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POST-DRAINAGE SECONDARY SUCCESSION OF SOIL NEMATODES ON FEN PEAT MEADOWS IN BIEBRZA WETLANDS, POLAND

ABSTRACT: After the drainage of fens and their permanent use as meadows, peat-forming process is being replaced by moorshing (mucking) process (mineralization and humification of peat), and then by turf-forming process. Secondary succession of soil nematodes was examined by using the chronosequence of meadow sites (period I: 1978–1983) and also by analysing the same sites 15–17 years later (period II: 1994–1997). The analysis was focused on the taxa (genera) of nematodes and on 19 to 29 parameters describing the community as total density, density of trophic groups, diversity indices and maturity indices. The pattern of successional changes was obtained for periods from 2 to 117 years after drainage. Natural not-drained fens were used for comparison. Soil structure and soil processes occurring over the time considered can be characterized as follows: soil moisture (by weight) 80–52%, total soil porosity 90–77%, bulk density 0.16–0.44 (to 0.92) g cm⁻³, total C content in soil 47–7%, total N content in soil 4.4–0.5%, ranges in the sequence from Mt I (poorly moorshified soils) to Mt III (strongly moorshified soils). In natural fens, soil moisture was 80%, soil porosity 90%, bulk density 0.15–0.35 g cm⁻³, and peat-forming processes (Pt) were continued. As compared with natural fens, drainage and management of fens was associated with increasing density of total nematodes and their components such as bacterivores, fungivores, facultative plant feeders, obligate plant feeders, omnivores, and predators. In drained fens the density of nematodes declined with succession with the exception of omnivores. The increase in the density of omnivores was positively correlated

with the number of years after drainage ($r = 0.48$, $P < 0.01$). The indices of taxa diversity and maturity indices were positively correlated with years after drainage ($P < 0.001–0.05$). In natural fens, ranges of density of all trophic groups were lower, and maturity indices higher than in drained peat meadows. The mechanisms driving the first stage of succession in nematode communities (until about 30 years after the drainage of fens) seem to be tolerance to the droughts and to the excess of nitrogen what was accompanied with higher density of herbivores (mainly *Paratylenchus*). In later stages, interspecific competition is likely to play a more important role. Also a statistically significant relation was found of some taxa and parameters to peat type.

KEY WORDS: post-drained peat meadows, natural fens, soil nematodes, genera, trophic groups, density, diversity indices, maturity indices, peat types, nematode secondary succession

1. INTRODUCTION

In Poland, fen types of mires predominate, and its largest areas are located in the Biebrza Basin, North-Eastern part of the country. This is one of the last extensive fen areas in Europe. The major part of this area has been drained. Drainage was initiated already in the 19th century when three large strategic canals were made, draining underground waters. Later on a dense network of local channels was constructed.

After drainage, the accumulation of organic matter characteristic of peat-forming processes is replaced by moorsh- or muck-forming processes. Drying of peat and the associated aeration of the soil, followed by microbiological processes, give rise to decomposition and loss of organic matter. With respect to the degree of their transformation after drainage, peat soils can be categorized as poorly, moderately, and strongly moorshified, denoted by Mt I, Mt II, and Mt III, respectively (Okruszko 1993). Transformations of dehydrated peat mass, largely dependent on the kind of fen peat deposits (sedge-moss peat, tall sedge peat, and alder peat), concern chemical and biological properties of fen peat (Kajak *et al.* 1985, Kajak and Okruszko 1990, Okruszko 1995).

In the case of soil overdrying, the habitat acquires properties of stressed ecosystems (Odum 1985, Wasilewska *et al.* 1985, Pętal 1993).

After drastic dehydration, properties of both, the peat mass and the biota undergo changes with time. With reference to soil nematodes, time-related transformations after drainage of peat soils, as analysed by the method of the chronosequence of sites and previously described (Wasilewska 1991a), were used as a basis for further analysis of secondary succession. Namely, the same analysis was made at the same sites 15–17 years later, when secondary succession was directly observed. The problem of the dependence of nematodes on peat type, soil moisture, and on many other physical and chemical parameters at the study sites was presented earlier (Kajak *et al.* 1985, Wasilewska 1991b, c, d, 1994a). This paper will also consider the effect of peat type on succession. The analysis will concern taxa and also biocoenotic parameters describing nematode community. It should be added that a new approach to soil organisms was developed in the last decade that extended our understanding of the structure and function of ecosystems (Wardle and Giller 1996, Brussaard *et al.* 1997, Freckman *et al.* 1997, Ohtonen *et al.* 1997).

Soil nematodes have a key position in the soil trophic web as primary consumers (plant parasites), secondary consumers (predators) and consumers of decomposers (bacterivores and fungivores). They can influence soil processes as well as to reflect them. This is substantiated by the already rich

literature cited in overviews (Bongers 1990, Wasilewska 1997, Bongers and Bongers 1998, Bongers 1999, Bongers and Ferris 1999). According to Parmelee (1995), nematode communities are detectors of many changes in ecosystem parameters.

As the theory of ecosystem development states, the diversity of nematode communities increases with advancing succession, thus, the richness of taxa and diversity indices show trends (Pate *et al.* 2000). And this is the subject of the present paper.

The results of the study on nematode succession were published in more than ten papers. The habitats considered comprise seashore dunes (Góralczyk 1998), drifting sands to forest (de Goede 1993a, b), afforested dunes (Wasilewska 1970, 1971a), forests (Brzeski 1995, Armendáriz *et al.* 1996, Armendáriz and Arpin 1996, Hanel 1995, 2001), forest clear-cutting (Sohlenius 1997), fallow lands (Pate *et al.* 2000), grasslands (Wasilewska 1991a, 1994b), and highland peaty and drained meadows (Hanel 1997).

The present paper is focused on:

- an analysis of secondary succession of soil nematodes in peat soils drained for permanent use as hay meadows and pastures, and in a few not drained natural fens left without human interference, and
- an estimation of the effect of peat type on nematode taxa and communities.

2. STUDY AREA AND DIFFERENCES IN SOIL PROPERTIES AND PROCESSES

The Biebrza Basin is located in North-Eastern Poland (53°10'–53°30' N and 22°30'–23°60' E) and its fens are considered as temperate. Mean annual temperature is about 6°C and the annual sum of precipitation is 400–600 mm.

All the 19 study sites were located in the valleys of two rivers, Biebrza and Narew (North-Eastern Poland) (Fig. 1). Among four study sites (No. 1–No. 4, Table 1) on not drained peat (peat accumulating ecosystems), there was one sedge-moss fen, two sedge fluvial fens, and one alder swamp. The 15 sites on drained and managed grasslands (No. 5–No. 19, Table 1) comprised three on sedge-moss peat, five on sedge peat, and seven on alder peat. The nematode parame-

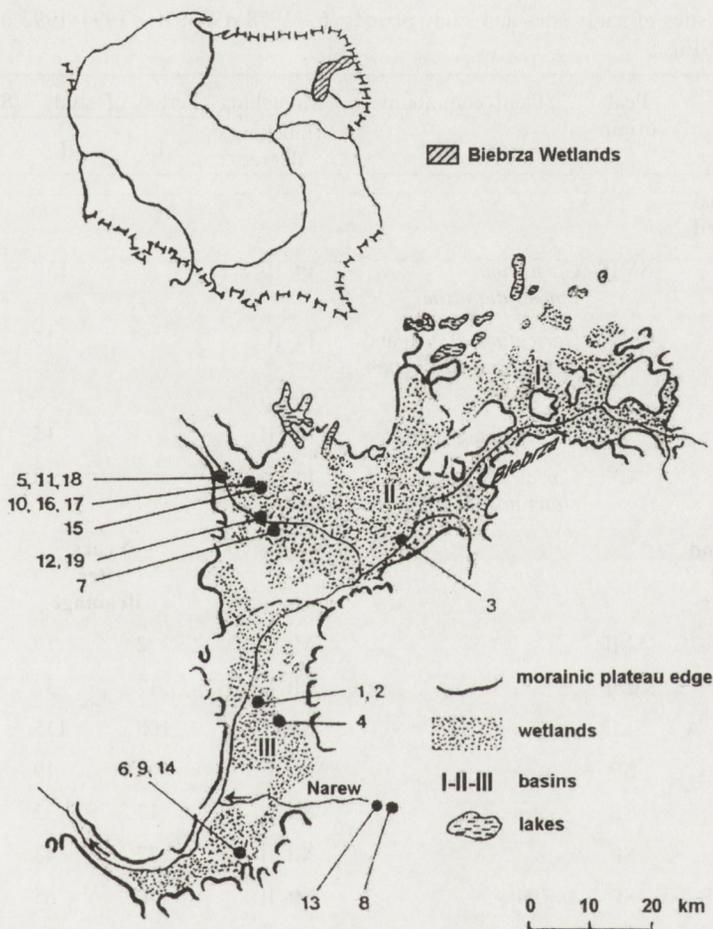


Fig. 1. Site sketch of the River Biebrza Valley (after Okruszko 1990) with denoted study sites (see No. in Table 1)

ters on site No. 17 (birch wood) were dependent on peat type and years after drainage in the same way as on the bordering meadow sites No. 16, and for this reason this site was included to the successional series of post-drained meadows. The soils derived from the sedge-moss community were characterized by a well developed moss layer, the highest water-holding capacity of the soil, and by a relatively stable moisture level throughout the year in natural and drained grasslands. The lowest moisture was observed in soils derived from alder peat. Alder peat soils were characterized by the highest bulk density, the lowest total porosity, and the lowest volume of mesopores; moorsh-forming processes were also most intense in alder peat (Okruszko 1993, also Wasilewska 1991a and Kaczmarek 1991 for the study sites). The total depth of the moorsh layer was below 20 cm on poorly moorshified soils (Mt I), typi-

cally 20–25 cm on moderately moorshified soils (Mt II), and over 30 cm on strongly moorshified soils (Mt III). Peat mineralization after drainage was also most intense in alder peat and least intense in wet sedge-moss peat (Kajak *et al.* 1985, Kajak and Okruszko 1990, Okruszko 1993).

Time-related changes in physical and chemical peat soil properties are illustrated (using the average values) for three study sites that differed in peat origin. Periods I and II refer to 15 and 30 years after fen drainage and subsequent meadow management, respectively (Table 2).

Over the period of 15 years, declines were observed in soil water content, total carbon and total N contents. Soil pH was reduced, whereas bulk density and nitrogen mineralization increased (Table 2). Nitrification rate followed the gradient sedge-moss peat, sedge peat, and alder peat, and was de-

Table 1. Characteristics of study sites and study periods: I – 1978–1983, II – 1994–1997. For more details see Wasilewska (1991a)

No. ¹⁾	Site ²⁾	Peat origin	Plant community	Moorshing (mucking) degree	Period of study		Sampling occasion	
					I	II	I	II
Natural fens – not drained								
1.	Dobarz	SMP ⁴⁾	<i>Caricetum limoso-diandrae</i>	Pt I		15 ⁷⁾	6	1
2.	Dobarz	SP ⁵⁾	<i>Caricetum elatae</i> and <i>Peucedano-Caricetum paradoxae</i>	Pt II		15	6	1
3.	Dolistowo	SP	<i>Caricetum gracilis</i>	Mt II		15	5	1
4.	Gugny	AP ⁶⁾	<i>Carici elongatae-Alnetum</i>	Pt		15	2	1
Drained and managed grasslands								
						Years after drainage		
5.	Toczyłowo A ³⁾	SMP		Mt I	2	17	7	1
6.	Wizna A	SMP		Mt I	17	32	19	6
7.	Sojczyn Gr. A	SMP		Mt	100	115	3	1
8.	Lipniki B ³⁾	SP		Mt I	2	19	19	1
9.	Wizna B	SP		Mt II	17	32	21	6
10.	Kuwasy B	SP		Mt II	27	43	8	1
11.	Toczyłowo B	SP	<i>Molinio-</i>	Mt II	50	65	7	1
12.	Modzelówka B	SP	<i>Arrhenatheretea</i>	Mt III	100	117	20	1
13.	Kiślaki C ³⁾	AP		Mt II	10	25	2	1
14.	Wizna C	AP		Mt II	17	32	19	6
15.	Pińczykowo C	AP		Mt II	30	45	1	1
16.	Kuwasy C	AP		Mt II	50	67	5	1
17.	Kuwasy C	AP		Mt II	50	65	3	1
18.	Toczyłowo C	AP		Mt II	50	65	2	1
19.	Modzelówka C	AP		Mt III	100	115	2	1

¹⁾ Consecutive numerals correspond to site numbers in Fig. 1; ²⁾ The original local names of site localities were maintained in order to make possible the comparison with another studies in which they are used (see Wasilewska 1991a); ³⁾ Soil moisture complex: A – wet, B – moist, C – dry; ⁴⁾ Sedge-moss peat; ⁵⁾ Sedge peat; ⁶⁾ Alder peat; ⁷⁾ Years between period I and II.

pendent on soil moisture. Rapid nitrification (over 300 kg N/growing season) of alder peat had many negative consequences such as high accumulation of nitrates in soil and their increasing concentrations in ground waters (Zimka and Stachurski 1996).

Further changes in soil processes also proceed with time after drainage. Peat is gradually converted into moorsh soil. Soil bulk density gradually increases. The con-

tents of carbon and nitrogen in soil and the rate of mineralization of organic matter decline (Table 3). Biological activity of moorshified soils and peat was evaluated by Maciak (1995), based on carbon and nitrogen compounds.

As a result of the subsidence of drained soils and mineralization of organic matter, their surface gradually lowers. On site No. 10, 16 and 17 (Table 1) the rate of subsidence

Table 2. Yearly average values of physical and chemical properties of peat soils on three sites (No. 6, 9 and 14, Table 1) in first period (I) and second period (II), that is, 15 and 30 years after drainage and management as meadows (top soil layer 0–15 cm); SMP – soil originated from sedge-moss peat, SP – from sedge peat, AP – from alder peat (adapted from Gotkiewicz 1977, Pętał and Churski 1991, Zimka and Stachurski 1996, Stachurski and Zimka 1998; cited in Kajak and Pętał 2001)

Properties	Period	SMP	SP	AP	Probability		
		1	2	3	1–2	1–3	2–3
Water content (% by weight)	I	79.6	76.2	66.0			
	II	74.2	71.7	61.4	*	***	***
Bulk density (g cm ⁻³)	I	0.209	0.208	0.236			
	II	0.217	0.220	0.252	NS	***	***
Thickness of peat deposit (cm)	I						
	II	400	400	265			
Total C content (%)	I	47.4	46.1	45.5			
	II	35.6	35.1	34.5	*	*	*
Total N content (%)	I	3.11	3.60	3.80			
	II	2.92	2.86	2.72	***	***	***
pH (in KCl)	I	5.8	5.9	5.8			
	II	5.0	5.4	5.2	***	***	***
N-mineralization rate (g m ⁻² season)	I	6.5	16.5	34.6			
	II	13.4	17.3	35.8	**	***	***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; NS – not significant.

Table 3. Long-term changes in soil processes after drainage of fens (adapted from Walczyna 1973, cited in Kajak and Okruszko 1990)

	Number of years after drainage of fens			
	30	100	115	170
Type of soil	moorsh peat	moorsh peat	moorsh	black earth
Bulk density (g cm ⁻³)	0.24	0.44	0.92	0.99
Organic C (%)	47.5	23.8	6.9	4.4
Total N (%)	4.45	2.13	0.52	0.36
Mineralization of:				
organic C ^{a)} (g C dm ⁻³ yr ⁻¹)	3.45	2.09	2.39	1.49
nitrogen N ^{a)} (g NO ₃ -N dm ⁻³ yr ⁻¹)	0.42	1.24	0.23	0.20

^{a)} Laboratory data.

was 1.35 cm per year (Szuniewicz and Chrzanowski 1995). It has been found that the subsidence of peatlands intensively drained is mainly due to peat mineralization (in 77%) and to a lesser extent to peat density (in 23%). The process of self-deepening of river channels can also contribute to a slight subsidence of natural, not drained peatlands, as this can be the case on site No. 3 (Table 1).

The mean rate of the subsidence of the fen drained in 1963–64 where sites No. 6, 9 and 14 were located (Table 1), was estimated at 0.3 cm per year in the wet part (site No. 6), and it was twice as fast, that is, 0.6 cm per year in the dry part (site No. 14) (Nazaruk and Kaca 1999).

Restoration of drained fens, mainly through the control of the ground water level, has already been initiated in Poland

(Okruszko 1995, Nazaruk 1996) and in other parts of the world (Wösten *et al.* 1997).

The succession of nematode communities will be analysed with reference to changes in peat soils drained and managed as meadows for periods from 2 to 117 years. Not drained natural fens will serve as comparison (Table 1). Drained meadows were partly treated with fertilizers, mown two-three times a year, and in some years grazed extensively in late autumn. Soil processes and the composition of plant communities of natural and drained fens are given by Pałczyński (1972, 1984), Okruszko (1990), Kajak and Okruszko (1990), and Kotowska *et al.* [1996 (1998)].

3. METHODS

3.1. SOIL SAMPLING FOR NEMATODES

Soil samples for nematodes were taken with a soil sampler 2 cm² in surface area, 50 cm³ in volume, and 25 cm deep. On each sampling occasion, 20 cores were taken at random, representing a collective sample. Nematodes were extracted by using a modified Baermann method (4 × 25 cm³ of mixed soil) (Wasilewska 1991a). The extracted nematodes were identified to genus or genus *sensu lato* (according to Andrassy 1984 and Bongers 1988) and then allocated to trophic groups (Wasilewska 1971b, Yeates *et al.* 1993).

The material was collected in two periods: period I (1978–1983, after Wasilewska 1991a) and period II (1994–1997), using the same methods and sites, only the number of sampling occasions being different (Table 1). In the second period of study 16 sites were sampled only once, what was significantly less times than in the first period. Nevertheless, more nematode taxa were found in the second period. It indicates, together with a suitable number of subsamples, the confidence to the results.

3.2. PARAMETERS RELATED TO NEMATODE COMMUNITY

In period I, nematode succession was analysed by using the chronosequence of sites. The sequence reflected the response of nematodes to physical and chemical changes in soil properties. In period II successional changes were evaluated for the same sites,

but under later stages. Period I included meadows of span of years from 2 to 100 after drainage of fens and period II – span of years from 17 to 117.

The basic unit for recalculation of parameters was the density of taxa, expressed as individuals per m².

From 19 to 29 parameters were used to describe the structure of nematode communities in periods I and II, separately:

D – density

– Total density of nematodes – D total

– Density of bacterivores – D B

– Density of fungivores – D F

– Density of facultative plant feeders – D FPF

– Density of obligate plant feeders – D OPF

– Density of omnivores – D O

– Density of predators – D P

R – ratio

– Ratio of density of bacterivores to density of fungivores – B/F, also in the variant with potential fungivores (FPF) that is – B/(F+FPF). This ratio can be indicative of decomposition pathway: mainly through bacteria or mainly through fungi

– Ratio of density of bacterivores + fungivores, also in the variant with potential fungivores, to density of obligate plant feeders – (B+F)/OPF and (B+F+FPF)/OPF. The trophic status of facultative plant feeders is known only in part. This ratio can be indicative of differences in mineralization between dead and live plant tissues, that is, between the detritus – or grazing food webs (Wasilewska 1997)

S – number of taxa

– The number of taxa (genera) in the community – S total

– The number of taxa in the group of bacterivores + fungivores – S (B+F)

– The number of taxa in the group of facultative plant feeders + obligate plant feeders – S (FPF+OPF)

– The number of taxa in the group of omnivores + predators – S (O+P)

H' – diversity index

– Shannon diversity index – $H' = - \sum p_i \log_2 p_i$ where p_i is the proportion of each taxon (genus) in the total population or group (Shannon and Weaver 1949), calculated for the total community (H' total), the group of bacterivores + fungivores (H' (B+F)), the group of facultative plant feeders (H' FPF), the group of obligate plant feeders (H' OPF)

and the group of omnivores + predators (H^+ (O+P));

MI – maturity index

– This index is based on differing life strategies of the species in the community (Bongers 1990, 1999, Bongers *et al.* 1995). Taxonomic units (genera) are classified here from colonizers (short life cycle, high rate of reproduction, tolerance to disturbance), which were assigned rank 1, to persisters (long life cycles, poor colonizers, few offspring, sensitivity to disturbance), which were assigned rank 5. The remaining taxa were intermediate on the colonizers-persisters (c-p) scale (Bongers 1990). In the broad sense, the position of a taxon on the c-p scale is becoming equivalent to the position on the r-K continuum. Formula of maturity index according to Bongers (1990) is as follows: $MI = \sum v_i p_i$; where v_i is the rank of i-taxon on c-p scale and p_i is the proportion of i-taxon in nematode community. Indicated below maturity indices differ in what part of nematode community is considered and c-p indicates the range of ranks of that part of taxa. The following indices were calculated:

– MI (c-p = 1–5) (Bongers 1990) based on the taxa without plant feeders. Lower MI is indicative of earlier successional stages, or of environmental perturbations, whereas higher values are indicative of later successional stages, or smaller environmental perturbations;

– Sum MI (c-p = 1–5). It is calculated using all taxa in a nematode community (Yeates 1994, Wasilewska 1994b) and c-p 1–5 as Bongers (1990). It serves the same purpose as MI (c-p = 1–5) and reacts similarly, albeit under natural or semi-natural conditions;

– MI (c-p = 2–5) (Bongers *et al.* 1995) based on the same taxa as MI (c-p = 1–5), but without taxa allocated to c-p = 1, that is, those developing under food rich conditions and which form dauerlarvae when microbiological activity declines. The exclusion of the taxa with c-p = 1 precludes the monitoring of short-lasting changes such as the application of nitrogen fertilizers in agroecosystems;

– Sum MI (c-p = 2–5) – based on all taxa, but with exclusion of taxa c-p = 1

– Ba MI – maturity index of bacterivore nematodes. It should increase with succession;

– PPI – (Bongers 1990) is constructed using phytoparasitic nematodes (c-p = 2–5).

It is positively correlated with primary production, and higher values indicate nutrient enrichment in the environment;

– Ratio PPI/MI (*sensu* Bongers *et al.* 1997) might reflect ecosystem enrichment by indicating divergence in the values of the two indices;

Class *Secernentea* versus class *Adenophorea*

– N S/A – ratio of numbers of nematodes from the class *Secernentea* to the numbers of nematodes from the class *Adenophorea*. It informs of the relation of all more r-strategists s. l. in the community to all more K-strategists s. l. (Bongers 1999). I suggest that the ratio of these two groups characterizes the divergence from natural conditions. The higher the value of S/A, the greater divergence. This is substantiated by the fact of a more abundant occurrence of dorylaimids (*Adenophorea*) in natural or little by man transformed habitats (Wasilewska 1974).

– S S/A – ratio of the number of taxa from the class *Secernentea* to the number of taxa from the class *Adenophorea*.

C – constancy index

– Constancy index $C = q:Q \cdot 100$, where q is the number of sites with the taxon present, and Q is the total number of sites (in percentage). The constancy index characterizes the degree of the association of a taxon with the biocoenosis.

Brief form of nematode community parameters is presented in Appendix.

3.3. STATISTICS

All the data across 19 sites, two periods, and three peat types were subjected to statistical analysis of variance (two-way ANOVA).

These tests were used to estimate the effects of the two sampling periods (period I and period II, controlled for sites) and peat types (controlled for periods). The significance of differences between periods I and II was additionally analysed by using the non-parametric Friedman test. These two methods appeared to be complementary in searching significance of differences. Sites on natural fens (No.1–No. 4, Table 1) were included to this statistical analysis.

Time-related changes in nematode community parameters and in the density of the taxon *Paratylenchus* (transformed to $\ln(n+1)$) were analysed by linear regression. The significance was tested by ANOVA for correlation. The sites on natural, not drained

fens are excluded from this analysis, though they were graphically compared with drained sites.

4. RESULTS

4.1. TAXA: PERIOD I (1978–1983) VERSUS PERIOD II (1994–1997)

In total, 122 taxa were identified in the collected material, including 90 in period I and 104 in period II (Table 4). Most frequent were taxa associated with only one meadow site: 23 taxa in period I and 28 taxa in period II. Only 3 taxa (*Acroboloides*, *Aphelenchoides*, and *Eudorylaimus*) occurred at all sites (natural fens and drained grasslands).

The 18 taxa present only in period I included those occurring in habitats considered as aquatic, fresh-water, or at least as moist soils. These were *Calolaimus*, *Ethmolaimus*, *Ironus*, *Prodesmodora*, *Aphanolaimus* (present on 1 to 4 sites). Other fresh-water taxa, that were present on a smaller number of sites in period II than in period I, were represented by *Hirschmaniella* (2 vs 10), *Tripyla* (2 vs 18), and *Tobrillus* (4 versus 7).

32 taxa were present only in period II. Except for *Filenchus* and *Miculenchus*, these taxa occurred only on 1–3 meadows, were not abundant, and of different trophic groups.

72 taxa were present in both periods, and many of them were dominant. Of this number, 15 had significantly higher densities (ANOVA or Friedman test) in period I: *Paratylenchus*, *Tylenchus*, *Panagrolaimus*, *Rhabditis*, *Acroboloides*, *Aphelenchoides*, *Aphelenchus*, *Eudorylaimus*, *Pratylenchus*, *Rhabdolaimus*, *Cephalobus*, *Ditylenchus*, *Tylencholaimus*, *Hemicycliophora*, *Paraphelenchus*, *Neotylenchus*, *Chronogaster*, *Tripyla*, and *Hirschmaniella*. In period II, only 4 taxa had significantly higher densities: *Filenchus*, *Mononchus*, *Miculenchus*, and *Cervidellus* (Table 4).

The difference between periods I and II was reflected in the ratio of nematodes from two taxonomic classes: *Secernentea* and *Adenophorea*. The S/A ratio in terms of abundance was much higher in period I than in period II, although this was not the case of the number of taxa (Table 5). The reduced prevalence of *Secernentea* over *Adenophorea* in period II, thus with advancing secondary succession, provides evidence for approaching "natural" conditions.

4.2. THE EFFECT OF PEAT TYPE ON NEMATODE TAXA

To analyse the relationship between densities of taxa and peat type, two-way ANOVA analysis of variance was used, where period was controlled (it was tested if the association of a taxon with a peat type was repeated in both periods). This analysis was performed for taxa present on at least four sites in periods I or II (there were 4 sites on sedge-moss peat, 7 sites on sedge peat, and 8 sites on alder peat). A total of 66 taxa were tested.

The density of most taxa did not show significant relationships with peat type. A significant relationship was found for three taxa: *Aphelenchoides*, *Hirschmaniella*, and *Wilsonema*. For *Panagrolaimus* this relationship approached significance. For two taxa, *Alaimus* and *Helicotylenchus*, an interaction was found between peat type and period in their effects on density (Table 6). It means that the dependence of these taxa on peat type differed between period I and period II. In addition, Table 6 shows several taxa for which no statistical significance was found but of the 61 remaining taxa they were closest to significance.

For *Panagrolaimus*, the dependence of density on peat type approached significance. A tendency to such dependence was found for *Paratylenchus*, *Euteratocephalus*, and *Pratylenchus*. All the above taxa represented three trophic groups: bacterivores, fungivores, and obligate plant feeders (Table 6). The most frequent sequence of peat types with respect to nematode density was SMP < SP < AP, except for *Hirschmaniella* that followed an opposite pattern.

If all the 9 taxa cited above can be considered as dependent on peat type, they account for about one-seventh of the analysed taxa, thus the major part of taxa did not depend on peat type. The dependence on peat type was observed for taxa noted on all sites (*Aphelenchoides*), as well as for those noted on few sites (*Hirschmaniella*), what indicate constancy indices (Table 6).

The dependence on soil type is clearly reflected in the ratio of *Secernentea* to *Adenophorea*. The numerical dominance of the former over the latter was 1.8 times higher on alder peat and 1.2 times higher on sedge peat as compared with sedge-moss peat. The number of taxa did not follow the same proportions (Table 5).

Table 4. List of taxa occurring on 19 study sites and mean densities ($D \cdot 10^3$ indiv. m^{-2}) in period I (1978–1983) and period II (1994–1997); B – bacterivores, F – fungivores, FPF – facultative plant feeders, OPF – obligate plant feeders, O – omnivores, P – predators

No.	c-p ¹⁾	Taxon	D I	D II	P ²⁾	P ³⁾	R ⁴⁾
1.	2	<i>Paratylenchus</i> – OPF	2453.37	160.26	NS	**	15/14
2.	2	<i>Tylenchus</i> – FPF	1379.23	85.00	**	***	19/17
3.	1	<i>Panagrolaimus</i> – B	910.81	193.47	**	***	18/16
4.	1	<i>Rhabditis</i> – B	778.76	230.74	**	*	19/17
5.	3	<i>Helicotylenchus</i> – OPF	706.91	356.16	NS	NS	16/17
6.	2	<i>Acrobeloides</i> – B	765.30	240.37	***	**	19/19
7.	3	<i>Tylenchorhynchus</i> – OPF	443.89	371.16	NS	NS	16/16
8.	2	<i>Aphelenchoides</i> – F	478.89	98.32	***	***	19/19
9.	2	<i>Plectus</i> – B	286.53	211.79	NS	NS	18/18
10.	2	<i>Aglenchus</i> – FPF	163.75	184.47	NS	NS	17/15
11.	2	<i>Aphelenchus</i> – F	231.43	90.53	*	*	17/14
12.	2	<i>Eucephalobus</i> – B	129.68	190.89	NS	NS	15/16
13.	4	<i>Eudorylaimus</i> – O	199.39	96.42	*	*	19/19
14.	3	<i>Pratylenchus</i> – OPF	193.95	97.47	NS	*	14/12
15.	3	<i>Rhabdolaimus</i> – B	172.67	114.21	NS	*	18/15
16.	2	<i>Wilsonema</i> – B	211.00	70.21	NS	NS	18/13
17.	3	<i>Rotylenchus</i> – OPF	82.95	159.21	NS	NS	12/16
18.	2	<i>Cephalobus</i> – B	155.51	31.21	**	**	17/12
19.	2	<i>Ditylenchus</i> – FPF	143.85	41.32	*	*	18/16
20.	2	<i>Filenchus</i> – FPF	0.00	181.53	**	***	0/17
21.	3	<i>Prismatolaimus</i> – B	115.44	58.95	*	NS	17/15
22.	3	<i>Teratocephalus</i> – B	85.89	84.11	NS	NS	16/14
23.	5	<i>Mesodorylaimus</i> – O	71.30	52.89	NS	NS	17/16
24.	3	<i>Euteratocephalus</i> – B	64.03	58.53	NS	NS	8/14
25.	2	<i>Gracilacus</i> – OPF	67.05	35.58	NS	NS	5/5
26.	4	<i>Tylencholaimus</i> – F	90.40	10.63	*	*	13/7
27.	2	<i>Monhystera</i> – B	65.53	32.89	NS	NS	17/13
28.	3	<i>Meloidogyne</i> – OPF	78.26	12.47	NS	NS	9/10
29.	2	<i>Coslenchus</i> – FPF	26.71	52.74	NS	NS	10/13
30.	4	<i>Alaimus</i> – B	39.55	19.21	NS	NS	16/12
31.	4	<i>Mononchus</i> – P	12.84	39.74	**	***	12/18
32.	5	<i>Aporcelaimellus</i> – O	17.87	29.26	NS	*	9/16
33.	2	<i>Heterocephalobus</i> – B	15.36	31.21	NS	NS	14/12
34.	2	<i>Acrobeles</i> – B	21.75	16.58	NS	NS	8/8
35.	3	<i>Heterodera</i> – OPF	14.37	20.21	NS	NS	5/7
36.	3	<i>Hemicyclophora</i> – OPF	27.16	4.58	**	***	13/2
37.	2	<i>Malenchus</i> – FPF	7.63	22.95	NS	NS	5/7
38.	2	<i>Seinura</i> – P	25.32	4.42	NS	NS	10/6
39.	2	<i>Chiloplacus</i> – B	20.59	7.58	NS	NS	6/4
40.	2	<i>Paraphelenchus</i> – F	19.53	5.53	*	NS	9/6

Table 4. Continued

No.	c-p ¹⁾	Taxon	D I	D II	P ²⁾	P ³⁾	R ⁴⁾
41.	2	<i>Miculenchus</i> – FPF	0.00	20.26	*	**	0/9
42.	3	<i>Cylindrolaimus</i> – B	8.51	10.84	NS	NS	9/11
43.	2	<i>Cervidellus</i> – B	11.01	4.63	NS	*	10/3
44.	2	<i>Neotylenchus</i> – F	13.23	1.74	NS	*	8/1
45.	2	<i>Anaplectus</i> – B	7.42	7.42	NS	NS	8/4
46.	2	<i>Basiria</i> – FPF	3.32	8.53	NS	NS	6/7
47.	4	<i>Dorylaimidae others</i> – O	8.99	2.74	NS	NS	9/5
48.	2	<i>Psilenchus</i> – FPF	7.07	2.16	NS	NS	12/4
49.	3	<i>Bastiania</i> – B	7.00	1.11	– ⁵⁾	–	1/2
50.	4	<i>Dorylaimoides</i> – O	0.05	7.95	–	–	1/4
51.	1	<i>Diploscapter</i> – B	0.42	7.32	–	–	1/3
52.	1	<i>Diplogaster</i> – B	2.95	4.53	–	–	5/2
53.	4	<i>Pungentus</i> – O	5.31	2.11	–	–	3/3
54.	5	<i>Dorylaimellus</i> – O	5.26	1.74	–	–	2/1
55.	3	<i>Chronogaster</i> – B	5.37	1.58	*	**	11/2
56.	3	<i>Aphanolaimus</i> – B	6.93	0.00	–	–	3/0
57.	3	<i>Tripyla</i> – P	5.13	1.79	NS	*	8/2
58.	3	<i>Geocenamus</i> – OPF	0.00	6.84	–	–	0/3
59.	3	<i>Diphtherophora</i> – O	5.82	0.84	–	–	5/3
60.	2	<i>Nothotylenchus</i> – F	5.07	1.37	NS	NS	6/4
61.	5	<i>Prodorylaimus</i> – O	4.55	1.47	NS	NS	6/4
62.	4	<i>Enchodelus</i> – O	2.79	3.00	–	–	2/4
63.	2	<i>Tylocephalus</i> – B	0.00	5.11	–	–	0/1
64.	5	<i>Longidorus</i> – OPF	0.29	4.53	–	–	2/5
65.	3	<i>Tobrilus</i> – B	1.95	2.58	NS	NS	7/4
66.	3	<i>Hirschmaniella</i> – OPF	3.58	0.63	*	*	10/2
67.	3	<i>Chromadora</i> – B	0.53	3.32	–	–	1/2
68.	3	<i>Pratylenchinae others</i> – OPF	3.53	0.00	–	–	1/0
69.	1	<i>Bunonema</i> – B	3.51	0.00	–	–	1/0
70.	2	<i>Deladenus</i> – F	3.21	0.16	–	–	3/1
71.	4	<i>Eudorylaimus "I"</i> – O	3.11	0.00	–	–	1/0
72.	2	<i>Boleodorus</i> – F	0.00	3.05	–	–	0/5
73.	2	<i>Drilocephalobus</i> – B	0.03	3.00	–	–	1/2
74.	2	<i>Zeldia</i> – B	1.89	0.89	–	–	4/1
75.	3	<i>Criconemella</i> – OPF	0.00	2.79	–	–	0/2
76.	4	<i>Amphidelus</i> – B	2.63	0.00	–	–	1/0
77.	2	<i>Ditylenchus "I"</i> – FPF	2.63	0.00	–	–	1/0
78.	2	<i>Neopsilenchus</i> – FPF	0.00	2.63	–	–	0/1
79.	5	<i>Aporcelaimus</i> – O	0.00	2.26	–	–	0/3
80.	3	<i>Tetylenchus</i> – OPF	1.71	0.16	–	–	2/1
81.	3	<i>Aulolaimus</i> – B	1.74	0.00	–	–	1/0

82.	5	<i>Chrysonemoides</i> – O	0.00	1.58	–	–	0/1
83.	3	<i>Criconemoides</i> – OPF	1.53	0.00	–	–	1/0
84.	3	<i>Chromadoridae</i> – B	0.26	1.26	–	–	1/2
85.	3	<i>Trophurus</i> – OPF	0.00	1.37	–	–	0/3
86.	5	<i>Nygotaimus</i> – P	0.37	0.89	–	–	1/1
87.	5	<i>Axonchium</i> – O	0.00	1.26	–	–	0/2
88.	3	<i>Odontolaimus</i> – B	0.00	1.11	–	–	0/2
89.	4	<i>Leptonchus</i> – O	0.00	1.05	–	–	0/2
90.	5	<i>Thornenema</i> – O	0.00	1.05	–	–	0/2
91.	3	<i>Ethmolaimus</i> – B	1.00	0.00	–	–	2/0
92.	4	<i>Ironus</i> – P	0.97	0.00	–	–	4/0
93.	3	<i>Anonchus</i> – B	0.03	0.89	–	–	1/1
94.	3	<i>Euteratocephalus</i> "1" – B	0.00	0.89	–	–	0/1
95.	3	<i>Metateratocephalus</i> – B	0.00	0.89	–	–	0/1
96.	1	<i>Pristionchus</i> – B	0.00	0.89	–	–	0/1
97.	1	<i>Panagrolaimidae</i> "1" – B	0.84	0.00	–	–	5/0
98.	4	<i>Trichodorus</i> – OPF	0.58	0.21	–	–	1/1
99.	1	<i>Panagrobelum</i> – B	0.00	0.74	–	–	0/1
100.	2	<i>Lelenchus</i> – FPF	0.00	0.63	–	–	0/2
101.	2	<i>Monhystrella</i> – B	0.21	0.37	–	–	1/1
102.	5	<i>Actinolaimus</i> – P	0.57	0.00	–	–	3/0
103.	2	<i>Tylenchus</i> "1" – FPF	0.53	0.00	–	–	1/0
104.	4	<i>Tylencholaimellus</i> – F	0.00	0.53	–	–	0/2
105.	1	<i>Panagrolaimidae</i> others – B	0.00	0.47	–	–	0/1
106.	1	<i>Mesorhabditis</i> – B	0.37	0.00	–	–	1/0
107.	4	<i>Dorylaimus</i> – O	0.00	0.37	–	–	0/2
108.	1	<i>Protorhabditis</i> – B	0.00	0.37	–	–	0/1
109.	3	<i>Prodesmodora</i> – B	0.34	0.00	–	–	3/0
110.	3	<i>Desmolaimus</i> – B	0.08	0.16	–	–	1/1
111.	4	<i>Longidorella</i> – OPF	0.00	0.21	–	–	0/1
112.	1	<i>Panagrobelus</i> – B	0.00	0.21	–	–	0/1
113.	3	<i>Steratocephalus</i> – B	0.00	0.21	–	–	0/1
114.	3	<i>Achromadora</i> – B	0.00	0.16	–	–	0/1
115.	2	<i>Acrolobus</i> – B	0.00	0.16	–	–	0/1
116.	5	<i>Belondira</i> – O	0.00	0.16	–	–	0/1
117.	5	<i>Chrysonema</i> – O	0.00	0.16	–	–	0/1
118.	3	<i>Microilaimus</i> – B	0.00	0.16	–	–	0/1
119.	4	<i>Thornia</i> – O	0.00	0.16	–	–	0/1
120.	4	<i>Calolaimus</i> – O	0.11	0.00	–	–	1/0
121.	2	<i>Cephalobidae</i> others – B	0.05	0.00	–	–	1/0
122.	3	<i>Axonolaimidae</i> "1" – B	0.04	0.00	–	–	1/0

¹⁾ c-p (rank on colonizers-persisters scale) according to Bongers (1990); ²⁾P – significance level of density between periods: two-way ANOVA. Tests were performed only for taxa that in periods I and II occurred on at least 9 sites; ³⁾P – significance level: Friedman test (for 19 sites); ⁴⁾R – ratio of the number of sites where a taxon occurred in period I to the number of sites where it occurred in period II; ⁵⁾ no statistical analysis was possible;

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS – not significant difference.

Table 5. Ratio of numbers (N) and of the number of taxa (S) of nematodes of the class *Secernentea* (S) to nematodes of the class *Adenophorea* (A) for period I (1978–1983) and II (1994–1997) and different peat types; Peat types as in Table 1

Parameter	Period		Type of peat		
	I	II	SMP	SP	AP
N S/A	7.03	3.89	4.62	5.71	8.15
S S/A	48/42 = 1.14	57/47 = 1.21	52/39 = 1.33	50/39 = 1.28	54/39 = 1.38

4.3. TAXON: *PARATYLENCHUS*

This taxon is considered as an index of the degradation of overdried alder peat in the first years after drainage (Wasilewska 1991a), and it needs analysis of the time-related situation.

Numbers of *Paratylenchus* were several times higher (15 times with respect to the mean density per site) in period I than in period II ($P < 0.01$ Friedman test) (Table 4), and they were most dependent on alder peat and least dependent on sedge-moss peat ($P < 0.06$, ANOVA) (Table 6). Although the mean density of *Paratylenchus* on alder peat sites was the highest of all found taxa, the probability of dependence of that taxon density on peat type was much lower ($P < 0.06$, ANOVA) than of the two other genera like *Aphelenchoides* and *Wilsonema* ($P < 0.02$, ANOVA) (Table 6). The reason of above is, that only *Paratylenchus* was extremely abundant on few, but not on all, alder peat sites. Thus, genus *Paratylenchus* is not dependent just on alder peat, but is strongly dependent on peat with high rate of nitrogen mineralization.

Densities of *Paratylenchus* in alder peat showed differences between periods I and II (Table 6). The correlation of density with years after drainage in period I was negative and highly significant ($r = -0.9$, $P < 0.001$). The correlation in period II, that is 15–17 years later, was not significant ($r = -0.29$, NS) (Fig. 2). The highest densities of *Paratylenchus* were observed 10–30 years after drainage (20 million and 13.4 million individuals m^{-2} , respectively, on alder peat).

4.4. NEMATODE COMMUNITY ANALYSIS

4.4.1. THE EFFECT OF TWO PERIODS AFTER DRAINAGE

The following parameters describing nematode community will be considered: densities of trophic groups, number of taxa

(genera), diversity indices and maturity indices of the community. To compare the values of these parameters in periods I and II, two tests were used (Table 7).

The mean density of all trophic groups and the mean total density were significantly higher in period I compared with period II – by factors of 2.8 for total nematodes, 2.4 for bacterivores, 4.0 for fungivores, 2.9 for facultative plant feeders, 3.3 for obligate plant feeders, and 1.6 for omnivores ($P < 0.05–0.000$). No difference between periods was found for predators. This pattern was obtained for a significant number of sites (Table 7 – A). The decrease in densities in period II (except for obligate plant feeders and predators) was also confirmed by the non-parametric Friedman test (Table 7 – B).

Two ratios: bacterivores to fungivores – B/F and fungivores combined with potential fungivores – B/(F+FPF) were higher in period II (respectively, 1.4 times, $P < 0.08$ and 1.5 times, $P < 0.03$) (Table 7 – A). Thus, the numerical dominance of bacterivores over fungivores increased.

The next two ratios of trophic groups, indicating the association of nematodes with detritus or grazing food webs – (B+F)/OPF, and with facultative plant feeders – (B+F+FPF)/OPF show a decrease in the dominance of nematode association with the detritus food web in favour of the grazing food web in period II, but this is not statistically confirmed (Table 7 – A).

No significant differences were found in the mean total number of taxa (S total) and in the functional groups between periods I and II (Table 7 – A and B).

The Shannon diversity index increased for the group of facultative plant parasites (H' FPF) and for the group of omnivores + predators (H' O+P) in period II (Table 7 – A and B). The diversity for remaining trophic categories – H' (B+F), H' OPF, and H' total did not significantly differ between periods (Table 7 – A and B).

Table 6. Statistics (two-way ANOVA) for estimating densities ($D \pm SE$) of several taxa in relation to peat type, and the index of constancy (C), period I – 1978–1983, period II – 1994–1997; B – bacterivores, F – fungivore, OPF – obligate plant feeders; SMP – sedge-moss peat – 4 sites, SP – sedge peat – 7 sites, AP – alder peat – 8 sites

Taxon	Peat type	Period I $D \pm SE \cdot 10^3 m^{-2}$	Period II $D \pm SE \cdot 10^3 m^{-2}$	d.f. A B AB	Period – A		Peat – B		Interactions AB		C (%)
					F-value	P	F-value	P	F-value	P	
					<i>Aphelenchoides</i> – F	SMP	392 ± 76	50 ± 18	1	31.4	
	SP	330 ± 102	75 ± 24	2							100
	AP	651 ± 103	142 ± 33	2							100
<i>Hirschmaniella</i> – OPF	SMP	12.5 ± 9.1	2.2 ± 2.2	1	4.2	0.049*	4.1	0.025 *	1.9	0.158	63
	SP	2.0 ± 0.8	0.4 ± 0.4	2							43
	AP	0.5 ± 0.5	0	2							6
<i>Wilsonema</i> – B	SMP	11 ± 6	74 ± 62	1	1.3	0.258	3.5	0.043 *	2.5	0.095	100
	SP	50 ± 24	45 ± 18	2							86
	AP	451 ± 187	89 ± 41	2							75
<i>Helicotylenchus</i> – OPF	SMP	186 ± 76	803 ± 389	1	0.9	0.341	0.1	0.926	3.7	0.034 *	75
	SP	734 ± 219	272 ± 80	2							86
	AP	943 ± 333	205 ± 75	2							94
<i>Alaimus</i> – B	SMP	7.2 ± 3	17.5 ± 12	1	0.8	0.368	2.4	0.105	4.0	0.027 *	75
	SP	10.6 ± 5	26.4 ± 10	2							71
	AP	80.9 ± 30	13.7 ± 5	2							88
<i>Panagrolaimus</i> – B	SMP	340 ± 170	124 ± 96	1	6.4	0.016	3.2	0.054	2.2	0.132	88
	SP	523 ± 152	164 ± 74	2							93
	AP	1535 ± 503	253 ± 108	2							88
<i>Paratylenchus</i> – OPF	SMP	50 ± 42	17 ± 13	1	2.4	0.129	2.9	0.069	2.7	0.082	63
	SP	273 ± 77	182 ± 148	2							71
	AP	5562 ± 2605	212 ± 101	2							88
<i>Euteratocephalus</i> – B	SMP	1.7 ± 1.7	18.5 ± 12	1	0.0	0.991	2.8	0.072	0.8	0.455	63
	SP	1.7 ± 1.4	50.5 ± 29	2							57
	AP	149.7 ± 86	85.5 ± 28	2							63
<i>Pratylenchus</i> – OPF	SMP	19 ± 13	59 ± 26	1	0.7	0.419	2.8	0.078	0.7	0.496	63
	SP	103 ± 56	53 ± 25	2							79
	AP	360 ± 162	155 ± 85	2							63

* $P < 0.05$.

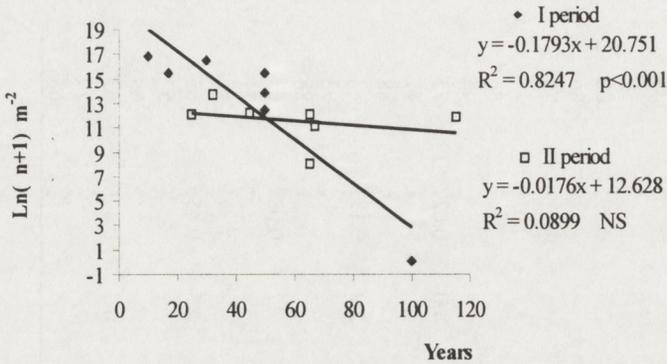


Fig. 2. Changes in density of *Paratylenchus* on drained and meadow-managed alder peats ($n = 7$) with time after drainage

All variants of maturity indices, including Ba MI and PPI, were significantly higher in period II. The difference between ratio PPI/MI in period I and II was insignificant (Table 7 – A and B).

It can be stated in short that after 15–17 years, nematode densities declined and the maturity of nematode communities increased.

4.4.2. THE EFFECT OF PEAT TYPE

Like in the case of taxa, two-way ANOVA was performed to estimate the effect of peat type on various nematode community parameters, after controlling for period effects (Table 7 – C). A significant effect of peat type (sedge-moss peat – SMP, sedge peat – SP, and alder peat – AP) was found for only three parameters (D total, D B, and D OPF). This means that the effect of peat type on nematode densities in the sequence $SMP < SP < AP$ in periods I and II occurred in a significant number of sites. The interaction for group OPF was due to the fact that in period II the abundance of this group on alder peat sites was not as high as in period I. This situation influenced the significance of the interaction for the parameter D total (Table 7 – C).

The remaining parameters do not follow the pattern: $SMP < SP < AP$. In that sense they do not show relation to peat type.

Thus, only the density of most abundant groups, and not taxa diversity or community maturity, was related to peat type.

4.4.3. SEQUENTIAL TIME-RELATED CHANGES ON DRAINED AND MANAGED MEADOWS IN PERIODS I AND II, AND THEIR COMPARISON WITH NATURAL NOT DRAINED FENS

Changes with time after drainage were analysed for most parameters that significantly differed between period I and II and

for some other parameters (Fig. 3). Period I was started earlier after drainage and also terminated earlier than period II (Table 1, Fig. 3). Thus, period II did not include first years after drainage, when some trophic groups increased rapidly (Wasilewska 1991a). The scattering within sites was large, thus significant differences with time after drainage were found for few parameters. Densities of total nematodes, bacterivores, fungivores, facultative plant feeders, and obligate plant feeders decreased with years after drainage in period I (higher density) and period II (lower density), but the correlation was not statistically significant (Fig. 3: 1, 2, 3, 4, and 5). In period I, fungivores tended to increase with time. Densities on natural fens, not included into regression, were much lower, closer to values in period II than in period I.

Omnivores were the only trophic group significantly increasing with years after drainage in both periods (Fig. 3: 6). Densities of predators were not significantly correlated with years after drainage.

The two ratios (B/F, Fig. 3: 7 and $B/(F+FPF)$, Fig. 3: 8) showed similar trends: i.e. in period I they decrease, in period II they increase with years after drainage but in both cases correlation was statistically not significant.

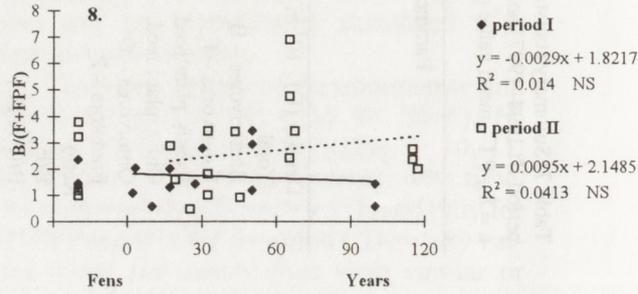
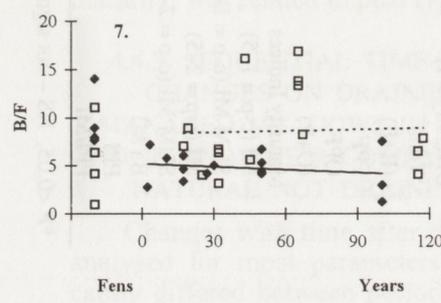
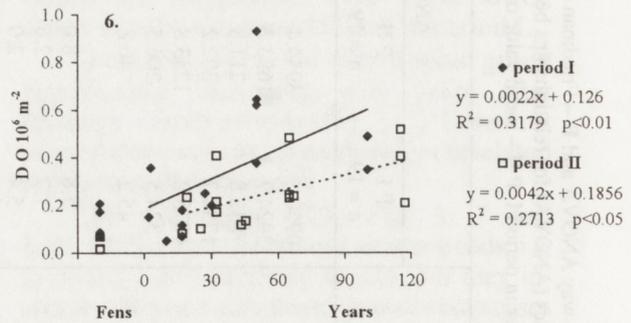
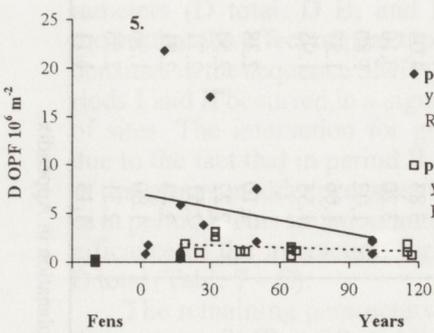
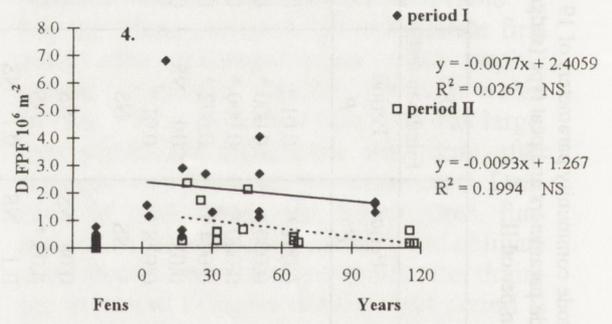
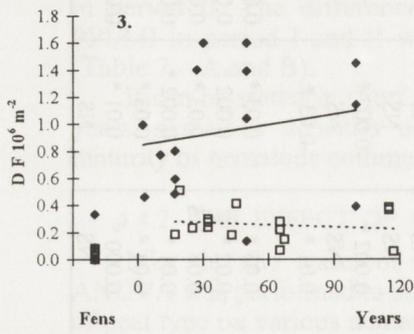
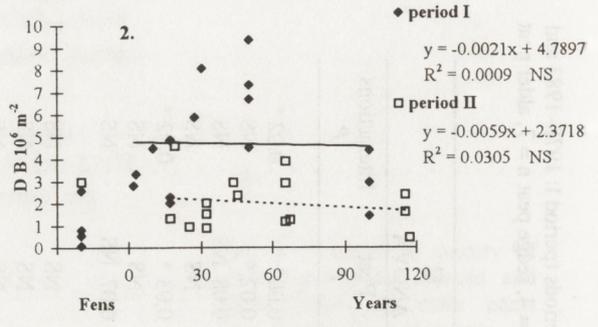
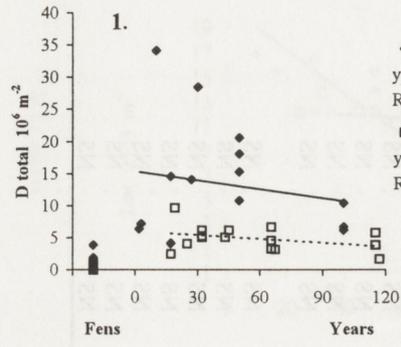
The ratio of nematodes associated with the detritus food web to those associated with the grazing food web ($(B+F)/OPF$, Fig. 3: 9) also was not significantly correlated with time in both periods.

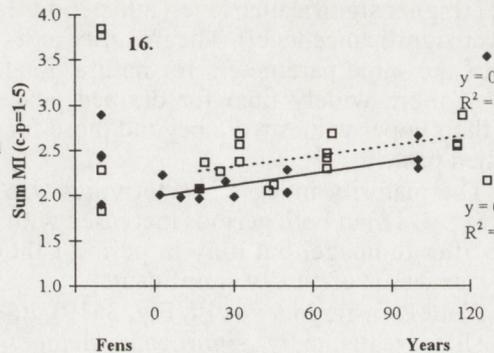
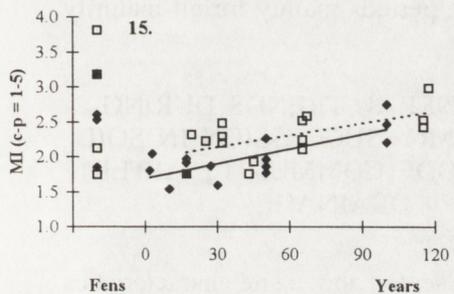
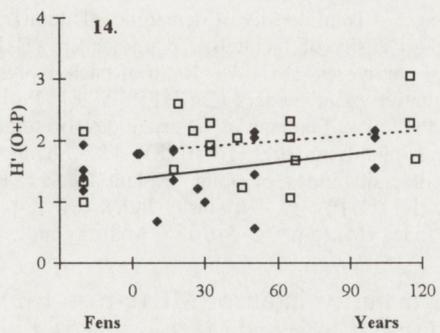
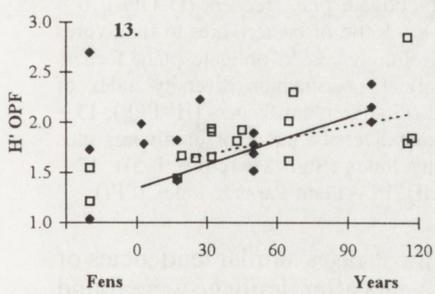
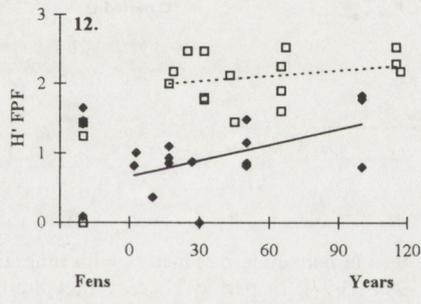
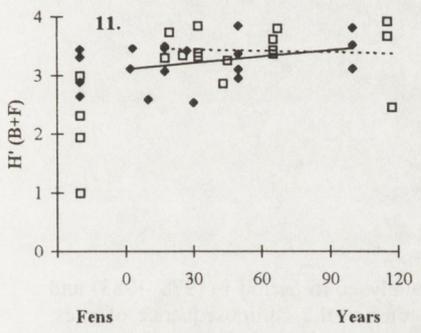
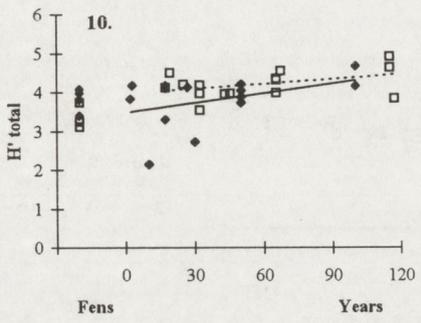
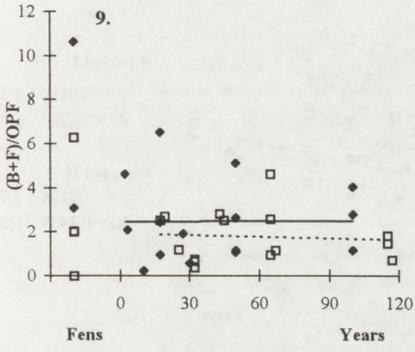
Diversity indices of the community and functional groups (H' total, H' (B+F), H' FPF, H' OPF and H' (O+P) (Fig. 3: 10, 11, 12, 13, and 14) tended to increase with time, but statistical significance was found only for H' FPF and H' OPF in period I. Diversity values found for natural fens were similar or lower to that for drained peat.

Table 7. Summary statistics (A – two-way ANOVA and B – Friedman test) for nematode community parameters of 19 sites in two periods (period I: 1978–1983 and period II: 1994–1997) and C – statistics (ANOVA) for relationships between nematode parameters and peat type (sedge-moss peat n = 4, sedge peat n = 7, alder peat n = 8); P I – mean value of a parameter in period I, P II – mean value of a parameter in period II

Parameter ¹⁾	A ANOVA				B Friedman test	C ANOVA		
	P I n = 19	P II n = 19	F-value	Period P	Period P	Period P	Peat P	Interactions P
Density (D) · 10 ³ m ⁻²								
Total	10950.2	3954.4	13.1	0.002 *	0.01 *	0.003 *	0.007 *	0.02 *
Bacterivores – B	3924.7	1653.2	23.1	0.000 *	0.000 *	0.002 *	0.02 *	NS
Fungivores – F	842.8	211.8	29.3	0.000 *	0.000 *	0.000 *	0.08 NS	NS
Facult. plant feed. – FPF	1734.7	602.2	10.4	0.004 *	0.002 *	0.01 *	NS	NS
Oblig. plant feed. – OPF	4078.2	1233.8	4.3	0.05 *	0.1 NS	0.09 NS	0.03 *	0.02 *
Omnivores – O	324.5	206.5	5.6	0.028 *	0.01 *	NS	NS	NS
Predators – P	45.2	46.8	0.0	NS	NS	NS	0.07 NS	NS
Ratio								
B/F	5.8	8.0	3.2	0.08 NS	NS	NS	NS	NS
B/(F+FPF)	1.7	2.6	5.3	0.03 *	NS	0.06 NS	NS	NS
(B+F)/OPF	5.4	2.0	2.9	0.1 NS	0.1 NS	NS	NS	NS
(B+F+FPF)/OPF	7.3	2.5	3.3	0.08 NS	0.1 NS	0.01 *	NS	0.07 NS
Number of taxa – S								
Total	38.2	35.5	0.6	NS	NS	NS	NS	0.03 *
(B+F)	21.1	17.5	3.5	0.07 NS	NS	0.02 *	NS	0.03 *
(FPF+OPF)	11.1	11.8	0.5	NS	NS	NS	NS	NS
(O+P)	5.9	6.2	0.1	NS	NS	NS	NS	NS
Diversity – H'								
Total	3.83	4.04	1.7	NS	NS	NS	NS	NS
(B+F)	3.20	3.10	0.1	NS	NS	NS	NS	NS
FPF	1.02	1.80	13.1	0.002 *	0.002 *	0.003 *	NS	NS
OPF	1.66	1.57	0.2	NS	NS	NS	NS	NS
(O+P)	1.55	1.95	8.2	0.01 *	0.03 *	0.02 *	NS	NS
Maturity Indices								
MI (c-p = 1–5)	2.10	2.38	5.0	0.03 *	0.03 *	0.08 NS	NS	NS
SUM MI (c-p = 1–5)	2.22	2.54	5.8	0.02 *	0.002 *	0.01 *	NS	NS
MI (c-p = 2–5)	2.51	2.71	3.4	0.08 NS	0.03 *	0.07 NS	NS	NS
SUM MI (c-p = 2–5)	2.43	2.71	6.7	0.01 *	0.002 *	0.006 *	NS	NS
Ba MI	1.80	1.96	4.8	0.04 *	0.03 *	NS	NS	NS
PPI	2.31	2.55	16.9	0.000 *	0.01 *	0.000 *	NS	NS
PPI/MI	1.13	1.11	0.6	NS	NS	NS	NS	NS

*P < 0.05, NS – not significant; ¹⁾ Explanation in Appendix.





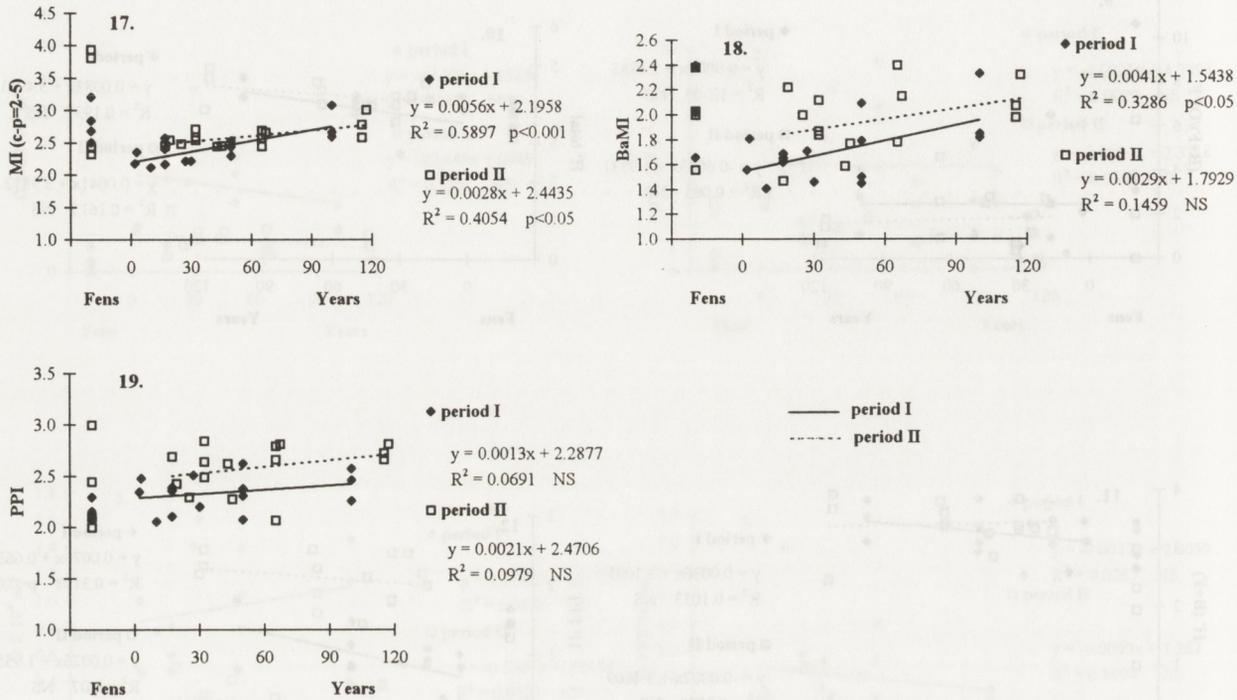


Fig. 3. Changes in nematode parameters with time after drainage on sites analysed in period I (1978–1983) and period II (1994–1997). In period I, years after drainage (from 2 to 100) refer to the chronosequence of sites, whereas in period II, they refer to the comparison of the same sites after 15–17 years. Regressions are calculated for meadows developed after drainage and management of fens ($n = 15$). The values of parameters for not drained natural fens ($n = 4$) denoted as “Fens”, (also analysed in periods I and II) are shown in the figure for comparison, but not included to the regression. Explanation of parameters in Appendix.

Parameters: 1 – Total density of nematodes (D total), 2 – Density of bacterivores (D B), 3 – Density of fungivores (D F), 4 – Density of facultative plant feeders (D FPF), 5 – Density of obligate plant feeders (D OPF), 6 – Density of omnivores (D O), 7 – Ratio of bacterivores to fungivores (B/F), 8 – Ratio of bacterivores to fungivores plus facultative plant feeders (B/(F+FPF)), 9 – Ratio of bacterivores plus fungivores to obligate plant feeders ((B+F)/OPF), 10 – Shannon diversity index of total community (H' total), 11 – Shannon diversity index of bacterivores plus fungivores (H' (B+F)), 12 – Shannon diversity index of facultative plant feeders (H' FPF), 13 – Shannon diversity index of obligate plant feeders (H' OPF), 14 – Shannon diversity index of omnivores plus predators (H' (O+P)), 15 – Maturity Index (MI (c-p = 1–5)), 16 – Maturity Index (Sum MI (c-p = 1–5)), 17 – Maturity Index (MI (c-p = 2–5)), 18 – Maturity index of bacterivores (Ba MI), 19 – Plant Parasite Index (PPI)

All maturity indices (MI (c-p = 1–5), Sum MI (c-p = 1–5) and MI (c-p = 2–5), Fig. 3: 15, 16, and 17) showed significant positive correlations with years after drainage in period I (higher significance level) and period II (lower significance level). The maturity indices of the same parameters for natural fens ranged more widely than for drained peat, and their upper values were beyond those for drained peat.

The maturity index of bacterivores (Ba MI, Fig. 3: 18) in both periods increased with time after drainage, but only in period I the increase was statistically significant.

Plant Parasite Index (PPI, Fig. 3: 19) did not show statistically significant changes with time after drainage in both periods.

Thus, in most cases similar tendencies of changes with years after drainage were found in period I and II. It was mainly decrease in density of nematodes, but increase in diversity and maturity. These changes, if described by linear regression, were statistically significant in both periods mainly for all maturity indices.

4.5. GENERAL TRENDS DURING SECONDARY SUCCESSION IN SOIL NEMATODE COMMUNITY AFTER DRAINAGE

The presented above site characteristics such as soil structure and processes (Tables 2

and 3 and Wasilewska 1991a) and the analysis of succession for periods ranging from 2 to 117 years after drainage and management of fens, makes possible the estimation of the range of variations of site conditions important for nematode succession. These were as follows: soil moisture (by weight) 80–52%, total soil porosity 90–77%, bulk density 0.16–0.44 g cm⁻³ (up to 0.92), total C content in soil 47–7%, total N content in soil 4.4–0.5%, ranges in a sequence from Mt I (poorly moorshified soils) to Mt III (strongly moorshified soils). In natural not

drained fens: soil moisture 80%, soil porosity 90%, bulk density 0.15–0.35 g cm⁻³, and peat-forming process (Pt) was continued.

Below are presented parameters describing nematode community (density, diversity and maturity) during the secondary succession from 2 to 117 years after drainage. Time related changes were described by linear regressions, calculated for all drained meadow sites, including values of both periods, arranged according to years after drainage (Table 8).

Table 8. Biocoenotic parameters illustrating secondary succession of soil nematodes during a period from 2 to 117 years after drainage of fens and their permanent use as meadows. Time related changes are presented as linear regressions, correlations and probability (n = 30)

Parameter ¹⁾		Slope	Intercept	Correlation coefficient – R ²	P
A Density					
1	D total	-0.0599	12.0830	0.0744	NS
2	D B	-0.0125	3.9849	0.0367	NS
3	D F	-0.0013	0.7095	0.0078	NS
4	D FPF	-0.0125	2.0240	0.0950	NS
5	D OPF	-0.0364	5.1278	0.0710	NS
6	D O	0.0030	0.1643	0.2257	<0.01
7	D P	-4E-05	0.0618	0.0007	NS
B Ratio					
8	B/F	0.0100	6.2121	0.0085	NS
9	B/(F+FPF)	0.0072	1.8604	0.0348	NS
10	(B+F)/OPF	-0.0033	2.3105	0.0056	NS
11	(B+F+FPF)/OPF	-0.0061	3.1331	0.0118	NS
C Number of taxa					
12	S total	0.0540	37.1760	0.0422	NS
13	S (B+F)	0.0002	20.8220	3E-06	NS
14	S (FPF+OPF)	0.0236	11.5710	0.0726	NS
15	S (OP)	0.0301	4.7832	0.1174	NS
D Diversity					
16	H' total	0.0071	3.6776	0.2039	<0.01
17	H'(B+F)	0.0019	3.2463	0.0293	NS
18	H' FPF	0.0085	1.1238	0.1800	<0.05
19	H' OPF	0.0065	1.4220	0.2094	<0.01
20	H' (O+P)	0.0049	1.5345	0.0987	NS
E Maturity					
21	MI (c-p = 1-5)	0.0063	1.8115	0.4328	<0.001
22	SUM MI (c-p = 1-5)	0.0047	2.0659	0.4251	<0.001
23	MI (c-p = 2-5)	0.0046	2.2915	0.5079	<0.001
24	SUM MI (c-p = 2-5)	0.0036	2.3244	0.3710	<0.001
25	Ba MI	0.0041	1.6339	0.2644	<0.01
26	PPI	0.0024	2.3467	0.1278	<0.05
27	PPI/MI	-0.0023	1.2924	0.2191	<0.01

¹⁾ See explanation in Appendix.

Table 9. Correlations and linear regressions of the maturity index – MI (c-p = 1–5)¹⁾ on years after drainage at sites that differed in peat type; SMP – sedge-moss peat, SP – sedge peat, AP – alder peat

	SMP	SP	AP
N	6	10	14
Slope	0.005776	0.008411	0.007139
Intercept	1.849	1.790	1.747
Correlation coefficient – r	0.88	0.75	0.61
P	0.05	0.05	0.05

¹⁾ Explanation in Appendix.

Table 10. Ranges of soil nematode parameters on not drained natural fens and on drained fens managed as meadows from 2 to 117 years

Parameter ¹⁾	Natural fens n = 8	Drained peat meadows n = 30
D total 10 ³ m ⁻²	34–3939	4067–34150
D B 10 ³ m ⁻²	3–2584	475–9377
D F 10 ³ m ⁻²	3–335	60–1600
D FPF 10 ³ m ⁻²	0–765	176–6825
D OPF 10 ³ m ⁻²	0–301	426–21775
D O 10 ³ m ⁻²	16–206	50–930
D P 10 ³ m ⁻²	0–17	0–225
B / F	1.0–14.07	1.27–16.93
B/(F+FPF)	1.0–3.80	0.48–6.91
(B+F)/OPF	2.0–52.0	0.24–6.53
(B+F+FPF)/OPF	2.0–53.0	0.56–8.06
S total	10–47	22–57
S (B+F)	2–26	12–28
S (FPF+OPF)	1–12	7–20
S (O+P)	2–9	2–17
H' total	3.13–4.08	2.15–4.92
H' (B+F)	1.00–3.44	2.46–3.92
H' FPF	0–1.65	0–2.53
H' OPF	0–2.70	0.50–2.86
H' (O+P)	1.00–2.72	0.57–3.05
MI (c-p = 1–5)	1.75–3.82	1.54–2.75
Sum MI (c-p = 1–5)	1.83–3.85	1.97–2.89
MI (c-p = 2–5)	2.33–3.94	2.12–3.08
Sum MI (c-p = 2–5)	2.31–3.85	2.07–2.90
Ba MI	1.56–2.40	1.41–2.40
PPI	2.00–3.00	2.06–2.84
PPI/MI	0.52–1.20	0.93–1.53

¹⁾ Explanation in Appendix.

Drainage and management of fens were followed by an increase in the density of total nematodes, that is, bacterivores, fungivores, facultative plant feeders, obligate plant feeders, omnivores and predators. In the course of succession their densities decreased, with the exception of omnivores. That decrease described by linear regression was statistically insignificant (Table 8 – A: 1, 2, 3, 4, 5, and 7). Only omnivores showed a statistically significant increase of density throughout succession (Table 8 – A: 6).

Positive correlation with years after drainage of two ratios, B/F and B/(F+FPF) were not significant (Table 8 – B: 8 and 9). Similarly, negative correlation with years of the ratios (B+F)/OPF and (B+F+FPF)/OPF were not significant (Table 8 – B: 10 and 11).

No statistically significant changes during succession were found in all the parameters describing the number of taxa in the community and functional groups (Table 8 – C: 12, 13, 14, and 15).

The Shannon diversity index for total community and functional groups increased with succession, but statistically significant only for H' total, H' FPF, and H' OPF (Table 8 – D).

All maturity indices measured succession in a similar way. They increased significantly with years after drainage (Table 8 – E: 21, 22, 23, and 24). Both MI and Sum MI similarly evaluated the course of changes with time. Regressions of the communities without taxon c-p = 1 (Table 8 – E: 23 and 24) were calculated with higher MI values (the intercept of MI c-p (1–5) = 1.81 and of MI c-p. (2–5) = 2.29, the intercept of Sum MI (c-p 1–5) = 2.07 and Sum MI (c-p 2–5) = 2.32).

Maturity index for bacterivores (Ba MI) also statistically increased during succession (Table 8 – E: 25).

Plant Parasite Index (PPI) showed a positive and statistically significant correlation with time (Table 8 – E: 26), and the ratio PPI/MI a negative significant correlation (Table 8 – E: 27).

The maturity index MI calculated for each peat type separately showed very similar trends in succession from 2 to 117 years. And although the intercept of the linear correlation followed the pattern $SMP > SP > AP$, the rate of increase (slope) in the for-

mula followed the other pattern i.e. $SP > AP > SMP$ (Table 9).

On natural fens, the ranges of the lowest and highest densities of all the trophic groups and the number of taxa were lower, and the maturity indices were higher than on drained peat meadows. The maximum ranges of diversity indices were higher on drained fens (Table 10).

5. DISCUSSION¹

The problem of peat drainage and the management drained peatlands as hay meadows and pastures has broadly been analysed in the literature. The contribution of soil biota to transformations after drainage was also extensively covered and some of the present study sites were previously described (Andrzejewska *et al.* 1985, Kajak *et al.* 1985, Wasilewska *et al.* 1985, Kaczmarek 1991, 1993, 1998, Makulec 1991, 1993, Burakowski and Nowakowski 1993, Pętal 1994, Nowak and Pilipiuk 1997, Olejniczak 1998), including nematodes (Wasilewska 1991a, b, 1994a, Dmowska 1993, Ilieva-Makulec 2000). A general conclusion from these papers is that soil biological activity increases after drainage.

The method of nematofauna analysis during the post-drainage succession, based on both the chronosequence of sites and the secondary succession on the same sites, seems to be one of the first with reference to meadows on drained peat soils. The method of the chronosequence of sites was also used to study the succession of soil mesofauna in forests that developed on drained peat soils in Finland (Laiho *et al.* 2001).

The effects of peat type on many nematode community parameters such as abundance, individual body size, production and root consumption by phytophagous nematodes were examined elsewhere (Wasilewska 1991a, b, c, d, 1999). Presented in this paper mean densities of nematodes in periods I (i.e. from 2 to 100) and period II (i.e. from 17 to 117 years after drainage) revealed the following sequence arising from peat type: $SMP < SP < AP$. Although the scatter of values of the parameters around linear regression regressed on time was large, also due to the influence of peat type, it was possible to

¹ For symbols see also Appendix.

reveal and statistically document succession in terms of the MI index.

5.1. TAXA

The species richness has never been studied in natural fens of the Biebrza Wetlands. Most probably it includes some species new to science.

The estimates of the number of described nematode species largely differ: 15000 according to Bongers and Bongers (1998), 20000 according to Bongers and Ferris (1999), 5600 in terrestrial habitats (Andrássy 1991), 5000 of soil species (Wall and Moore 1999), and in Poland 1000 soil and aquatic species described, the estimated number of present species being 5000 (Brzeski cited in Andrzejewski and Weigle (1991)). Biebrza fens could increase these numbers, but several representatives of so called aquatic taxa were absent after 15–17 years. It is difficult, however, to classify typically aquatic species, as those cited by Prejs (1986), Gerber and Smart (1987), Cox and Smart (1994), and Bongers (1999) occur not only in freshwater ecosystems but also in terrestrial ecosystems. Some of them are predators of large body sizes (*Actinolaimus*, *Ironus*, *Tripyla*) that die first when stressed.

It is assumed that nematodes of class *Secernentea* are more resistant to habitat transformation than are nematodes of class *Adenophorea* (Bongers 1999). It has been found that the ratio of the former to the latter was lower in period II of the study (7.03 versus 3.89). This implies that in period II a more "natural state" of the habitat was restored, as the number of taxa with higher energy costs declined, and as a result the loss of energy from the system was reduced.

A more abundant occurrence of *Secernentea* in period I was due to the fact that this was the period of the first 10–30 years after drainage, when rapid changes occurred in alder peat. The persistence of this "natural" habitat condition was dependent on peat type as indicated by the values of the *Secernentea/Adenophorea* ratio following the sequence SMP < SP < AP. In contrast, the S/A ratio on maize fields varied from 40 to 90 (Wasilewska in press). According to Yeates and King (1997), a decrease in the proportions of adenophorean nematodes under improved compared to those under natural grasslands was related with slower carbon cycling.

The 122 nematode genera recorded from the grasslands of the river Biebrza Basin are comparable with their number in a more diversified area of Europe. Ekschmitt *et al.* (1999) noted 123 genera in six grassland types along transect from the northern Sweden to Greece (40–68°N and 0.5–23°E).

In later years after drainage (period II), the mean density of most taxa was lower than in earlier years (period I). The decline was most pronounced for bacterivorous so called by Bongers (1999) "enrichment opportunists" (living in enriched nutrient conditions i.e. in excess of nitrogen and by fast growing bacteria) like *Panagrolaimus* and *Rhabditis* and less pronounced for the other bacterivores such as *Acrobeloides*, *Plectus*, *Rhabdolaimus*, *Cephalobus*, *Prismatolaimus*, and *Acrobeles*. Some other bacterivores such as *Eucephalobus*, *Heterocephalobus*, *Cylindrolaimus*, *Teratocephalus*, *Euteratocephalus*, and *Anaplectus* increased or did not change their abundance between the two periods. This composition of bacterivorous taxa reflects the process of their replacement with changing soil trophic conditions. This process, as reflected in the proportions of taxa allocated on the colonizers-persisters (c-p) scale (i.e. r-strategists *s.l.* – K-strategists *s.l.* scale) during succession on alder peat in period I, indicated a decline in bacterivorous extreme colonizers in favour of nematodes with higher c-p value as was earlier stated by Wasilewska (1998). This process was continued in period II, as indicated by higher values of maturity index for bacterivores (BaMI) in this period compared with period I (1.96 vs. 1.80, $P < 0.03$).

Also the most abundant taxa from obligate plant feeder (OPF) group followed the same pattern. The mean density of *Paratylenchus* (c-p = 2), i.e. having rank 2 on colonizers-persisters scale, decreased in period II to about 6.5% of the density in period I, taxa of the group c-p = 3, such as *Helicotylenchus*, *Pratylenchus*, and *Tylenchorhynchus* were reduced to 50–83%, whereas *Rotylenchus* increased to 192%. Thus the group OPF was also maturing, as evidenced by the statistically significant PPI increase in period II ($P < 0.0007$). According to van Bruggen and Semenov (2000), a soil system in which densities of an abundant pathogen as *Paratylenchus* decline some time after peat drainage, is returning to the state

of stable and healthy soil. Increasing abundance of *Paratylenchus* in specified situations was reported in earlier papers of the author (Wasilewska 1991a, b) and also was announced by other authors. For example, after the burning of tussock-grasslands in New Zealand (Yeates and Lee 1997) and in improved pastures compared with native (Yeates and King 1997), densities of *Paratylenchus* increased 100 and 265 times, respectively. An adaptive ability of this taxon is connected with the presence of a highly resistant subadult stage. Density of *Paratylenchus* increases in strongly overdried habitats and in habitats with fluctuating soil moisture (drained alder peat, soil after grass burning), and also where the development of root system follows the lowering water level. It becomes the major dominant among phytophages.

The taxon *Filenchus* appeared in a later period of succession (period II). *Filenchus* can feed and reproduce on fungal cultures, including mycorrhizal species (after Hanel 2000, 2001). Abundance of this genus could indicate an increase in population of mycorrhizal fungi and establishment of ectomycorrhiza.

5.2. COMPARISON OF NATURAL FENS AND DRAINED PEAT MEADOWS

Conversion of fens into managed grasslands by drainage, that releases moorshing processes, is associated with manifold increases in the abundance of total nematodes and their trophic groups, along with changes in the community structure (Table 10 and Fig. 3). An increase in nematode abundance on improved grasslands compared with native grasslands was also presented by Yeates and King (1997).

The rule that the key feature of natural ecosystems is a soil community dominated by fungal pathway of decomposition (Bardgett and McAlister 1999) does not hold for natural fens if the structure of nematode communities is considered.

The prevalence of bacterivores over fungivores (ratio B/F) does not differentiate clearly natural and drained fens. In contrast, the group of obligate plant feeders, that was scarce or absent at the time of sampling on natural fens, accounted for large differences in the ratio (B+F)/OPF. This provides evidence that the contribution of nematodes to rapid nutrient cycling in natural fens was neg-

ligible. Drainage accounted for an increase in the number of taxa. Taxon diversity in the community, measured by the Shannon diversity index, did not differentiate natural and drained fens, although the ranges of H' were larger on drained fens. Significant differences were observed in all maturity indices, as reflected in the fact that the ranges were shifted towards lower values on drained fens managed as grasslands.

5.3. NEMATODE SUCCESSION IN POST-DRAINED FEN MEADOWS

As compared with natural ecosystems, cultivated ecosystems enriched with organic or mineral fertilizers shift to early successional stages, as stated with reference to nematodes, by Wasilewska (1994a) and Neher and Olson (1999). Ecosystems in early stages of secondary succession are characterized by the prevalence of energy dissipation over accumulation. Processes occurring in these early stages involve fast mineralization of matter, fast nutrient turnover (Yeates and King 1997), and a possible loss of released nutrients and compounds from the ecosystem (Kajak and Wasilewska 1996). The next stages of secondary succession, in the case of post-drained fen meadows with human interference (fertilizing, grazing), are characterized by slower processes. A specific feature of secondary succession on post-drained fen meadows is the presence of a continuous source of additional organic matter and released carbon and nitrogen, though at a diminishing rate. This makes difference between these meadows and meadows on mineral soils.

The rate of organic matter decomposition decreases with succession. According to Okruszko (1993), in the first stage, associated with the decomposition of weakly humified, overdried peat mass, the intensity of decomposition depends on the supply of mineral nitrogen to microorganisms. At a moderate level of soil matter humification, optimum conditions for mineralization occur when the contents of mineral nitrogen and carbon in the soil are sufficient for microorganisms. The third stage involves the mineralization of strongly humified organic matter with N and C fixed in cyclic humic compounds or in bitumen and lignin remainder, highly resistant to decay. Under such conditions N and C mineralization is slow, and only *Actinomyces* are capable of decom-

posing substances hard to breakdown (Okruszko 1993). The first several to ten or so years after drainage are a period of intensive microbial activity. Bacterial feeders increase in numbers as a result of increasing microbial activity (Yeates and King 1997, Bongers and Bongers 1998). Bacteria and fungi are the primary decomposers directly affecting nutrient cycling and nutrient supply to plants (Ingham *et al.* 1985, Liang *et al.* 1999). Bacterial-based food webs exhibit higher decomposition rates than fungal webs (Liang *et al.* 1999), though, for example, under organically managed grasslands there was a greater abundance of fungal feeding nematodes (Yeates and Bongers 1999). Bacteria and their consumers reproduce and turnover nutrients at faster rates than fungi and their consumers (after Wall and Moore 1999). In post-drained fens, the ratio of bacterivores to fungivores nematodes (B/F) was higher than one in all cases (and in most cases in the variant with potential fungivores i.e. B/F+FPF), and it showed no trends with succession. Thus, if mineralization rate was declining with succession on post-drained fen meadows, this occurred on both, bacterial and fungal pathways. This is implied by the significant decrease in density of two groups of the consumers of decomposers (bacterivorous and fungivorous nematodes) with advancing succession (by comparison of period I and II). The reduction of microbiological activity with succession can also be substantiated by a steady increase in the maturity index for bacterivores (Ba MI) ($P < 0.01$). In some situations, however, the B/F ratio increased with succession, as found by Hanel (2001) in pine forests on coal-mining sands. It was also much higher in soils under improved grassland than under native grassland (Yeates and King 1997), this being confirmed by a significantly higher fungal/bacterial biomass ratio in unfertilized compared with fertilized grasslands (Bardgett and McAlister 1999).

As exemplified by the three study sites, it has been found that the rate of nitrogen mineralization in soil was not reduced 30 years after drainage, and in sedge-moss peat it was even twice as high as 15 years after drainage (Table 2). This would explain a steady, though going slower with years of succession, reduction in the abundance of bacterivorous nematodes. Ettema *et al.* (1999) observed a significant increase in the abundance of bacterivorous but not fungivorous

nematodes after an experimental soil treatment with inorganic nitrogen.

Obligate plant feeders (OPF) together with facultative plant feeders (FPF) were the most abundant trophic groups that emerged after the drainage of fens. Their occurrence was more associated with the alder peat type than with the other two types (Table 7). This group was more abundant earlier after drainage ($P < 0.05$ for OPF and $P < 0.004$ for FPF) but the decrease of their density with advancing succession was not significant. The maturity index of this group (PPI) increased with succession. It has higher value in the period more distant from drainage ($P < 0.0007$) and was positively correlated with years after drainage ($P < 0.05$). It is difficult to find a confirmation of this situation in the literature. The Plant Parasite Index (PPI) was higher in fertilized than unfertilized grasslands (Bongers *et al.* 1997). It was positively correlated with soil moisture, soil organic matter, and soil nitrate (Liang *et al.* 1999), and it decreased with increased fallow lands combined with an increase in the abundance of herbivores (Pate *et al.* 2000). According to Bongers and Ferris (1999), enrichment increases the carrying capacity of plants for plant feeding nematodes, resulting in higher PPI values, and then probably a high turnover is continued due to surplus of nutrients in the food web (Bongers *et al.* 1997).

The ratio of Plant Parasite Index to Maturity Index (PPI/MI) is an indicator of the soil nutrient status (Bongers and Bongers 1998), thus its decline is indicative of lower soil fertility (Bongers *et al.* 1997). On the study sites, PPI/MI was negatively correlated with years after drainage ($r = -0.47$, $P < 0.01$). A negative correlation of this ratio with age of mineral meadows was found by Wasilewska (1994b), although PPI itself did not show trends with advancing succession. According to Dutch authors, the PPI/MI ratios not exceeding 0.9 indicate natural habitats, the values of about 1.2 show slight nutrient disturbances, and above 1.6 – high soil enrichment with nutrients (Bongers *et al.* 1997, Bongers 1999). The range of the PPI/MI ratio for the natural fens under study was 0.5–1.2, whereas for post-drained meadows it was 0.93–1.53. Thus, the negative correlation of this ratio with years after drainage, as found in the present study, provides evidence for habitat impoverishment.

Yeates and Bongers (1999) argue that the ratio of bacterivores + fungivores to obli-

gate plant feeders ((B+F)/OPF) may indicate changes in the pathways of organic matter decomposition (through microflora or through phytophages). Thus, in the natural fens under study, decomposition proceeded through the detritus food chain (ratio 2.0–52.0), whereas in the post-drained meadows, phytophages played an important part (ratio 0.2–6.5). Values of this ratio did not change significantly with years. There is known an example of an successional trend of this ratio with age of meadows on mineral soils ($r = -0.596$, $P = 0.04$) (Wasilewska 1994b). This ratio needs a deeper insight into the factors influencing its value, such as a feedback between root herbivory by nematodes and microbial activity (Bardgett *et al.* 1999).

The density of omnivorous nematodes increased with advancing secondary succession ($P < 0.01$). Positive correlations with years after drainage were obtained for period I ($P < 0.01$) and period II ($P < 0.05$), the density level being higher in period I ($P < 0.01$). The latter and also the fact that this group was more abundant in the soil of drained fens compared with natural fens are indicative of their dependence on the total abundance of nematodes. The omnivorous character of this group is due to their predation on nematodes, in some cases only in adult forms, and feeding on bacteria (sometimes only in juveniles). They “assist” carnivores, bacterial and fungal feeders, where necessary (Bongers and Bongers 1998).

Predators were very scarce, occasionally present, and they did not show successional trends.

In the new, so called “post-drained” situation there was an increase in the taxon richness and in the diversity index compared with natural fens. The only exception was the value of H' in separate meadows on alder peat in the period of 10–25 years after drainage, when it was lowest (Wasilewska 1991a). Almost all diversity parameters such as H' total ($P < 0.01$), H' FPF ($P < 0.05$), and H' OPF ($P < 0.01$) increased with years after drainage.

The increasing trend in the diversity of soil nematode communities with years after drainage corresponds to the trend in soil succession, which signifies approaching oligotrophic (van Bruggen and Semenov 2000) and relatively stable conditions (Bongers and Bongers 1998). This increasing trend in diversity seems to be especially important in the light of the hypothesis proposed

by Bongers and Bongers (1998) that in temperate zones nematode diversity decreases with the changing conditions such as fluctuating temperature, humidity, osmotic value of capillary water, CO_2 and O_2 contents in soil air, pH, seasonal inputs of organic material, and nutrient leaching. The increase of soil biota diversity could be a proof of diminishing the variation at the above conditions.

A high nematode diversity (H') was noted by Hanel (1997) on pristine peat meadows and drained meadows. Yeates and King (1997) observed a higher diversity on native than on improved (i.e. fertilized) grasslands. Diversity was shown to be independent of the age of mineral meadows while maturity index (MI) significantly increased with age (Wasilewska 1994b).

Bongers and Ferris (1999) have proposed a general rule that a value of maturity index (MI(c-p = 1–5)) less than 2.0 indicates to much nutrient-enriched (i.e. disturbed) systems, and a value of 4.0 indicates undisturbed, pristine environment. This cannot be exactly applied to the values of this parameter obtained in the present study (Table 10), but the general tendency is valid.

The maturity index (MI) decreases in enriched nutrient conditions as evidenced by many field studies (Bongers *et al.* 1977, Yeates and King 1997, Liang *et al.* 1999), whereas it increases with decreasing microbial activity, and soil fertility (Bongers and Ferris 1999). Thus, MI increases as a result of the loss of r-strategists – bacterial feeders and the increase in K-strategists – omnivores (Bongers 1990). Moreover, Bongers and Ferris (1999) argue that during late succession, opportunists are replenished – but not replaced – by persisters.

Reduction in the rate of mineralization of organic matter many years after drainage of moorshing soils is caused by accumulation of large amounts of humus and lignin, i.e. fractions resistant to decomposition by soil microorganisms. Mineralization of organic carbon compounds goes in parallel with mineralization of organic nitrogen compounds, including humus, this leading to a gradual decline in N-total in these soils and to their impoverishment (Walczyna 1973). Consequently, these processes should underlie trends in the maturity index.

Trends in the nematode communities analysed in the present paper are consistent with theories of recovery after stress (Odum 1985) and have much in common with the

theory of fallow succession analysed for nematode communities (Pate *et al.* 2000). Also, they show some similarity to the pattern of age-related succession on mineral meadows (Wasilewska 1994b) and in forests on coal-mining sands (Hánel 2001). Functional aspects of soil nematode diversity on peat meadows are also largely consistent with conclusions of Bardgett and Cook (1998) concerning the life strategy of organisms involved in "fast" and "slow" cycles of decomposition, but they need to be complemented. Although succession within a range from 2 to 117 years proceeded towards a low input system (lower percentage of carbon and nitrogen in soil and their lower mineralization) with more heterogeneous resources (a higher diversity of functional groups – lower niche width), and was characterized by more persistent taxa, no clear dominance of the fungal decomposition pathway was developed, as indicated by the relatively stable ratios of bacterivores to fungivores (B/F) and bacterivores to fungivores + facultative plant feeders (facultative fungivores) (B/(F+FPF)). Thus, within the study period, nematode parameters did not show a clear transition from eutrophy to oligotrophy. But with respect to the increase in soil acidity (as exemplified by three sites in Table 2), and a significant increase ($P < 0.05$) in the diversity of facultative plant feeders – partially mycophilous (H' FPF), along with the increase in the density of mycorrhizal taxa such as *Filenchus* (according to Hánel 2000), a specific approaching more oligotrophic conditions of late succession should be noted.

Some short-term fluctuations in soil moisture and the associated mineralization rate of peat and some anthropogenic factors such as fertilization and grazing, influence taxa $c-p = 1$ (i.e. r-strategists) quicker than other taxa. This can be inferred in part from correlation coefficients with years of succession, which were lower for MI ($c-p = 1-5$) ($r = 0.66$, $P < 0.001$) and higher for MI ($c-p = 2-5$) (excluded $c-p = 1$) ($r = 0.71$, $P < 0.001$), as well as from the intercept (1.81 and 2.29, respectively).

In the course of 117 years succession in nematode communities, near all parameters of density do not reveal significant trends with time, described by linear regression. Scattering values within sites is the reason for these. All parameters of community diversity and maturity did show statistically significant trends with time. Densities were more influ-

enced by short-lasting fluctuations. The long-lasting process of community maturity showed successional trend with time on the way of exchange of taxa of different life strategies.

Maturity is thus a quantitative and "directional" parameter during nematode succession in drained peat soils used as permanent meadows. It seems that the successional pattern of nematode dynamics mainly depends on food resources (in the detritus and grazing pathways) that are released or limited, depending on a physical factor such as water content of peat soils. A question arises whether it is possible to predict the direction of succession after drainage of peat soils from soil biota. According to Laiho *et al.* (2001), peatland forests developed after drainage evolve into upland forests, where decomposition in general is much faster than in pristine peatland. Hánel (1997) suggests that nematodes in drained peat meadows in southern Czech Republic evolve towards mesic meadow nematode communities.

It seems that the acceleration of successional processes is equivalent to saving peat resources. It may happen only by raising the water level of peat lands.

Some authors predict that predacious and omnivorous nematodes (that is, persistent taxa (K-strategist *s.l.*) influencing MI increase) would increase in response to increased fine root production under elevated atmospheric CO_2 in the high-N soil (Hoeksema *et al.* 2000).

No single model can explain successional changes (Walker and Chapin 1987, Morin 1999). In the river Biebrza and river Narew valleys, both life history traits and competitive displacement were observed to affect nematode succession. One of the possible mechanisms in the initial stages (until about 30 years after drainage of fens), biota are tolerant of periods of drought and nitrogen excess. During that period also a higher herbivory abundance is pronounced. This is a period of rapid peat transformation. In later stages, when nitrogen resources are being reduced and turfing processes are involved, presumably the role of interspecific competition is increasing (e.g., disappearance of *Paratylenchus* in favour of *Rotylenchus* and *Helicotylenchus*).

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6. SUMMARY

After the drainage of fens and their permanent use as meadows, peat-forming process is being replaced by moorsh (muck) -forming process, and then by turf-forming process. Properties of both the peat mass and the biota of such ecosystems undergo time-related changes.

The study sites were selected on fens located in the valleys of the Biebrza and Narew rivers (Fig. 1). They comprised natural and drained fens used as permanent meadows, which differed in terms of the number of years after drainage, peat origin, plant communities, mucking degree, and physico-chemical soil properties (Table 1).

Changes in soil nematode communities with years after drainage, analysed by the method of site chronosequence, and previously described (Wasilewska 1991a) for period I (1978–1983), were the basis for further analyses of the secondary succession. The same sites were sampled 15–17 years later, in so called period II (1994–1997), when the density of taxa (genera) of nematodes were evaluated (Table 4) and biocoenotic parameters (19–29) describing the community (density, diversity and maturity) were measured (Table 7). As period II was shifted by 15–17 years compared with period I, it did not include the most drastic changes in soil and in nematode fauna occurring after drainage. Hence, in period I the density of almost all nematode trophic groups and of the indicator taxon *Paratylenchus* was several times higher (ANOVA, $P < 0.000–0.02$) and the ratio of nematodes of the class *Secernentea* to nematodes of the class *Adenophorea* (index of undisturbed conditions) was also higher (Table 5). At the same time, i.e. in earlier period after drainage almost all maturity indices: MI (c-p = 1–5), SUM MI (c-p = 1–5), MI (c-p = 2–5), Ba MI, and PPI were lower (ANOVA, $P < 0.000–0.04$), as well as diversity indices of some trophic groups.

Also the pattern of successional changes was analysed in the period from 2 to 117 years after fen drainage and management as meadows. Not drained natural fens were used for comparison (Fig. 3 and Table 10). Site characteristics such as soil structure and processes were as follows: soil moisture (by weight) 80–52%, total soil porosity 90–77%, bulk density 0.16–0.44 (to 0.92) g cm⁻³, total C content in soil 47–7%, total N content in soil 4.4–0.5%, ranges in the sequence from Mt I (poorly moorshified soils) to Mt III (strongly moorshified soils). On natural fens, soil moisture was 80%, soil porosity 90%, bulk density

0.15–0.35 g cm⁻³, and peat-forming process (Pt) was continued (Tables 2 and 3).

Drainage and management of fens was always followed by an increase in density of total nematodes and in component trophic groups such as bacterivores – B, fungivores – F, facultative plant feeders – FPF, obligate plant feeders – OPF, omnivores, and predators, as compared with their abundance in natural fens. Later in succession, their densities declined, but the negative correlation with time was not significant. The only exception was the group of omnivores that showed an increasing trend in density (ANOVA for correlation, $P < 0.01$). No significant successional trends were observed in ratios B/F and (B+F)/OPF, and in the number of taxa. Indices of taxa diversity and maturity were positively correlated with years after drainage (ANOVA for correlation, $P < 0.001–0.05$) (Table 8).

On natural fens, the ranges of the densities of all trophic groups were lower, and of maturity indices were higher than on drained peat meadows. The maximum ranges of diversity indices were higher on drained peat meadows compared with natural fens (Table 10).

One of the possible mechanisms driving the first stages of nematode succession in the Biebrza and Narew river valleys seems to be periods of drought and the excess of nitrogen. In later stages, probably interspecific competition becomes more important, as implied, for example, by the disappearance of *Paratylenchus* in favour of *Rotylenchus* and *Helicotylenchus* (Fig. 2, Table 4).

Also the effect of peat type on the density of taxa and the values of community parameters was evaluated (Tables 6 and 7). The taxa significantly influenced by peat type comprised *Aphelenchoides*, *Hirschmaniella*, *Wilsonema*, *Panagrolaimus*, and *Paratylenchus* (ANOVA, $P < 0.02–0.06$). The dependence on peat type was found for only three parameters: density of total nematodes, bacterivores, and obligate plant feeders, according to the pattern: sedge-moss peat < sedge peat < alder peat during period I and period II (ANOVA, $P < 0.007–0.02$). The growth rate of the maturity index MI (c-p = 1–5) during succession from 2 to 117 years followed the pattern: sedge peat > alder peat > sedge-moss peat (Table 9).

7. REFERENCES

- Andrássy I. 1884 – Klasse Nematoda – Akademie-Verlag, Berlin, 509 pp.
 Andrássy I. 1991 – A short census of free-living nematodes – *Fundam. appl. Nematol.* 15: 187–188.
 Andrzejewska L., Chmielewski K., Kaczmarek M., Kajak A., Wasilewska L. 1985 – The effect of peat meadow management on biocoenosis – *Pol. ecol. Stud.* 11: 53–78.

- Andrzejewski R., Weigle A. 1991 – Polskie studium różnorodności biologicznej [Polish Studium of Biodiversity] – Narodowa Fundacja Ochrony Środowiska, Warszawa, 186 pp.
- Armendáriz I., Arpin P. 1996 – Nematodes and their relationship to forest dynamics: 1. Species and trophic groups – *Biol. Fertil. Soils*, 23: 405–413.
- Armendáriz I., Hernández M. A., Jordana R. 1996 – Temporal evolution of soil nematode communities in *Pinus nigra* forest of Navarra, Spain – *Fundam. Appl. Nematol.* 19: 561–577.
- Bardgett R. D., Cook R. 1998 – Functional aspects of soil animal diversity in agricultural grasslands – *Appl. Soil Ecol.* 10: 263–276.
- Bardgett R. D., Cook R., Yeates G. W., Denton C. S. 1999 – The influence of nematodes on below-ground processes in grassland ecosystems – *Plant and Soil*, 212: 23–33.
- Bardgett R. D., McAlister E. 1999 – The measurement of soil fungal: bacterial biomass ratios as an indicator of ecosystem self-regulation in temperate meadow grasslands – *Biol. Fertil. Soils*, 29: 282–290.
- Bongers T. 1988 – De Nematoden van Nederland – *Natuurhistorische Bibliotheek van de KNNV* 46, Pirola, Schoorl, 408 pp.
- Bongers T. 1990 – The maturity index: an ecological measure of environmental disturbance based on nematode species composition – *Oecologia*, 83: 14–19.
- Bongers T. 1999 – The maturity index, the evolution of nematode life history traits, adaptive radiation and c-p scaling – *Plant and Soil*, 212: 13–22.
- Bongers T., Bongers M. 1998 – Functional diversity of nematodes – *Appl. Soil Ecol.* 10: 239–251.
- Bongers T., Ferris H. 1999 – Nematode community structure as a bioindicator in environmental monitoring – *TREE*, 14: 224–228.
- Bongers T., de Goede R. G. M., Korthals G. W., Yeates G. W. 1995 – Proposed changes of c-p classification for nematodes – *Russian J. Nematol.* 3: 61–62.
- Bongers T., Van der Meulen H., Korthals G. W. 1997 – Inverse relationship between nematode maturity index and plant parasite index under enriched nutrient conditions – *Appl. Soil Ecol.* 6: 195–199.
- Brussaard L., Behan-Pelletier V. M., Bignell D. E., Brown V. K., Didden W. A., Folgarait P. J., Fragoso C., Wall-Freckman D., Gupta V. V. S. R., Hattori T., Hawksworth D., Klopatek C., Lavelle P., Malloch D., Rudek J., Söderström B., Tiedje J. M., Virginia R. A. 1997 – Biodiversity and ecosystem functioning in soil – *Ambio*, 26: 563–570.
- Brzeski M. W. 1995 – Changes of the nematode fauna in the successive age classes of a Scots pine forest – *Fragm. faun.* 38: 339–345.
- Burakowski B., Nowakowski E. 1993 – Beetles (Coleoptera) of meadows on peat soils in Biebrza Valley – *Zesz. probl. Post. Nauk roln.* 406: 153–159.
- Cox R. J., Smart G. C. 1994 – Nematodes associated with plants from naturally acidic wetland soils – *J. Nematol.* 26: 535–537.
- de Goede R. G. M., Georgieva S. S., Verschoor B. C., Kameron J.-W. 1993a – Changes in nematode community structure in a primary succession of blown-out areas in a drift sand landscape – *Fundam. appl. Nematol.* 16: 501–513.
- de Goede R. G. M., Verschoor B. C., Georgieva S. S. 1993b – Nematode distribution, trophic structure and biomass in a primary succession of blown-out areas in a drift sand landscape – *Fundam. Appl. Nematol.* 16: 525–538.
- Dmowska E. 1993 – Nematode communities of hydrogenic soils – *Zesz. probl. Post. Nauk roln.* 406: 139–152.
- Ekschmitt K., Bakonyi G., Bongers M., Bongers T., Boström S., Dogan H., Harrison A., Kallimanis A., Nagy P., O'Donnel A. G., Sohlenius B., Stamou G., Wolters V. 1999 – Effects of the nematofauna on microbial energy and matter transformation rates in European grassland soils – *Plant and Soil*, 212: 45–61.
- Ettema C. H., Lowrance R., Coleman D. C. 1999 – Riparian soil response to surface nitrogen input: the indicator potential of free-living soil nematode populations – *Soil Biol. Biochem.* 31: 1625–1638.
- Freckman D. W., Blackburn T. H., Brussaard L., Hutchings P., Palmer M. A., Snelgrove P. V. R. 1997 – Linking biodiversity and ecosystem functioning of soils and sediments – *Ambio*, 26: 556–562.
- Gerber K., Smart G. C. Jr. 1987 – Plant-parasitic nematodes associated with aquatic vascular plants – *Vistas on Nematol.*: 488–501.
- Gotkiewicz J., 1977 – Mineralization course of nitrogen compounds in distinguished sites of the Wiza fen – *Pol. ecol. Stud.* 3: 33–43.
- Góralczyk K. 1998 – Nematodes in a coastal dune succession: Indicators of soil properties? – *Appl. Soil Ecol.* 9: 465–496.
- Hánel L. 1995 – Secondary successional stages of soil nematodes in cambisols of South Bohemia – *Nematologica*, 41: 197–218.
- Hánel L. 1997 – Soil nematodes (Nematoda) of peaty and drained meadows at Senotin in South Bohemia, Czech Republic – *Časopis Národního muzea, Řada přírodovědná*, 166: 15–25.
- Hánel L. 2000 – Seasonal changes of soil nematodes, other soil microfauna and fungus fruiting bodies in a spruce forest near České Budejovice, Czech Republic – *Biologia (Bratislava)*, 55: 435–443.
- Hánel L. 2001 – Succession of soil nematodes in pine forests on coal-mining sands near Cottbus, Germany – *Appl. Soil Ecol.* 16: 23–34.

- Hoeksema J. D., Lussenhop J., Teeri J. A. 2000 – Soil nematodes indicate food web responses to elevated atmospheric CO₂ – *Pedobiologia*, 44: 725–735.
- Ilieva-Makulec K. 2000 – Nematode fauna of a cultivated peat meadow in relation to soil depth – *Ann. Zool. (Warszawa)* 50: 247–254.
- Ingham R. E., Trofymov J. A., Ingham E. R., Coleman D. C. 1985 – Interactions of bacteria, fungi and their nematode grazers: Effects on nutrient cycling and plant growth – *Ecol. Monogr.* 55: 119–140.
- Kaczmarek M. 1991 – Characteristics of the studied habitats in the Biebrza and Narew old river valleys – *Pol. ecol. Stud.* 17: 7–18.
- Kaczmarek M. 1993 – Characteristic of Collembola communities occurring on meadows on variously degraded hydrogenous soil – *Zesz. probl. Post. Nauk roln.* 406: 129–133.
- Kaczmarek M. 1998 – Long term changes (15 years) of Collembola communities on drained fens – *Pol. J. Ecol.* 46: 237–242.
- Kajak A., Okruszko H. 1990 – Grasslands on drained peats in Poland (In: *Managed Grasslands*, Ed. A. Breymeyer) – Elsevier Science Publishers, B. V., Amsterdam, pp. 213–253.
- Kajak A., Pętał J. 2001 – Drained fens: comparison of N mineralization rate and biotic structures in the periods of secondary succession – *Pol. J. Ecol.* 49: 261–270.
- Kajak A., Wasilewska L. 1996 – Różnorodność gatunkowa organizmów a przebieg rozkładu materii w glebach uprawnych [The species diversity of organisms and the course of the decomposition of matter in cultivated soils] – *Zesz. nauk. Komit. Człow. Środ.* 15: 129–144.
- Kajak A., Andrzejewska L., Chmielewski K., Ciesielska Z., Kaczmarek M., Makulec G., Pętał J., Wasilewska L. 1985 – Long-term changes in grassland communities of heterotrophic organisms on drained fens – *Pol. ecol. Stud.* 11: 21–52.
- Kotowska J., Pasternak-Kuśmierska D., Wilpiszewska I. 1996 (1998) – Comparative analysis of the sward of hay-growing meadows on peat-muck soils – *Pol. ecol. Stud.* 22: 141–157.
- Laiho R., Silvan N., Carcamo H., Vasander H. 2001 – Effects of water level and nutrients on spatial distribution of soil mesofauna in peatlands drained for forestry in Finland – *Appl. Soil Ecol.* 16: 1–9.
- Liang W., Lavian I., Steinberger Y. 1999 – Dynamics of nematode community composition in a potato field – *Pedobiologia*, 43: 459–469.
- Maciak F. 1995 – Ocena aktywności biologicznej murszów i torfów na podstawie mineralizacji związków węgla i azotu [Estimation of the biological activity in moorshs and peats on the basis of carbon and organic nitrogen mineralization] – *Roczn. Glebozn.* 46: 19–26.
- Makulec G. 1991 – The effect of long term drainage of peat soil on earthworm communities (Oligochaeta: Lumbricidae) – *Pol. ecol. Stud.* 17: 203–219.
- Makulec G. 1993 – Abundance and biomass of earthworms (Lumbricidae) in hydrogenous soils under various degree of mucking – *Zesz. probl. Post. Nauk roln.* 406: 119–127.
- Morin P. J. 1999 – *Community ecology* – Blackwell Science Inc. Abingdon, 424 pp.
- Nazaruk M. 1996 – Zatrzymać degradację łąk położonych na glebach torfowo-murszowych [Reserve the degradation of meadows located on peat-moorsh soils] – *Wiad. mel. łąk.* 39: 153–157.
- Nazaruk G., Kaca E. 1999 – Peatland subsidence on the Wizna study area with a functioning irrigation-drainage system made of ceramic drains – *J. Water Land Develop.* 3: 77–89.
- Neher D. A., Olson R. K. 1999 – Nematode communities in soils of four farm cropping management systems – *Pedobiologia*, 43: 430–438.
- Nowak E., Pilipiuk I. 1997 – The influence of drainage on enchytreids (Enchytraeidae, Oligochaeta) of fens in the Biebrza ice-marginal valley – *Ekol. pol.* 45: 423–440.
- Odum E. P. 1985 – Trends expected in stressed ecosystems – *BioScience*, 35: 419–422.
- Okruszko H. 1990 – Wetlands of the Biebrza Valley. Their value and future management – *Pol. Acad. Sci., Warszawa*, 107 pp.
- Okruszko H. 1993 – Transformation of fen-peat soils under the impact of draining – *Zesz. probl. Post. Nauk roln.* 406: 3–75.
- Okruszko H. 1995 – Influence of hydrological differentiation of fens on their transformation after dehydration and on possibilities for restoration (In: *Restoration of temperate wetlands*, Eds. B. D. Wheeler, S. C. Shaw, W. J. Fojt, R. A. Robertson) – John Wiley and Sons Ltd. pp. 113–119.
- Olejniczak I. 1998 – The carabid communities of natural and drained peatlands in the Biebrza Valley, NE Poland – *Pol. J. Ecol.* 46: 243–260.
- Ohtonen R., Aikio S., Väre H. 1997 – Ecological theories in soil biology – *Soil Biol. Biochem.* 29: 1613–1619.
- Pałczyński A. 1972 – Bagna Jaćwieskie. Pradolina Biebrzy – *Roczn. Nauk roln.* D. 145: 1–232. (in Polish with German summary)
- Pałczyński A. 1984 – Natural differentiation of plant communities in relation to hydrological conditions of the Biebrza Valley – *Pol. ecol. Stud.* 10: 347–385.
- Parmelee R. W. 1995 – Soil fauna: linking different levels of the ecological hierarchy (In: *Linking species and ecosystems*, Eds. C. G. Jones, J. H. Lawton) – Chapman and Hall, Inc., New York, London, 107–115.

- Pate E., Ndiaye-Faye N., Thioulouse J., Villenave C., Bongers T., Cadet P., Debouzie D. 2000 – Successional trends in the characteristics of soil nematode communities in cropped and fallow lands in Senegal (Sonkorong) – *Appl. Soil Ecol.* 14: 5–15.
- Petal J. 1993 – Communities of soil invertebrates in meadows on transformed hydrogenous soil – *Zesz. probl. Post. Nauk roln.* 406: 111–117.
- Petal J. 1994 – Ant communities in Biebrza marschland (In: Proc. Intern. Symp. "Conservation and management of fens", June 6–10, 1994, Warsaw–Biebrza, Poland) – Institute of Land Reclamation and Grassland Farming in Falenty, pp. 399–406.
- Petal J., Churski T. 1991 – Basic physical, chemical and biotic processes in meadow ecosystems on hydrogenous soils – *Pol. ecol. Stud.* 17: 347–358.
- Prejs K. 1986 – Nematodes as a possible cause of rhizome damage in three species of *Potamogeton* – *Hydrobiologia*, 131: 281–286.
- Shannon C. E., Weaver W. 1949 – The mathematical theory of communication – Urbana, University of Illinois Press, 117 pp.
- Sohlenius B. 1997 – Fluctuations of nematode populations in pine-forest soils. Influence by clear-cutting – *Fundam. appl. Nematol.* 20: 103–114.
- Stachurski A., Zimka J. R. 1998 – The influence of nitrogen and sulphur mineralization in peat soils on nutritional status of plants – *Pol. J. Ecol.* 46: 101–116.
- Szuniewicz J., Chrzanowski S. 1995 – Przeobrażanie się i spływanie odwodnionych gleb torfowych na przykładzie torfowiska Kuwasy [Transformation and shallowing of dehydrated peat soils on example of Kuwasy fen] (In: Torfoznawstwo w badaniach naukowych i praktyce. Sesja naukowa z okazji jubileuszu 45-lecia działalności naukowej oraz 70 rocznicy urodzin prof. dr hab. Henryka Okruszko, Falenty 6–7.11.1995) [In: Peat science in researches and practice. Scientific session on 45 jubilee of scientific activity and 70 anniversary of birthday of prof. dr Henryk Okruszko, Falenty 6–7.11.1995] – Wyd. IMUZ, Materiały seminaryjne IMUZ, 34, pp. 241–246.
- van Bruggen A. H. C., Semenov A. M. 2000 – In search of biological indicators for soil health and disease suppression – *Appl. Soil Ecol.* 15: 13–24.
- Walczyzna J. 1973 – Przeobrażenia substancji organicznej w dawno odwodnionych murszach i czarnych ziemiach użytkowanych jako pola orne i łąki [Transformation of organic matter in mucks and black earths drained long ago and utilized as arable land and meadow] – *Zesz. probl. Post. Nauk roln.* 146: 163–188 (in Polish with English summary).
- Walker L. R., Chapin F. S. III. 1987 – Interactions among processes controlling successional change – *Oikos*, 50: 131–135.
- Wall D. M., Moore J. C. 1999 – Interactions underground: soil biodiversity, mutualism and ecosystem processes – *BioScience*, 49: 109–119.
- Wardle D., Giller K. E. 1996 – The quest for a contemporary ecological dimension to soil biology – *Soil Biol. Biochem.* 28: 1549–1554.
- Wasilewska L. 1970 – Nematodes of the sand dunes in the Kampinos Forest . I. Species structure – *Ekol. pol.* 18: 429–443.
- Wasilewska L. 1971a – Nematodes of the dunes in the Kampinos Forest . II. Community structure based on numbers of individuals, state of biomass and respiratory metabolism – *Ekol. pol.* 19: 651–688.
- Wasilewska L. 1971b – Klasyfikacja troficzna nicieni glebowych i roślinnych [Trophic classification of soil and plant nematodes] – *Wiad. ecol.* 17: 379–388 (in Polish).
- Wasilewska L. 1974 – Rola wskaźnikowa wszytkożernej grupy nicieni glebowych [The role of the omnivores group of soil nematodes as ecological indicator] – *Wiad. ecol.* 20: 385–390 (In Polish with English summary).
- Wasilewska L. 1991a – Long-term changes in communities of soil nematodes on fen peat meadows due to the time since their drainage – *Ekol. pol.* 39: 59–104.
- Wasilewska L. 1991b – Communities of soil nematodes of drained fen differentiated by peat origin – *Pol. ecol. Stud.* 17: 155–178.
- Wasilewska L. 1991c – The role of nematodes in the process of element cycling on drained fen differentiated by peat origin – *Pol. ecol. Stud.* 17: 179–190.
- Wasilewska L. 1991d – The effect of moisture content of drained peat soils on nematode communities – *Pol. ecol. Stud.* 17: 191–201.
- Wasilewska L. 1994a – Changes in biotic indices in meadow ecosystems after drainage of fens (In: Proc. Intern. Symp. "Conservation and management of fens", June 6–10, 1994, Warsaw–Biebrza, Poland) – Institute for Land Reclamation and Grassland Farming in Falenty, pp. 407–416.
- Wasilewska L. 1994b – The effect of age of meadows on succession and diversity in soil nematode communities – *Pedobiologia*, 38: 1–11.
- Wasilewska L. 1997 – Soil invertebrates as bioindicators, with special reference to soil-inhabiting nematodes – *Russ. J. Nematol.* 5: 113–126.
- Wasilewska L. 1998 – Changes in the proportions of groups of bacterivorous soil nematodes with different life strategies in relation to environmental conditions – *Appl. Soil Ecol.* 9: 215–220.
- Wasilewska L. 1999 – Soil nematode response to root production in grasslands on fen peat soils – *Pol. J. Ecol.* 47: 231–246.

- Wasilewska L., Andrzejewska L., Chmielewski K., Kaczmarek M., Kajak A., Makulec G., Pełal J. 1985 – Biocenoses of drained peat meadows in the Biebrza ice-marginal valley as compared to other types of meadows and crop fields – *Pol. ecol. Stud.* 11: 87–105.
- Wasilewska L. (in press) – Nematofauna and tree-belts in agricultural landscape of Turew region, Poland.
- Wösten J. H. M., Ismail A. B., Van Wijk A. L. M. 1997 – Peat subsidence and its practical implications: a case study in Malaysia – *Geoderma*, 78: 25–36.
- Yeates G. W. 1994 – Modification and qualification of the nematode maturity index – *Pedobiologia*, 38: 97–101.
- Yeates G. W., Bongers T. 1999 – Nematode diversity in agroecosystems – *Agric. Ecosyst. Environ.* 74: 113–135.
- Yeates G. W., Bongers T., de Goede R. G. M., Freckman D. W., Georgieva S. S. 1993 – Feeding habits in soil nematode families and genera – an outline for soil ecologists – *J. Nematol.* 25: 315–331.
- Yeates G. W., King K. L. 1997 – Soil nematodes as indicators of the effect of management on grasslands in the New England Tablelands (NSW): Comparison of native and improved grasslands – *Pedobiologia*, 41: 526–536.
- Yeates G. W., Lee W. G. 1997 – Burning in New Zealand snow-tussock grassland: effects on vegetation and soil fauna – *New Zealand J. Ecol.* 21: 73–79.
- Zimka J. R., Stachurski A. 1996 – Intensity of nitrification and sulphur oxidation in peat soils of meadows of Biebrza river valley (Poland): An effect of cation release and eutrophication of groundwater – *Ekol. pol.* 44: 311–332.

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APPENDIX

Brief form of used nematode community parameters:

D total	Total density of nematodes
D B	Density of bacterivores
D F	Density of fungivores
D FPF	Density of facultative plant feeders
D OPF	Density of obligate plant feeders
D O	Density of omnivores
D P	Density of predators
B/F	Ratio of density of bacterivores to density of fungivores
B/(F+FPF)	Ratio of density of bacterivores to density of fungivores + facultative plant feeders
(B+F)/OPF	Ratio of density of bacterivores + fungivores to density of obligate plant feeders
(B+F+FPF)/OPF	Ratio of density of bacterivores + fungivores + facultative plant feeders to density of obligate plant feeders
S total	Total number of taxa
S (B+F)	Number of taxa of bacterivores + fungivores
S (FPF+OPF)	Number of taxa of facultative plant feeders + obligate plant feeders
S (O+P)	Number of taxa of omnivores + predators
H' total	Shannon diversity index of total community
H' (B+F)	Shannon diversity index of bacterivores + fungivores
H' FPF	Shannon diversity index of facultative plant feeders
H' OPF	Shannon diversity index of obligate plant feeders
H' (O+P)	Shannon diversity index of omnivores + predators
c-p scale	Colonizers-persisters scale (r-strategists sl – K strategists sl scale)
c-p = 1	Taxa with rank 1
c-p = 1–5	Taxa with ranks from 1 to 5
MI (c-p = 1–5)	Maturity Index based on all taxa with exclusion of plant feeders
SUM MI (c-p=1–5)	Maturity Index based on all taxa
MI (c-p = 2–5)	Maturity Index based on taxa with exclusion of plant feeders and of taxa c-p=1
SUM MI (c-p=2–5)	Maturity Index based on all taxa with exclusion of taxa c-p=1
Ba MI	Maturity Index of bacterivores
PPI	Plant Parasite Index
PPI/MI	Ratio of PPI to MI
N S/A	Ratio of numbers of nematodes from the class <i>Secernentea</i> to numbers of nematodes from the class <i>Adenophorea</i>
S S/A	Ratio of number of taxa from the class <i>Secernentea</i> to number of taxa from the class <i>Adenophorea</i>