 (2)	1 (1)	0.6
Dorylaimida	4.6 (16)	0.1 (2)	0.6	58 (19)–	0.4 (1)	2.1	16 (19)+	0.3 (2)	1.2
Total Nematoda	42	5.1	0.6	84 (19)+	6.5 (1)	0.8	32.9 (19)	7 (1)	0.6

ORF = obligatory root feeders; FFF = facultative fungal feeders; BF = bacterial feeders; IhV = uncut stand; Ih0+ = cut area with slash; Ih0– = cut area without slash. Max and min = number/g soil dw; CV = coefficient of variation (sd/$\bar{x}$); + and – show differences of at least two times the extreme values of the reference stand (IhV).

* Figures between parentheses refer to number of years after cutting.

control forest (IhV) also the fluctuations were large and sometimes there were trends of directed changes in abundance over longer periods (Tables 3-5). The temporal variation of some species in the humus layer are indicated on Fig. 2 and the mean values in various soil layers for periods I an II on Fig. 3.

During the first 5 years after the cutting some nematode species increased pronouncedly and others decreased rather rapidly in numbers in the litter and humus layers of the cut plots (Tables 3, 4). As was the case with the semitaxonomic feeding groups the increases were generally more pronounced in Ih0+ than in Ih0-. During the second period these differences had disappeared in most cases and were sometimes replaced by a tendency towards higher numbers of animals in soil from Ih0- than from IH0+.

The most abundant genus among Tylenchida facultative fungal feeders, *Aphelenchoides,* decreased rather markedly and rapidly in the cut plots (Fig. 2). The number of *Ditylenchus* was much less influenced during the first period but decreased markedly during the second period (Fig. 3). *Tylenchus s.l.* was obtained in rather high numbers also during the second period in the cut plots (Fig. 3).

The most abundant member of Rhabditida, *Acrobeloides nanus,* had higher mean values in plots with (Ih0+) than without (Ih0-) cutting-wastes during the first period (Figs 2, 3). However, already after the first years there were much lower abundances of *Acrobeloides nanus* in the cut areas than in the control forest and as was the case with several other taxa, the abundances in IhV fluctuated considerably. The graphs for *Wilsonema otophorum. Plectus* spp. and *Eudorylaimus* sp. show similarities, with distinct increases, especially in Ih0+, during the first part of the study (Figs 2, 3).

Plectus spp. differed markedly in their patterns of fluctuation in population numbers. Thus *Plectus longicaudatus* increased more rapidly but also decreased more markedly than *P. acuminatus* (Fig. 2). During period II, hardly any *P. longicaudatus* were found in the cut plots

Table 3. *Maximum and minimum abundance of various taxa of nematodes in the litter layer in soil samples taken in a cut (Ih0) and an uncut (IhV) pine forest soil up to 19 years after a clear-cutting.*

TAXA	TREATMENT								
	IhV			Ih0+			Ih0–		
	Max	Min	CV	Max	Min	CV	Max	Min	CV
TYLENCHIDA ORF									
Geocenamus	0	0	0	0.9 (15)	0	3	0	0	0
TYLENCHIDA FFF									
Tylenchus	178 (4)*	18	0.8	61 (15)*	0.4	0.7	28 (15)*–	2.6	0.8
Ditylenchus	80 (5)	9.8	0.5	126 (3)	0	1.8	14 (2)–	0	1.2
Aphelenchoides	180 (14)	47	0.4	216 (2)	6.4	1.4	168 (15)	0.2	1.8
Paraphelenchus	0	0	0	0.9 (4)	0	3	0.5 (5)	0	3
RHABDITIDA BF									
Rhabditis	87 (14)	2.8	1.1	1.2 (5)–	0	3	0.7 (3)–	0	3
Bunonema	113 (15)	0	0.8	16 (2)–	0	0.9	73 (15)	0	2.6
Acrobeloides nanus	42 (1)	2.4	0.9	138 (2)+	0.9	2.3	14 (2)	0	1.1
ADENOPHOREA BF									
Teratocephalus deconincki	85 (16)	0	0.9	93 (2)	0	1.1	18 (4)–	0	0.9
T. terrestris	16 (2)	0	1.1	88 (2)+	0	1.8	45 (3)+	0	1.1
Metateratocephalus crassidens	48 (3)	0	1.6	19 (3)–	0	1.7	9.6 (3)–	0	2.2
Plectus acuminatus	428 (15)	130	0.4	295 (3)	18	1	210 (15)–	8.3	1.1
P. rhizophilus	75 (19)	0	2.7	3.1 (19)–	0	2.5	0	0	
P. longicaudatus	121 (2)	2.2	1.3	52 (2)–	0	1.8	82 (2)	0	2.8
P. minimus	45 (15)	0	1.1	6.4 (1)–	0	1.9	2.4 (1)–	0	3
Plectidae unidentified	0	0	0	1.3 (16)	0	3	0	0	0
Wilsonema otophorum	20 (16)	0	2.1	41 (2)+	0	2.2	1.4 (4)–	0	3
Rhabdolaimus	1.4 (19)	0	3	0	0	0	0	0	0
Eumonhystera	65 (19)	0	0.8	36 (2)	0	1.4	11 (3)	0	1.5
Prismatolaimus	6.6 (4)	0	2.1	7.6 (3)	0	3	3.1 (1)	0	2.1
Achromadora	181 (3)	0	1.8	53 (3)–	0	1.7	7 (3)–	0	2.6
Alaimus	2.1 (16)	0	3	4 (5)	0	2	0.8 (19)	0	3
DORYLAIMIDA									
Eudorylaimus	162 (14)	24	0.6	123 (2)	0.7	1.4	35 (2)–	0	1.1
Aporcelaimellus	3.6 (14)	0	2.4	1.3 (14)	0	2.1	1 (16)	0	3
Tylencholaimus stecki	21 (14)	0	1.5	6.1 (3)–	0	1.8	2.4 (2)–	0	2.4
T. mirabilis	0	0	0	6.4 (14)	0	2.4	2.7 (19)	0	2.7
Diphtherophora	0	0	0	1.3 (5)	0	2	0	0	0
Dorylaiminae	17 (4)	0	1.7	1.2 (5)	0	3	0	0	0

ORF = Obligatory root feeders; FFF = facultative fungal feeders; BF = bacterial feeders; IhV = uncut stand; Ih0+ = cut area with slash; Ih0– = cut area without slash. Max and min = numberg/g soil dw; CV = coefficient of variation $(sd/\bar{x})$; + and – show differences of at least two times the extreme values of the reference stand (IhV).
* Figures between parentheses refer to number of years after cutting.

(Fig. 3). The two *Teratocephalus* spp. also differed in their patterns of change. Both species increased in the cut plots during period I, but, during period II, *T. terrestris* remained in high numbers in the cut areas, whereas, *T. deconincki* decreased markedly (Fig. 3). *Eudorylaimus* sp., which increased very distinctly during period I, had much lower numbers in Ih0 than in IhV during period II (Figs. 2, 3).

Certain taxa, viz. *P. longicaudatus* and *Rhabditis* sp., were almost absent in samples from Ih0 during the second period. Conversely, other genera which were not found during the first part of the study appeared and increased towards the end of the study period (e.g. *Diphtherophora, Rhabdolaimus*). Strangely enough, these species appeared simultaneously in soil from IhV.

The strong increasers, according to the definition giv-

Table 4. *Maximum and minimum abundance of various taxa of nematodes in the humus layer in soil samples taken in a cut (Ih0) and an uncut (IhV) pine forest soil up to 19 years after a clear-cutting.*

TAXA	TREATMENT								
	IhV			Ih0+			Ih0–		
	Max	Min	CV	Max	Min	CV	Max	Min	CV
Tylenchida ORF									
Geocenamus	0	0		0.1 (19)	0	3	0		
Tylenchida FFF									
Tylenchus	159 (16)*	13	1.1	91 (2)*	7	0.8	66 (14)*–	5	0.7
Ditylenchus	70 (5)	4.5	1	66 (3)	2	1.2	63 (2)	1	1.4
Nothotylenchus	1.9 (14)	0	3	0	0		4 (14)	0	3
Aphelenchoides	280 (4)	31	0.8	83 (2)–	2	1.5	51 (1)–	0	1.2
Rhabditida BF									
Rhabditis	71 (4)	2	1.2	4 (2)–	0	1.5	2 (4)–	0	3
Bunonema	15 (15)	0	1	10 (15)	0	0.9	21 (15)	0	1.5
Acrobeloides nanus	134 (16)	29	0.6	127 (1)	5	1.1	58 (2)–	3	0.9
Cervidellus	0	0		4 (5)	0	3	0		
Adenophorea BF									
Teratocephalus deconinicki	58 (16)	0	1.2	70 (4)	0	1.2	41 (3)	0	1.1
T. terrestris	21 (14)	0	0.7	52 (4)+	0	0.9	34 (2)	0	0.8
Metateratocephalus crassidens	7 (19)	0	0.7	46 (2)+	0	2	11 (4)	0	1.5
Plectus acuminatus	160 (4)	13	1	99 (2)	5	0.8	73 (2)–	4	0.9
P. rhizophilus	2 (19)	0	2.2	1 (19)	0	3	0.6 (19)	0	3
P. longicaudatus	91 (4)	2	1.1	79 (2)	0	1.7	34 (2)–	0	1.9
P. minimus	9 (15)	0	1.6	1 (15)	0	3	0.6 (15)	0	1.8
Plectidae unident.	0	0		0	0		0		
Wilsonema otophorum	32 (5)	2	0.7	142 (4)+	0	1.3	78 (4)+	0.2	1.3
Rhabdolaimus	9 (19)	0	3	0.8 (19)	0	2.1	2 (16)	0	1.6
Eumonhystera	14 (16)	0	1	17 (2)	0	1.2	12 (2)	0	2.1
Prismatolaimus	9 (19)	0	0.7	0.8 (4)	0	1.1	11 (4)	0	1.8
Achromadora	15 (3)	0	1.6	18 (3)	0	1.8	15 (3)	0	2.5
Alaimus	1 (3)	0	1.6	8 (5)	0	1.7	2 (3)	0	1.8
Dorylaimida									
Eudorylaimus	120 (3)	19	0.6	191 (3)	4	1.2	72 (4)	8	0.8
Aporcelaimellus	2 (3)	0	0.9	1 (14)	0	1.2	5 (14)	0	1.2
Tylencholaimus stecki	17 (16)	0	1.5	11 (16)	0	1.1	6 (15)–	0	1.8
T. mirabilis	7 (19)	0	1.9	76 (19)+	0	2.5	22 (16)+	0	1.4
Diphtherophora	0.2 (16)	0	2.8	1 (19)	0	3	0	0	0
Dorylaiminae	10 (1)	0	2.1	0.6 (5)	0	2.8	0	0	0

ORF = obligatory root feeders; FFF = facultative fungal feeders; BF = bacterial feeders; IhV = uncut stand; Ih0+ = cut area with slash; Ih0– = cut area without slash. Max and min = number/g soil dw; CV = coefficient of variation (sd/$\bar{x}$); + and – show differences of at least two times the extreme values of the reference stand (IhV).

* Figures between parentheses refer to number of years after cutting.

en in materials and methods, compiled from Tables 3-5 are listed in Table 6. Most cases of strong increases (eleven cases) were found in the mineral soil. All species in Table 6 increased strongly in Ih0+ (fifteen cases), and five increased also in Ih0- (seven cases).

It can be seen that the frequency of strongly decreasing species was the highest in the litter layer and lowest in the mineral soil (Tables 3-5). It is also evident that the number of species which decreased markedly was higher in Ih0- than in Ih0+.

Table 5. *Maximum and minimum abundance of various taxa of nematodes in the mineral soil in soil samples taken in a cut (Ih0) and an uncut (IhV) pine forest soil up to 19 years after a clear-cuting.*

TAXA	TREATMENT								
	IhV			Ih0+			Ih0−		
	Max	Min	CV	Max	Min	CV	Max	Min	CV
TYLENCHIDA ORF									
Geocenamus	0.5 (19)*	0	1.6				0.2 (16)*	0	1.5
TYLENCHIDA FFF									
Tylenchus	2.6 (4)	0.4	0.6	6 (4)+	0.3	1	3.1 (4)	0.3	0.8
Ditylenchus	1.7 (5)	0.1	0.8	2.6 (5)	0	1	2.7 (15)	0.03	0.9
Aphelenchoides	25 (5)	0.5	1.5	2.8 (2)−	0.4	0.8	6.4 (14)−	0.2	1
RHABDITIDA BF									
Rhabditis	0.4 (3)	0	1.2	0.2 (3)	0	2.1	0.06 (15)	0	3
Bunonema	0.1 (3)	0	2	0.2 (4)	0	2.1	0.1 (3)	0	1.7
Acrobeloides nanus	11 (16)	1.8	0.6	17 (2)	2.4	0.7	6.7 (19)	1.8	0.4
Cervidellus	0.3 (1)	0	2.1	7.8 (5)+	0	2.3	0.7 (5)	0	2
Heterocephalobus	0	0	0	0.06 (15)	0	3	0	0	
ADENOPHOREA BF									
Teratocephalus deconincki	1.7 (4)	0	1.8	2.3 (4)	0	0.8	0.7 (4)	0	1.1
T. terrestris	2.9 (4)	0	1	3.1 (4)	0.07	1	6 (2)+	0	1.4
Metateratocephalus crassidens	0.2 (3)	0	0.2	0.4 (2)	0	2	0.1 (5)	0	1.5
Plectus acuminatus	2.4 (4)	0.5	2.4	7.7 (4)+	0.4	1.1	1.8 (5)	0.3	0.5
P. rhizophilus	0.07 (19)	0	3	0	0	0	0	0	0
P. longicaudatus	0.8 (16)	0	1.1	2.1 (3)+	0	1.4	1.7 (2)+	0	1.8
P. minimus	0.1 (19)	0	3	0.2 (15)	0	3			
Plectidae unident.	0	0	0	0	0	0	1.3 (19)	0	2.5
Wilsonema otophorum	0.3 (4)	0	1.4	1.4 (3)+	0	1.4	0.5 (4)	0	1.2
Rhabdolaimus	1 (19)	0	2.3	12 (5)+	0	1.7	5.8 (16)+	0	1.7
Eumonhystera	0.2 (5)	0	1.4	0.6 (2)	0	1.5	0.2 (4)	0	1
Prismatolaimus	1.7 (16)	0	1.3	1.9 (19)	0	1.3	0.8 (4)−	0	0.7
Achromadora	0.9 (3)	0	3	0.5 (4)	0	1.5	1 (3)	0	2.7
Alaimus	0	0		0.1 (19)	0	2.2	0.4 (3)	0	2.5
DORYLAIMIDA									
Nygolaimoides	0	0	0	0.3 (19)	0	3	0	0	
Eudorylaimus	2.1 (3)	0	1.1	2.4 (3)	0.1	0.9	0.8 (3)−	0.2	0.4
Aporcelaimellus	0.5 (15)	0	0.8	0.4 (14)	0	0.8	0.6 (14)	0	1.7
Tylencholaimus stecki	0.08 (16)	0	3	0.7 (14)	0	1.7	0.2 (3)	0	2.3
T. mirabilis	3.8 (16)	0	0.8	53 (19)+	0.1	2.4	15 (19)+	0	1.5
Diphtherophora	0.5 (14)	0	2.7	2.8 (19)+	0	2.1	0.6 (15)	0	1.6
Dorylaiminae	0.4 (5)	0	2.1	0.3 (5)	0	3	0.2 (5)	0	2.3

ORF = obligatory root feeders; FFF = facultative fungal feeders; BF = bacterial feeders; IhV = uncut stand; Ih0+ = cut area with slash; Ih0− = cut area without slash. Max and min = number /g soil dw; CV = coefficient of variation (sd/$\bar{x}$); + and − show differences of at least two times the extreme values of the reference stand (IhV).

* Figures between parentheses refer to number of years after cutting.

Discussion

This study clearly shows that the nematode populations may react rather markedly to such a large scale disturbance as a clear-cutting represents. The increase during the first period of the study was certainly related to the liberation of nutrients from dying roots and the destruction of soil organisms (Sohlenius, 1982). The clear effects of slash on several taxa also indicate that the extra energy input from the leaching slash material had an impact on the soil microorganisms which serve as food sources for several nematode species. Bååth (1980)

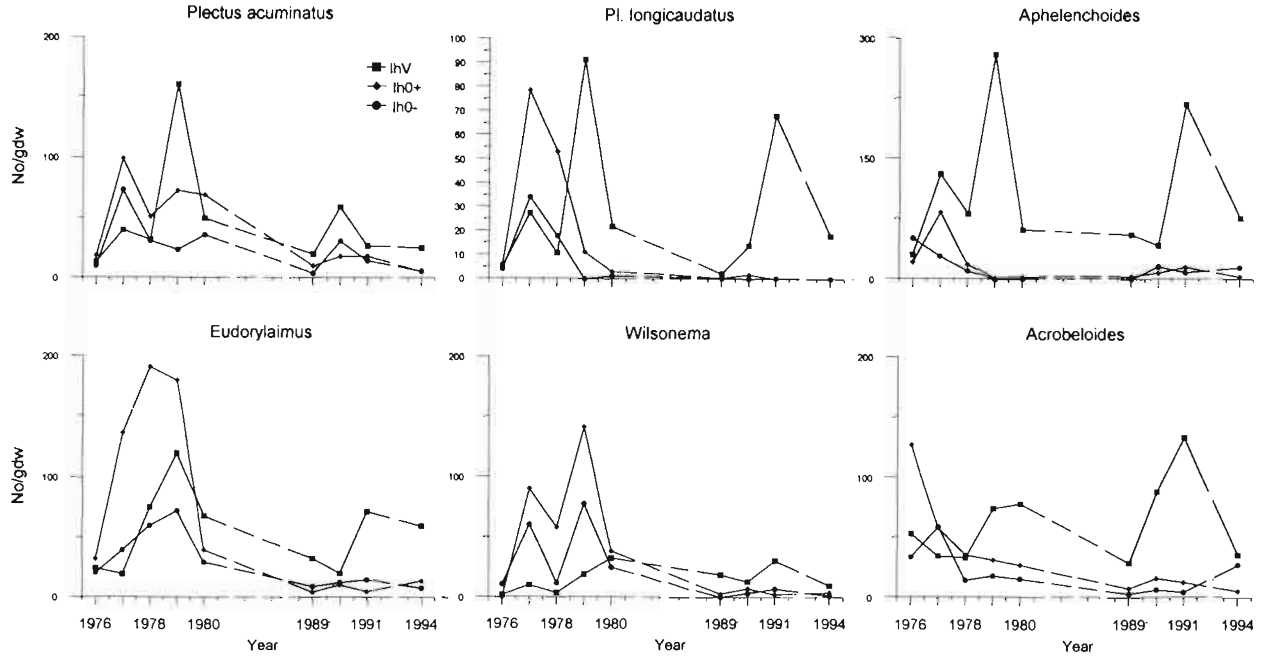

Fig. 2. *Fluctuations in abundance of some nematode taxa in the humus layer in pine forest soil.* ■ = *uncut stand;* ♦ = *cut stand with cutting wastes;* ● = *cut stand without cutting wastes.*

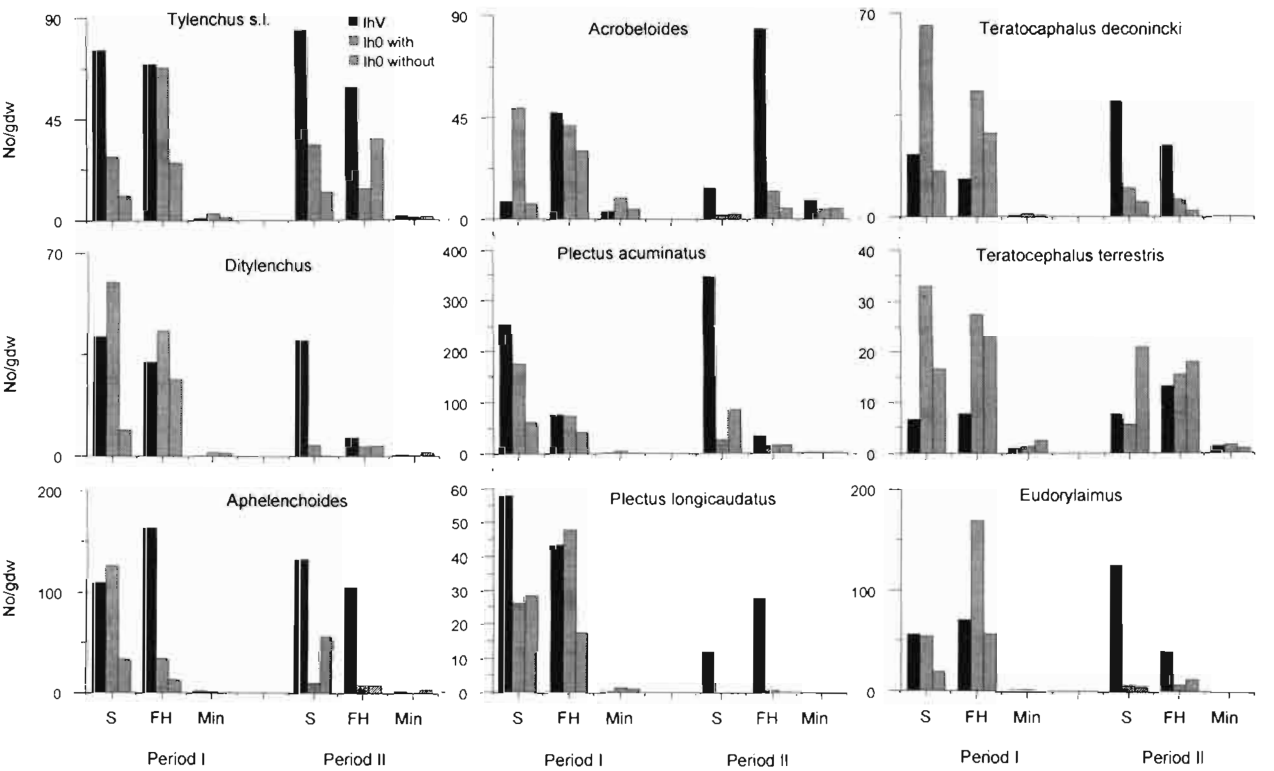

Fig. 3. *Mean abundance of various nematode taxa in different soil layers during period I (2-4 years cutting) and period II (14-16 years after cutting). S = litter layer; FH = humus layer; Min = mineral soil.*

Table 6. *Behaviour of nematode taxa according to soil layers and treatment.*

	Behaviour	Soil layer	Treatment	c-p scale
Tylenchus	Si	mineral	Ih0+	2
Acrobeloides nanus	Ri	litter	Ih0+	2
Cervidellus	Si	mineral	Ih0+	2
Teratocephalus terrestris	Ri	litter	Ih0+, Ih0–	3
	Si	humus	Ih0+	
	Ri	mineral	Ih0–	
Metatertocephalus crassidens	Ri	humus	Ih0+	3
Plectus acuminatus	Si	mineral	Ih0+	2
P. longicaudatus	Si	mineral	Ih0+	2
	Ri	mineral	Ih0–	
Wilsonema otophorum	Ri	litter	Ih0+	2
	Si	humus	Ih0+, Ih0–	
	Si	mineral	Ih0+	
Rhabdolaimus	Si	mineral	Ih0+	3
	Li	mineral	Ih0–	
Tylencholaimus mirabilis	Li	humus	Ih0+, Ih0–	4
	Li	mineral	Ih0+, Ih0–	
Diphtherophora	Li	mineral	Ih0+	3

Ri = rapid increasers, reaching peak abundance 1-2 years after cutting; Si = slow increasers, reaching peak abundance 3-5 years after cutting; Li = late increasers, reaching peak abundance 14-19 years after cutting;
Ih0+ = cut area with slash; Ih0– = cut area without slash; c-p scale : classification by Bongers (1990).

Table 7. *Bongers' maturity index (MI) during period I and period II.*

Soil layer	PERIOD I			PERIOD II		
	IhV	Ih0+	Ih0–	IhV	Ih0+	Ih0–
Litter	2.27	2.35	2.33	2.20	2.23	2.06
Humus	3.00	2.63	2.53	2.22	2.51	2.58
Mineral	2.56	2.24	2.38	2.26	2.79	2.72
M^2	2.32	2.40	2.42	2.23	2.56	2.55

m^2 = all layers; IhV = uncut stand; Ih0+ = cut area with slash; Ih0– = cut area without slash.

and Lundgren (1982) found higher abundances of fungi and bacteria in plots with than without slash. The much reduced abundance of several nematode species during the second period indicated a depletation of food supply which certainly was, in part an effect of a very slow recovery of vegetation after the cutting and the depletion of the initial pulse of food supply. Also, Arpin *et al.* (1995) demonstrated the large effects of litter removal on nematode numbers in a deciduous forest.

The pattern of reaction of various species is somewhat in contrast with what would be expected from previous publications. For instance some members of the Secernentea, which have a high potential growth rate, generally decreased or developed poorly in the cut plots. It was unexpected that a genus such as *Rhabditis,* which is classified by Bongers (1990) as a colonizer or an r-strategist and which generally increase if there is a surplus of easily available food sources (Sohlenius, 1973), did not increase but rather disappeared from the cut plots. It was also unexpected that *A. nanus,* which has a low c-p value, did not increase more. In laboratory incubated humus there was a tremendous increase in number of *A. nanus,* and sometimes of *Rhabditis,* in humus soil from plots in IhV and Ih0 (Sohlenius, 1993). The low abundance of these species in the field samples from Ih0 could be due to a sensitivity to the relative hard and fluctuating climatic conditions which prevailed on the cut areas. Thus climatic conditions may prevent certain species from exploiting available resources. *Plectus* species on the other hand are known from habitats with extreme and fluctuating climatic conditions (Nielsen, 1948; Yeates, 1970; Sohlenius *et al.,* 1996).

The decrease of some other members of the Secernentea such as *Aphelenchoides,* which are considered to be fungal feeders, would be expected, since there was a decrease of fungal biomass which could be due to a natural decrease of roots and mycorrhiza fungi, after the cutting (Bååth, 1980).

Those species which increased most markedly during the first period after the cutting belonged to the Adenophorea bacterial feeders or the Dorylaimida, which are placed by Bongers (1990) in the middle of the c-p scale or more towards the persisters. The pronounced increase of *Wilsonema* can be compared with observations in incubation experiments (Sohlenius, 1985; Hyvönen & Huhta, 1989) and field experiments (Sohlenius & Wasilewska, 1984). *Wilsonema* spp. apparently increase greatly in certain rather narrow ranges of environmental conditions and may thus be a useful indicator of certain types of disturbances. The early increase of *Eudorylaimus* is also in disagreement with the common conclusion that dorylaims are sensitive to disturbances (Zullini & Peretti, 1986; Wasilewska, 1989). The dorylaims were generally considered as persisters and given a high c-p value by Bongers (1990). *Eudorylaimus* is known from extreme climatic conditions in Antarctica (Yeates, 1970).

Contrary to what could be expected from Bongers (1990) hypothesis, the maturity index for the various layers in the cut areas was higher than in the uncut areas (Table 7) which indicates that these nematode faunae were more mature than those of the forest. So, for the kind of disturbance that clear-cutting represents and for this type of forest, the maturity index did not respond as proposed by Bongers – that such a disturbance should generally result in a lower MI value. Certainly, the index will change if other types of disturbances such as forest fertilization or acidification are considered. Such disturbances will to a higher degree promote rapidly growing members of the Secernentea, which seem to be more tolerant to chemical stresses than the Adenophorea. Calculations of MI on data of Sohlenius and Wasilewska (1984) showed that the index was clearly lower after fertilization and irrigation of a young pine forest stand in the same area as that used for the present investigation (unpubl.). The stress on the populations following a clear-cutting is largely due to hard climatical-physical conditions. It appears that some species among the Adenophorea are very tolerant of harsh environmental conditions, whereas most members of the Secernentea may be more sensitive. Ruess and Funke (1995) found no effect on the maturity index in forests damaged by atmospheric pollution. However, in another study Ruess (1995) found lower MI values in acidified than in more undisturbed spruce stands.

Some of the responses of various taxa are in line with Bongers' classification (Table 6). Those species which reached maximum abundance during the first years after the cutting should correspond to taxa with a low value on the c-p scale, whereas those which increased more slowly should be more in agreement with what Bongers calls persisters. If we compare the result for the rate of reaching maximal density for the taxa presented on Table 6 with Bongers' index values, perhaps *Teratocephalus* and *Metateratocephalus* should have a lower c-p value than 3, since they increased rather rapidly after the cutting. *P. acuminatus* should have a higher c-p value than *P. longicaudatus,* which increased more rapidly. Maybe *T. mirabilis* and *Diphtherophora* should have an even higher value than proposed by Bongers (1990) since they increased at a very late stage of this investigation.

A criticism of Bongers' classification is that it is based on family level, which may be a too large an unit since there are large differences in growth rate and patterns of reaction even between various species in the same genus. An example of this in the present study are the differences in reactions between the *Plectus* spp. and probably also between the *Teratocephalus* spp. and the *Tylencholaimus* spp. This difficulty has earlier been discussed by Yeates (1994) and by Ruess and Funke (1995).

There are indications of long-term changes of the nematode fauna in the area. There were synchronic changes in both the forest and in the cut plots indicating certain long-term changes due to factors influencing all sites in the area. Also the occurrence of synchronized increases of taxa on all sites such as *Bunonema* (with maximum abundance in all sites 15 years after the cutting) and *Achromadora* (with maximum abundance in all sites 3 years after cutting) indicated overriding influences by climatic conditions influencing all soils in the area simultaneously. Thus, for some taxa, the variability in abundance between years was certainly influenced by long-term environmental changes or overriding weather conditions. Arpin *et al.* (1995) also found long-term changes which sometimes coincided in time in various treatments.

The results clearly show the importance of considering time dependent changes after disturbances and the necessity of a control site for comparisons of changes in faunal composition after a disturbance. The contribution to total nematode numbers by various species may change rather rapidly after a disturbance and thus the results of monitoring faunal effects is strongly time dependent. This may be one reason for the large differences in effects of treatment on faunal composition in various studies where the time after the treatment may differ (*cf.* for instance Hyvönen & Huhta, 1989; Hyvönen & Persson, 1990).

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