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Soil nematodes in five spruce forests of the Beskydy mountains, Czech Republic

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Summary – Soil nematode communities were studied in five 5 to 138 year-old spruce forests in the Beskydy Mountains, Northern Moravia, Czech Republic. A total of 92 species was found in all stands studied. Nematode abundance ranged from 272.9 to 6238.9×10^3 ind·m^{-2} (mean value 1409.6×10^3 ind·m^{-2}), biomass varied from 33.6 mg·m^{-2} to 1.197 mg·m^{-2} (mean value 337.2 mg·m^{-2}). Myco-phytophagous nematodes of the order Tylenchida had the greatest abundance but individual genera differed in their preference for the spruce forests studied. The abundance of bacteriophagous nematodes was similar in all localities. The composition of nematode communities was influenced by the age of spruce trees, herbaceous undergrowth and altitude.

Résumé – ***Nématodes du sol de cinq forêts d'épicéas des Monts Beskydy, République Tchèque*** – Cette étude concerne les peuplements de nématodes du sol de cinq forêts d'épicéas âgées de 5 à 138 ans, situées dans les Monts Beskydy, Moravie du Nord, République Tchèque. Au total, 92 espèces ont été répertoriées dans les sites étudiés. L'abondance des nématodes varie de 272,9 à $6238,9 \times 10^3$ ind·m^{-2}, la valeur moyenne de cette abondance étant de $1409,6 \times 10^3$ ind·m^{-2}. La biomasse fluctue de 33,6 mg·m^{-2} à 1197,0 mg·m^{-2} (moyenne : 337,2). Les nématodes myco-phytophages de l'ordre des Tylenchida présentent l'abondance la plus élevée. Considérés individuellement, les genres montrent des préférences variables. L'abondance des nématodes bactériophages est semblable dans tous les sites. La structure des communautés de nématodes est influencée par l'âge des arbres, la nature du sous-bois et l'altitude.

Key-words : soil nematodes, community structure, spruce forests.

Spruce forests cover large areas of Europe and, in the Czech Republic, they represent about 60 % of the woodland (20 % of the 78 862 km^2 national territory). The spruce ecosystem consists mostly of man-made plantations which have replaced the original natural plant associations and, in consequence, they are diverse in their growth rate, undergrowth composition, animal and microfloral assemblages, and soil qualities. Concerning nematodes, spruce forests are mostly inhabited by myco-phytophagous Tylenchida and bacteriophagous populations of the orders Rhabditida and Araeolaimida. Omniphagous nematodes of the order Dorylaimida are less abundant and predacious species of the order Mononchida are frequently absent (Bassus, 1962; Háněl, 1992). The total nematode densities in European spruce stands varies greatly, from 0.44×10^6 ind·m^{-2} (Háněl, 1993 *a*) to 13.00×10^6 ind·m^{-2} (Byzova *et al.*, 1986).

This paper deals with the diversity, abundance, biomass and composition of soil nematode communities of five spruce plantations in the Beskydy Mountains, Czech Republic, and is part of an extensive program for the study of soil invertebrates in spruce forests and the effect of industrial immissions upon them as well.

Materials and methods

SITE DESCRIPTION

Investigations were carried out from 1988 to 1992 in spruce forests [*Picea abies* (L.) Karst.] of the Protected Landscape Area Beskydy in Northern Moravia/Southern Silesia regions, Czech Republic. Mean long-term annual air temperature of the area is 5-6 °C, sum of precipitation 1200-1400 mm. Parent rocks are cretacious sandstones accompanied by claystones of the Silesian unit of the West-Carpathian flysh. Original plant formations were mostly *Abieto-Fagetum* forests, which have been replaced by spruce and, to a lesser extent, by beech and pine plantations or agricultural land. The original forests are limited to small natural reserves. The territory is exposed to winds polluted by immissions from north-west industrial agglomerations in North Moravia and South Silesia. In the latest decade, ambient concentrations of pollutants in the region studied were about 20-200 μg·m^{-3} year^{-1}of dust, 2-100 μg·m^{-3} year^{-1} of SO_2, and 1-30 μg·m^{-3} year^{-1} of NO_x. Nematodes were studied in five spruce forest plantations situated in two localities as follows :

Locality I : Research station Bílý kříž

18 ° 33′ E, 49 ° 30′ N, 880-900 m a.s.l., slope 12-14° with SW orientation, parent rocks Godula sandstones of Mesozoic (Cretaceous) age, acidic sand-loam brown soil (dystric cambisol) on the sandstone base, locally podzolized, ambient pollutant concentrations of 60-80 $\mu g \cdot m^{-3}$ $year^{-1}$ of dust, 10-16 $\mu g \cdot m^{-3}$ $year^{-1}$ of SO_2, and 10-15 $\mu g \cdot m^{-3}$ $year^{-1}$ of NO_x.

Site A : Five year-old spruce forest (in 1988; i.e. spruce trees were planted in 1984) with sparse shrubs of *Betula pubescens* Ehrh. and *Fagus sylvatica* L. and dense undergrowth of *Calamagrostis villosa* (Chaix) Gmel., patches of *Vaccinium myrtillus* L., tufts of *Avenella flexuosa* (L.) Parl. and sparse *Rubus fruticosus* L. sp. aggreg. C_{Org} (3-10 cm) = 3.5-12.0 %, pH (H_2O) (3-10 cm) = 4.31.

Site B : 105 year-old spruce forest with sparse shrubs of *Picea abies* and *Betula pubescens*, undergrowth of *Rubus idaeus* L., *Luzula sylvatica* (Huds.) Gaud., *Calamagrostis villosa, Vaccinium myrtillus*, tufts of *Avenella flexuosa, Polytrichum formosum* Hedw. and seedlings of *Picea abies*. C_{Org}(0-3 cm) = 18.9-21.2 %, C_{Org} (3-6 cm) = 10.0-20.7 %, C_{Org}(6-11 cm) = 2.9-16.7 %, pH (H_2O) (0-10 cm) = 3.63.

Site C : 134 year-old spruce forest with *Fagus sylvatica* (5 %) and *Abies alba* L. (2 %), herbaceous undergrowth of *Calamagrostis villosa, Vaccinium myrtillus, Oxalis acetosella* L., sparse *Rubus idaeus, Dryopteris carthusiana* (Vill.) H.P. Fuchs, *Luzula sylvatica*, and patches of bare litter. C_{Org}(0-3 cm) = 19.2-22.0 %, C_{Org}(3-6 cm) = 8.5-18.9 %, C_{Org}(6-11 cm) = 3.4-12.2 %, pH (H_2O) (0-10 cm) = 3.43.

Locality II : Kněhyně mountain

18° 19′ E, 49° 29′ N, 1257 m a.s.l., slope 30-40° with N orientation, shallow, stony, acidic brown – podzol soil (dystric cambisol – leptic podzol), ambient pollutant concentrations of 90-110 $\mu g \cdot m^{-3}$ $year^{-1}$ of dust, 8-10 $\mu g \cdot m^{-3}$ $year^{-1}$ of SO_2, and 4-5 $\mu g \cdot m^{-3}$ $year^{-1}$ of NO_x.

Site D : 52 year-old spruce forest on the North slope of the mountain, undergrowth (about 50-70 %) of *Dryopteris spinulosa* (F.O. Muller) Sch. et Thell., tufts of *Calamagrostis villosa*, sparse *Luzula sylvatica, Avenella flexuosa, Rubus idaeus* and small patches of *Vaccinium myrtillus*, sporadic but uniform growth of *Oxalis acetosella*. C_{Org}(0-3 cm) = 8.4-21.5 %, C_{Org}(3-6 cm) = 5.1-17.1 %, C_{Org}(6-11 cm) = 3.8-4.9 %, pH (H_2O) (0-10 cm) = 4.18.

Site E : 52 year-old spruce forest on the North slope of the mountain, dense undergrowth (about 100 %) of *Dryopteris spinulosa* and *Oxalis acetosella* accompanied with *Vaccinium myrtillus, Calamagrostis villosa, Luzula sylvatica, Avenella flexuosa, Rubus idaeus, Polytrichum formosum* on stones and stubs. C_{Org}(0-3 cm) = 16.4-21.7 %, C_{Org}(3-6 cm) = 4.9-21.5 %, C_{Org}(6-11 cm) = 4.3-13.4 %), pH (H_2O) (0-10 cm) = 3.98.

The degree of damage to spruce trees by immissions was studied in 1988-1989 and expressed in the following scale of canopy defoliation : spruce damage degree 0 (0-10 % needle loss), 1 (10-30 %), 2 (30-50 %). Individual values for spruce forests studied were as follows : A (0), B (2), C (1), D (2.5), E (2).

METHODS

Soil samples were take on June 24, 1988, October 11, 1988, June 26, 1989, October 23, 1989, October 12, 1990, June 13, 1991, November 5, 1991, June 18, 1992 and October 21, 1992 using a cylindrical corer with an area of 10 cm^2 in cross section to the depth of 10 cm in locality I and of 5-7 (10) cm in locality II (depending on the depth of soil profile) with ten replicates. Cores were divided into two subsamples 0-5 cm of organic layer and 5-10 cm of mineral layer (in locality I), and the soil was thoroughly mixed. Nematodes were isolated from four 5 g soil (layer of 0-5 cm in locality I and total soil cores in locality II) or 10 g soil (layer 0-5 cm at locality I) by means of a modified Baermann funnel method (flat double muslin cloth sieve, exposition 24 h at 20-23 °C). Animals were fixed by FAA and studied in glycerin mounts (Seinhorst, 1959).

The biomass of adult nematodes was estimated according to Andrássy (1956), and the biomass of juveniles was taken as one half of the adult biomass. Depending on the feeding habits of the species observed nematodes were divided into six trophic groups : bacteriophagous (genera 1-17, 35, 37, 38 in Table 1), mycophagous (18, 19, 33, 34), myco-phytophagous (20-25), phytophagous (26-32), omniphagous (41-46) and predators (36, 39, 40). The Shannon-Wiener information formula ($H' = -\Sigma\, pi\, ln\, pi$) for species ($H'$ spp), genera (H' gen) and families (H' fam) diversity, and the Maturity Index and the Plant Parasite Index (Bongers, 1990) for families (Bongers, 1988) were calculated from nematode abundance.

Most of the adult nematode specimens in localities studied were identified to species level. Species similarity of nematode assemblages was evaluated using the Sørensen's index $Sø = (2\, s/s_1 + s_2) \times 100$ (s_2 = number of species in locality 1; s_2 = number of species in locality 2; s = number of species common to localities 1 and 2). However, majority of quantitative analyses was produced from genera abundance as the great proportion of juveniles in nematode populations decreased the reliability of species abundance estimates. Species abundance was used for Shannon-Wiener index as the pattern of its changes is usually similar to variations in the generic index; species data approximate the greatest diversity value but the error can be higher than for genera. The species were mostly assigned to genera following the monographs on nematode orders (Andrássy, 1984; Siddiqi, 1986; Jairajpuri & Ahmad, 1992).

The ordination of samples and genera was calculated using the CANOCO program, method DCA, detrending by the 2nd order polynomials (Ter Braak, 1987 *a*, *b*), data genera abundance, eigenvalues X 1 0.47649, X 2 0.28149, X 3 0.11918, X 4 0.0814. The divisive classification of samples and genera was produced by the TWINSPAN program (Hill, 1979), cut levels 0, 2, 4, 8, 16, 32, 64, 128, 256, range of values 0-523.88.

Results

A total of 92 species were identified in nematode assemblages in all of the localities studied, and most species were found in the 5-9 year-old spruce forest. The number of species was greater in localities at the Bílý Kříž station than in those at Kněhyně mountain (Table 1).

The highest mean values of the Shannon-Wiener indices (except for H' spp.) and the top Plant Parasite Index (PPI) were found in the 5-9 year-old spruce forest. In the other sites the PPI, and in all of the localities Maturity Indices (MI) were almost constant, with a slight exception for MI in site E (Table 2).

The most abundant nematode genera were *Filenchus, Acrobeloides, Aglenchus, Plectus, Eudorylaimus* s.l., *Rhabditis* and *Rotylenchus.* The total abundance of nematode populations varied from 272.9 to 6238.9×10^3 ind·m^{-2}, with a mean value of 1409.6×10^3 ind·m^{-2}. Fig. 1 shows changes during the investigated period. The greatest nematode population densities occurred in October 1992, and the abundance was mostly greater in localities at a lower altitude than in a higher one.

The total nematode biomass varied from 33.6 mg·m^{-2} to 1197.0 mg·m^{-2}. Table 2 gives long-term mean values for individual sites. The greatest biomass was in the 5-9 year-old spruce forest and tended to decrease with

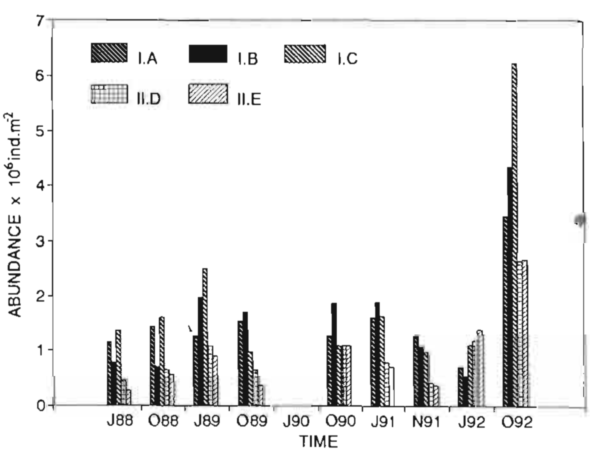

Fig. 1. *Abundance changes of soil nematode communities in spruce forests A, B, C, D, E.*

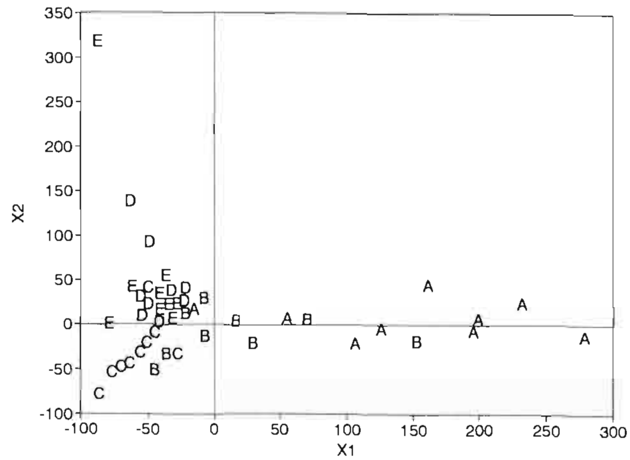

Fig. 2. *Ordination of samples from nematode communities in spruce forest A, B, C, D, E.*

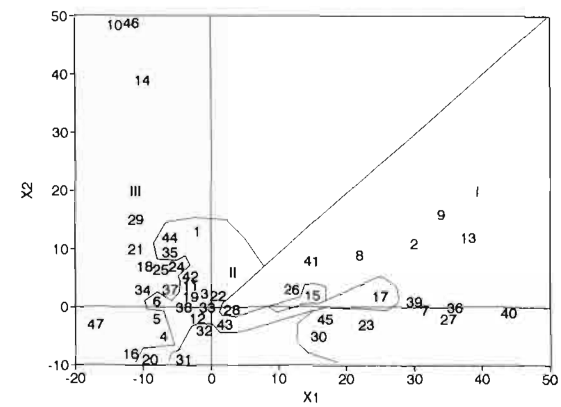

Fig. 3. *Ordination of nematode genera (explanation for numerals see Table 2) in spruce forests A, B, C, D, E; TWINSPAN groups of genera I - III (up to the second level of division).*

the increasing age of spruce trees. Consequently, the greatest mean individual biomass of a nematode specimen was in the 5-9 year-old forest and the lowest one in the 134-138 year-old forest.

Fig. 2 shows the ordination of samples. It can be seen that the nematode fauna in the youngest spruce forest was different from the others : however, it developed into a community similar to those in older spruce stands. Samples taken from the 134-138 and the 52-56 year-old forests were grouped into two relatively homogeneous but intersecting clusters. Fig. 3 gives the ordination of genera encircled in TWINSPAN groups up to the second level of division. The group I contains nematode genera characteristic of the 5-9 year-old spruce forest. The genera *Rotylenchus, Clarkus, Prionchulus, Bursilla* reached their greatest abundance in this stand (Table 2). Group II is composed of the dominant genera *Filenchus, Acrobeloides, Plectus* and *Eudorylaimus* s.l., the subdominant genera *Aphelenchoides, Ditylenchus* and

Table 1. *List of nematodes in soil of five spruce forests.*

	A	B	C	D	E
MONHYSTERIDA					
1 *Eumonhystera vulgaris* de Man, 1880	+	+	+	+	+
2 *Geomonhystera aenariensis* Meyl, 1953	+		+		
ARAEOLAIMIDA					
3 *Plectus acuminatus* Bastian, 1865	+	+	+	+	+
4 *Plectus cirratus* Bastian, 1865	+				
5 *Plectus geophilus* de Man, 1880	+	+	+	+	+
6 *Plectus longicaudatus* Bütschli, 1873	+	+	+	+	+
7 *Plectus parietinus* Bastian, 1865			+		
8 *Plectus parvus* Bastian, 1865	+	+	+	+	+
9 *Plectus rhizophilus* de Man, 1880	+				
10 *Plectus sambesii* Micoletzky, 1915	+	+	+	+	
11 *Plectus silvaticus* Andrássy, 1985		+	+		
12 *Wilsonema otophorum* de Man, 1880	+	+	+	+	+
13 *Tylocephalus auriculatus* Bütschli, 1873	+				
TERATOCEPHALIDA					
14 *Metateratocephalus crassidens* de Man, 1880	+	+	+	+	+
15 *Teratocephalus lirellus* Anderson, 1969	+	+	+	+	+
16 *Teratocephalus paratenuis* Eroshenko, 1973	+	+	+	+	+
17 *Teratocephalus tenuis* Andrássy, 1958	+				
18 *Teratocephalus terrestris* Bütschli, 1873	+		+		
RHABDITIDA					
19 *Heterocephalobus elongatus* de Man, 1880	+	+		+	
20 *Heterocephalobus* sp.		+			
21 *Cephalobus persegnis* Bastian, 1865	+	+			
22 *Eucephalobus striatus* Bastian, 1865	+				
23 *Chiloplacus* sp.				+	
24 *Acrobeloides nanus* de Man, 1880	+	+	+	+	+
25 *Panagrolaimus rigidus* Schneider, 1866	+	+	+	+	+
26 *Bursilla monhystera* Bütschli, 1873	+	+		+	+
27 *Rhabditis* sp.	+	+	+	+	+
28 *Bunonema reticulatum* Richters, 1905		+			
29 dauer larvae		+	+	+	+
DIPLOGASTERIDA					
30 *Diplogaster* sp. s.l.	+	+	+		
APHELENCHIDA					
31 *Paraphelenchus* sp.					+
32 *Aphelenchoides composticola* Franklin, 1957	+			+	
33 *Aphelenchoides minimus* Meyl, 1953					+
34 *Aphelenchoides pusillus* Thorne, 1929	+	+	+	+	+
35 *Aphelenchoides saprophilus* Franklin, 1957	+	+	+	+	+
36 *Aphelenchoides* sp. 1	+	+	+	+	+
37 *Aphelenchoides* sp. 2	+	+	+		
38 *Aphelenchoides* sp. 3				+	
TYLENCHIDA					
39 *Filenchus annulatus* Siddiqui & Khan, 1983	+	+	+	+	+
40 *Filenchus discrepans* Andrássy, 1954	+	+	+	+	+
41 *Filenchus helenae* Szczygiel, 1969	+	+	+	+	+
42 *Filenchus polyhypnus* Steiner & Albin, 1946		+			
43 *Filenchus vulgaris* Brzeski, 1963	+	+	+		
44 *Filenchus* sp. 1	+	+	+	+	+
45 *Filenchus* sp. 2				+	

Table 1 *(continued).*

46 *Tylenchus butteus* Thorne & Malek, 1968				+	
47 *Tylenchus* sp.				+	
48 *Malenchus acarayensis* Andrássy, 1968	+	+	+	+	+
49 *Malenchus bryophilus* Steiner, 1914		+	+	+	+
50 *Malenchus* sp.	+		+	+	
51 *Aglenchus agricola* de Man, 1884	+	+	+	+	+
52 *Lelenchus leptosoma* de Man, 1880	+	+	+	+	
53 *Ecphyadophora tenuissima* de Man, 1921		+		+	
54 *Bitylenchus dubius* Bütschli, 1873	+				
55 *Rotylenchus buxophilus* Golden, 1956	+	+	+	+	+
56 *Pratylenchus* sp.	+	+	+		
57 *Hoplotylus femina* s'Jacob, 1960					+
58 *Paratylenchus microdorus* Andrássy, 1959	+				
59 *Paratylenchus nanus* Cobb, 1923	+	+	+		
60 *Criconema demani* Micoletzky, 1925		+	+		
61 *Criconemella macrodora* Taylor, 1936		+			
62 *Ditylenchus parvus* Zell, 1988	+	+	+		+
63 *Ditylenchus silvaticus* Brzeski, 1991	+	+	+	+	+
64 *Ditylenchus* sp. 1			+		
65 *Ditylenchus* sp. 2				+	
66 *Neoditylenchus* sp.			+	+	+
67 *Deladenus saccatus* Andrássy, 1954		+			
ENOPLIDA					
68 *Prismatolaimus dolichurus* de Man, 1880	+	+	+	+	+
69 *Prismatolaimus intermedius* Bütschli, 1873	+				+
70 *Tripyla setifera* Bütschli, 1873	+				
71 *Bastiania gracilis* de Man, 1876		+	+		
72 *Alaimus macer* Andrássy, 1958	+		+		
73 *Alaimus meyli* Andrássy, 1961	+	+			
74 *Alaimus primitivus* de Man, 1880		+			+
75 *Alaimus* sp.	+	+	+	+	+
MONONCHIDA					
76 *Clarkus papillatus* Bastian, 1865	+	+	+	+	+
77 *Prionchulus punctatus* Cobb, 1917	+	+	+		+
DORYLAIMIDA					
78 *Mesodorylaimus bastiani* Bütschli, 1873	+				+
79 *Eudorylaimus brevis* Altherr, 1952				+	+
80 *Eudorylaimus carteri* Bastian, 1865		+	+		
81 *Eudorylaimus parvus* de Man, 1880	+	+	+	+	+
82 *Eudorylaimus* sp. 1	+		+		
83 *Eudorylaimus* sp. 2		+	+	+	+
84 *Eudorylaimus* sp. 3		+	+		
85 *Eudorylaimus* sp. 4		+			
86 *Aporcelaimellus obtusicaudatus* Bastian, 1865	+	+	+		+
87 *Aporcelaimellus simus* Andrássy, 1958	+	+	+		
88 *Pungentus silvestris* de Man, 1912	+				
89 *Pungentus* sp.				+	+
90 *Tylencholaimus mirabilis* Bütschli, 1873			+		+
91 *Tylencholaimus stecki* Steiner, 1914	+	+	+		
92 *Trichodorus* sp.				+	
UNIDENTIFIED			+		+
NUMBER OF SPECIES	60	59	57	47	45
SØRENSEN'S INDEX					
B	72				
C	74	81			
D	62	66	65		
E	63	67	71	74	

Table 2. *Mean abundance* (× 10^3 ind·m^{-2}) *of soil nematodes in five spruce forests, H' - Shannon-Wiener indices for species (spp), genera (gen) and family (fam) abundance, MI - Maturity Index, PPI - Plant Parasite Index, CL - Confidence Limits P = 0.05.*

	I.A	I.B	I.C	II.D	II.E
MONHYSTERIDA					
1 *Eumonhystera*	2.6	2.1	1.6	4.0	8.4
2 *Geomonhystera*	3.4	–	0.4	–	–
Σ	6.1	2.1	2.0	4.0	8.4
ARAEOLAIMIDA					
3 *Plectus*	131.5	105.3	132.5	161.1	65.4
4 *Wilsonema*	2.4	2.1	21.6	4.7	2.6
Σ	134.0	107.4	154.1	165.8	68.0
TERATOCEPHALIA					
5 *Metateratocephalus*	0.7	10.3	17.9	10.8	1.9
6 *Teratocephalus*	4.4	6.2	11.0	7.7	16.6
Σ	5.1	16.6	28.9	18.5	18.5
RHABDITIDA					
7 *Heterocephalobus*	7.2	0.7	–	0.4	–
8 *Cephalobus*	0.6	0.3	–	–	–
9 *Eucephalobus*	0.1	–	–	–	–
10 *Chiloplacus*	–	–	–	0.2	–
11 *Acrobeloides*	115.3	154.5	200.4	147.9	172.5
12 *Panagrolaimus*	30.2	27.3	3.1	7.6	2.2
13 *Bursilla*	60.2	0.6	–	1.0	0.5
14 *Rhabditis*	27.6	67.3	50.1	114.3	193.4
15 *Bunonema*	–	0.2	–	–	–
16 dauer larvae	–	1.6	13.8	0.4	5.0
Σ	241.3	252.5	267.4	271.7	373.6
DIPLOGASTERIDA					
17 *Diplogaster* s.l.	0.4	0.2	0.2	–	–
Σ	0.4	0.2	0.2	–	–
APHELENCHIDA					
18 *Paraphelenchus*	–	–	–	–	0.4
19 *Aphelenchoides*	51.1	72.9	73.0	43.4	24.9
Σ	51.1	72.9	73.0	43.4	25.4
TYLENCHIDA					
20 *Filenchus*	139.9	595.4	1165.1	235.1	255.9
21 *Tylenchus*	–	–	–	4.8	–
22 *Malenchus*	75.4	37.9	32.4	51.1	5.1
23 *Aglenchus*	336.9	323.8	40.8	0.2	1.0
24 *Lelenchus*	0.8	0.6	0.4	1.8	–
25 *Ecphyadophora*	–	0.4	–	0.8	–
26 *Bitylenchus*	0.4	–	–	–	–
27 *Rotylenchus*	325.0	51.0	0.5	2.5	1.6
28 *Pratylenchus*	1.1	0.2	3.6	–	–
29 *Hoplotylus*	–	–	–	–	1.8
30 *Paratylenchus*	0.8	0.5	0.1	–	–
31 *Criconema*	–	0.2	1.3	–	–
32 *Criconemella*	–	0.2	–	–	–
33 *Ditylenchus*	51.2	60.2	74.5	41.9	18.6
34 *Neoditylenchus*	–	–	0.2	0.4	0.5
Σ	931.5	1070.4	1318.9	338.7	284.5
ENOPLIDA					
35 *Prismatolaimus*	0.7	1.2	1.1	3.3	5.9
36 *Tripyla*	1.7	–	–	–	–
37 *Bastiania*	–	0.3	0.4	–	–

Table 2 *(continued).*

38 *Alaimus*	3.0	3.1	6.5	3.7	1.1
Σ	5.4	4.6	8.0	7.1	6.9
MONONCHIDA					
39 *Clarkus*	30.8	0.3	0.4	4.1	1.1
40 *Prionchulus*	36.8	0.3	0.3	–	1.1
Σ	67.6	0.7	0.7	4.1	2.2
DORYLAIMIDA					
41 *Mesodorylaimus*	0.3	–	–	–	0.3
42 *Eudorylaimus* s.l.	76.3	130.6	88.5	139.4	131.4
43 *Aporcelaimellus*	0.4	0.4	0.4	–	0.6
44 *Pungentus*	0.1	–	–	0.4	2.9
45 *Tylencholaimus*	7.0	0.3	1.4	–	0.6
46 *Trichodorus*	–	–	–	0.4	–
Σ	84.1	131.3	90.3	140.2	135.7
UNIDENTIFIED					
47 A	–	+	0.4	–	2.5
TOTAL ABUNDANCE	1526.5	1658.7	1943.8	993.5	925.7
± CL	± 592.5	± 889.0	± 1291.8	± 521.6	± 576.5
BIOMASS $mg \cdot m^{-2}$	667.8	279.8	207.6	289.6	241.4
± CL	± 188.3	± 140.5	± 99.2	± 179.9	± 135.3
MEAN INDIVIDUAL BIOMASS μg	0.494	0.182	0.122	0.302	0.270
± CL	± 0.176	± 0.061	± 0.048	± 0.148	± 0.122
NUMBER OF SPECIES	60	59	57	47	45
H'spp	2.67	2.55	2.16	2.79	2.46
NUMBER OF GENERA	34	35	31	28	29
H'gen	2.42	2.05	1.59	2.19	1.99
NUMBER OF FAMILIES	23	24	22	18	21
H'fam	1.98	1.58	1.38	1.97	1.93
MI	2.30	2.30	2.25	2.27	2.15
PPI	2.37	2.05	2.04	2.01	2.01

Malenchus, and some others *(Eumonhystera, Prismatolaimus, Teratocephalus, Alaimus* and *Panagrolaimus)* being ubiquitous in all spruce forests of the investigated area. The genus *Rhabditis* (group III) was most abundant in spruce forests at the Kněhyně mountain. The genus *Aglenchus* reached great population densities in the 5-9 and 105-109 year-old spruce stands, evidently in connection with the dense herbaceous (grass) undergrowth there.

Correlation coefficients of some environmental variables with the ordination axes are given in Table 3. Generic composition of nematode assemblages was correlated mostly with the age of spruce trees and the altitude of localities. Sampling date had relatively little influence on nematode populations and site effect was probably hidden by many factors connected with the biological qualities of spruce forest-type ecosystem.

Fig. 4 shows the TWINSPAN dendrogram for samples and indicator genera, their signs and borderline cut levels for five levels of division. Four clusters of samples can be distinguished. The cluster W is mostly composed of samples taken in the youngest spruce forest and is characterized by a high abundance of the genus *Rotylenchus.* The cluster X includes samples with a high abundance of the genera *Rhabditis, Eudorylaimus, Malenchus, Plectus, Filenchus,* and *Aphelenchoides.* The cluster Y is mostly composed of samples from sites B and C, whereas the cluster Z includes only samples of nematode assemblages in sites D and E. In general, the

Table 3. *Weighted correlation coefficients between axes of ordination of nematode genera and some environmental variables.*

	X 1	X 2	X 2	X 4
Site	– 0.052	0.485	0.122	0.041
Sampling date	– 0.294	– 0.112	– 0.451	– 0.096
Altitude of site	– 0.333	0.553	0.118	– 0.103
Age of spruce trees	– 0.624	– 0.396	– 0.015	– 0.057

Table 4. Mean abundance and biomass of nematode trophic groups in five spruce forests.

	I.A	I.B	I.C	II.D	II.E
ABUNDANCE ($\times 10^3$ ind·m^{-2})					
Bacteriophages	390.5	383.5	461.0	467.1	477.9
Mycophages	102.3	133.1	147.6	85.7	44.5
Myco-phytophages	553.0	958.1	1238.7	293.9	262.1
Phytophages	327.3	52.1	5.5	2.5	3.4
Omniphages	84.1	131.3	90.3	140.2	135.7
Predators	69.3	0.7	0.7	4.1	2.2
BIOMASS (mg·m^{-2})					
Bacteriophages	91.3	78.8	86.9	114.0	119.8
Mycophages	5.1	7.8	9.3	5.3	2.9
Myco-phytophages	36.6	46.0	42.1	11.4	7.5
Phytophages	223.8	35.7	1.0	2.2	1.9
Omniphages	140.4	110.2	66.9	153.6	105.0
Predators	170.6	1.3	1.3	3.1	4.3

TWINSPAN analysis of nematode assemblages reflected the altitude of localities, a factor which is connected with different composition of herbaceous undergrowth in the spruce forests studied.

The myco-phytophages of the family Tylenchidae were the most abundant trophic group of nematodes (Table 4). In the spruce forest at the research station Bílý kříž the abundance ratio *Filenchus/Aglenchus* increased with the age of spruce plantation (0.42 in site A, 1.84 in site B, 28.56 in site C). At the Kněhyně mountain, the ratio was extremely high in consequence of a negligible abundance of the genus *Aglenchus*. The abundance of mycophagous genera was higher at Bílý Kříž station than at the Kněhyně mountain. The abundance of bacteriophagous nematodes was similar in all localities; greater variations were found in omnivorous populations. Phytophagous and predaceous nematodes reached the greatest abundance in the youngest spruce forest.

Bacteriophagous and omniphagous nematodes had the greatest biomass in all stands except for the 5-9 year-old forest (Table 4). In this stand, phytophages represented 33.5 % of the total nematodes biomass, predators 25.6 % and omniphages 21.0 %, while the proportion of bacteriophages was only 13.7 %.

Discussion

The number of species in the spruce forests studied was relatively low, especially at the Kněhyně mountain. Popovici (1980) found 69 and 93 species in two mountain spruce forests (South-East Carpathians) in Rumania, Šály *et al.* (1986) identified 48 species in three spruce forests (West Carpathians) in Slovakia. Some spruce forest nematode assemblages at lower altitudes of temperate European regions seem to be more diverse than those at the higher ones. Bassus (1962) distinguished 50 nematodes species in two spruce woods in Germany, Solovyeva (1986) found 34 but Novikova (1970) 163 species in spruce forests in Russia (Moscow region).

As concerns the generic composition of nematode communities in spruce woods studied, the age of spruce trees and the altitude were the important influential factors. Low correlation between sites and nematode assemblages can be explained by similar composition of herbaceous udergrowth in sites D and E (A and B) depending on both altitude and the age of spruce trees. Another factor influencing nematodes in coniferous forests might be the soil pH. De Goede (1993) found a correlation between nematodes and pH in forest ecosystems in the Netherlands. On the other hand, spruce plantations in Western Bohemia of similar age, altitude and soil pH had different composition of nematode communities (Háněl, 1993 *a*). In the sites studied, the soil pH decreased with the age of spruce trees, and this might exert an influence upon nematode populations.

Different cumulative characteristics of nematode showed a different dependence. Number of species, total abundance, and abundance of the order Tylenchida were higher at Bílý kříž station (lower altitude) than at Kněhyně mountain (higher altitude). On the other hand, H'gen, H'fam, total biomass, mean individual biomass of a nematode specimen, and abundance of the order Mononchida tended to decrease with the increasing age of spruce trees whereas the abudance of the genus *Filenchus* increased. Changes connected with tree age can be related to successional development of the ecosystems studied. Especially, the decrease in mean individual body weight seems to be a characteristic of old growing coniferous (mixed coniferous) forests in Europe – similar changes were found by Wasilewska (1971) and De Goede (1993) in pine woods. In some genera, the key factor influencing their distribution was probably the composition of herbaceous plant cover – especially the genus *Aglenchus* clearly reflected the density of grass roots.

There was a visible trend in decreasing abundance of predacious and phytophagous nematodes (especially the genus *Rotylenchus*) with the age of spruce plantations. *Rotylenchus* spp. are important parasites on young spruce trees (Gubina, 1980) and the data in the present study indicate that their population density was regulated by mononchid nematodes. However, the decline in population density of the genus *Rotylenchus* cannot fully explain the extinction of mononchid predators as they can feed upon various nematode species (Small, 1987). It is possible that they are sensitive to acid substrates (see Szczygiel, 1971; Winiszewska-Slipinska & Skwiercz, 1987) or to some chemicals in spruce forest soil; their sensitivity to chemical composition of humus was proved by Arpin *et al.* (1984, 1988).

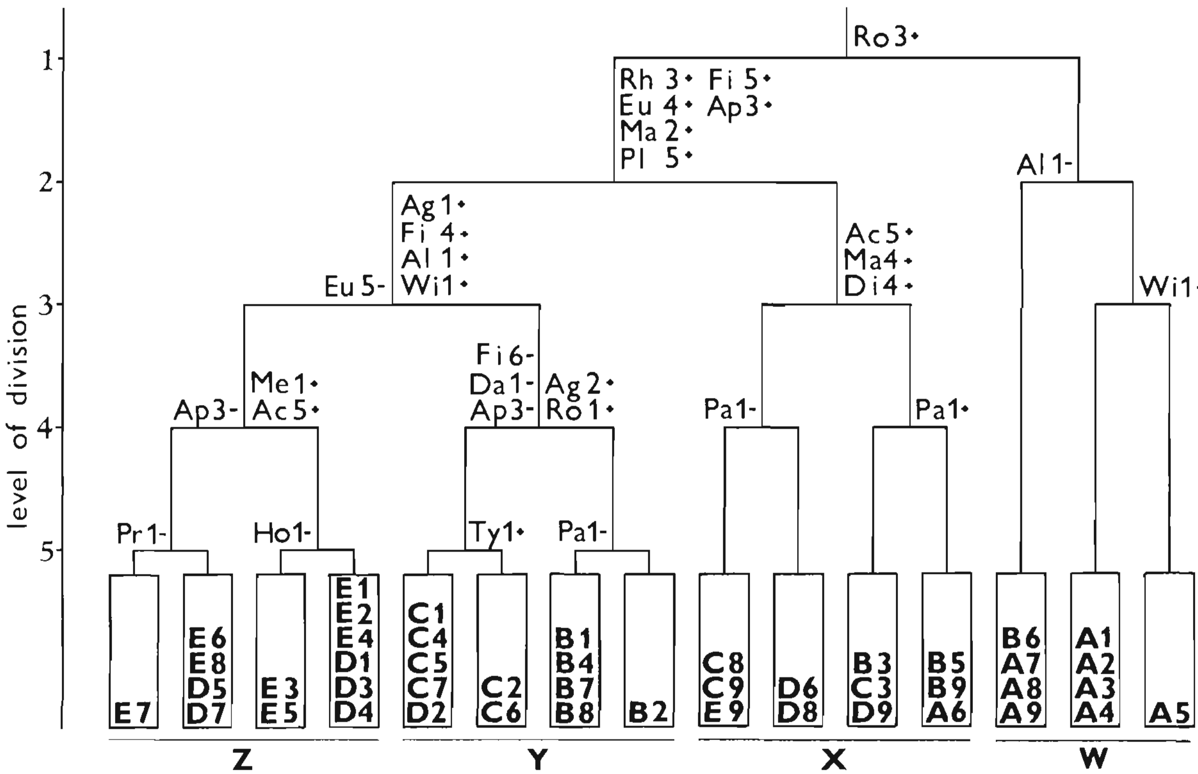

Fig. 4. *TWINSPAN dendrogram (up to the fifth level of division) of nematode populations in spruce forests A, B, C, D, E; sampling dates : 1 = June 24, 1988, 2 = October 11, 1988, 3 = June 26, 1989, 4 = October 23, 1989, 5 = October 12, 1990, 6 = June 13, 1991, 7 = November 5, 1991, 8 = June 18, 1992, 9 = October 21, 1992; indicator nematode genera with their signs and borderline cut levels as specified in " materials and methods " : Ro =* Rotylenchus, *Rh* = *Rhabditis*, *Eu* = Eudorylaimus *s.l.*, *Ma* = Malenchus, *Pl* = Plectus, *Fi* = Filenchus, *Ap* = Aphelenchoides, *Al* = Alaimus, *Ag* = Aglenchus, *Wi* = Wilsonema, *Ac* = Acrobeloides, *Di* = Ditylenchus, *Me* = Metateratocephalus, *Da* = *dauer larvae*, *Pa* = Panagrolaimus, *Pr* = Prionchulus, *Ho* = Hoplotylus, *Ty* = Tylencholaimus; *clusters of samples W, X, Y, Z separated at the first level of division (W), the second level (X) and the third level (Y, Z).*

Data in Table 2 show that, while the total population density of nematodes in spruce forests was comparable with their abundance in deciduous forests and meadows, their diversity was lower (Háněl, 1993 *b*). An interesting phenomenon was the decrease in the Shannon-Wiener index values with the age of the forest whereas the Maturity Index was stable. Moreover, the mean abundance of all " maturity families " was very similar in localities studied and ranged from 646×10^3 ind·m^{-2} to 696×10^3 ind·m^{-2}; so that variations in the total nematode abundance mainly resulted from population densities of the order Tylenchida (see Table 2). An explanation can be as folows : while the Shannon-Wiener index indicated changes in nematode assemblages reflecting the age of spruce trees, the Maturity Index showed that besides those changes nematode populations maintained their identity with a certain type of ecosystem (spruce forest). This can be in concordance with Bongers' (1990) hypothesis that the Maturity Index can visualize structural changes in nematode assemblages and therefore the disturbance of ecosystem. The Maturity Index values also support Háněl's (1992) conclusion that moderate immission damage of spruce trees in the localities studied was hardly detectable in soil nematodes.

Proportion of individual trophic groups in the overall nematode communities varied in the different spruce forests. Mean abundance and biomass of bacteriophagous nematodes showed insignificant differences among individual stands (Table 4). Also, little variation was seen in the abundance of omniphages. This agrees with the data given by Háněl (1993 *a*), although the abundance of omniphages in spruce forests of the Krušné hory Mountains (heavily injured by immissions) was much lower than in the localities under study. The greatest differences were found in the abundance of phytophagous nematodes and myco-phytophagous species of the family Tylenchidae. The abundance of the genus *Filenchus* increased with the age of the spruce ecosystem. In the Krušné hory Mountains spruce forests were of similar age, 30-40 years and the abundance of the genus *Filenchus* decreased with increasing impairment of spruce forests by immissions and decreasing diversity of mycorrhizal fungi (Háněl, 1993 *a*). Therefore, the root system of both spruce trees and herbaceous undergrowth in relation to mycorrhizal mycoflora is probably another important factor influencing nematodes populations in spruce ecosystems. Their mutual development likely depends on tree age and altitude, and on the impairment of spruce trees by immissions (Cudlín *et al.*, 1991). Those relationships can be especially important for myco-phytophagous nematodes, as bacteriophages show lesser abundance variations in different localities. Further investigations should be aimed at rhizosphere interactions in spruce forests ecosystems with particular attention to nematodes – roots – mycorrhizal fungi dependence.

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