

## Changes in nematode community structure in a primary succession of blown-out areas in a drift sand landscape

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**Summary** – Nematode community structure and nematode abundance in a primary succession of blown-out areas in a drift sand landscape were studied. The successional stages sampled included drift sands without vegetation, *Spergulo-Corynephorum* and Scots pine (*Pinus sylvestris* L.) forest of different age. Samples were taken from the 0-10 cm mineral soil and, in the forested stages, also from the organic layer. In order to study succession of the nematode fauna in relation to soil development, the organic layer was divided into a litter, fermentation and humus horizons. Multivariate analyses showed gradual changes in nematode faunal structure as succession proceeded. The colonization of the sites by higher plants, and the subsequent invasion of Scots pine coincided with marked differences in the composition of the nematode fauna. The diversity of the nematode fauna increased as soil development proceeded. Differences in nematode fauna structure between the soil horizons within any successional stage appeared larger than differences between the successional stages of the soil horizons. The successional changes in the composition of the nematode fauna are discussed in terms of the colonizers-persisters model of Bongers, and the prospect for nematodes to contribute to a soil classification system are indicated.

**Résumé – Modifications de la structure des peuplements de nématodes dans une succession végétale primaire d'une zone de dunes sableuses balayée par le vent** – Cette étude a concerné la structure des peuplements et l'abondance des nématodes dans une succession primaire de végétation d'une zone balayée par le vent dans un paysage de dunes sableuses. Des prélèvements ont été effectués dans les aires correspondant aux différentes étapes de cette succession végétale : dunes sans végétation, *Spergulo-Corynephorum*, forêts de pins d'Écosse (*Pinus sylvestris* L.) d'âges variés. Les échantillons de sol ont été prélevés dans la couche minérale, à 0-10 cm de profondeur, et également dans la couche organique pour les zones reforestées. Pour étudier l'évolution de la faune nématologique en relation avec le changement de composition du sol, la couche organique a été divisée en litière, couche F (« fermentation ») et humus. Des analyses multivariées démontrent un changement graduel de la faune nématologique au cours de la succession végétale. La colonisation des sites par les végétaux supérieurs, puis l'invasion par les pins d'Écosse, coïncident avec des différences marquées dans la composition de la faune nématologique. La diversité de cette faune s'accroît au fur et à mesure que le sol se constitue. Les différences de structure de la faune entre couches du sol sont, quel que soit le stade de la succession, plus grandes que celles observées dans ces couches au cours des différents stades de la succession végétale. Les séquences de changement dans la composition de la faune nématologique sont discutées en terme de « colonisateurs-permanents », suivant le modèle de Bongers, tandis que les perspectives d'utilisation des nématodes pour une classification des sols sont évoquées.

**Key-words** : Nematodes, succession, *Pinus sylvestris*, community structure, c-p triangle.

Studies on primary forest succession concentrate mainly on the development of the vegetation (West *et al.*, 1981). Below-ground processes are usually included in terms of horizon development, and root and nutrient dynamics. While studies on changes in soil faunal population structure in relation to primary forest succession are rare (Heal & Dighton, 1986), extensive information is available about the occurrence and functioning of the

soil fauna of various habitats (Swift *et al.*, 1979; Peterson & Luxton, 1982; Mitchell & Nakas, 1986).

Studies of short-term successional changes in soil fauna populations on freshly fallen leaves or during the colonization of litterbags (e.g. Twinn, 1974; Anderson, 1975; Sohlenius & Boström, 1984; Zell, 1989; Siepel, 1990) and further analyses of later stages of decomposition can reveal a picture of soil faunal changes during

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natural succession within various ecosystems (Twinn, 1974; Rusek, 1978; MacMahon, 1981). However, despite their usefulness, trends deduced will often be crude due to climatological, geological, pedological and methodological differences between different studies. Fine-scale investigations of successional changes in soil faunal populations, either derived from long-term sampling programmes or from studying successional seres, are necessary to test the significance of the suggested patterns of faunal succession (e.g. Odum, 1969; Rusek, 1978; Heal & Dighton, 1986) under field conditions. In addition, with growing interest in soil faunal community structure as an indicator of environmental disturbance, knowledge concerning both short-term and long-term natural changes in community structure, become a prerequisite to identify such disturbance.

We studied changes in nematode faunal composition in relation to primary vegetation succession of blown-out areas in a drift sand landscape in the Netherlands. Nematodes are among the soil faunal groups which offer possibilities for assessing soil ecosystem quality (Samoiloff, 1987; Freckman, 1988; Bongers, 1990), and are potentially useful in ecological soil classifications (Bongers *et al.*, 1989). Drift sands are among the most nutrient poor soils in North-Western Europe. *Cladonio-Pinetum* as the first forested stage of drift sands is consequently highly sensitive to stresses such as those which may be imposed by atmospheric deposition (Van der Werf, 1991). In view of the relatively high levels of deposition of especially nitrogenous compounds in the Netherlands (Heij & Schneider, 1991), knowledge of the natural soil community and its succession within these habitats is urgently needed. The blown-out areas at "Hulshorst sand" and "Leuvenum forest" offer possibilities to sample across a vegetation succession of the drift sand habitat. Past forest development of the area is well documented, prior soil development of the blown-out soils is lacking, and the texture and mineralogical composition of the parent material of the soil remains more or less constant during the first centuries of succession (Fanta, 1986; Emmer *et al.*, 1991). Moreover, succession of vegetation (Fanta, 1986; Prach, 1989), its nutrient dynamics (Moszynska, 1991) and soil development (Van Berghem *et al.*, 1986; Emmer *et al.*, 1991) are well documented. However, as this area is subjected to atmospheric deposition, the influence of this deposition on the biological succession, as well as the influence of changing climatic conditions on the succession, cannot be excluded.

This paper presents details on nematode community structure and nematode abundance at blown-out areas at Hulshorst sand and Leuvenum forest. Distribution of nematode taxa within the soil profile, trophic group distribution and nematode biomass in various successional stages have also been published (De Goede *et al.*, 1993).

## Materials and methods

### SITE DESCRIPTION

The study was undertaken in "Hulshorst sand" and "Leuvenum forest", two adjacent nature reserves near Harderwijk in the Netherlands. Descriptions of the geology, pedology and vegetation of the area are given in Prach (1989), Van Berghem *et al.* (1986), Emmer *et al.* (1991) and Fanta (1986).

The area is a former cover sand landscape which was covered with forests and heathlands. Mainly due to overgrazing, the sand became active, and the area was converted into a drift sand landscape. However, since the first half of the 19th century the drift sands were reforested by both spontaneous establishment and planting (Prach, 1989). Our research was conducted in blown-out areas. Their substrate is a gravel-rich, coarse fluvio-periglacial sand, with a very low organic content (0.2-0.4 % by weight) (Emmer *et al.*, 1991).

The first stages of primary succession are characterized by the occurrence of algae, lichens, and low growing plants such as *Corynephorus canescens* (L.) Beauv., *Spergula morisonii* Bor. and *Polytrichum piliferum* Hedw. (Prach, 1989; Fanta, 1986). The subsequent invasion of Scots pine (*Pinus sylvestris* L.) coincides with the occurrence of *Festuca ovina* L. At the same time an organic horizon starts to develop. With increasing thickness of the organic horizon, *Deschampsia flexuosa* (L.) Trin. becomes the dominant species in the herb layer. After the forest reaches an age of about 90-100 years, *Empetrum nigrum* L., *Vaccinium vitis idaea* L., *Vaccinium myrtillus* L., as well as second generation Scots pine, start to develop. A Scots pine forest about 105 years old (Stille Eenzaamheid, located in "Leuvenum forest"), characterized by a herb layer composed of *D. flexuosa*, *E. nigrum*, *V. vitis idaea*, *V. myrtillus* forms the oldest stage of succession present. This stage is considered to be a disclimax, because broadleaved tree and shrub species characteristic of the next successional stages (*Betulo-Quercetum*), cannot regenerate successfully due to animal browsing (Fanta, 1986). *Deschampsia flexuosa* is still the dominant herb species, but because the density of flowering shoots is low and the density of dead roots is relatively high, its vitality seems to be reduced (Moszynska, 1991).

Soil development took place, reflecting succession of the vegetation, with mull and mor type humus in the unforested and forested stages respectively. So far, during succession soil texture and mineralogical composition of the parent material of the soil remained fairly constant, but some chemical properties, like pH and amount of organic matter, changed (Emmer *et al.*, 1991).

## SAMPLING, EXTRACTION, COUNTING AND IDENTIFICATION

Nematode samples were taken in two spontaneous primary succession seres (sere A and B), with Scots pine forests of about 105 years old as the oldest stage studied.

Sere A consisted of six vegetation successional stages : (1) bare drift sand; (2) *Spergulo-Corynephorum*; Scots pine forests of (3) 5-8, (4) 30-35, (5) 80 and (6) 105 years old. Stages 1-5 were located at "Hulshorst sand", whereas the oldest stage (stage 6) was located 2.3 km away at De Stille Eenzaamheid.

Samples were taken on 24 and 25 October 1988. Within each stage, three representative 100 m<sup>2</sup> plots were selected. The organic horizons and mineral soil were sampled separately.

From the organic horizons ten cores (core diameter 79 mm) were taken, and combined into one bulk-sample per plot. From stage 4 onwards organic horizons covered the whole soil surface. In stages 1 and 2 no organic horizon was present. In stage 3 the organic horizon was present only under the canopy of the scattered, young Scots pine trees within each plot. Therefore, the organic horizon of stage 3 was sampled specifically under the canopy of those trees.

The mineral soil was sampled to a depth of 10 cm. Fifty cores (core diameter 17 mm) were taken in a regular pattern over the whole plot, and combined into one bulk-sample per plot.

Sere B consisted of seven successional stages and an eighth stage which was thought to be an example of an early variant of *Betulo-Quercetum* (forest composed of *P. sylvestris*, *Quercus robur* L. and *Betula* spec., with a herb layer dominated by *E. nigrum* or *V. myrtillus*; *D. flexuosa* covered  $\leq 5\%$  of the area of these plots). The first six stages were located at "Hulshorst sand" along a transect with a length of 950 m, about 500 m south of sere A. Stage 7 was located 2.6 km away at De Stille Eenzaamheid, and stage 8 was located 1 km north-east of stage 7 at "Leuvenum forest". The stages sampled can be characterized as : (1) bare drift sand; (2) *Spergulo-Corynephorum*; Scots pine forests of (3) 3-5, (4) 25-30, (5) 45-50, (6) 80-90 and (7) 105 years old; (8) *Betulo-Quercetum* of approximately 105 years old.

Within every stage, three (four in stages 2 and 8) representative 100 m<sup>2</sup> plots were selected. The mineral soil and organic horizons (stage 3-8) were sampled separately on 11 and 12 June 1990. The organic layer was divided into litter (L), fermentation (F) and humus (H) horizons following Klinka *et al.* (1981).

The samples of the organic horizons were composed of one sample per plot only, and were taken 1.5 m from a tree trunk. The L-horizon, present from stage 3 onwards, was sampled by hand from 900 cm<sup>2</sup>. The F- and H-horizons, present respectively from stages 4 and

5 onwards, were sampled with a Shallow Profile Sampler (internal surface area 36.5 cm<sup>2</sup>; Wardenaar, 1987).

The mineral soil was sampled as described for sere A. In the stages 3 and 4 samples were taken specifically under the canopy of the scattered trees and each bulk-sample consisted of fifty cores, evenly distributed under 5 and 2 different trees respectively.

Nematode extraction, counting, processing and identification followed De Goede and Dekker (1993). Nematodes were extracted from 100 g fresh mass mineral soil, 25 g fresh mass organic horizon (sere A), 10 g fresh mass L-horizon and 20 g fresh mass F- and H-horizon. Extractions were completed within two days of sampling. Using known total sample weight, results were converted to a m<sup>-2</sup> basis.

Water content of each sample was determined after 24 h drying at 105 °C.

## STATISTICS

Changes in population structure following succession were analyzed using correspondence analysis (CA) (Ter Braak, 1988). The analyses were based on relative generic abundances, which were transformed as follows : 2<sup>n</sup> % becomes (n + 1) %, when n = 0-7. Genera with a frequency less than 20 % of the commonest taxon, were downweighted in proportion to their frequency (Ter Braak, 1988).

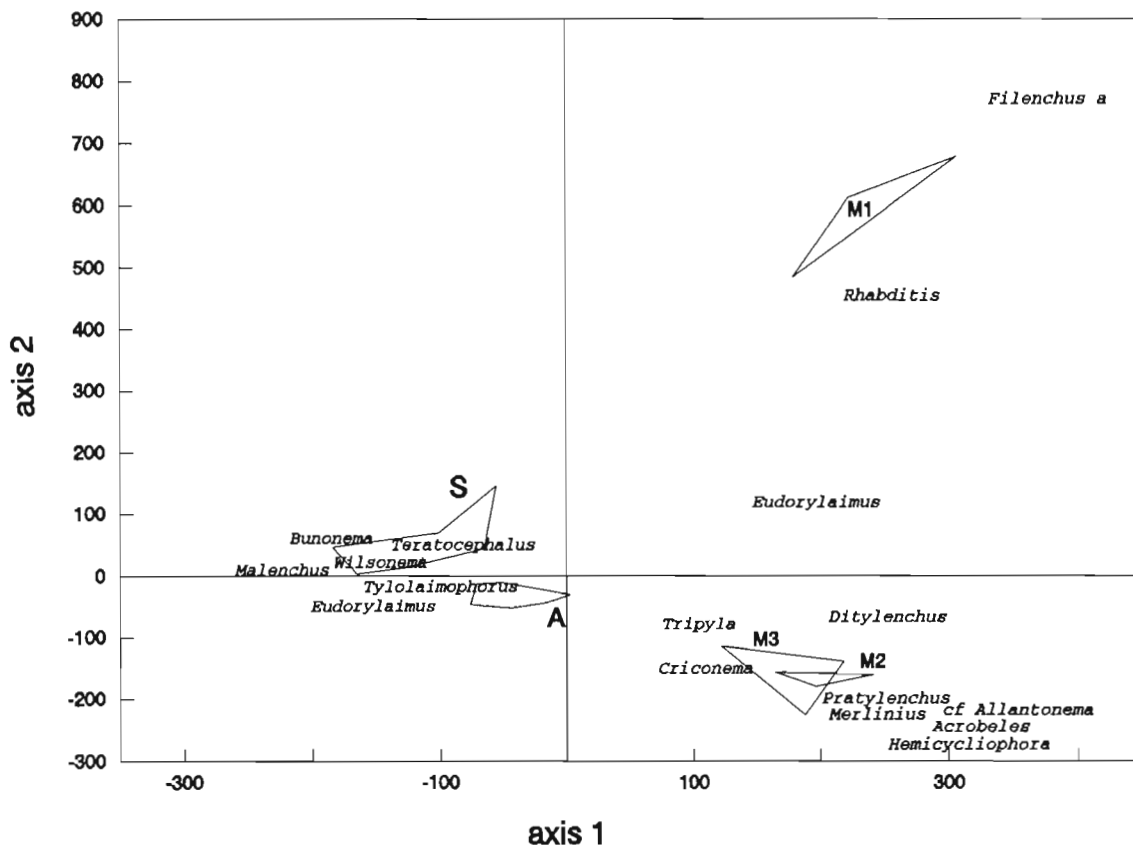
Similarities between samples were calculated with the Similarity ratio (SR) (e.g. Jongman *et al.*, 1987);  $SR_{ij} = \sum_k Y_{ki} Y_{kj} / (\sum_k Y_{ki}^2 + \sum_k Y_{kj}^2 - \sum_k Y_{ki} Y_{kj})$  with  $Y_{ki}$  and  $Y_{kj}$  being the proportion of taxon  $Y$  in sample  $i$  and  $j$  respectively. Prior to calculation, data were transformed as described above.

To calculate the c-p value distribution (De Goede, 1993) of the nematode samples, the c-p scores as given by Bongers (1990) were used.

Differences in nematode abundance and similarity between the successional stages were tested by Mann-Whitney U-test (Sokal & Rolf, 1981).

## Results

The correspondence analyses gave clearly differing groups which could be related to the stage of succession and soil horizons. The nematode faunal composition of bare drift sand (M1), differed greatly from the subsequent stages where vegetation was present (Fig. 1 for sere A; data for sere B are not shown, but were comparable to Fig. 1). In bare drift sand, relatively low numbers of nematodes occurred (Tables 1, 2) and compared to the mineral soil of the subsequent successional stages, fewer nematode taxa were found (Tables 1, 2). *Eudorylaimus* was present in all samples from stage 1, and was the dominant taxon. In sere A *Filenchus* a and *Rhabditis* were also found in all three replicate stage 1 samples, but in relatively low numbers.



**Fig. 1.** Ordination diagram (CA) of the axes 1 and 2 based on the nematode fauna of the organic horizons and 0-10 cm mineral soil of primary succession sere A. Contour lines indicate the position of the samples of the organic horizons (S) and of the 0-10 cm mineral soil of stages 1, 2, 3 and 4-6 (M1, M2, M3 and A respectively). Some common taxa are indicated (each name is centered at the position of the taxon in the diagram).

**Table 1.** Mean nematode abundance and total number of genera (n = 38) in the 0-10 cm mineral soil (M) and organic horizon (S) of the successional stages of sere A. (For M and S are the nematode abundances given in numbers per gdw and in numbers  $\times 10^3$  per  $m^2$  respectively, abundances within one column followed by a different letter differ significantly,  $p \leq 0.05$ , - organic horizon not present).

| Successional stage | Nematode abundance |                 | Number of taxa |    |
|--------------------|--------------------|-----------------|----------------|----|
|                    | M <sup>1)</sup>    | S <sup>2)</sup> | M              | S  |
| 1                  | 49 a               | -               | 13             | -  |
| 2                  | 721 b              | -               | 17             | -  |
| 3                  | 942 b              | 1186            | 17             | 8  |
| 4                  | 910 b              | 12 690          | 24             | 18 |
| 5                  | 399 c              | 12 070          | 17             | 18 |
| 6                  | 204 c              | 15 460          | 18             | 17 |
| Total              |                    |                 | 33             | 25 |

**Table 2.** Mean nematode abundance (numbers  $\times 10^3$  per  $m^2$ ) and total number of genera (n = 56) in different soil horizons of the successional stages of sere B. (0-10 cm mineral soil (M), humus (H), fermentation (F), litter (L) horizon, total organic horizon (O) and total profile (T = M + O), abundances within one column followed by a different letter differ significantly,  $p \leq 0.05$ , - horizon not present).

| Successional stage             | Nematode abundance |        |         |         | Number of taxa |    |    |    |    |    |
|--------------------------------|--------------------|--------|---------|---------|----------------|----|----|----|----|----|
|                                | M                  | H      | F       | L       | M              | H  | F  | L  | O  | T  |
| 1                              | 56 a               | -      | -       | -       | 4              | -  | -  | -  | -  | 4  |
| 2                              | 461 bce            | -      | -       | -       | 26             | -  | -  | -  | -  | 26 |
| 3                              | 485 bce            | -      | -       | 240 ab  | 21             | -  | -  | 9  | 9  | 25 |
| 4                              | 363 bcde           | -      | 539 a   | 196 ad  | 20             | -  | 9  | 6  | 11 | 22 |
| 5                              | 412 b              | 264 a  | 1136 b  | 427 b   | 25             | 12 | 13 | 8  | 20 | 33 |
| 6                              | 824 c              | 476 b  | 1940 bc | 261 bd  | 22             | 14 | 15 | 8  | 21 | 29 |
| 7                              | 156 d              | 284 ab | 2339 c  | 150 adc | 20             | 14 | 18 | 6  | 22 | 28 |
| 8                              | 247 e              | 763 ab | 5000 c  | 68 c    | 33             | 20 | 19 | 10 | 28 | 37 |
| Total number of different taxa |                    |        |         |         | 51             | 26 | 21 | 16 | 35 | 56 |

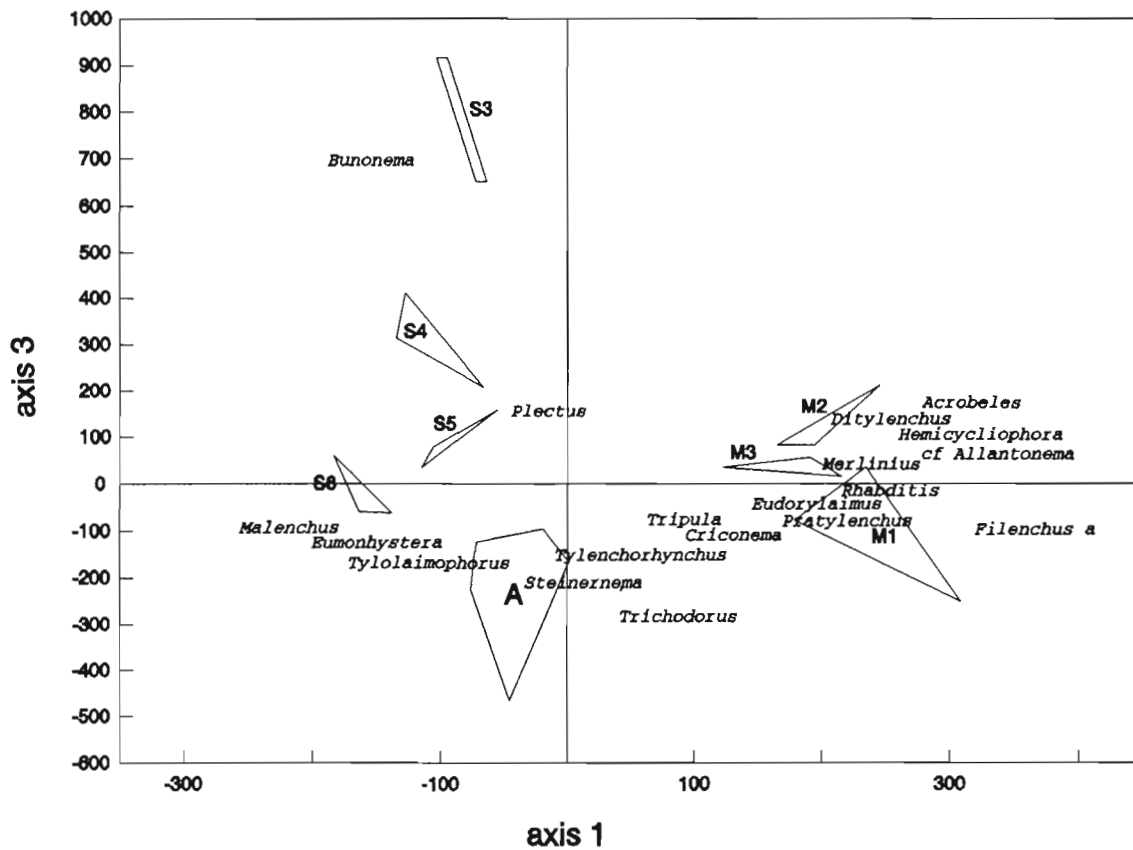


Fig. 2. As figure 1, but for the axes 1 and 3 of succession sere A. Contour lines indicate the position of the samples of the organic horizons of the stages 3 to 6 (S3-6) and of the 0-10 cm mineral soil of the stages 1, 2, 3 and 4-6 (M1, M2, M3 and A respectively). Some common taxa are indicated (see Fig. 1).

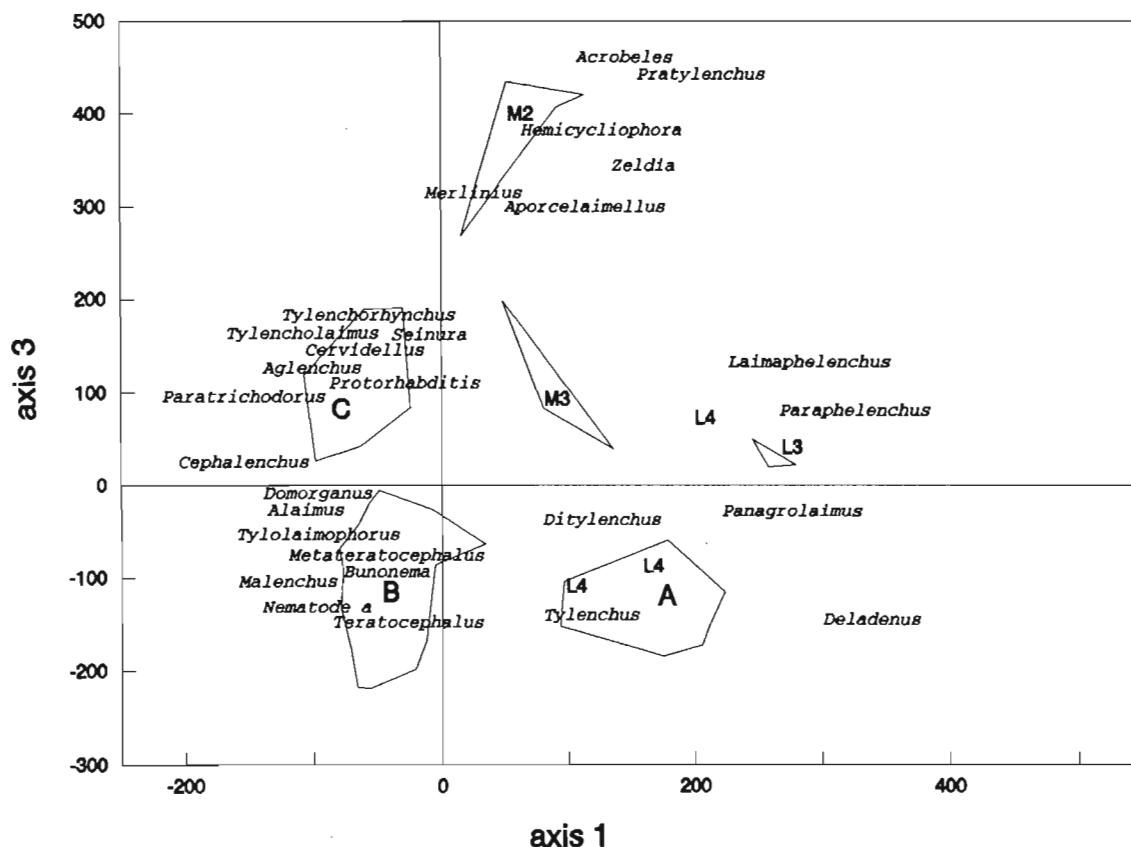
Based on the composition of the nematode fauna the stages with vegetation present, were divided in two groups differing in stage of succession (stages 2-3 and stages 4-9; Figs 1, 3). This division was most evident in the composition of the nematode fauna of the mineral soil, but appeared also for the litter horizon of stage 3 (Figs 2, 3). In both successional seres *Hemicycliophora*, *Pratylenchus*, *Acrobeles* and *Merlinius* were characteristic for stages 2 and 3, whereas *Wilsonema*, *Tyrolaimophorus*, *Filenchus* b, *Teratocephalus* and *Steinernema* were absent or rare in the early stages but common in the older stages of succession. Moreover, the taxa *Ditylenchus* and cf *Allantonema* and the genera *Zeldia*, *Aporcelaimellus* and *Paraphelenchus* were restricted to these early stages of the successional seres A and B respectively.

Independent of the stage of succession, a further sub-division of the forested sites (stage 4-9) was related primarily with soil horizon (Figs 1, 3), which itself is part of succession. In sere B, where the most detailed sub-division in soil horizons was carried out, analysis of the composition of the nematode fauna revealed three groups of soil horizons: litter horizon, fermentation-humus horizon, and 0-10 cm mineral soil. However,

subsequent correspondence analyses showed gradual shifts in nematode fauna structure within the horizons, which were related to the stage of succession of the vegetation (Figs 3, 4, 5).

The litter horizon was distinguished from the underlying horizons by the low number of taxa (Table 2) and by the occurrence of *Panagrolaimus*, *Laimaphelenchus* and *Deladenus*. The first two taxa were abundant also in the 0-10 cm mineral soil of the stages 2 and/or 3, which explained the joint classification of the 0-10 cm mineral soil of the stages 2-3 and the L horizons on the first CA axis (Fig. 3), despite a relative low similarity between litter horizons and 0-10 cm mineral soil (SR 25-42 %).

Differences in nematode fauna composition between the F/H horizon and the 0-10 cm mineral soil were primarily based on *Cervidellus* (relative frequencies (%) in 0-10 cm mineral soil and F/H horizon 100, 6; n = 16), *Tylenchorhynchus* (100, 12), *Tylencholaimus* (50, 0), *Aglenchus* (44, 6) and *Paratrichodorus* (38, 0), which were characteristic for the 0-10 cm mineral soil, and *Teratocephalus* (6, 56) and Nematode A (6, 50; an undescribed alaimid) which occurred more frequently in the F/H horizon.



**Fig. 3.** Ordination diagram (CA) of the axes 1 and 3 based on the nematode fauna of the organic horizons and 0-10 cm mineral soil of primary succession sere B. Contour lines indicate the position of the samples of the litter, fermentation/humus and 0-10 cm mineral horizons of stages 4-8 (A, B and C respectively), of the 0-10 cm mineral soil of stages 2 and 3 (M2, M3) and of the litter horizon of stages 3 (L3) and 4 (L4). The pattern extracted by the axis 2 is not shown, but was comparable to the gradient extracted by axis 2 of the CA based on the nematode fauna of sere A. Some common taxa are indicated (see Fig. 1).

Nematode diversity was highest in the 0-10 cm mineral soil where 33 and 51 different taxa were found in seres A and B respectively (Tables 1, 2). In the organic horizon of seres A and B, 25 and 35 taxa were detected respectively. Exclusion of the successional stages without an organic horizon (stages 1-2) and/or those with only a litter horizon present (stage 3), only partly explained this higher diversity in the 0-10 cm mineral soil; the total number of taxa found in the 0-10 cm mineral soil of the stages  $\geq 3$  and  $\geq 4$ , was 30 and 26 for sere A and 48 and 43 for sere B respectively. Except for an increase in nematode taxa related to the development of vegetation (stage 2), another remarkable increase in nematode taxa occurred at the change from stage 4 to 5 of sere B (Table 2). This increase was brought about mainly because of the development of the organic horizon, as genera increased in the organic horizon and 0-10 cm mineral soil by 82 % and 25 % respectively. In the subsequent successional stages total numbers of genera remained fairly constant, but shifts in the composition of the nematode fauna still occurred (Figs 4, 5).

The relation between successional stages and the composition of the nematode fauna of the various horizons of sere B are summarized in Table 3, where the similarity between stage 7 and the other successional stages is given for each horizon. The similarity between the stages 1-6 and stage 7 increased with proceeding succession, whereas a subsequent decrease was found for stage 8. The relatively large increase in similarity when going from stage 3 to stage 4, is in line with the results from the correspondence analysis (Fig. 3). Thus, the development of an organic horizon concurs with major changes in the composition of the nematode fauna, even in the 0-10 cm mineral soil.

In the field seral stages 3 and 4 form a patchwork surrounded by stage 2 vegetation and nematode species occurring in stages 3 or 4 and which do not occur in stage 2, have to colonize these stages. This colonization can take place from *i*) nearby stage 3 and 4 patches, or from *ii*) the older forested stages (stage  $\geq 5$ ). Of the 19 taxa which had to colonize the stages 3-4 (Table 4), *Laimaphelenchus penardi*, *Acrobeloides tricornis* and *Apor-*

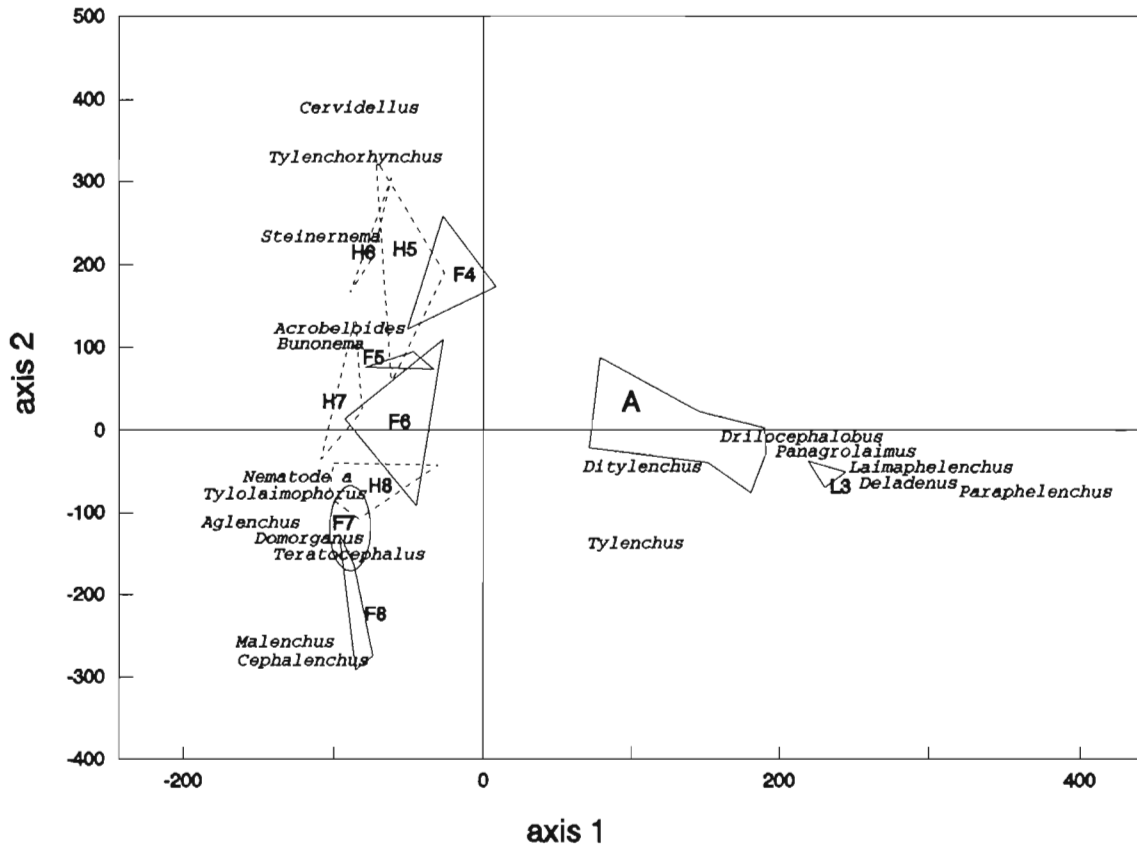


Fig. 4. Ordination diagram (CA) of the axes 1 and 2 based on the nematode fauna of the organic horizons of primary succession sere B. Contour lines indicate the position of the samples of the litter horizons of the stages 3 and 4-8 (L3 respectively A) and of the fermentation (F) and humus (H) horizons of the stages 4-8 (F4-8, L4-8). Some common taxa are indicated (see Fig. 1).

*celaimium* occurred only in the stages 3-4, and are probably examples of type *i*) colonization. Compared to the taxa occurring both in stage 2 and in the stages  $\geq$  3-4, a greater proportion of taxa which had to colonize the stages 3-4 belonged to c-p classes 1 or 2 (colonizers, opportunists) (55 and 79 % respectively). This illustrates the colonizing potential within the type *i*) and/or *ii*) group of taxa (Table 4). Only 33 % of the taxa which were restricted to the forested stages 5-8 belonged to c-p classes 1-2 (Table 4).

Colonization of the soil horizons by nematodes is exemplified by changes in c-p value group distribution of nematode fauna (excluding root feeding nematodes) during horizon development (Fig. 6). In the first representatives of the various soil horizons, greater part of the non-root feeding nematode fauna consisted of opportunistic taxa, with c-p score 1 (litter horizon; Fig. 6 D) or c-p score 2 (fermentation and humus horizon; Fig. 6 B, C). However, during the subsequent development of the fermentation and humus horizons, a relative increase of persisters or K-strategists *sensu lato* (c-p group 3-5) was observed. In the 0-10 cm mineral soil similar trends were observed after first establishment of an organic

horizon (Fig. 6 A). In the litter horizon, no population of persisters was found to develop, but taxa with c-p score 2 dominated the older stages.

Table 3. Similarity (SR) between the nematode fauna of successional stage 7 and the other stages of sere B by horizon. (For stage 7 the internal-similarity between replicates is given, abbreviations as in Table 2, similarities within one column followed by a different letter differ significantly,  $p \geq 0.05$ , - combination not present.)

| Successional stage | Soil horizon |        |        |         |
|--------------------|--------------|--------|--------|---------|
|                    | M            | H      | F      | L       |
| 1                  | 5.8 a        | -      | -      | -       |
| 2                  | 29.1 b       | -      | -      | -       |
| 3                  | 33.4 b       | -      | -      | 56.1 a  |
| 4                  | 66.7 cd      | -      | 53.4 a | 65.5 ad |
| 5                  | 79.0 e       | 68.1   | 73.1 b | 82.2 bc |
| 6                  | 70.9 c       | 68.2   | 70.9 b | 85.6 c  |
| 7                  | (83.2)       | (78.4) | (84.8) | (90.0)  |
| 8                  | 64.9 d       | 64.5   | 75.9 b | 75.8 bd |

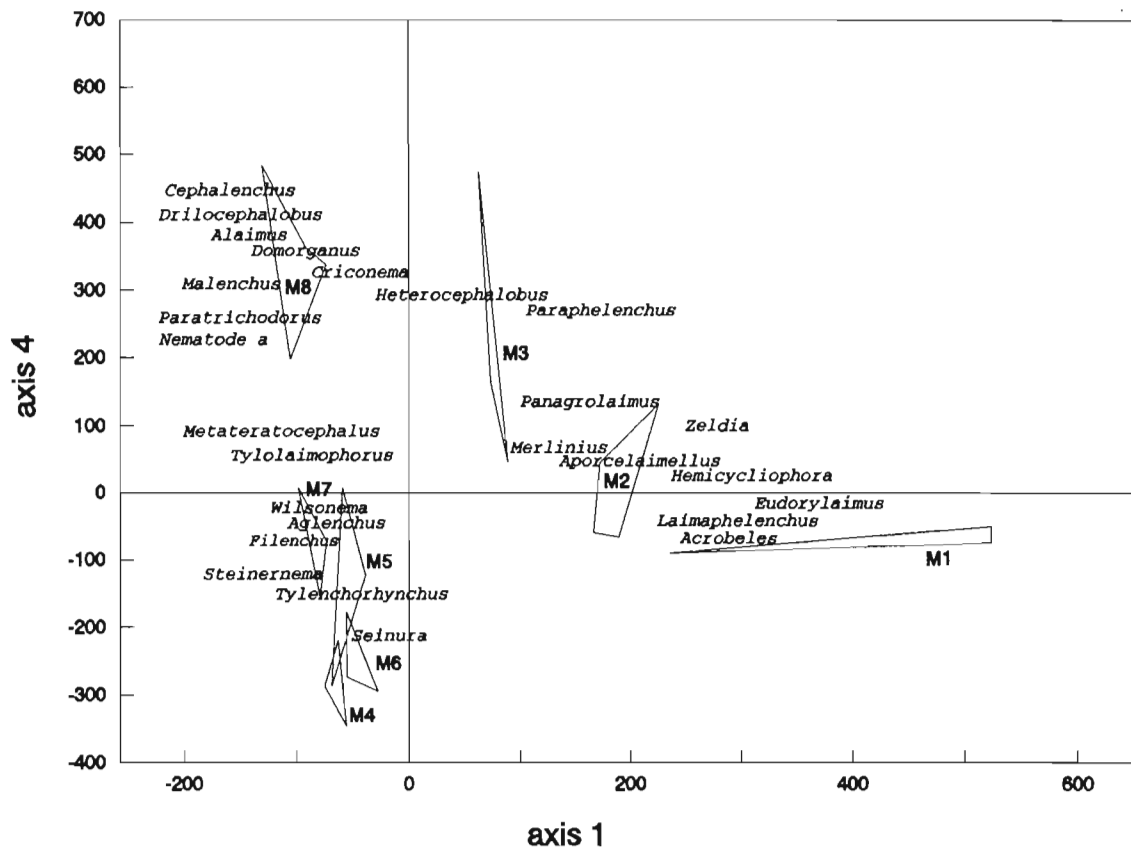


Fig. 5. Ordination diagram (CA) of the axes 1 and 4 based on the nematode fauna of the 0-10 cm mineral soil of primary succession sere B. The positions of the samples of the stages 1-8 are indicated with close fitting contour lines (M1-8). The patterns extracted by the axes 2 and 3 are not shown, but were similar to those extracted by the axes 2 and 3 respectively of the CA based on both organic and mineral soil horizons. Some common taxa are indicated (see Fig. 1).

Table 4. Number of nematode taxa (n = 36, excluding the plant feeding taxa) of successional sere B tabulated by c-p group and distribution within successional sere.

| c-p group | Taxa present in the stages |       | Taxa present only in stages 5-8 |
|-----------|----------------------------|-------|---------------------------------|
|           | ≥ 2                        | ≥ 3-4 |                                 |
| 1         | 0                          | 3     | 0                               |
| 2         | 6                          | 12    | 2                               |
| 3         | 2                          | 3     | 2                               |
| 4         | 2                          | 0     | 2                               |
| 5         | 1                          | 1     | 0                               |

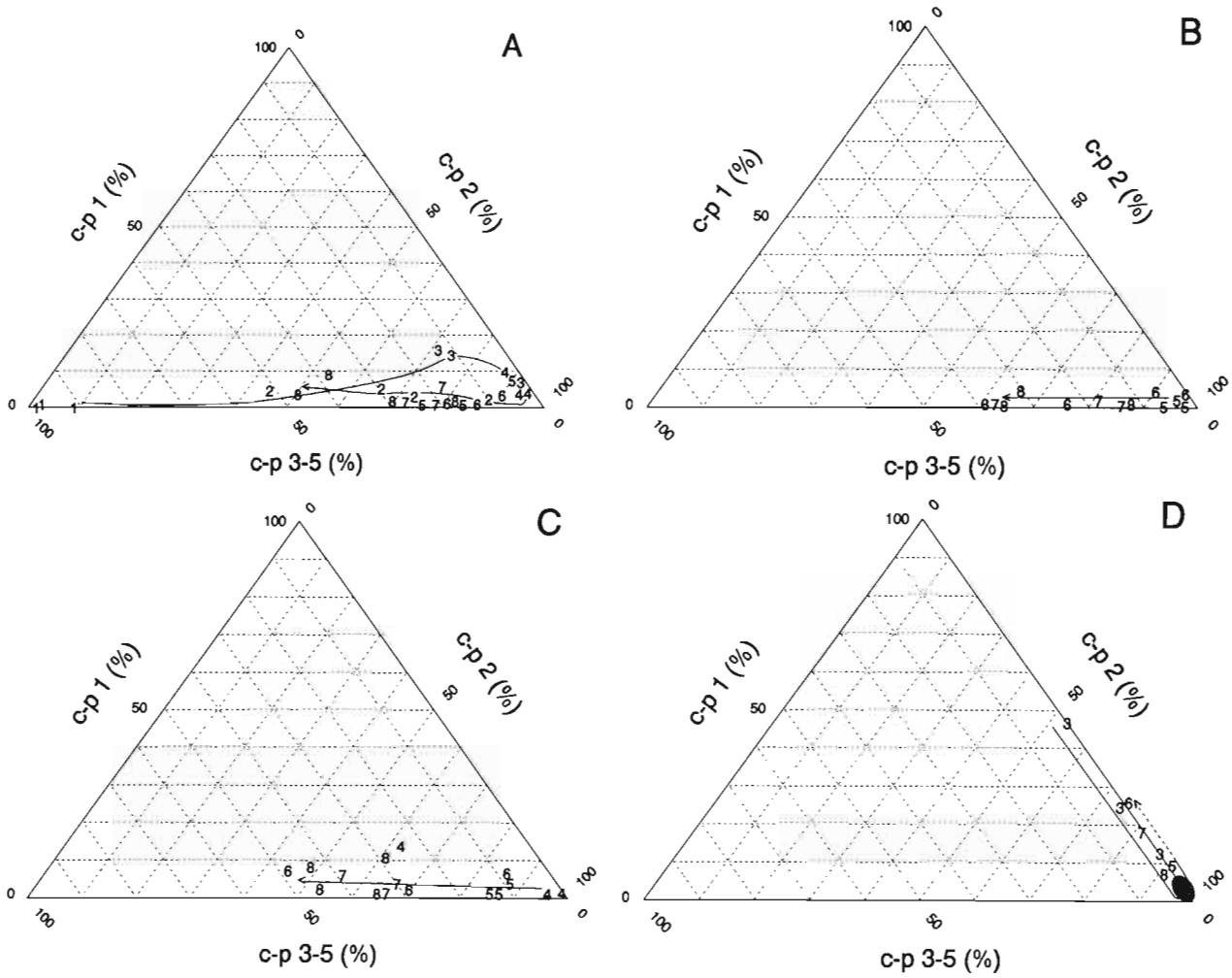
In the course of succession, the total number of nematodes found in the profile (0-10 cm mineral soil including the horizons on top) increased from  $56 \times 10^3$  in stage 1 to  $6078 \times 10^3 \text{ m}^{-2}$  in stage 8 (Table 2). Also in the fermentation horizon, highest numbers of nematodes were found in the oldest stages. However, nematode abundance in the 0-10 cm mineral soil and litter horizon decreased in the stages 7-8 compared to the

preceding stages. No trends were found in the humus horizons. In the stages 7 and 8 80-82 % of the total nematode population in the profile occurred in the fermentation horizon, whereas 10-13 % were found in the humus horizon, 4-5 % in the 0-10 cm mineral soil and 1-5 % in the litter horizon.

### Discussion

The primary succession of the vegetation, the nutrient dynamics within the vegetation and the organic profile of the "Hulshorts sand" and "Leuvenum forest" are well documented. The present study of the nematode fauna is the first on animal populations. Changes in the composition of the nematode fauna in the course of primary succession in a drift sand landscape appeared to be related to changes in vegetation and the development of an organic soil profile. During succession from bare drift sand to forest, different phases in nematode community composition could be recognized: *i*) bare drift sands without vegetation present, *ii*) vegetation of higher plants, but without trees, *iii*) Scots pine trees or forest.





**Fig. 6.** C-p triangles of successional changes in nematode fauna composition within the 0-10 cm mineral soil (a), humus (b), fermentation (c) and litter (d) horizons of primary succession sere B. Numbers refer to the corresponding stages of succession. Trends are indicated (arrows). The samples which are not shown separately in Fig. 6 d lay all within the hatched area.

The nematode fauna of the bare drift sands was dominated by the genus *Eudorylaimus*. Species of this genus are classified as omnivores (Yeates *et al.*, 1993), and because of their common occurrence in mosses and airborne dust (Orr & Newton, 1971; Krnjaic & Krnjaic, 1972; Zullini & Peretti, 1986) are expected to survive dehydration. During midsummer, maximum temperatures as well as temperature fluctuations in the top layer of the bare sand will be most extreme. Only well-adapted species can survive these climatic conditions. However, in autumn when maximum temperatures are lower, other taxa would also be able to survive in the top layer of the bare drift sand. It is not known whether they colonized the 0-10 cm drift sand from deeper soil horizons or relied on dispersal by wind each year. Except for the surface of the drift sand, where layers of algae can be found (Prach, 1989), the low water table and organic

matter content  $\leq 0.4\%$  (Emmer *et al.*, 1991) mean food conditions are very poor, especially in deeper soil layers. Thus, wind dispersion seemed most likely, as was shown by Orr and Newton (1971) for some of the taxa present in the October samples (*Aphelenchoides*, *Rhabditis*, *Ditylenchus*, Tylenchidae and Cephalobidae). The occurrence of the plant feeding ectoparasite *Trichodorus* in the October samples of the bare drift sand, supports this view.

The development of a vegetation composed of higher vascular plants, coincided with increased absolute nematode abundance and diversity. Introduction of trees in the primary succession led to further major shifts in nematode fauna composition. Some genera (*Acrobeles* and *Hemicycliophora*) could not be detected in the first stage where trees were present. They were not found in the third stage of sere B, where samples were taken only

under the canopy of 3-5 year old Scots pine trees. However, they were present in the third stage of sere A, where the 0-10 cm mineral soil was also sampled outside the canopy. Other taxa (cf *Allantonema*, *Aporcelaimellus* and *Zeldia*) characteristic of the treeless vegetation also occurred under the canopy of the 3-5 year old Scots pine trees, but were absent in the subsequent successional stages (age of trees  $\geq$  25-30 years). In addition, taxa like *Wilsonema*, *Tylolaimophorus*, *Filenchus* b, *Steinernema* and *Teratocephalus* only occurred in the forested stages, where they were generally present.

De Goede (1993), studied relationships between the composition of the nematode fauna of a variety of habitats within the Netherlands and the pedological and floristic characteristics of those habitats, also found significant differences between forested and unforestated habitats with soils of comparable texture. When the nematode samples from 0-10 cm mineral soil of sere B were projected onto the correspondence analysis graph of the axis 1 and 2 of the data of De Goede (1993), they coincided with those clusters composed of samples with related habitat types (Sample Groups; Fig. 7). Stages 2 and 3 coincided with Sample Group A, which is composed of grassland and dwarf-shrub vegetations on sandy soils. Stages 1 and 4-7 were positioned onto Sample Group G, the Scots pine forests. Stage 8, an early variant of a *Betulo-Quercetum*, was separated from the stages 1, 4-7 and coincided with Sample Group F. Just within this Sample Group F, the majority of sites with a *Betulo-Quercetum roboris* were classified (De Goede, 1993). These similarities between nematode community structure and habitat type as found in both investigations, support the classification of soils based on their nematode fauna as proposed by De Goede (1993). Nematode sampling in the study of De Goede (1993) was restricted to the 0-10 cm mineral soil. From our results it can be seen that as a consequence of such a restriction, the major part of the nematode fauna of soils with a mor type humus will be excluded from the classification, and this may result in lower discrimination between some successional stages.

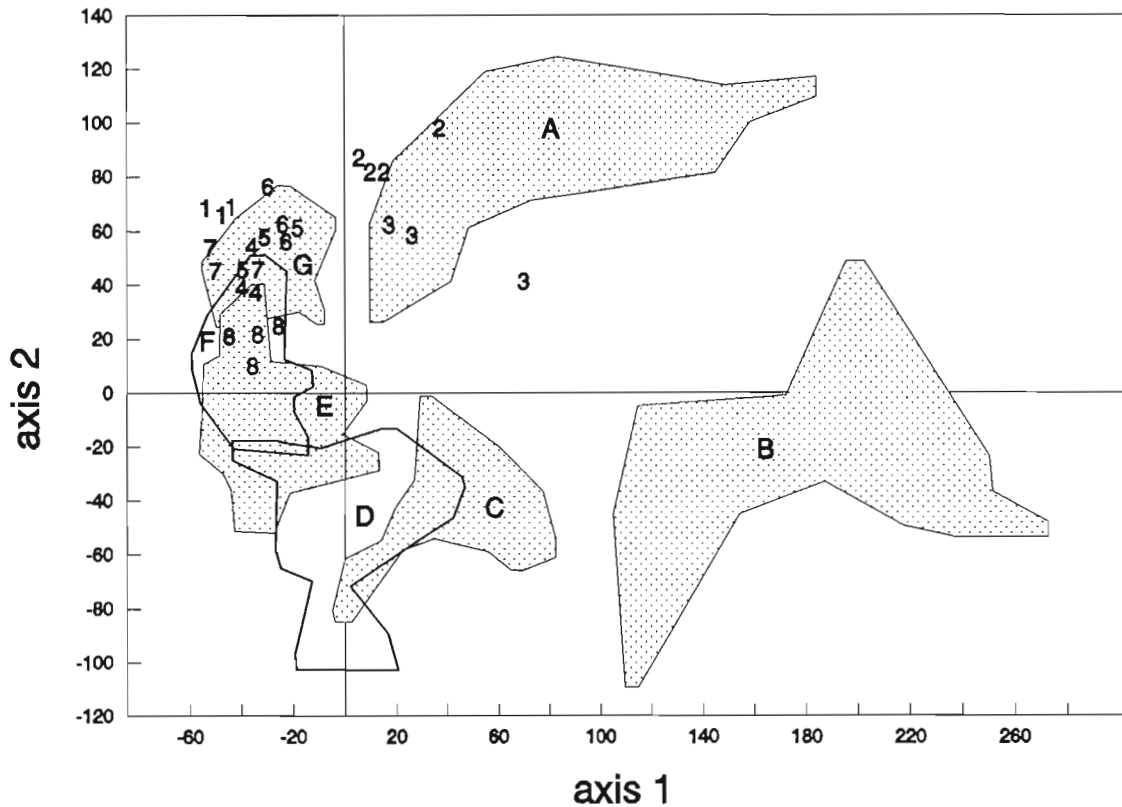
Fanta (1986) found that, mainly due to game browsing, natural succession of the Scots pine forest towards a poor variant of birch-oak forest (*Betulo-Quercetum*) does not occur in the 105 year old stand of De Stille Eenzaamheid (stage 7). Our results showed successional relationships between the nematode fauna of stage 8 (a mixed Scots pine-birch-oak forest with a herb layer dominated by *V. myrtilus* and *E. nigrum* located in the same area), a possible example of subsequent development of the Scots pine forest towards a vegetation characterized by the presence of deciduous trees, and the preceding Scots pine stages. Moreover, Fig. 7 showed high similarity between the nematode fauna of this stage and other *Betulo-Querceta*. Reconstruction of the geological development, former vegetation and

chemical-physical soil properties of site 8, are needed to determine its successional status.

As 67 % of the nematode taxa of the 0-10 cm mineral soil of sere B were restricted to either the stages 2-3 or to the forested stages ( $\geq$  4), it is likely that some common environmental parameters determined the differences in nematode community structure between the unforestated and forested habitats. Although specific causal connections are difficult to demonstrate, development of the vegetation and derived changes in microclimate and distribution of organic matter within the soil, will represent the driving forces. This is illustrated by the distribution of the plant feeding nematode taxa over both habitat types. Of the 16 plant feeding nematode genera which occurred in the 0-10 cm mineral soil of the stages 2-8 of sere B, 31 and 50 % were restricted to the unforestated and forested habitats respectively (De Goede *et al.*, 1993). Only three plant feeding taxa occurred in both habitats, and of those only *Tylenchorhynchus microphasmis* was common throughout sere B. Furthermore, application of results of a preliminary study of the sensitivity of nematodes to dehydration (Booyink, pers. comm.) to the data of sere B, showed a relative increase of taxa sensitive to dehydration in the deeper soil horizons. The observation of a similar increase of taxa sensitive to dehydration when going from the 0-10 cm mineral soil of the unforestated stages to the forested stages, suggests influences of microclimatological nature, which will be associated with soil and vegetation development.

After Scots pine trees invaded the *Spergulo-Corynephoretum*, parallel to the progression of the vegetation succession, a mor type organic horizon started to develop. Besides implications of the presence of an organic horizon on the occurrence of nematodes discussed above, the occurrence of the nematodes will also depend on the morphological differentiation and subsequent changes in chemical-physical properties of the organic horizons (Emmer *et al.*, 1991). Wasilewska (1970) who also studied the nematode fauna of Scots pine forests of different age, concluded that the colonization of nematodes in the forested habitat was primarily influenced by the cover with vascular plants in combination with the humus content of the soil. Above certain threshold settlement conditions, she observed a clear increase in number of nematode taxa. Such an increase in nematode genera was observed also in the "Hulshorst sand" sere B by the change from stage 4 to stage 5, and was brought about mainly because of the development of the organic horizon. Stage 5 was the first successional stage in which all three master organic horizons (L, F and H horizon; Klinka *et al.*, 1981) could be distinguished. In the subsequent Scots pine stages the total number of genera remained fairly constant, as was found also by Wasilewska (1970), but shifts in the composition of the nematode fauna still occurred (Figs 4, 5).

The assumption of a dominant influence by the stage of development of the organic layer on the occurrence of



**Fig. 7.** Ordination diagram (detrended correspondence analysis, DCA) of the axes 1 and 2 based on the nematode fauna of the 0-10 cm mineral soil of 209 nematode samples from a variety of habitats within the Netherlands (De Goede, 1993). Seven clusters of samples (A-G), each characterized by a specific combination of soil and floristic properties, are indicated. The 26 samples of the 0-10 cm mineral soil of sere B were included passively in the DCA. Their position within the diagram is indicated by numbers corresponding to the stage of succession.

nematodes, is further supported by changes in c-p value group distribution within the various soil horizons. Relating the colonizing abilities of the nematode taxa, as expressed by their c-p score (Bongers, 1990), with the stage of development of the various soil horizons, showed that the nematode faunae of the initial stages of the master horizons distinguished were composed mainly of taxa characterized as opportunists (c-p score 1 or 2). These taxa are among the first to respond to increased food availability or to colonize vacant niches (Bongers, 1990; Bongers *et al.*, 1991). In the next stages the relative importance of persisters or K-strategists *sensu lato* increased, a trend which was observed also in the 0-10 cm mineral soil after first establishment of an organic horizon. However, such a development of persisters was not found for the litter horizon. Moreover, here relatively large numbers of the opportunist *Panagrolaimus* (c-p score 1) were found also in the older stages, indicating unstable and/or temporarily *ad libitum* food sources. Thus, the initial community of the various horizons was characterized by a considerable degree of opportunism (Swift *et al.*, 1979). However, in the litter horizon this was found to be independent of the stage of

succession, which probably is related to varying food and feeding conditions in this horizon.

The soil profile was characterized by distinct morphological differences between litter, fermentation and humus horizons, and a sharp change from the organic horizon to mineral soil. Moreover, when going from litter via fermentation to humus, pH decreased and bulk density increased, indicating that the morphological differentiation paralleled chemical and physical differentiation (Emmer *et al.*, 1991). The correspondence analyses and similarity measurements showed that comparable soil horizons of the older ( $\geq$  stage 5) forested sites, had higher similarity than different horizons within the same profile (Figs 3, 4). Arpin and Ponge (1986) achieved similar results when studying the nematode fauna of *P. sylvestris* and *Quercus petraea* plantations and a mixed plantation of these tree species. Thus within each master organic horizon as well as in the 0-10 cm mineral soil a nematode fauna developed, which can be related to specific environmental conditions of the horizon. Nematode taxa composition (e.g. in the litter horizon) appeared to be mainly due to food conditions (De Goede *et al.*, 1993) and resistance to adverse microclimatolog-

ical characteristics (e.g. dehydration). As far as species were identified, none of the common species of the deeper soil horizons were common in the litter layer (De Goede *et al.*, 1993). However, such an absolute segregation in species distribution was not found for the deeper horizons, although some species were restricted to a selection of horizons (De Goede *et al.*, 1993). Thus, in addition to "lateral orientated habitats" for soil animals (Emmer *et al.*, 1991), vertical migration of certain nematode species, as probably can be derived also from the colonization process of the fermentation and humus horizons in the course of succession, cannot be ignored.

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