Nematode distribution, trophic structure and biomass in a primary succession of blown-out areas in a drift sand landscape

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Summary – The nematode fauna of a successional sere in a blown-out area in a drift sand landscape, including drift sands without vegetation, *Spergulo-Corynephoretum* and Scots pine (*Pinus sylvestris* L.) forests of different ages, was studied. Samples were taken from the 0-10 cm mineral soil and, in the forested stages, also from the organic layers. The organic layers were divided into litter, fermentation and humus horizons. The initial stages of succession were dominated by omnivorous nematodes. Nematodes feeding on lower plants were restricted to the surface layers and different species occurred during the succession. In litter horizons nematode trophic structure followed microfloral succession. The occurrence of plant feeding nematodes could be related to rooting patterns of herb and tree species. Bacterial and plant feeding nematodes reached highest densities and biomass m^{-2} in the fermentation horizons and increased during succession. Predatory nematodes were rare and occurred only in mineral soil. Average nematode length differed by soil horizon and decreased in the 0-10 cm mineral soil during succession. Relations between nematode morphometrics and micro-climatological conditions are discussed.

Résumé – *Répartition, composition trophique et biomasse des nématodes dans une succession végétale primaire d'une zone de dunes sableuses balayée par le vent* – La présente étude porte sur la faune nématologique de la succession végétale d'une zone sableuse balayée par le vent dans un paysage de dunes sableuses comprenant des dunes sans végétation, un *Spergulo-Corynephoretum* et des forêts de pin d'Écosse (*Pinus sylvestris* L.) de différents âges. Dans les zones en voie de reforestation, les échantillons ont été prélevés dans la couche minérale 0-10 cm ainsi que dans les couches organiques. Ces couches organiques ont été divisées en litière, couche F (« fermentation ») et couche humifère. Aux premiers stades de la succession, les espèces omnivores sont dominantes. Les nématodes se nourrissant sur les végétaux inférieurs sont limités aux couches superficielles, différentes espèces apparaissent au cours de la succession. Dans la couche de litière, la structure trophique du peuplement nématologique évolue suivant la succession de la microflore. La présence des espèces phytoparasites est liée à la végétation. Les types de répartition verticale des nématodes phytoparasites ont pu être mis en relation avec le type de système racinaire des herbes et des arbres. Les nématodes bactério- et phytophages atteignent leurs plus fortes densités et biomasses m^{-2} dans les couches F et leur nombre augmente au cours de la succession. Les prédateurs sont rares, présents seulement dans la couche minérale. La longueur moyenne des individus composant la faune nématologique diffère suivant les couches du sol et décroît au cours de la succession dans la zone 0-10 de la couche minérale. Les relations entre morphométrie des nématodes et conditions microclimatiques sont discutées.

Key-words : Nematodes, succession, *Pinus sylvestris*, feeding groups, biomass, soil horizons.

Short-term nematode population dynamics has been studied extensively during the past two decades. For the temperate regions, annual nematode population dynamics have been described for various natural ecosystems, including grasslands, deciduous and coniferous forests, bogs and heatland (Peterson & Luxton, 1982). Grouping nematode species into ecological groups, mostly based on their feeding requirements, and subsequent relating of the abundance and biomass of these groups to other soil biota and ecological soil processes, has given insight to the position of nematodes in soil processes. In contrast, data on long-term changes in the

occurrence of nematodes in relation to habitat development are scarce, but are valuable both to the understanding of changes in soil ecological processes during habitat development and to evaluation of the ecological condition of soils (" soil health ") (De Goede *et al.*, 1993).

Only Wasilewska (1970, 1971) and De Goede *et al.* (1993) have described nematode community development in relation to successional changes in temperate forests. Vegetation succession of afforested dunes paralleled increasing nematode diversity, abundance and biomass, and decreasing average nematode body weight

(Wasilewska, 1970, 1971). Furthermore, shifts were observed in feeding group proportions; a relative increase of " facultative " plant feeding nematodes as compared with obligatory plant feeders, and a decreasing importance of omnivorous nematodes being the most marked changes. Wasilewska (1971) concluded that these changes were related to differences in plant cover and humus content of the successional stages. De Goede *et al.* (1993), who studied nematode community structure in a primary succession of blown-out areas in a drift sand landscape, found a comparable increase in nematode diversity during forest succession. This increase was found to be related to the development of the organic horizon. As succession proceeds on these soils, the organic horizon of Scots pine forests (the primary colonizing tree species) develops into a mor type organic profile (Emmer *et al.*, 1991). At full development within such an organic profile litter, fermentation and humus horizons, which reflect different stages of decomposition of the organic matter, can be recognized (Klinka *et al.*, 1981). The maximum number of nematode species coincided with the first occurrence of a fully developed mor humus (De Goede *et al.*, 1993). Each horizon was also characterized by its nematode faunal composition. These changes in nematode species distribution during succession and within the soil profile, showed relationships to vegetation and micro-climatological conditions, and indicated significant differences in ecological conditions between the various soil horizons.

The present study describes the trophic group distributions, the spatial and successional species distributions, and the total biomass and body dimensions of the nematode fauna of this primary succession of blown-out areas in a drift sand landscape described by De Goede *et al.* (1993). Effects of succession on the nematode community are discussed with emphasis on the ecological processes with which the various trophic groups are associated, and changes in habitat conditions related to the development of the organic horizon and the vegetation.

Materials and methods

The results presented are based on the nematode samples taken from successional sere B near Harderwijk in the Netherlands, as described by De Goede *et al.* (1993). Briefly summarizing, the nematode fauna of eight successional stages, characterized as (1) bare drift sand, (2) *Spergulo-Corynephoretum*, Scots pine (*Pinus sylvestris* L.) forests of respectively (3) 3-5, (4) 25-30, (5) 45-50, (6) 80-90 and (7) 105 years old and (8) an early variant of *Betulo-Quercetum* with age comparable to stage 7, were investigated. At each site the 0-10 cm mineral soil was sampled and, depending on the state of development of the organic horizon, samples were taken from the litter, fermentation and humus horizons. No significant differences in thickness of each of the organic horizons were found between the successional stages. Thickness of the fermentation and humus horizons (mean and standard deviation in parentheses) was 6.1 (1.28) and 1.7 (0.69) cm respectively; thickness of the litter horizon was < 0.5 cm.

At stage 3 no herb layer but only pine needles were present. The herb layer of stage 4 was composed of *Festuca ovina* L., *Corynephorus canescens* (L.) Beauv. and *P. sylvestris* needles. From stage 5 onwards the herb layer was composed of *Deschampsia flexuosa* (L.) Trin. and mosses, with in the stage 7 also *Empetrum nigrum* L., *Vaccinium myrtillus* L. and seedlings of *Prunus* sp., *Betula* sp. *Quercus* sp. and *Sorbus aucuparia* L. *Empetrum nigrum* and *V. myrtillus* dominated the herb layer of stage 8, whereas *D. flexuosa* and mosses were present in low densities.

Adult nematodes were identified to species level. However, as in some samples juveniles could not adequately be attributed to species, because of either the lack of adults or the presence of mixed species populations, the results will generally be presented at genus level. Allocation of nematodes to trophic groups followed Yeates *et al.* (1993). Nematodes feeding by piercing algae, lichens or mosses and those feeding on unicellular eucaryotes were combined into one group : nematodes feeding on lower plants. The taxa found (see Bongers (1988) for authorities), with their trophic habit are (for plant feeding nematodes subgroups are indicated by a. sedentary parasites, b. migratory parasites, c. semi-endoparasites, d. ectoparasites and e. epidermal and root hair feeders) :

Plant feeding nematodes : *Aglenchus agricola* (e), *Cephalenchus hexalineatus* (d), *Criconema sphagni* (d), *Filenchus ditissimus* (e), *F. helenae* (e), *Hemicycliophora epicharoides* (d), *Heterodera* sp. (a), *Malenchus bryophilus* (e), *M. sulcus* (e), *Merlinius microdorus* (d), *Merlinius* sp. (d), *Nagelus obscurus* (d), *Paratrichodorus teres* (d), *Pratylenchus* sp. (b), *Rotylenchus* sp. (c), *Tylenchorhynchus microphasmis* (d) and *Tylenchorhynchus* sp. (d).

Hyphal feeding nematodes : *Aphelenchoides* spp., *Deladenus durus*, *Ditylenchus* spp., *Paraphelenchus pseudoparietinus*, *Pseudhalenchus minutus*, *Tylencholaimus mirabilis* and *Tylolaimophorus typicus*.

Bacterial feeding nematodes : *Acrobeles mariannae*, *Acrobeloides nanus*, *A. tricornis*, *Alaimus mucronatus*, *Bunonema richtersi*, *Cephalobus* sp., *Cervidellus serratus*, *Cylindrolaimus* sp., *Domorganus* sp., *Drilocephalobus* sp., *Eucephalobus mucronatus*, *Eumonhystera vulgaris*, *Heterocephalobus elongatus*, *Metadiplogaster* sp., *Metateratocephalus crassidens*, nematode A (undescribed alaimid), *Panagrolaimus rigidus*, *Plectus acuminatus*, *P. longicaudatus*, *P. pusillus*, *Prismatolaimus intermedius*, *Prodesmodora* sp., *Protorhabditis* sp., *Rhabditonema propinquum*, *Steinernema* sp., *Teratocephalus* sp. *Wilsonema otophorum* and *Zeldia punctata*.

Predators : *Seinura* sp. and *Tripyla* sp.

Nematodes feeding on lower plants : *Laimaphelenchus penardi, L. pini, L. pannocaudus* and *Tylenchus davainei.*

Omnivores : *Aporcelaimellus obtusicaudatus, Aporcelaimium* sp. and *Eudorylaimus* sp.

From every successional stage, the total length (L, μm) and longitudinal section (A, μm²) of 50-60 randomly selected nematodes were measured using a GOP 302 image-analyzer (Context Vision, Sweden). Nematode biomass (G) was calculated from the Andrássy equation $G (\mu g) = (W^2 \times L) \times (16 \times 10^{-5})$. Body width W (μm) was calculated as the A/L ratio, and therefore consequently was an underestimation of maximum body width, which is generally used in the Andrássy equation. In principle the Andrássy equation is based on nematode volume multiplied by a constant (1.0625×10^{-6}). Robinson (1984) showed that nematodes' volume calculated using the area/length ratio, resulted in an underestimation of nematode volume in the range of 3-12 %, whereas bias in the Andrássy method ranged from − 2 to + 23 %. Thus biomass estimates presented in this study will be on average 0-28 % lower than those obtained using W.

Differences in trophic group composition between the various successional stages were tested by the Mann-Whitney U-test. Body length was log transformed, and differences in mean population body length between the various successional stages and soil horizons were tested by an analysis of variance.

Results

Genera and trophic group distribution

Omnivorous nematodes, represented by three genera only, dominated the early successional stages, especially the drift sands where no vegetation was present (Fig. 4). *Aporcelaimellus* and *Aporcelaimium* (present only at stage 3) predominantly occurred in the 0-10 cm mineral soil of the *Spergulo-Corynephoretum* and under the invading young Scots pine trees. On the other hand, *Eudorylaimus* was present throughout most of the succession, and occurred both in the mineral soil and the organic horizons. The absence of omnivorous nematodes in the samples taken in successional stage 4 is remarkable (Table 1; Fig. 4). The discontinuous distribution of the genus *Eudorylaimus* with respect to succession indicates that several species may be involved. In the forested stages, *Eudorylaimus* reached highest densities in the fermentation horizon, with their numbers increasing in this horizon during the succession.

Laimaphelenchus and *Tylenchus* (nematodes feeding on lower plants) mainly occurred in the superficial soil horizons (Figs 1, 2; Table 1), corresponding to the distribution of mosses, lichens and algae. They reached highest densities in the *Spergulo-Corynephoretum*. The sharp decrease in numbers in stage 5, coincided with the closure of the herb layer (in stage 3 and 4 still > 30-50 %

of the area was pine litter). The species of *Laimaphelenchus* showed different optima in the succession, with *L. pini, L. penardi* and *L. pannocaudus* having their peak occurrence in stage 2, 3-4 and 5 respectively (Fig. 5). *Tylenchus* replaced *Laimaphelenchus* in the oldest successional stages.

Together with the nematodes feeding on lower plants, the bacterial feeding nematodes dominated the nematode community of the *Spergulo-Corynephoretum* where the two groups composed 23 and 45 % of the total numbers respectively (Table 1). Only three of the total 25 bacterial feeding genera found in this study were restricted to the first successional stages *(Acrobeles, Zeldia, Eucephalobus)* (Figs 2, 3).

The abundance and relative proportion of the bacterial feeding nematodes depended both on the soil horizon and on the stage of succession. In the 0-10 cm mineral soil, their numbers remained fairly constant $(178-299 \times 10^3 \text{ m}^{-2})$ until stage 6 (the 80-90 years old Scots pine forest), but decreased significantly to 61-$76 \times 10^3 \text{ m}^{-2}$ in the older forests. The highest abundance of bacterial feeding nematodes was found in the fermentation horizon, where numbers increased from 221×10^3 in stage 4 to $858 \times 10^3 \text{ m}^{-2}$ in the *Betulo-Quercetum*. However, in this horizon the proportion of bacterial feeding nematodes reached a peak in stage 5 (50 %) and decreased subsequently to 27-31 % in the oldest stages. This was mainly due to a strong increase in plant feeding nematodes as succession proceeded.

In the litter horizon the hyphal feeding nematodes outnumbered the bacterial feeding nematodes. Here the bacterial feeders : hyphal feeders (BF : HF) ratio was 0.2-0.3 (exceptionally 0.6 at stage 3), whereas it was ⩾ 1 in the 0-10 cm mineral soil and in most of the samples taken from the fermentation horizon (see below for exceptions). Only two bacterial feeding genera *(Panagrolaimus, Plectus)* were common in the litter horizon. The distribution of *Panagrolaimus* was mainly restricted to this layer, whereas *Plectus* occurred throughout the profile. However, some spatial segregation of the three *Plectus* species present in this study, seemed to occur (Fig. 5); *P. acuminatus* and possibly also *P. pusillus* predominantly occurred in the surface layers, whereas *P. longicaudatus* was rare in the litter horizon, but common in the deeper horizons. Most other bacterial feeding genera also showed characteristic distribution patterns within the soil profile and/or succession. In the forested stages *Bunonema,* Nematode A and *Teratocephalus* were found mainly in the fermentation and humus horizons. *Cervidellus* and *Eucephalobus* were mainly restricted to the 0-10 cm mineral soil, whereas *Wilsonema, Metateratocephalus, Acrobeloides, Prismatolaimus, Protorhabditis, Heterocephalobus* and *Steinernema* were found both in the 0-10 cm mineral soil and in the fermentation and humus horizons. *Alaimus, Domorganus, Drilocephalobus* and *Prodesmodora* were found mainly in the oldest successional stages.

Table 1. Mean densities (numbers × 10³ m⁻²) of trophic groups per soil horizon and stage of a succession. (Bacterial feeding (BF), hyphal feeding (HF), plant feeding (PF), omnivores (OV), predators (PR) and feeding on lower plants (LF), in the 0-10 cm mineral soil plant feeding nematodes are divided into endo- and ectoparasites (a-d) and epidermal and root hair feeders (e) in a given line numbers followed by different letters differ significantly (p ≤ 0.05; one sided).

Successional stage	1	2	3	4	5	6	7	8
Litter								
BF			65 *a*	29 *bc*	86 *a*	50 *ac*	21 *bc*	16 *bc*
HF			108 *ac*	132 *a*	336 *b*	205 *a*	126 *ac*	50 *c*
PF			0	0	0	0	0	< 1
OV			0	0	0	0	0	0
PR			0	0	0	0	0	0
LF			67 *a*	35 *ab*	5 *bc*	6 *b*	2 *bc*	1 *c*
Fermentation								
BF				202 *a*	572 *b*	697 *bc*	730 *c*	1 326 *bc*
HF				221 *a*	268 *ab*	414 *ab*	519 *ab*	858 *b*
PF				116 *a*	253 *ab*	752 *bc*	1 010 *c*	2 656 *d*
OV				0 *a*	43 *b*	77 *bc*	80 *bc*	130 *c*
PR				0	0	0	0	0
LF				0	0	0	0	30
Humus								
BF					83	226	82	147
HF					159	124	127	184
PF					23 *a*	121 *b*	74 *b*	421 *ab*
OV					0 *b*	4 *ab*	0 *b*	11 *a*
PR					0	0	0	0
LF					0	1	0	0
0-10 cm Mineral soil								
BF	1 *a*	209 *bd*	269 *b*	161 *bd*	178 *d*	299 *bd*	61 *c*	76 *c*
HF	1 *a*	27 *b*	183 *cd*	97 *bcd*	110 *cd*	212 *c*	35 *b*	70 *d*
PF	0 *a*	48 *bd*	6 *a*	105 *bcd*	116 *c*	285 *e*	59 *df*	97 *cf*
a-d	0 *a*	46 *bd*	6 *ac*	10 *c*	45 *bd*	72 *bd*	16 *b*	34 *d*
e	0 *a*	2 *a*	0 *a*	95 *bc*	71 *b*	212 *c*	43 *b*	62 *b*
OV	55 *ac*	62 *a*	25 *bc*	0 *d*	7 *bd*	13 *b*	1 *d*	3 *d*
PR	0 *ac*	9 *abc*	3 *abc*	0 *ac*	3 *b*	16 *ab*	0 *ac*	0 *c*
LF	0 *a*	106 *b*	0 *a*	2 *ab*	0 *a*	0 *a*	0 *a*	< 1 *a*

The distribution of six of the eight hyphal feeding genera is shown in Figure 4. *Aphelenchoides* occurred in all horizons and in all stages. The only other genus with such an extensive distribution was the bacterial feeding *Plectus,* and as with *Plectus* several species of *Aphelenchoides* were involved. The hyphal feeding *Ditylenchus* had a similar distribution to *Aphelenchoides,* but was found less frequently in the humus horizon. *Paraphelenchus* and *Deladenus* occurred in the topmost horizons, with peak occurrences in stage 3 and 6-7 respectively. The remaining hyphal feeding genera predominantly occurred in the 0-10 cm mineral soil. Among these, *Tylolaimophorus* reached highest relative abundances in the oldest stages [stages (6) 7-8], where it also occurred in the fermentation and humus horizons.

The absolute numbers of hyphal feeding nematodes were highest in the oldest successional stages (stages 5-8), mainly because of increasing numbers in the organic horizon (Table 1). In the 0-10 cm mineral soil maximum abundances were found in the stages 3-6. In the litter horizon the hyphal feeding nematodes were the most abundant trophic group, where they composed 45-84 % (weighted mean 70 %) of the total nematode fauna. In all other horizons their proportion was ≤ 45 % (one exception : humus horizon of stage 5, proportion 60 %). The relatively high proportion of hyphal feeding nematodes in the first stages of the various organic horizons as well as in the 0-10 cm mineral soil of stage 3 as compared to the same horizons of the subsequent stages is notable (fermentation horizon stage 4 and 5-8, 41 and
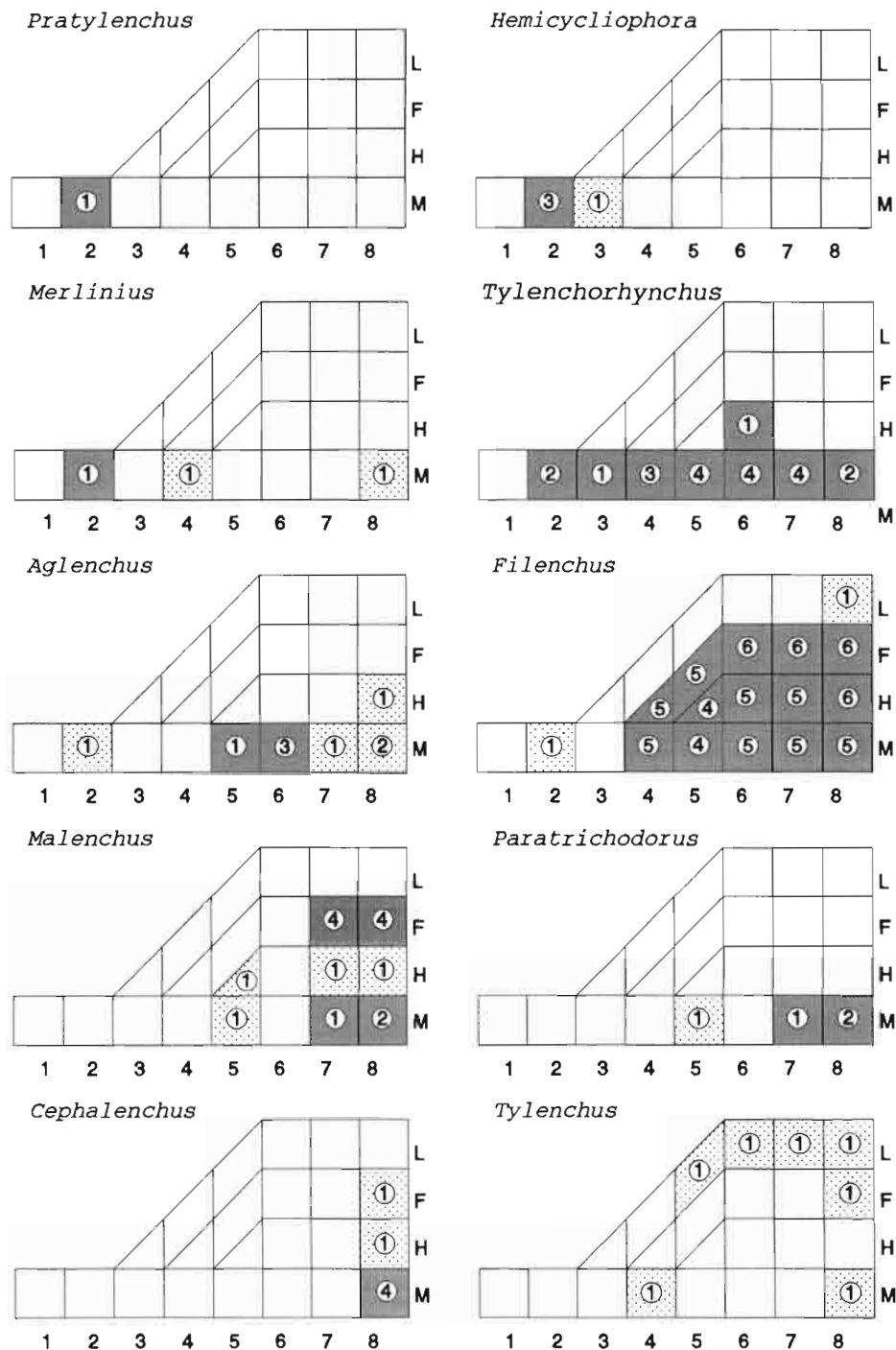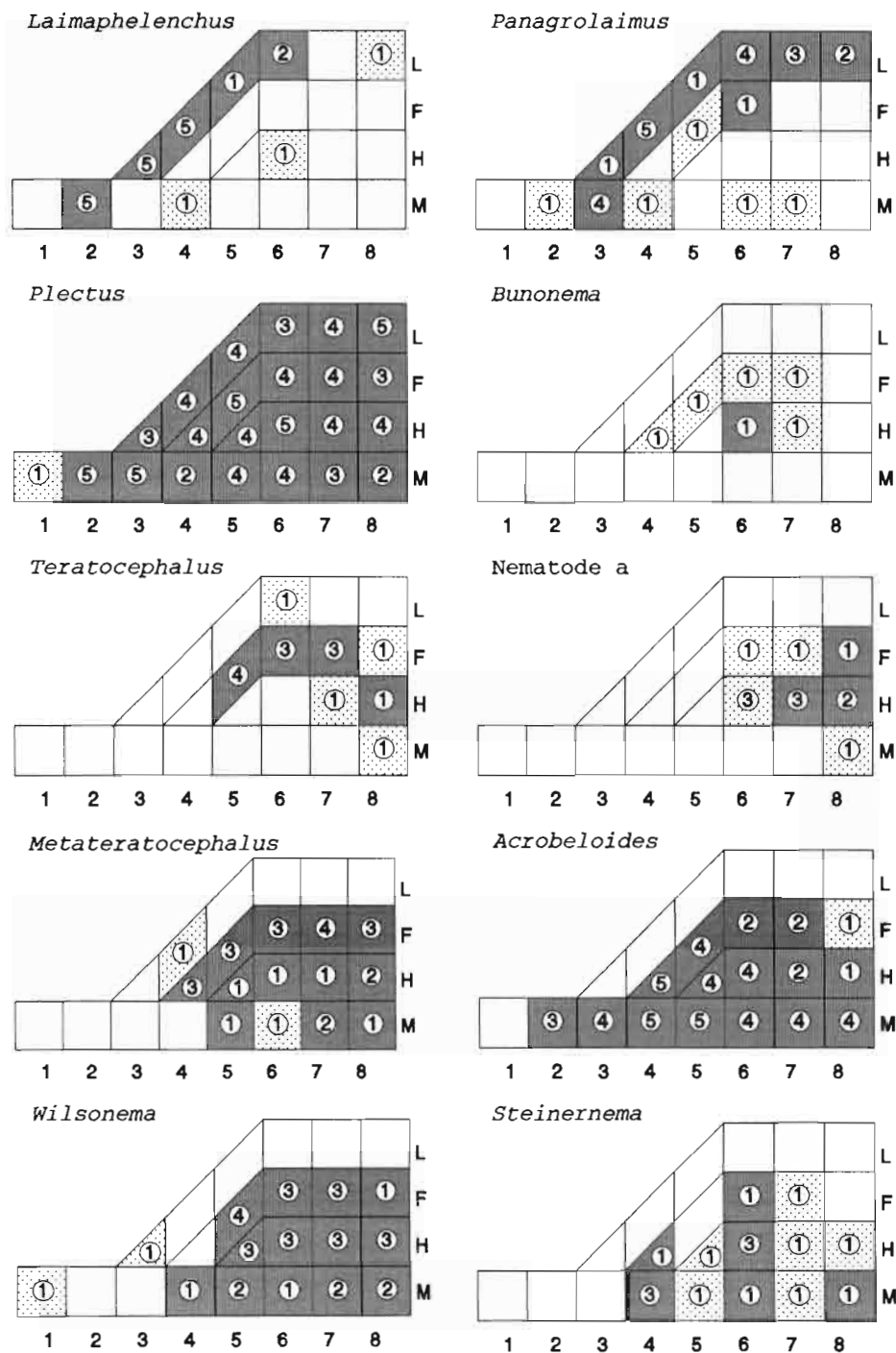
Fig. 1. Vertical distribution of nine plant feeding and one lower plant feeding nematode genera in stages 1-8 of a primary succession on blown-out areas on a drift sand. Soil horizons are litter (L), fermentation (F), humus (H) and 0-10 cm mineral soil (M). Indicated is whether genera were absent (white), present in ≤ 50 % of the samples (stippled), or present in > 50 % of the samples (solid). Average nematode population density is given by relative abundance classes : 1 < 0;2], 2 < 2;4], 3 < 4;8], 4 < 8;16], 5 < 16;32], 6 < 32;64] and 7 < 64;100] % (n = 3 for the stages 1, 3-7 and n = 4 for the stages 2 and 8).

Fig. 2. Vertical distribution of one lower plant feeding and nine bacterial feeding nematode genera in stages 1-8 of a primary succession on blown-out areas on a drift sand (See Fig. 1 for details).
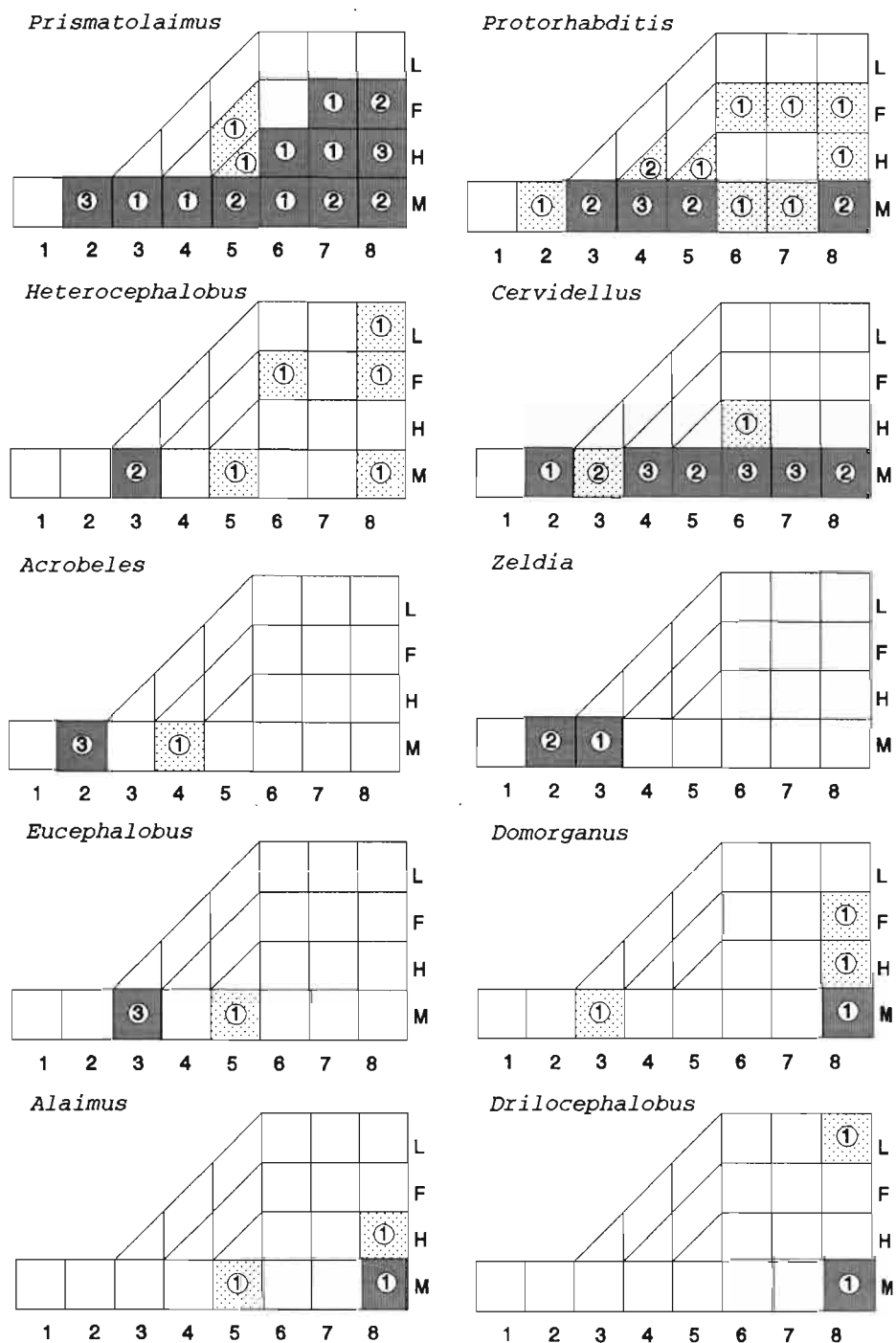
Fig. 3. Vertical distribution of ten bacterial feeding nematode genera in stages 1-8 of a primary succession on blown-out areas on a drift sand (See Fig. 1 for details).
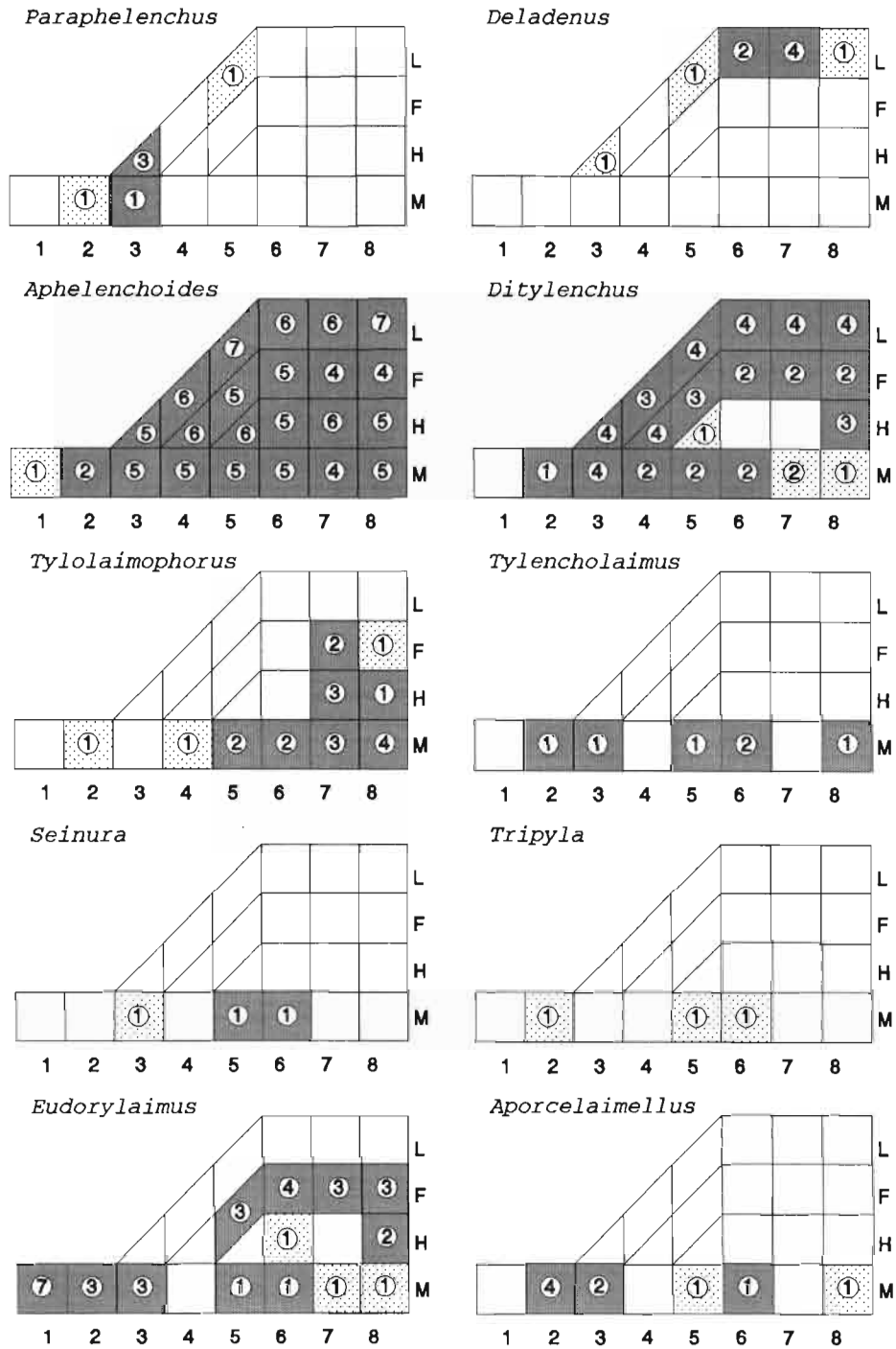
Fig. 4. Vertical distribution of six hyphal feeding, two predatory and two omnivorous nematode genera in stages 1-8 of a primary succession on blown-out areas on a drift sand (See Fig. 1 for details).
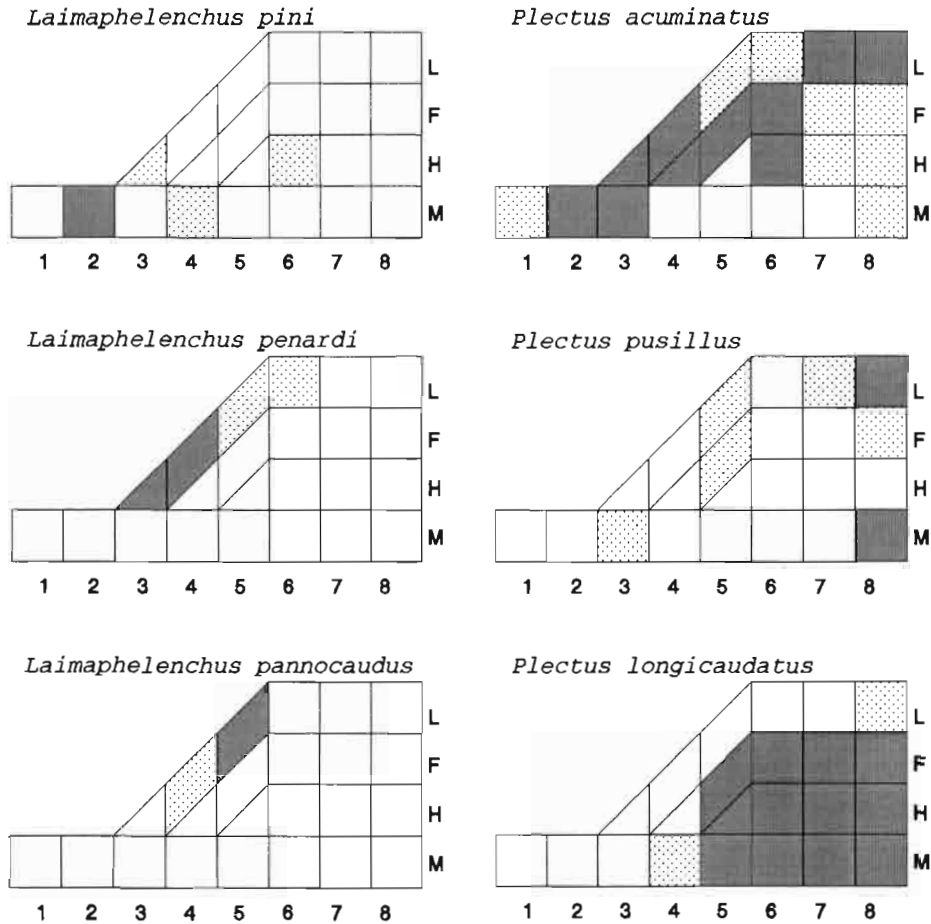
Fig. 5. Vertical distribution of the species of *Laimaphelenchus* and *Plectus* in stages (1-8) of a primary succession on blown-out areas on a drift sand (See Fig. 1 for details).

17-24 % respectively; humus horizon stage 5 and 6-8, 60 and 24-45 %; 0-10 cm mineral soil stage 3 and 4-8, 40 and 22-28 %). However, no significant differences in absolute numbers were found (Table 1); thus the relatively high percentages of hyphal feeding nematodes resulted from changes in other trophic groups.

An exceptionally high BF : HF ratio 9.7 (4.52) (mean and standard deviation in parentheses) was found for the 0-10 cm mineral soil of the *Spergulo-Corynephoretum,* as the second highest value was only 2.1 (1.40) (fermentation horizon stage 5).

Invasion by Scots pine and related changes in the composition of the vegetation, paralleded profound changes in the occurrence of the plant feeding nematodes. The numbers of plant feeding nematodes decreased significantly from 48×10^3 m^{-2} in the *Spergulo-Corynephoretum* to only 6000 m^{-2} under the 3-5 year old Scots pine trees of stage 3 (Table 1). However, in the subsequent stages the numbers in 0-10 cm mineral soil increased to a peak of 285×10^3 m^{-2} in stage 6, and then subsequently decreased again to 59-97×10^3 m^{-2}. In

both cases the decrease in numbers was accompanied by shifts in the generic composition. With the development of the young forest, *Pratylenchus, Hemicycliophora, Merlinius, Nagelus* and *Tylenchorhynchus* decreased below detection level or disappeared, and populations of *Filenchus* and *Aglenchus* started to develop (Fig. 1). Greatest development of populations of *Paratrichodorus, Cephalenchus* and *Malenchus* were found after stage 6, whereas *Aglenchus* seemed to decrease. *Tylenchorhynchus* is the only plant feeding genus which is common in all stages with vegetation present, both outside and inside the forest.

The diversity of plant feeding nematodes in the organic horizons was relatively low. Of the fifteen plant feeding genera only *Filenchus* and *Malenchus* were frequently found in these horizons, where they were mainly responsible for a significant increase in absolute numbers of plant feeding nematodes, from 116×10^3 m^{-2} in stage 4 to 2.658×10^6 m^{-2} in stage 8 (respectively 22 and 54 % of total numbers in the fermentation horizon). Subdivision of plant feeding nematodes in groups based

Table 2. Nematode biomass (mg·m⁻²) in the different soil horizons of the various stages of a primary succession on blown-out areas on drift sand. (Litter (L), fermentation (F), humus (H) horizon, 0-10 cm mineral soil (M) and total (T); percentages within soil profile are given between brackets).

Stage	Soil horizon									
	L		F		H		M		T	
1							47	(100)	47	
2							99	(100)	99	
3	32	(27)					85	(73)	117	
4	17	(22)	31	(41)			30	(38)	79	
5	32	(22)	67	(46)	8	(6)	39	(27)	146	
6	23	(12)	75	(41)	38	(21)	49	(27)	185	
7	14	(8)	138	(80)	13	(8)	9	(5)	173	
8	5	(2)	243	(87)	13	(5)	19	(7)	280	

on aspects of their feeding biology, showed the almost exclusive occurrence of epidermal and root hair feeders in the fermentation and humus horizons (groupe e; Fig. 1). Plant feeding nematodes of groups a-d (sedentary parasites, migratory endoparasites, semi-endoparasites and ectoparasites respectively) were mainly restricted to the mineral soil where they occurred together with epidermal and root hair feeders. The latter were absent or rare in the 0-10 cm mineral soil of the early stages of succession (stages 2 and 3; Table 1).

Predatory nematodes were found only in 0-10 cm mineral soil and then only in stages 2-3 and 5-6 (Table 1; Fig. 4). Their population reached 16×10^3 m⁻², and they comprised 1-2 % of the total nematode fauna of this horizon.

NEMATODE BIOMASS AND LENGTH

In 0-10 cm mineral soil nematode biomass was highest in stages 2 and 3 (99 and 85 mg.m⁻² respectively) (Table 2). Relatively low values (< 20 mg.m⁻²) were obtained for the oldest forests of stages 7 and 8. In the fermentation horizon a gradual increase in biomass from 31 mg.m⁻² in stage 4 to 243 mg.m⁻² in stage 8 was found, reflecting the increase in absolute numbers in this horizon. Compared with the absolute abundance of nematodes in the litter horizon, the total nematode biomass in this horizon was relatively high. The nematodes in the litter horizon were on average significantly longer than those in the underlying horizons (Table 3). With increasing depth nematode length decreased significantly in the organic horizons, with minimum lengths in the humus horizon. In the underlying 0-10 cm mineral soil, average length of nematodes was significantly larger than in the humus horizon, but it did not differ from the lengths in the litter layers of the stages 4 and 5 and the fermentation layers. Average length of nematodes in the mineral soil was maximum in the drift sands of stage 1, and decreased gradually with increasing age of the forests.

Table 3. Average length (μm) of nematodes per soil horizon in the various stages of a primary succession on blown-out areas on drift sand. (Numbers within the table followed by different letters differ significantly (p ≤ 0.05), see Tab. 2 for abbreviations.)

Stage	Soil horizon			
	L	F	H	M
1				890 *a*
2				484 *bc*
3	539 *b*			439 *ce*
4	455 *cd*	370 *fgh*		403 *def*
5	436 *ce*	362 *fgi*	264 *m*	389 *eg*
6	445 *cd*	325 *ijl*	342 *gl*	357 *fgj*
7	462 *c*	340 *hijkl*	274 *m*	341 *hijkl*
8	438 *ce*	326 *hijkl*	266 *m*	353 *gk*

Longer nematodes tended to have greater body width; the average nematode width in stages 3-8, calculated as the A : L ratio, was 15.2, 12.6, 11.7 and 14.4 μm for the litter, fermentation and humus horizon and 0-10 cm mineral soil respectively. The relatively large average nematode length in the humus horizon of stage 6 compared with stages 5, 7 and 8 is remarkable. As a result of this and greater absolute nematode abundance, the total biomass of the nematode fauna of stage 6 was also relatively high (Table 2).

Discussion

Successional changes in the vegetation and related soil development of the blown-out areas were correlated with changes in nematode community structure (De Goede *et al.,* 1993). These successional changes in nematode community structure showed a pattern of initial dominance of nematode taxa generally characterized as

colonizers (*sensu lato* Bongers, 1990), followed by the development of nematode faunae characteristic for the stage of succession and soil horizon (De Goede *et al.*, 1993). The present study showed that, depending on the stage of succession, the nematode fauna of these soil horizons also had characteristic trophic structures (Table 1).

The surface layers of successional stages 2-8 were characterized by the occurrence of relatively high numbers of hyphal feeding nematodes and the presence of nematodes feeding on lower plants. Greatest abundances of the latter were found in stage 2 where algae, mosses and lichens constituted 39-98 % of total biomass of the herb layer (Moszynska, 1991). As total biomass of lower plants in the forested stages remained high (450-2170 and 560-8840 kg/ha for the forests and *Spergulo-Corynephoretum* respectively (Moszynska, 1991)), this does not explain the decrease in numbers of nematodes feeding on lower plants and the disappearance of *Laimaphelenchus* as succession proceeded. However, the increasing cover of the herb layer and tree canopy during succession, are likely to depress the occurrence of photosynthetic unicellular organisms (e.g. algae) in the litter horizons, and the three *Laimaphelenchus* species found in this study were probably associated with such algae, as they are common inhabitants of algae layers covering tree trunks (Bongers, 1988). On the other hand, *Tylenchus* specifically occurred in the late successional stages (stage ≥ 5) where it probably fed on mosses (Procter, 1984; Yeates *et al.*, 1993).

The nematode fauna of the litter horizons was characterized by the extreme dominance of hyphal feeding nematodes (Table 1). Studies on the succession of microflora and soil organisms during the decomposition of pine needles, showed a dominance of fungi in the initial stages of decomposition (Kendrick & Burges, 1962; Ponge, 1991). Sizeable bacterial populations were found to develop only at the more advanced stages of decay (Richards, 1987; Ponge, 1991). Thus the trophic structure of the nematode fauna of the litter horizon in this study (with BF : HF ratio's < 1) reflected the generally observed composition of the microflora of these horizons. The reported minor importance of bacteria in the initial stages of decomposition of pine needles are further supported by the occurrence of only two common bacterial feeding nematode taxa *(Panagrolaimus, Plectus)* in the litter horizons. The occurrence of *Panagrolaimus* is possibly related to its opportunistic life strategy which may be advantageous in microhabitats with unpredictable feeding conditions (De Goede *et al.*, 1993). However, life strategies of the species within the Plectidae are supposed to be less opportunistic (Schiemer, 1983; Bongers, 1990). Three species of *Plectus* were found in this study, from which *P. acuminatus* and *P. pusillus* occurred in the surface horizons, and *P. longicaudatus* only beneath the litter horizon. Zell (1989) also found *P. acuminatus*, together with the opportunist

Rhabditis silvatica, to be the first bacterial feeding colonizers of fallen beech leaves, whereas the surface horizons of another beech forest were dominated by *Plectus cirratus* (Voltz, 1951 *in* Twinn, 1974). Twinn (1974) suggested that the large *Plectus* spp. of surface horizons, occupy a niche different from that of other bacterial feeding nematodes. This then should resolve such cases as the absence of the eurytopic bacterial feeding nematodes *Acrobeloides nanus*, *Wilsonema otophorum* and *Metateratocephalus crassidens* in the litter horizon. Schiemer (1983) hypothesized that the relatively long reproductive phase of *Plectus palustris/P. cirratus* can be advantageous in tiding over periods of food shortage. Moreover, the associated occurrence of some *Plectus* species with mosses and lichens (Nielsen, 1949, 1967; Procter, 1984; Zullini & Peretti, 1986; Bongers, 1988) and their dominance in high latitude and altitude nematode communities (Proctor, 1984) indicate their ability to survive extreme climatological conditions, which is most pronounced in the litter horizon.

The occurrence of soil fauna in surface horizons largely depends on the physiological tolerance of the species to fluctuations in microclimatological conditions (Anderson, 1977; Rusek, 1978; De Goede *et al.*, 1993), such as fluctuating temperature and moisture conditions. The presence of water films is essential to the activity of nematodes. Thus species living in the surface horizons will exhibit a relatively efficient water retention and greater ability to survive dessication through anhydrobiosis. Because of the physical structure of the litter horizon, avoidance of dessication by migration to deeper soil horizons is not expected. Because loss of water due to transpiration decreases exponentially for animals with smaller surface : volume ratio's (Vannier & Verhoef, 1978), the occurrence of relatively large nematodes in the 0-10 cm mineral soil of the stages 1 and 2 and in the litter horizons (Table 3 and text), may reflect selection to reduce such water loss. However, as nematode movement depends on adequate water film thickness surrounding soil particles, and as water loss may induce nematodes to enter the state of anhydrobiosis (Demeure *et al.*, 1979), the duration of activity of thicker nematodes like those found in the litter horizons, will be shorter than that of more slender specimens. If there is a trade-off between surface : volume ratio and body diameter it can be hypothesized that, body length : body-width ratio's of nematode faunae of surface horizons will be large compared to nematode faunae of microhabitats with less extreme fluctuations in moisture conditions. Thus, in relation to nematode size (body length) body width of the nematode fauna of the surface horizons will be relatively small. Average body length : body-width ratio's of the nematode fauna of the soil horizons of the successional stages 2-8 ranged from 29.7-30.6, 26.3-29.2, 22.1-27.7 and 25.8-27.2 for the litter, fermentation and humus horizons and 0-10 cm mineral soil respectively, and was 30.4 for stage 1. Although these re-

sults support the hypothesis, it needs validation as body width was not measured directly but was calculated from longitudinal section area divided by body length.

Odum (1969) listed trends to be expected in the successional development of ecosystems. He expected populations of relatively small animals in the initial stages of succession, and increasing body sizes as succession proceeds. Our results seem to contradict this hypothesis, because the largest nematodes were found in the bare drift sands of stage 1. With succession, average body length of the nematode fauna of the 0-10 cm mineral soil decreased. Similar results were obtained by Wasilewska (1971) for the nematode fauna of a successional sere of *P. sylvestris* in Poland. The organic matter content of the 0-10 cm mineral soil increased during succession (Emmer *et al.*, 1991) and will be related to altered soil micromorphology. Just as increased bulk density in the sequence litter, fermentation and humus horizon (Emmer *et al.*, 1991) was related to a decrease in average nematode length, this increase in organic matter content of the mineral soil may have resulted in selection for overall smaller nematodes in the course of succession.

In general, the distribution of plant feeding nematodes appears closely related to the distribution of roots, and many studies showed positive correlations between numbers of plant feeding nematodes and primary production (see Yeates, 1979, 1987 for discussion). In the litter horizons plant feeding nematodes associated with higher plants were absent, which can be explained by the absence of roots of herbs and *P. sylvestris* in these horizons. Root biomass in the fermentation and humus horizons increased during succession, and was highest in the fermentation horizons (van Berghem *et al.*, 1986). This corresponds with an increase in absolute numbers of plant feeding and bacterial feeding nematodes m^{-2} in the fermentation horizons, and with increasing biomass of the total nematode fauna of these horizons. Moreover, annual production of the herb layer of Scots pine forests of 45, 75 and 120 years old at Hulshorster sand also increased (947 (33 % of standing crop), 1783 (37 %) to 3206 (24 %) kg.ha^{-1}.y^{-1} respectively) (Moszynska, 1991). Our findings are also supported by observations from a succession of *P. sylvestris* in Poland, where an increase in abundance and biomass of bacterial, hyphal and plant feeding nematodes was observed in the succession (Wasilewska, 1971).

Densities of plant feeding nematodes were low in 0-10 cm mineral soil compared to numbers found in the fermentation horizons, indicating lower food supply in this horizon. Although root biomass estimates from the study area (Van Berghem *et al.*, 1986) were restricted to the organic horizons it is reasonable to expect such lower root biomass in the 0-10 cm mineral soil.

Besides quantitative differences in root biomass and density, differences in root quality (e.g. root anatomy, nutrition, exudates, growth pattern, mycorrhizas) will also effect plant feeding nematodes (Yeates, 1987). The

different vertical distribution patterns of epidermal/root hair feeding nematodes and endo- or ectoparasitic nematodes (respectively group e and a-d in Yeates *et al.*, 1993) in the forested stages probably relates to species-specific rooting patterns and morphometric characteristics of the nematodes.

In the organic horizons the plant feeding nematode fauna was composed predominantly of genera belonging to plant feeding group e *(Filenchus, Malenchus)* and nematodes belonging to plant feeding groups a-d only occurred incidently. The latter were mainly restricted to the mineral soil where they coexisted with the taxa from plant feeding group e. Similar nematode distribution patterns were found in a 67 years old Scots pine plantation (D63) located in the north-eastern part of the Netherlands, where plant feeding taxa belonging to groups c-d *(Rotylenchus, Tylenchorhynchus, Trichodorus, Paratrichodorus)* were restricted to the mineral soil, and group e taxa *(Filenchus, Malenchus)* occurred both in the mineral soil and organic horizons (De Goede, unpubl.). Also in a 15-20 years old Scots pine forest in Sweden, nematode taxa belonging to plant feeding groups c-d *(Rotylenchus, Paratylenchus)* and e *(Filenchus, Malenchus, Coslenchus)* reached highest abundances in the mineral soil and fermentation-humus horizons respectively (Magnusson, 1983).

As the occurrence of plant feeding nematodes depends on their hosts, the differences in distribution of group e and a-d plant feeding nematodes can probably be related to the rooting pattern of the plant species involved. In Scots pine plantations similar to Hulshorster sand, it was shown that the roots of the dominant herb species of the forested stages of the successional sere *(Deschampsia flexuosa, Empetrum nigrum, Vaccinium myrtillus)* mainly occurred in the organic horizons, and only few roots grew vertically into the mineral soil (Nabuurs, 1991). Persson (1980) found roots of *P. sylvestris* concentrated below the organic horizons, in the upper part of the mineral soil. And moreover, largest turnover rates of roots of *P. sylvestris* and dwarf shrubs occurred in the mineral soil and organic horizons respectively (Persson, 1980). Thus a greater part of the roots in the fermentation horizons probably belonged to plant species of the herb layer, whereas in the mineral soil the proportion of *P. sylvestris* roots was larger.

Deschampsia flexuosa was the dominant herb in the stages 5-7, and its roots have smaller diameter (diameter 0.1-0.5 mm; Nabuurs, 1991) than roots of *P. sylvestris, E. nigrum* and *V. myrtillus.* Yeates (1986, 1987) indicated that stylet length of nematodes functionally affects feeding, and differences in root diameter will influence the length of stylet required to utilise the root resource. The epidermal and root hair feeding *Filenchus* and *Malenchus* species from the organic horizons at Hulshorster sand, had shorter stylets than those nematode species restricted to the mineral soil (stylet lengths ≤ 10 μm and > 10 μm respectively). Stylet length of

Aglenchus agricola de Man 1881, also classified as epidermal and root hair feeder but mainly restricted to the mineral soil, is 13-16 μm (Sanwal & Loof, 1967). Thus, these observations indicate that distribution of plant feeding nematodes could be related to interspecific differences in food resource utilization.

The functional relationship between the epidermal and root hair feeders and roots of grasses like *D. flexuosa* is further supported by the observations that in the absence of a herb layer (stage 3) no group e taxa were found in the 0-10 cm mineral soil, and that in stage 4, where coverage of the herb layer was < 50 %, lower abundances of group e taxa were found than in the next stages with complete cover. In addition, experimental removal of the herb and organic layers from some parts of Scots pine plantation D63, dit not affect the occurrence of the group a-d genera *Tylenchorhynchus* and *Rotylenchus* in the 0-10 cm mineral soil one year after treatment (De Goede, unpublished data). Although these species can feed on *P. sylvestris* roots, grasses are important to *Rotylenchus* and other plant feeding group a-d taxa from Scots pine forest as well (Magnusson, 1983).

The total abundance of plant feeding nematodes, in particular epidermal and root hair feeders, in the 0-10 cm mineral soil of stage 6 (Table 1) coincided with maximum growing conditions for *D. flexuosa* (Van Berghem *et al.*, 1986; Fanta, 1986; Moszynska, 1991). Both the absolute and relative annual production of *D. flexuosa* (1660 kg.ha^{-1}.y^{-1} and 39 % of its standing crop respectively) were the highest recorded in the succession, and comprised 93 % of total production of the herb layer. In the oldest Scots pine stage these figures were 1541 kg.ha^{-1}.y^{-1}, 26 % and 48 % respectively. Besides, the proportion of above ground carbon stock transferred from the herb layer to the organic horizon by seasonal shoot death (42 % of total standing crop) almost doubled the estimates of younger and older forested stages (Moszynska, 1991). The increased abundance of plant feeding nematodes in stage 6 thus probably reflects a positive correlation with primary production (Yeates, 1987).

Acknowledgment

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