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THE INFLUENCE OF ACID RAIN ON SOIL NEMATODE COMMUNITIES: A COMPARISON OF CONTAMINATED HABITATS IN THE BELT OF THE KARKONOSZE AND IZERSKIE MOUNTAINS (SOUTH-WEST POLAND) WITH UNCONTAMINATED AREAS IN OTHER REGIONS OF POLAND

ABSTRACT: Taxonomic and trophic structure were described – along with indices of diversity and maturity – for nematode communities at six sites influenced by acid rain in the chain of the Karkonosze Mountains and at Hala Izerska (both in south-west Poland). The sites in question were spruce (*Picea abies*) forest with clear or else relatively limited signs of degradation, with the intensity of this phenomenon being determined in relation to the incidence of treefall, young spruce stands, and grass-herb communities. Intensified degradation was found to reduce the diversity and maturity of nematode communities and to increase the numerical representation of fungivorous species. Dry conditions intensified these changes.

The nematode communities of the aforementioned mountainous areas contaminated by acid rain were then compared with those studied by author about 20 years previously in other parts of Poland and considered uncontaminated. Communities from the contaminated areas were not found to have lower total numbers of nematodes, but did differ in the higher representation of fungivores and obligate plant parasites as well as in the absence of predators. A shift in the direction of feeding on fungi was noted among species feeding on reducers. Aspects unique to these communities which were noted on the scale of trophic differentiation were the loss of characteristic K-strategists (specially predators), and also loss of bacterivorous r-strategists in favour of more K-strategic bacterivores.

KEY WORDS: acid rain, soil nematodes, taxonomic composition, trophic groups, diversity index, maturity indices.

1. INTRODUCTION

The impact of acid rain has led to the death of forests over large areas of Europe and North America, with the most-damaged regions really constituting cases in which ecosystems have collapsed and forestcreating processes have disappeared. The result has been the replacement of forest by grasslands and scrub, with the creation of new groupings and assemblages of organisms (Rykowski 1993). Recent decades have seen the increased acidification of soils, largely as a result of acid precipitation, and those of very acid reaction should be considered chemically-degraded. Acidification accelerates many of the processes leading to the impoverishment of soils in cations like calcium, magnesium and potasium, as well as to the liberation of elements harmful to plants like aluminium and manganese. The mobility and hence availability to plants of heavy metals are also increased.

More than 25% of Poland's soils are very acid (i.e. of pH values below 4.5). A further 35% of soils lie within the pH range 4.6 to 5.5 and are thus considered acid (Ryszkowski and Bałazy 1993). Suffering most from the point of view of acidification is the region of the Western Sudetic Mountains, and specifically of the Izerskie and Karkonosze Ranges (NS 51–50°, WE 15–16°). Lying in the south-west of Poland, where the country borders with the Czech Republic and Germany, this is the infamous "Black Triangle" named by Andrzejewski and Baranowski (1993) and characterized by many large emission sources within Poland and across the borders. A circulation of air masses which is predominantly from the west ensures that the Sudetic Mountains are in the zone of the most direct impacts of the area's pollution sources. Emissions of sulphur dioxide here (above all from beyond the Polish border) amount to around $3 \cdot 10^6$ tones per year, and the resultant precipitation is Europe's most acidified. Estimates made in the winters between 1989 and 1992 suggest a "dry deposition" of sulphur dioxide equal to between 24 and 28 mg m^{-2} d^{-1}. The analogous figure for oxides of nitrogen was estimated at 0.4–0.6 mg m^{-2} d^{-1} (Andrzejewski and Baranowski 1993).

Degradational changes are very clearly seen in the area, where they take the forms of the death of forests and changes to the vegetation of the understorey (Fabiszewski et al. 1993).

Persson et al. (1989) and Wolters and Shaefer (1994) were able to show that the experimental acidification of soil does have an impact on soil fauna. Nevertheless, the reactions of soil organisms to acid rain are to a great extent unpredictable. Most studies have shown that acidification results in a fall in soil respiration and in the rate of decomposition, although microbiological processes do not display linear correlations with the intensity of this variable (Wolters and Schaefer 1994). Research also shows that the numerical representation of soil invertebrates increases in the cases of some groups, and decreases in the cases of others. It appears that the negative reactions of microfauna (protozoa and nematodes) are mainly the results of the lack of morphological structures hindering a direct contact between the body surface and the soil solution. Bearing this in mind, the reaction of nematodes to acidification ought therefore to involve decreased abundance.

Laboratory and field experiments with simulated acid rain have shown that communities of nematodes experience changes in their functional groups, with numbers of bacterivores, predators and omnivores declining, while those of so-called root feeders and fungal feeders either staying the same or even increasing (Hyvönen and Persson 1990, Persson et al. 1989, Ruess and Funke 1992, Ruess, Funke and Breunig 1995, Dmowska 1993). It is true that experimental simulations of acid rain do not really allow for estimations of long-term or more permanent impacts, but it is possible to compare severely-contaminated areas with less-contaminated or even uncontaminated areas, to the extent that the latter really existed in seventieth in Poland. Nevertheless *in situ* research on nematodes is largely lacking, with the exception of the works by Háněl (1993b) and Ruess (1995), and it was thus considered that even the preliminary orientation attempted in the present work was justified. Wolters and Schaefer (1994) underlined that there was a lack of research into microfaunas stressed by acid rain, in which there would also be developed the issues of biotic interactions, length of life, fertility, life strategies and the use made of resources by different species. The lack of such information would seem to be particularly significant where representatives of the decomposer fauna are concerned.

Presented in the present work are the abundances of nematode communities differing in their trophic status, as well as the biocoenotic parameters of these communities, in several ecosystems of the Karkonosze Mountains and Hala Izerska which are subjected to the strong influence of acid rain. Work was also done to compare the nematode faunas of these areas with those of areas elsewhere in Poland which are not considerd to be contaminated.

2. THE STUDY AREA AND STUDY SITES

Selected within the area of the Karkonosze Mountains were four sites near Jakuszyce. The locality in question is at the north-western extremity of the Polish part of the granite massif of the Karkonosze (Fig. 1). The area includes sources within the drainage basin of the River Kamienna, which are largely located within the zone of lower montane forest ascending here to 1000 m a.s.l. Sachanbiński (1994) has presented the area from the geochemical point of view, while air pollution has been addresses by Juda-Rezler and Abert (1994), Zwoździak et al. (1994), Kmieć et al. (1994) and Skiba et al. (1994).

The issue of acid precipitation is linked with changes in the emission of primary pollutants, including sulphur dioxide and nitrogen dioxide, and thence with the removal of their transformation products from the atmosphere as a result of dry de-

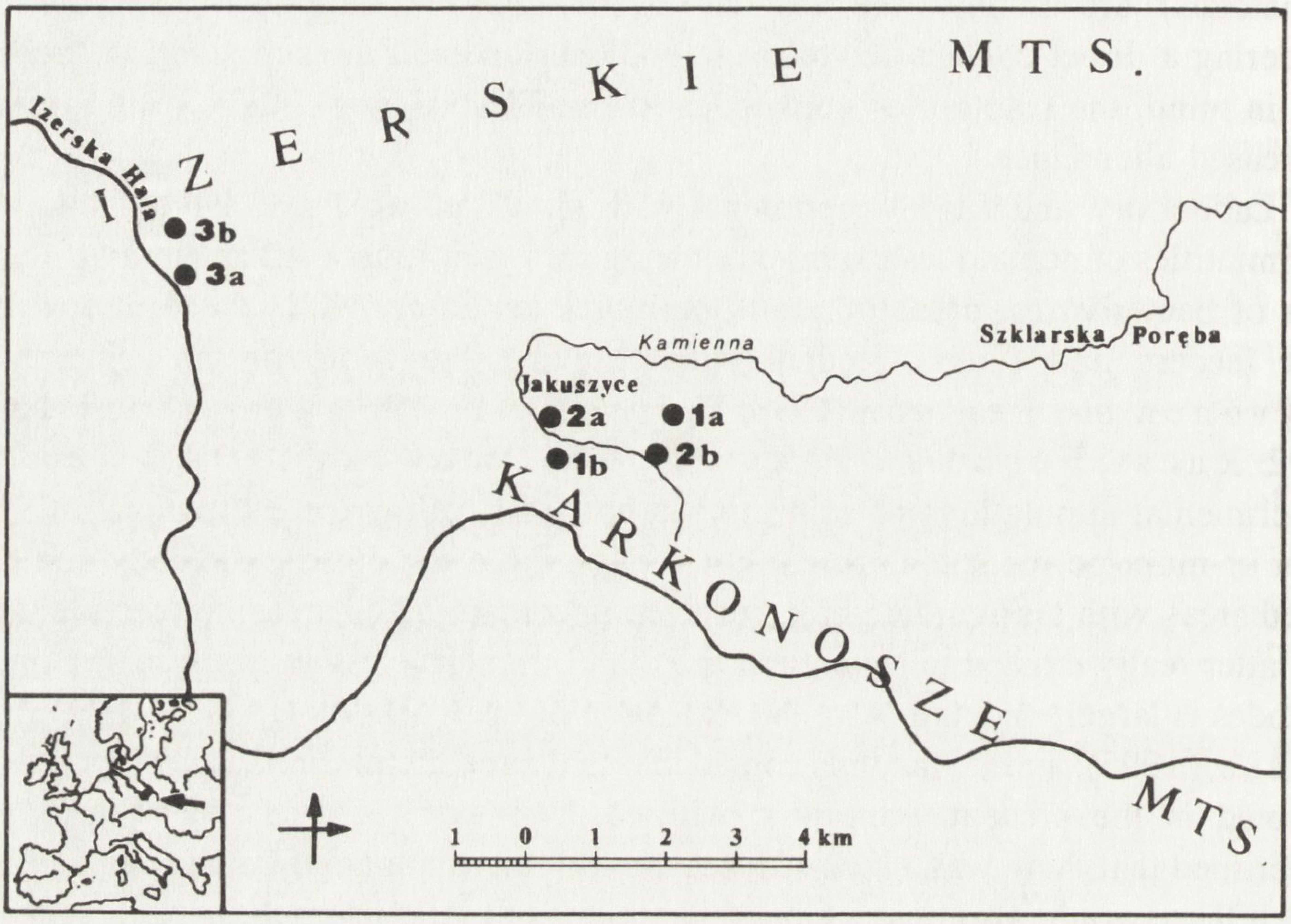

Fig. 1. Location of the study sites in the Karkonosze range (sites 1a, 1b, 2a and 2b) and at Hala Izerska in the Izerskie Mountains (sites 3a and 3b)

position or washing-out. The destruction of forest ecosystems began with the Izerskie Mountains part of the Western Sudety and then proceeded in an easterly direction (Zwoździak et al. 1995). The Karkonosze Mountains have high airborne concentrations of sulphur compounds, in the forms of SO_2 or sulphate aerosols (6–39 µg SO_2 m^{-3} d^{-1}, 37–52 µg SO_4^{-2} m^{-3} d^{-1}), of ammonia (14–16.5 µg NH_4^+ m^{-3} d^{-1}) and of the trace metals zinc (167 ng m^{-3} d^{-1} in the small airborne fractions) and cadmium (140 ng m^{-3} d^{-1}) (Zwoździak et al. 1995). The concentration of sulphurous compounds and ammonia exceed permitted levels for a forest ecosystem. In turn, the zinc and cadmium appear in amounts that are several times greater than the concentrations characteristic of the atmosphere in non-urbanized areas.

The two sites selected with spruce forest are at different stages of the destruction which also affects the grass and herb layer. The criterion used to define the intensity of degradation was the fall of spruce trees. The first site (Old Forest – site 1a) was in an area of spruce forests many years old in which the trees did not display external symptoms of degradation, while the second site (Dead Forest – site 1b) was in an area with the remnants of dead trunks and a luxuriantly-developed grass and herb layer. Sites were also selected in an area with self-regenerating, variously-aged young spruces and a luxuriantly-developed herb layer. The sites were a wet area (site 2a) and a dry area (site 2b) (Fig. 1, Table 1).

Table 1. Characteristics of the sites in the Karkonosze Mountains and at Hala Izerska (data for 1992), (Andrzejewska 1994; personal communication)

Geographical location (see Fig. 1)	Jakuszyce				Hala Izerska	
Ecosystems	Forest		Young stand		Meadow	
	old	dead	wet	dry	wet	dry
Symbol of site	1a	1b	2a	2b	3a	3b
Altitude a.s.l.	900–920 m				880–900 m	
Soil (depth 0–10 cm)						
Parent rock	biotite granits					
Soil type	peaty-podsol					podsol
Humidity (%)	56–77	59–64	56–69	47–61	77–82	33–49
Organic matter (%)	53.5	41.2	–	74.0	73.4	26.5
pH (H_2O)	3.6	3.7	3.7	3.7	3.9	4.1
Cellulose decomposition	12.26	40.41	24.51	16.41	25.86	21.54
Soil temperature (°C) (in October)	5.0	6.8	–	11.0	10.0	11.5
Plant cover:	spruce forest before destruction	cleared dead trunks	different aged regenerating stands of spruce (up to 17 years old)		unexploited meadow communities	

Montane meadows with grass-herb vegetation lie in a zone similarly--threatened by industrial emissions, but are charcterized by plant communities which have persisted without obvious structural changes. Hala Izerska – in the Polish part of the Izerskie Mountains – may be included among such areas, and it was at this location that sites 3a and 3b (patches of Wet Meadow and Dry Meadow respectively) were identified (Fig. 1, Table 1).

The sites selected were in the lower montane forest zone and did not differ in the substratum of the parent rock or in the type of soil (with the exception of the dry meadow site). Differences in the pH values of the soils were insignificant (albeit with rather greater acidity at the meadow sites). The sites did differ significantly in the contents of organic matter in their soils as well as in the rate of decomposition of cellulose (Table 1).

The spruce stands in the Jakuszyce area are substitute forest habitats which arose as a result of the economic utilization of habitats actually appropriate to communities of the Fagion alliance (mainly montane acid beechforests). Giving an aspect to this site is the presence of *Deschampsia flexuosa, Calamagrostis villosa* and clumps of *Vaccinium myrtillus*. The destruction of tree stands is followed by a change in the understorey vegetation towards grassy communities in which *Calamagrostis villosa* and *Deschampsia flexuosa* are dominant.

The spontaneous renewal of spruce forest occurs via a regeneration phase involving the growth of young spruce. The understorey beneath the growing trees witnesses a gradual increase in the importance of forest species such as *Vaccinum myrtillus, Oxalis acetosella, Maianthemum bifolium* and *Homogyne alpina.*

The wet meadow on Hala Izerska is in turn dominated by *Calamagrostis villosa, Eriophorum vaginatum, Deschampsia caespitosa, Nardus stricta, Molinia coerulea* and *Scirpus silvaticus*, as well as *Sphagnum* and *Polytrichum* mosses and various herbs.

The dry meadow differs in being dominated by *Deschampsia flexuosa* with an admixture of *Nardus stricta, Deschampsia caespitosa*, sedges and herbs.

The lack of differences in the soil pH values for the study sites (Table 1) restricted the possibilities for estimating the intensity of disturbance due to acid rain to the use of the state of the vegetation cover as an indicator. Thus:

Site 1a → Site 1b	Site 2a Site 2b	Site 3a Site 3b
degradation has become clear through dieback of trees	natural regeneration with differentiation in moisture levels	ongoing process of degradation with differentiation in moisture levels

3. METHODS OF DESCRIPTION AND COMPARISON OF SOIL NEMATODE COMMUNITIES

Nematodes are the best-represented group within the soil Metazoa, and have lately come to be seen as indicators of many soil processes, as well as bioindicators of the contamination and degradation of the natural environment (Arpin et al. 1984, Ferris and Ferris 1984/85, Arpin and Ponge 1986, Wasilewska 1974b, 1985, 1986, 1989, 1991a, 1991b, 1994a, 1995b, Samoiloff 1987). The selection of this group of animals as bioindicators is justified by: 1) small size and short (although varied) generation times; 2) ubiquitous occurrence, an ability to survive in even contaminated and highly-transformed ecosystems and a tendency to be the last group of soil invertebrates to die out in such circumstances; 3) the relative ease with which it is possible to make divisions into functional groups and hence the lack of a need to identify to the species level in every case; 4) the high diversity of taxa in communities; 5) the high degree of trophic diversity; 6) the varying sensitivity which different taxa exhibit in the face of dehydration, salinity and acidity changes, food shortages and low concentrations of oxygen; 7) the wide range of strategies adopted to make use of the resources of an environment.

Trophic classifications of soil nematodes make use of 5–8 group (Yeates et al. 1993). The basic groups are bacterivores, fungivores, facultative plant parasites, obligate plant parasites, omnivores and predators. Nematodes are thus represented at every trophic level, reflecting basic processes ongoing in the soil such as decomposition and mineralization, and having an influence on primary production (Ettema and Bongers 1993, Freckman 1988, Freckman and Ettema 1993, de Goede and Bongers 1994, Wasilewska 1979, 1989, Yeates 1979).

The following indices were adopted in the description and comparison of nematode communities:

1. The density and percentage numerical role of each of the trophic groups of nematode, namely:

– bacterivores (B), which have an impact on the breakdown of organic matter through their feeding on microbes (saprophytic or even pathogenic bacteria, as well as actinomycetes),

– fungivores (F), which feed on the hyphae of many species of fungi, including saprophytic, pathogenic and mycorrhizal species,

– plant parasites feeding on the leaves, buds and roots of vascular plants and having a direct effect on plant growth, or else an indirect effect entailing for example the transmission of other pathogenic agents. Distinquished within this group are facultative plant parasites (FPP) – which also feed on fungal hyphae – and obligate plant parasites (OPP). The FPP group poses great difficulties in ecological research, because it cannot be definitely assigned to either the phytophages or the fungivores,

– omnivores (O), which display links with all the levels of the trophic web as phytophages feeding on root hairs and algal cells, as predators on other nematodes, infusorians, rotifers and amoebae, and sometimes also as consumers of bacteria and fungi. Together with predators, the members of this group are considered to be indicators of disturbances in ecosystems (Wasilewska 1974a, 1985, 1989), being more numerous in those that are little-transformed from their natural state,

– predators (P), which feed on protozoa, enchytraeids, springtails, oligochaetes, nematodes and nematode eggs, as well as on bacteria and fungal spores in the juvenile stages.

2. The ratio of the numbers of bacterivores to fungivores (B/F), which – with account taken of potential fungivores (B/F + FPP) – gives information on the dominant way in which the breakdown of organic matter proceeds (i.e. with the participation of bacteria or fungi). Bacterivorous and mycophagous nematodes do have a significant role in the release of bioelements (Coleman et al. 1983, Ingham et al. 1985). It is also considered that bacteriophagous nematodes are indicators of bacterial activity (Freckman and Caswell 1985, Bååth et al. 1981) – indeed more certain indicators of current activity than plate counts or estimations of biomass (Griffiths 1994, Griffiths et al. 1992).

3. The ratio of the numbers of bacterivorous + fungivorous nematodes to that of obligatory plant parasites (B + F/OPP), as well as the form of relationship taking account of potential fungivores (i.e. B + F + FPP/OPP). These ratios point to the relationship between dead and live mineralization of plant tissues (Wasilewska 1991b), i.e. between the "detritus food web" and the "grazing

food web" of Yeates et al. (1993). The breakdown of dead tissue – subject first to the action of bacteria and fungi which are then fed upon by nematodes – leads to the release of bioelements at a rate that is slower than that possible via the sucking activities of phytophages. In addition, the ratios in question define the pressure exerted by obligate plant parasites on plant hosts in relation to the microbiological activity in the soil. It can be anticipated that ecosystems with slow cycling of elements will have higher values for the ratio, while those with faster cycling will have lower values.

4. Obligate plant parasites (OPP) and obligate + facultative fungivores (F, FPP) are morfologically adapted to suck out the contents of the living cells making up plant tissues and fungal hyphae (at this stage the pathogenic influence of obligatory plant parasites is excluded). The activity of sucking phytophages provides for the most rapid flow of matter and energy from the level of autotrophs to that of heterotrophs (Odum and Biever 1984). If the similar activity of mycophages (also in relation to mycorrhizal fungi) is added in, then a certain picture is given regarding the rapidity with which bioelements are released in a given ecosystem.

5. Shannon's index of taxonomic diversity (H'), which may be used while keeping in mind the latest assessments suggesting that taxonomic diversity is highest where environmental resources are of limited or average availability and where disturbances occur with moderate frequency (Hobbie, Jensen and Chapin 1993).

6. The numerical representation of the most abundant taxa (species or genera), where this creates a defined fraction (e.g. about 60%) of the entire grouping of nematodes. Stress situations more often than not exaggerate the dominance structure leaving fewer dominants but at an even higher level of abundance (Wasilewska 1995b).

7. Indices of the maturity of nematode communities. These are created on the basis of principles of succession or of the differential sensitivity of taxa to stress or discontinuities in succession. The hypothesis of succession is considered to be a function of the invasion and loss of species with different life strategies (Colinvaux 1986). Bongers (1990) presented original indices of maturity for nematode communities. Taxonomic families or genera are classified as "colonizers" (short life cycle, high reproductive rates, tolerant to disturbance) and assigned a numerical weighting of 1, or else as "persisters" (long life cycle, low colonization ability, few offspring, sensitive to disturbance) and assigned a weighting of 5. The Bongers (1990) formula for the Maturity Index (MI) is then:

$$MI = \Sigma\ vi\ pi$$

where vi is the value on the colonizers-persisters scale for the i-th taxon and pi is the proportion of the i-th taxon in the community.

a) The Maturity Index (MI) after Bongers (1990) is based only on free-living taxa of nematodes (on the colonizers-persisters scale of 1–5).

b) The Maturity Index total (Σ MI), based on all nematodes in the community (after Bongers 1990, Wasilewska 1994b, Yeates 1994). Yeates (1994) argued that combining the plant-feeding and free-living nematode taxa into a single maturity index enhanced the biological validity of the index by its holistic nature.

The MI and Σ MI indexes contain a quantitative assessment of taxa with different strategies for the utilization of environmental resources (the r-K strategy denoted by Pianka (1970)). Both indexes are reduced by ecosystemic disturbances, and are inclined to rise again with the return to the pre-stress situation (Ettema 1993, Ettema and Bongers 1993, Freckman and Ettema 1993, de Goede and Bongers 1994, de Goede and Dekker 1993, de Goede et al. 1993, Háněl 1995, Wasilewska 1994a, 1994b, 1995a). It seems that stress induces a return to earlier successional stages – as part of a process termed the retrogression of the system by Rapport et al. (1985). In the light of this, it was anticipated that there would be a similar reaction as a result of acid rain.

c) The Plant Parasite Index (PPI), based on plant-parasitic (FPP + OPP) taxa only on the c-p scale 2–5 (Bongers 1990). According to Freckman and Ettema (1993) and Neher and Campbell (1994), an increase in the PPI reflects increased plant production. It has also been stated that the value of the index rises with increased disturbance in nature, being for example higher in annual crops than perennial crops (Freckman and Ettema 1993), and higher in monoculture conditions than in multi-species cultivation (Wasilewska 1995a). However, Neher and Campbell (1994) did obtain higher PPI values for perennial crops than for annual ones, and in summary it can be said that index is still "in its infancy" and requires further evaluation.

The above indices and parameters were calculated on the basis of material obtained from the study sites on one occasion between 28th and 30th September 1992. The sites in question, located in the Karkonosze and Izerskie Mountains, have been described in Section 2. Collected from each site were 10 soil cores to depths of 25 cm. After mixing the samples were divided into several 25 ml samples for extraction using a version of Baerman's method modified in accordance with the earlier methodology devised by Wasilewska (1979). Classification of nematodes to the generic level was done for 3 samples of 25 ml, with about 500 individuals per site being identified. The trophic classification was performed in accordance with the method of Wasilewska (1971a), albeit with account taken of some changes made to the methodology by Yeates et al. (1993).

The comparison of the nematode communities from the Karkonosze and Izerskie Mountains on the one hand, and from other regions of Poland on the other, was carried out on the basis of an earlier study produced by the author. The parameters presented in the work – which have entered the literature only recently – were calculated on the basis of the author's materials.

4. THE RESULTS OF THE RESEARCH IN THE KARKONOSZE AND AT HALA IZERSKA

4.1. COMPOSITION AND DOMINANCE STRUCTURE

There were distinguished 53 genera of nematodes in the samples from the studied parts of the Karkonosze Mountains and Hala Izerska. The best-represented grouping within this total included those nematodes associated with the consumption of fungal hyphae in an obligate or facultative way. Furthermore, the taxa in this group were richest in dominants (those accounting from more than 10% of the community), with the three genera *Aglenchus, Filenchus* and *Aphelenchoides* being concerned. A similar dominance of three further taxa was noted only in the group of obligate plant parasites from sites 1a, 3a and 3b (Table 2).

Table 2. Trophic categorization of nematode genera occurring at the study sites in the Karkonosze Mountains and at Hala Izerska. Dominants within a trophic group are marked: + <20%, ++ ≥ 20–30%, +++ > 30%, while dominants in the grouping as a whole are marked by [1] > 10%
Site symbols as in Table 1

Ecosystem	Forest		Young stand		Meadow	
	Site symbol					
	1a	1b	2a	2b	3a	3b
Bacterivores						
1 *Acrobeloides*		++	++	+++	+++	++
2 *Alaimus*		+	+		+	
3 *Cervidellus*				+		
4 *Cylindrolaimus*	+					
5 *Domorganus*	++					
6 *Euteratocephalus*	+	+				
7 *Metateratocephalus*						+
8 *Panagrolaimus*	+	+	+		+	+
9 *Plectus*	+	+	++		+	+++
10 *Prismatolaimus*	+	+	+		+	
11 *Rhabdolaimus*		+	+			+
12 *Teratocephalus*	+++	+++	+	+	+	+
13 *Wilsonema*					+	
Fungivores + Facultative plant parasites						
1 *Aglenchus*	++[1]	+++[1]	+++[1]	+++[1]	+++[1]	+
2 *Aphelenchoides*	+	+++[1]	+	+	+	++
3 *Basiria*	+	+	+		+	
4 *Boleodorus*	+	+				
5 *Coslenchus*	+		+		+	

Ecosystem	Forest		Young stand		Meadow	
	Site symbol					
	1a	1b	2a	2b	3a	3b
6 *Deladenus*	+					
7 *Ditylenchus*	+	+	+	+	+	+
8 *Filenchus*	++[1)]	+	+	+++[1)]	++	+++[1)]
9 *Lelenchus*	+					
10 *Malenchus*	+		+	+		
11 *Miculenchus*		+	+			
12 *Nothotylenchus*		+	+		+	
13 *Paraphelenchus*					+	
14 *Polenchus*		+				
15 *Psilenchus*					+	
16 *Tylenchus*	+		+	+		+
17 *Tylenchida* others	+					
Obligatory plant parasites						
1 *Helicotylenchus*	+++[1)]	+	++		+++[1)]	+
2 *Heterodera* juv.		+				
3 *Paratylenchus*	+	+	+	+++	+	+++[1)]
4 *Pratylenchus*		+++			+	+
5 *Pratylenchoides*	+	+				
6 *Rotylenchus*	+++[1)]	+	+++			+
7 *Trichodorus*					+	
8 *Tylenchorhynchus*						+
Omnivores + predators						
1 *Dorylaimellus*						+++
2 *Eudorylaimus*	+++	+++	+++	+++	+++	+++
3 *Mesodorylaimus*					+	
4 *Prodorylaimus*					+++	
5 *Seinura*					+	

Presented below are the genera dominant in each of the trophic groups. Amongst the bacterivores, the genus *Teratocephalus* occurred at all sites and constituted a dominant of the group in the forest ecosystem (sites 1a and 1b). The genus *Acrobeloides* would seem to have been dominant at all the sites with the exception of 1a. In turn, the dominants of the fungivorous group coincided with the main dominants of the nematode community as a whole. The dominants among the obligate plant parasites differed from site to site (especially in relation to the host plants present) and were found to belong to the genera *Helicotylenchus*, *Rotylenchus* and *Pratylenchus*. The genus *Paratylenchus* occurred at all sites, albeit with a particularly marked dominance at the so-called dry sites (100% and 75% of all OPP species in the cases of sites 2b and 3b respectively). The group of omnivores and predators was dominated by the genus *Eudorylaimus*, although this was joined by *Prodorylaimus* in the case of site 3a. In fact, however, predators were mostly absent except for members of the genus *Seinura* (Table 2).

The core composition (55–61%) of the different nematode communities was found to involve species from group OPP and group F + FPP (Table 3). The sharpness of this dominance was greater at site 1b (where 3 taxa were involved) than at site 1a (with 4). The two remaining ecosystems of dry sites were characterized by more marked dominance (4 taxa at site 3a, 2 at 3b), with the same two taxa forming the core of the groupings at sites 2a and 2b, albeit with the percentage representation significantly higher at the dry site (Table 3).

Table 3. Dominant genera accounting together for 55–61% of the nematode community in the Karkonosze and at Hala Izerska – with an indication of trophic allegiances (for an explanation of the trophic symbol see Table 4)

Site					
1a			1b		
		%			%
Forest					
Helicotylenchus	(OPP)	20	*Aglenchus*	(FPP)	27
Rotylenchus	(OPP)	15	*Aphelenchoides*	(F)	19
Filenchus	(FPP)	12	*Pratylenchus*	(OPP)	9
Aglenchus	(FPP)	10		Σ	55
	Σ	57			
Site					
2a			2b		
Young stand					
Aglenchus	(FPP)	48	*Aglenchus*	(FPP)	39
Filenchus	(FPP)	12	*Filenchus*	(FPP)	36
	Σ	60		Σ	75
Site					
3a			3b		
Meadow					
Helicotylenchus	(OPP)	31	*Paratylenchus*	(OPP)	45
Aglenchus	(FPP)	14	*Filenchus*	(FPP)	16
Basiria	(FPP)	8		Σ	61
Acrobeloides	(B)	7			
	Σ	60			

The influence of acid rain on nematodes in the soils of highly-contaminated areas has only been studied in the north-western Czech Republic (H á n ě l 1993b) and in south-west Germany (R u e s s 1995). Both studies were concerned with spruce forest. The soils of the acid rain-contaminated stands studied by Ruess were found to have members of the genera *Teratocephalus, Metateratocephalus, Acrobeloides, Tylenchus* s.l. and *Aphelenchoides* as dominants, while those researched by Hánel revealed *Filenchus* and *Acrobeloides* species to be dominant, with populations of *Aphelenchoides* considered exceptionally low.

Noteworthy in the Karkonosze and Hala Izerska was the lack of rhabditids and diplogastrids, the exceptionally limited representation of cephalobids other than *Acrobeloides*, and the absence of the mononchids and predatory dorylaimids noted to differing degress of abundance in the forests and meadows of other parts of Poland (Wasilewska 1970, 1971a, 1974b, 1976). The great extent to which the forest environment was dominated by representatives of the Teratocephalidae is most probably linked with soil acidificiation (Buttner 1989), because this taxon does not attain a dominant position among bacteriophages in other forest environments (Wasilewska 1970, 1971c, Sandner and Wasilewska 1970). Spruce forest of the Czech Republic were characterized by the presence, but not the dominance, of representatives of this family in soils (Háněl 1993b). It is thus possible that the degree of dominance depends on the intensity of the stress.

4.2. NUMERICAL REPRESENTATION AND TROPHIC STRUCTURE

The young stands of spruce at sites 2a and 2b are poorer in nematodes than the forest and meadow environments (Table 4).

Table 4. Abundance (10^3 m^{-2}) of trophic groups of nematodes at sites in the Karkonosze and at Hala Izerska (n = 3)

Ecosystem	Forest		Young stand		Meadow	
Trophic group	Site					
	1a	1b	2a	2b	3a	3b
Bacterivores – B	1100	1350	550	500	1525	400
Fungivores – F	300	1800	125	25	700	375
Facultative plant parasites – FPP	1950	2925	2800	2950	3400	1450
Obligatory plant parasite – OPP	1950	1925	225	25	3625	3475
Omnivores	25	250	50	25	550	75
Predators					25	
Total	5325	8250	3750	3525	9825	5775
B/F	3.7	0.8	4.4	20.0	2.2	1.1
B/F + FPP	0.5	0.3	0.2	0.2	0.4	0.2
B + F/OPP	0.7	1.6	3.0	21.0	0.6	0.2
B + F + FPP/OPP	1.7	3.2	15.4	139.0	1.6	0.6

The best-represented and dominant group was made up of fungivorous species (F + FPP), which accounted for between 42 and 84% of the nematodes recorded in the forest environment. The highly-degraded site (1b) was shown to differ from less-degraded site (1a) in the elevated absolute and percentage representation of this group (Table 4, Fig. 2). The percentage share of fungivores was lover in the meadow environment, at 32–42%, but their absolute number (mainly at site 3a) was even higher than at two other forest sites (Table 4, Fig. 2).

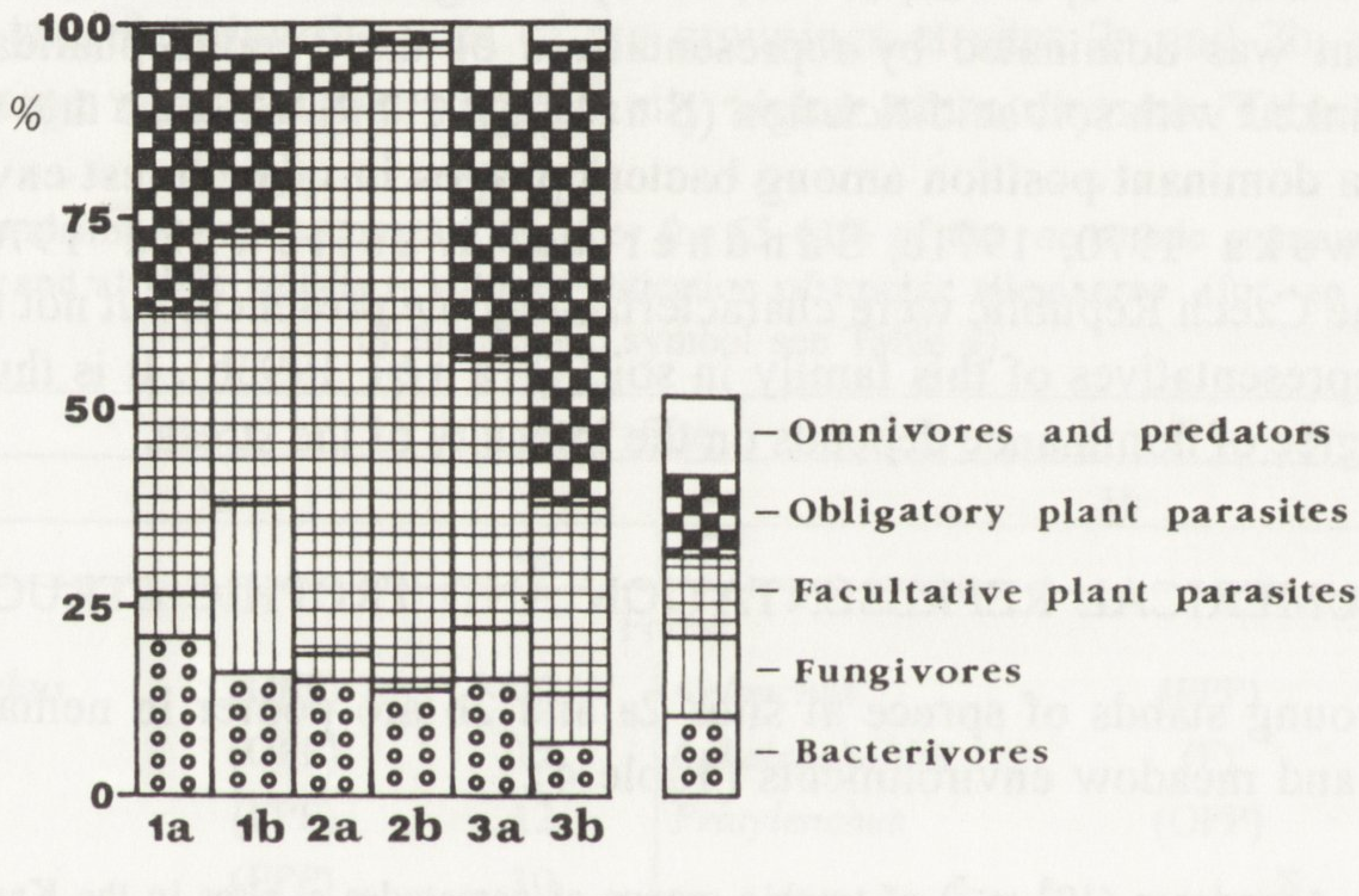

Fig. 2. Trophic structure (in % of total numbers) of nematode communities in ecosystems in the Karkonosze Mountains and at Hala Izerska
Site symbols as in Fig. 1 and Table 1

Populations of bacterivores varied, with the lowest being noted in young spruce stands (sites 2a and 2b) and the dry meadow (site 3b), and the highest in "dead forest" (site 1b). The percentage share taken by this groups varied between 7 and 21%, and thus nowhere reached even one-quarter of the total community (Table 4, Fig. 2).

Obligate plant parasites constituted the most abundant group in meadow soils but were only about half as numerous in the old forest environment (sites 1a and 1b). In turn, minimal representation of this group was noted in young stands of spruce (Table 4). Away from this last habitat, it was the OPP group which dominated in a significant manner (Fig. 2).

Values considerably below 1 were noted at all sites for the ratio between bacterivorous and fungivorous nematodes (B/F + FPP). This indicates that the prevailing form of decomposition involves fungi rather than bacteria. Advancing degradation of the environment (site 1b), or significant drying (sites 2b and 3b), both tend to reduce the value of the ratio (Table 4). The B/F ratio is in principle cited to visualize the role of obligate fungivores, and the lowest value for it was noted in the environment degraded to the greatest extent (i.e. site 1b) (Table 4).

At present it is difficult to determine if such a great abundance of fungivores (especially as degradation of the forest environment proceeds) reflects increased numbers of saprophytic fungi only, or if ecto- and endomycorrhizal species are also involved in the population increases. It is quite possible to envisage a rise in the numbers of all three types, with the different attendant effects on the biocoenosis involved.

The ratio linking nematodes with the release of bioelements via the feeding of reducers and directly by the feeding on primary producers (B + F/OPP and B + F + FPP/OPP) points above all to the greatest significance of this process in young stands (Table 4). The significance of the detritus chain is greater in a degraded site (value for site 1b > value for site 1a). Values of the ratio do not differ significantly between sites 3a and 1a, but the dry meadow environment (site 3b) did have a value considerably below 1 as a result of reduced populations of fungivorous nematodes and elevated numbers of phytophages. The highest value for the ratio under discussion was noted in young stands (with the value for site 2b exceeding that for site 2a). The reason here was the minimal representation of members of the OPP group at the first of these two sites (Table 4).

There is no doubt that the soils of the Karkonosze and Hala Izerska do have very low microbiological activity, irrespective of the form of decomposition which prevails. Thus the rate of decomposition of organic substances is a slow one (Pietr et al. 1993, Chmielewski 1994, Kidawa 1994).

4.3. DIVERSITY AND MATURITY

Shannon's (H') index of generic diversity joined the various indices showing the maturity of the community (MI, Σ MI and PPI) in displaying the highest values at the least-degraded forest site (1a), and values very little lower at the wet meadow site (3a) (Fig. 3). H' differed significantly ($p < 0.001$) between all the sites except 1a and 1b, for which it is only possible to describe a trend towards a fall in the value of the index ($p < 0.2$). The highly-degraded environment of site 1b recorded lower values for the indices, although values were lower still in young stands. Only the MI index appeared to be sensitive enough to "register" the process of regeneration, with values for sites 2a and 2b being greater than that for site 1b. Drier environments (2b and 3b) differed from their wetter analogues (2a and 3a) in displaying significantly lower values for all of the indices in question (Fig. 3).

The obvious conclusion to be drawn from this analysis is that the diversity and maturity of the community decline as a result of the stress imposed by acid rain, albeit in such a way that the process takes on a stronger form where soils

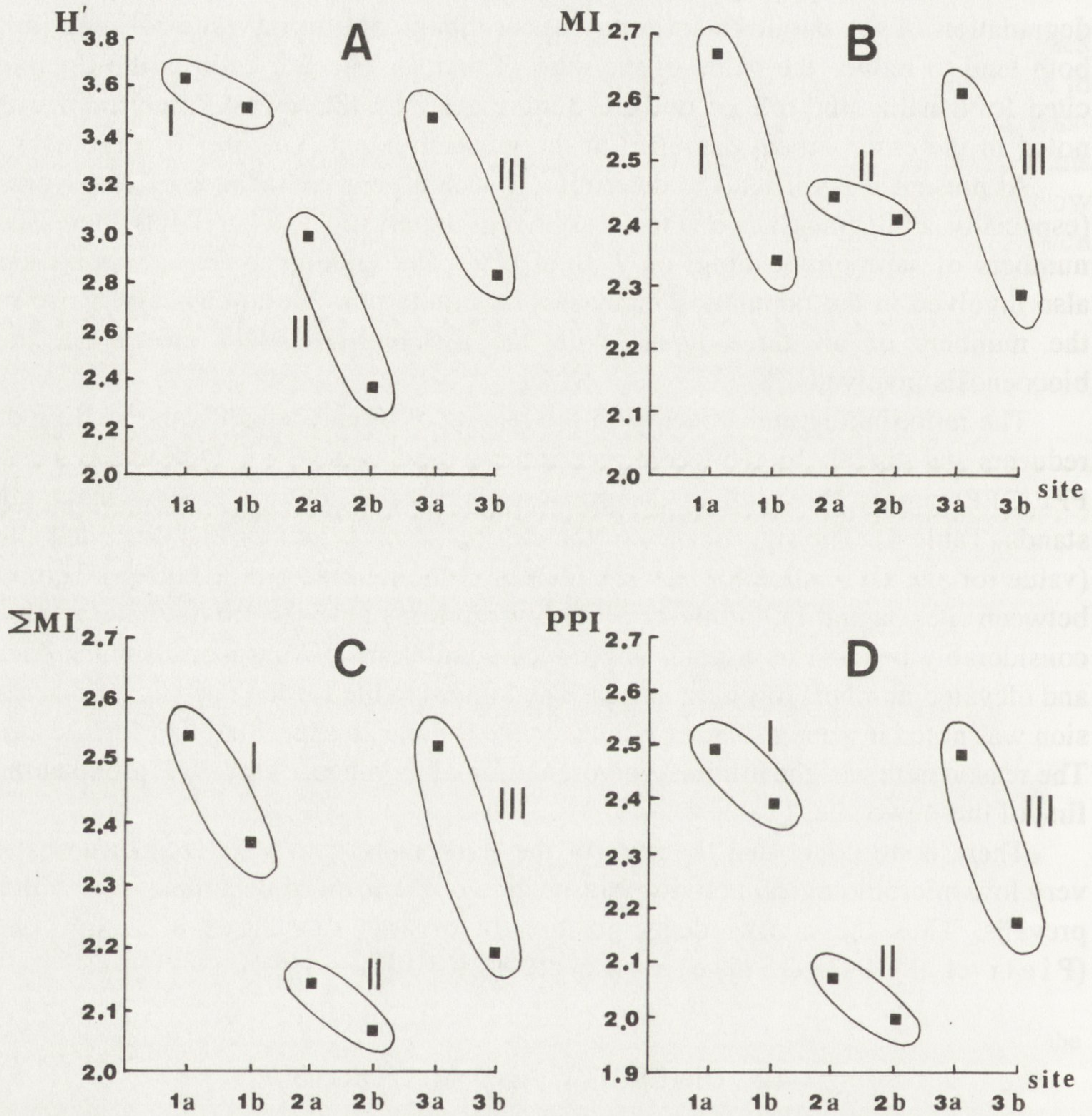

Fig. 3. Shannon index of generic diversity (H') – A, as well as indices of maturity for the nematode communities: MI – B, Σ MI – C and PPI – D in the ecosystems of the Karkonosze Mountains and Hala Izerska. Site symbols according to Fig. 1 and Table 1. Encircled are: I – forest ecosystems with degradation revealed through the death of trees; II – young stnads regenerating naturally in conditions of higher or lower humidity; III – grassy vegetation transformed by the long-term influence of acid rain – in more or less humid conditions

are drier. A similar phenomenon of enhanced stress brought about by the use of mineral fertilizers in dry conditions as opposed to moist conditions was noted for soil nematode communities in Scots pine forest in Sweden (Sohlenius and Wasilewska 1984).

Ecosystems with regenerating tree stands – as personified by sites 2a and 2b – show diversity and maturity indices that remain lower than those in old spruce forest (site 1a) or the permanent meadow ecosystem unstressed by desiccation (site 3a).

5. COMPARISON OF THE ACID RAIN-STRESSED NEMATODE COMMUNITIES OF THE KARKONOSZE AND HALA IZERSKA WITH THOSE FROM UNCONTAMINATED AREAS

It is currently difficult to single out an area of Poland not contaminated by acid rain. Relating the Karkonosze sites to forest and meadow ecosystems in central and northern Poland and in the Carpathian foothills gives a more reliable concept of "non-contamination" the greater the span of time between the research and 1992. Most of the sites available for comparison (Fig. 4) provide data for the 1970s and, while the comparisons are advantageous since they reflect work by the same author using the same methods, they also have a minus side in the impossibility of considering all the environmental and climatic differences between habitats, as well as inevitable minor methodological differences (e.g. in the number and seasonality of samples).

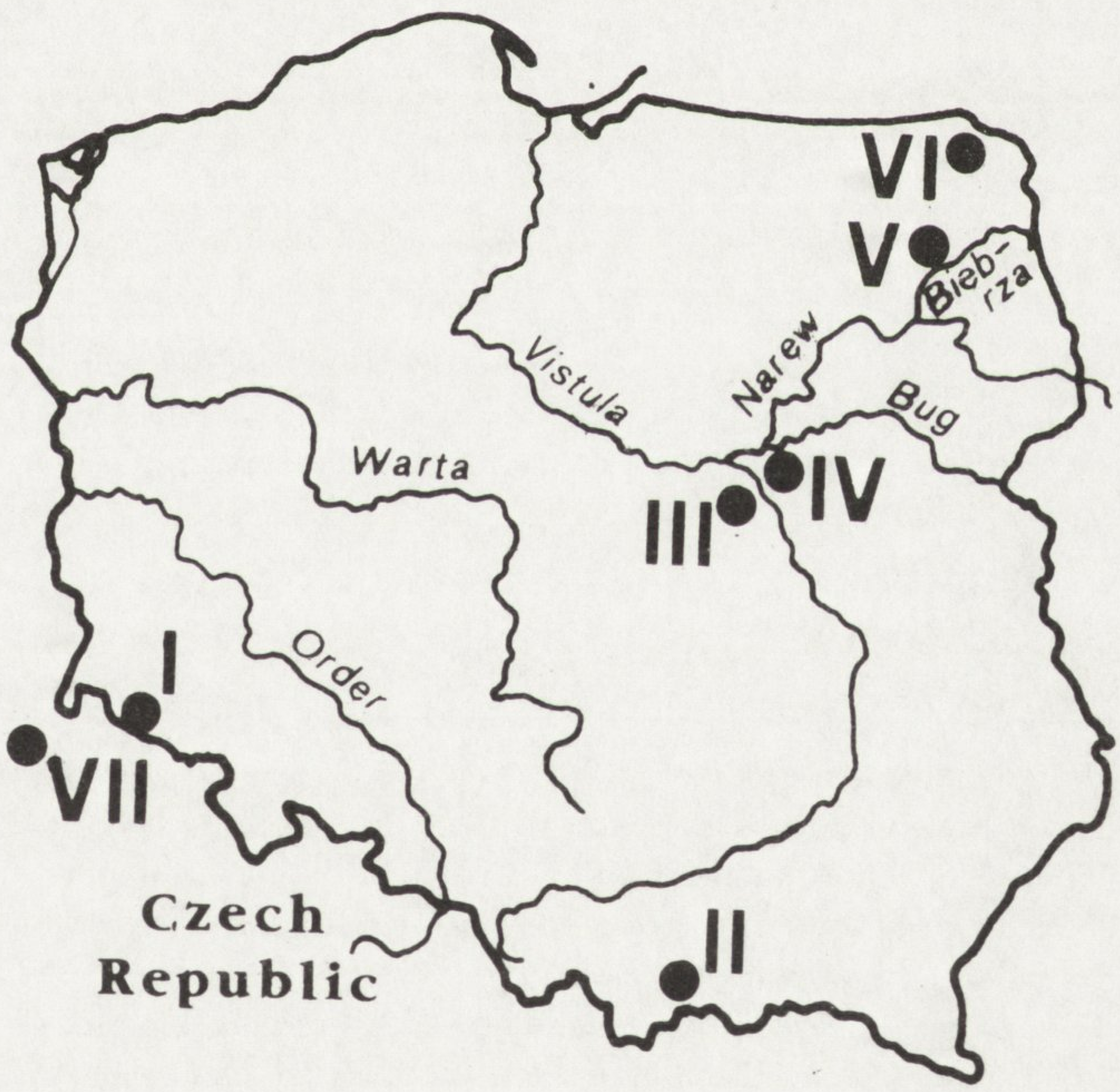

Fig. 4. Map of Poland with locations of sites providing comparative material marked (symbols and some descriptions of sites given in Table 5 along with cited papers)
I – the Karkonosze Mountains (site 1F: 1a, 1b, 2a, 2b) and Hala Izerska (site 1G: 3a, 3b); II – Carpathian Mts (site 3G); III – Kampinos Forest (sites 2F, 3F, 4F, 5F and 5G); IV – Vistula river terrace (site 4G); V – Biebrza and Narew River valleys (site 6G); VI – Suwałki region (site 2G); VII – Krušne Mts., Czech Republic (site 6F)

5.1. ABUNDANCE

The upper limits for total populations of nematodes in the forest ecosystems of the Karkonosze and in the grass-herb communities of Hala Izerska fall above the levels established for populations in other regions of Poland. As Fig. 4 and Table 5 make clear, it is only on drained peaty meadows in the Biebrza Marshes and in some meadows in the Suwałki area that the densities recorded for the Karkonosze and Hala Izerska sites are exceeded (in the first case several-fold).

However, the total population density is rarely an indicative feature since it says only that the given ecosystem remains in a position to maintain a numerically-abundant group of free-living nematodes. In the last sense, the nematode communities from contaminated spruce forest in the Czech Republic and Germany have been found to be decidely less numerous, especially when compared with those of the mature Karkonosze spruce forests only (Table 5).

Table 5. Range of abundance (10^3 m^{-2}) of soil nematodes in several forest and meadow ecosystems in Poland and in two (contaminated) forest ecosystems in neighbouring countries. Printed in bold are the sites contaminated by acid rain. The location of sites is given in Fig. 4

Site	Trophic group					Total
	Bacterivores	Fungivores	Facultative plant parasites	Obligatory plant parasites	Omnivores + predators	
Forest ecosystem						
1F	**500–1350**	**25–1800**	**1950–3000**	**1925–1950**	**25–250**	**3525–8325**
2F	2326	3300	1700	112	254	7962
3F	156–2644	182–1873	30–1380	41–277	100–222	509–6329
4F	1920	910	140	250	270	3490
5F	395	63	313	108	807	1686
6F	**319–438**	**11–26**	**38–785**	**4–64**	**4–9**	**436–1210**
7F	–	–	–	–	–	**1400–5100**
Grassland ecosystem						
1G	**400–1525**	**375–700**	**1450–3400**	**3475–3625**	**75–575**	**5775–9825**
2G	1600–5400	250–1400	700–1900	800–1950	450–2700	7350–11650
3G	750–1492	250–462	458–748	990–1490	680–2038	4184–5224
4G	1373	208	268	574	239	2662
5G	832–946	212–392	80–82	508–898	68–70	1700–2388
6G	2200–8100	400–1600	400–10600	400–31200	200–1200	4100–34100

Designations of sites:
1F – Site in the Karkonosze Mountains, present paper; **2F** - Acidophilous oak-pine forest (Pino-Quercetum), humus-rich podsolic soil, Puszcza Kampinoska (Sandner and Wasilewska 1970, Wasilewska 1970); **3F** – Afforested dunes, succession from 17–20 years-old pines to the Potentillo albae-Quercetum association, Puszcza Kampinoska (Wasilewska 1970, 1971b, 1979); **4F** – young 15-year-old pine stand on sandy ground, Kampinos Forest (Wasilewska 1971c); **5F** – Ecotone between Pino-Quercetum and Carici elongatae-Alnetum, wet forest with periodically stagnant water, Kampinos Forest (Sandner and Wasilewska 1970, Wasilewska 1979); **6F** – Spruce forest degraded by industrial emission, Kruśne Mts., The Czech Republic (Háněl 1993a); **7F** - Spruce forest degraded by industrial emission, south-west Germany, Bavaria and Schwabia (Ruess 1995);
1G – Site at Hala Izerska, present paper; **2G** – Permanent meadows in Suwałki Landscape Park (Wasilewska 1994b); **3G** – Montane pastures periodically grazed by sheep and differentiated by intensity of grazing, Pieniny Mts., (Wasilewska 1974a, 1979); **4G** – Cultivated meadow on fertile alluvial soil, medium fertilized, the upper Vistula River terrace (Wasilewska 1976, 1979); **5G** – Old hay meadow of the order Arrhenatheretalia, Łomna village, the vicinity of Kampinos Forest (Wasilewska, unpublished); **6G** – Fen peat meadows in Biebrza River and Narew River valleys, differentiated by peat origin and time after drainage (Wasilewska 1991b).

The density of fungivores and potential fungivores (group FPP) – considered together as the mycophilous group – is clearly at its peak in the Karkonosze and Hala Izerska. Here too, the Czech spruce forests display the lowest densities (Table 5).

The density of obligate plant parasites in the Karkonosze and on Hala Izerska exceeds in a very marked way the densities noted for all other sites on the list. This is the case for both forest ecosystems (excluding those associated with young stands) and meadow ecosystems (Table 5).

As mentioned previously, predatory nematodes are virtually absent from the Karkonosze and Hala Izerska sites (Table 2). This is also the case for the contaminated spruce forests of the Czech Republic. In turn, the abundance of omnivorous nematodes in the Karkonosze and Hala Izerska sites was also near the lower limits of abundance noted for omnivorous and predatory species in other regions of Poland (Table 5).

5.2. A COMPARISON BETWEEN THE KARKONOSZE SPRUCE FORESTS AND SOME OF THE FOREST ECOSYSTEMS OF KAMPINOS FOREST (CENTRAL POLAND)

The forest with which the comparison was made is 17–20 year-old pine forest covering dune elevation in Kampinos Forest, an extensive area of forest and wetland habitats just west of Warsaw. The forest in question is dominated by *Pinus silvestris, Juniperus communis, Quercus robur* and *Betula verrucosa*, with the understorey layers consisting of grasses, herbs amd mosses. At 1.58%, the humus content of the soils qualifies them for site D after Wasilewska (1970). The second site (identified as site E in the same paper) was on a high dune overgrown naturally by a multi-species stand dominated by a 135-year-old pine. The community present was *Potentillo albae-Quercetum* and the soil humus content was 2.13%. The sites in question had soils with pH values 1 or 2 units higher than those noted for Karkonosze sites (Table 6). The locations of both sites have been designed by the symbol 3F (Fig. 4).

Speaking in favour of the selection of these sites is the relatively high level of similarity between densities of all nematodes combined. However, the Karkonosze sites had lower densities of bacterivores, omnivores and predators, as well as significantly higher densities of obligate plant parasites (Table 6). This difference is further revealed in the percentage shares taken by the various trophic groups (Fig. 5). Fungivorous nematodes (F + FPP) are well-represented in both regions, but the ratio of bacterivores to fungivores (B/F + FPP) is much higher at the Kampinos Forest sites. Similarly, the ratio of bacterivores + fungivores to nematodes living at the cost of primary producers (i.e. B + F + FPP/OPP) is many times lower in the Karkonosze Mountains than in the Kampinos Forest (Table 6). This obviously results from the high numbers of phytophagous nematodes in the former area. Generic diversity H' is

Table 6. Abundance ($N \cdot 10^3 \cdot m^{-2}$) and biocoenotic parameters for soil nematodes in the two ecosystems in the Karkonosze (sites 1a and 1b) as well as two forest ecosystems in Kampinos Forest (central Poland) (site 3F in Fig. 4; the site referred to as D in the work of W a s i l e w s k a (1970, 1971b) – hence 3FD and the site referred to as E – hence 3FE)

Parameter		3FD	3FE	1a	1b
		Kampinos Forest		Karkonosze	
pH (H_2O) in the 0–10 cm soil layer		~ 4.6[1)]	~ 5.9[1)]	3.6	3.7
N	Total	6329	4480	5325	8250
	Bacterivores – B	2644	1581	1100	1350
	Fungivores – F	1873	1773	300	1800
	Facultative plant parasites – FPP	1380	910	1950	2925
	Obligatory plant parasites – OPP	210	72	1950	1925
	Omnivores	180	99	25	250
	Predators	42	45		
Ratio	B/F + FPP	1.2	1.7	0.5	0.3
	B + F + FPP/OPP	28.1	59.2	1.7	3.2
Number of genera		38	40	24	24
Shannon generic index (H')		3.6	3.1	3.6	3.5
Maturity indices: MI		2.2	2.1	2.7	2.3
Σ MI		2.2	2.2	2.5	2.4
PPI		2.1	2.1	2.5	2.4

1) obtained for 1965 from the unpublished materials

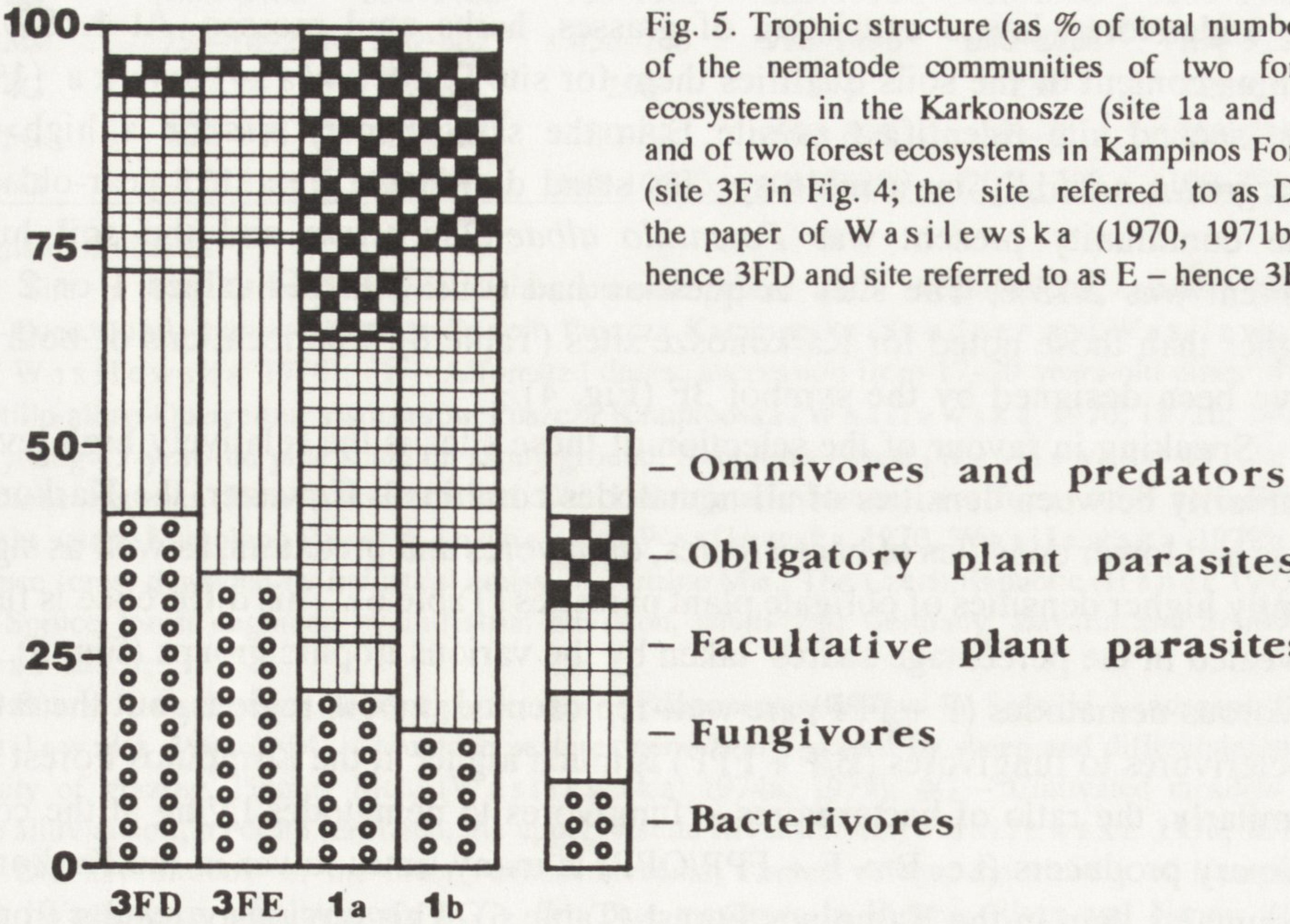

Fig. 5. Trophic structure (as % of total numbers) of the nematode communities of two forest ecosystems in the Karkonosze (site 1a and 1b) and of two forest ecosystems in Kampinos Forest (site 3F in Fig. 4; the site referred to as D in the paper of W a s i l e w s k a (1970, 1971b) – hence 3FD and site referred to as E – hence 3FE)

high in both regions, in spite of the smaller number of taxa in the Karkonosze. However, maturity indices attain a considerably higher values at the Karkonosze sites. It would at first seem that the low representation of omnivores and predators at these sites should have lowered the value for the maturity index, but in fact it is too low to be of significance. Reasons for the significantly higher MI and Σ MI values in the Karkonosze should be sought in the variable life strategies adopted by species within the bacterivorous group. The group of bacterivores from the Karkonosze sites is significantly richer in taxa that are higher-ranking where life strategy (c-p value) is concerned (Table 7). The PPI index predominates in a significant way at the Karkonosze sites (Table 6).

Table 7. Percentage share of nematode taxa with different life strategies (colonizer-persister (c-p) values after B o n g e r s 1990) in the group of bacterivores of forest ecosystems in the Karkonosze and Kampinos Forest (central Poland). Site symbols are as given in Table 6 and Fig. 4)

c-p value	Site			
	3FD	3FE	1a	1b
	Kampinos Forest		Karkonosze	
1	5	7	2	5
2	92	88	14	43
3	3	5	84	50
4				2

5.3. COMPARISON OF YOUNG SPRUCE STANDS IN THE KARKONOSZE WITH YOUNG PINE STAND IN KAMPINOS FOREST (CENTRAL POLAND)

The site in Kampinos Forest was a 15-year-old stand of Scots pine (*Pinus silvestris* L.) on sandy land near Izabelin within the Laski Forestry District (W a s i l e w s k a 1971c) (site 4F on Fig. 4). The stand in question extends over 1.5 ha and has a soil pH value more than 2 units higher than at the Karkonosze sites (Table 8).

The three compared sites had similar densities of nematodes, albeit with those in the Karkonosze having lower absolute and relative densities of bacterivores, and of omnivores + predators, as well as higher densities of fungivores + potential fungivores (F + FPP) (Table 8, Fig. 6). The value for the ratio of bacterivores to fungivores (B/F + FPP) was also lower in the mountains. It may be considered that role of nematodes in the release of bioelements takes place more *via* the detritus chain in the young stands in the Karkonosze. There is a high value for the ratio B + F + FPP/OPP than was noted for the young stand in Kampinos Forest. This is thus the reverse situation of that applying to the old stands in the Karkonosze (Table 6). Lower values for the index of diversity and for all three indices of maturity characterized the young stand in the Karkonosze when compared to that in the Kampinos Forest (Table 8). The high value for the PPI index observed in the young stand in the latter area was associated with the abundant occurrence of *Trichodorus pachydermus*

Table 8. Abundance $(N \cdot 10^3 \cdot m^{-2})$ and biocoenotic parameters for soil nematodes of two young spruce stands in the Karkonosze (sites 2a and 2b) and a young pine stand in Kampinos Forest (central Poland) Wasilewska (1971c) (site 4F in Fig. 4)

	Parameter	Site 4F	2a	2b
		Kampinos Forest	Karkonosze	
pH (H_2O) in the 0–10 cm soil layer		6.0[1)]	3.7	3.7
N	Total	3490	3750	3525
	Bacterivores – B	1920	550	500
	Fungivores – F	910	125	25
	Facultative plant parasites – FPP	140	2800	2950
	Obligatory plant parasites – OPP	250	225	25
	Omnivores	210	50	25
	Predators	60		
Ratio	B/F + FPP	1.8	0.2	0.2
	B + F + FPP/OPP	11.9	15.4	139.0
Number of genera		21	21	14
Shannon generic index (H')		3.2	3.0	2.3
Maturity indices:	MI	2.2	2.4	2.4
	Σ MI	2.3	2.1	2.1
	PPI	2.9	2.1	2.0

1) approximate estimate for the year 1970.

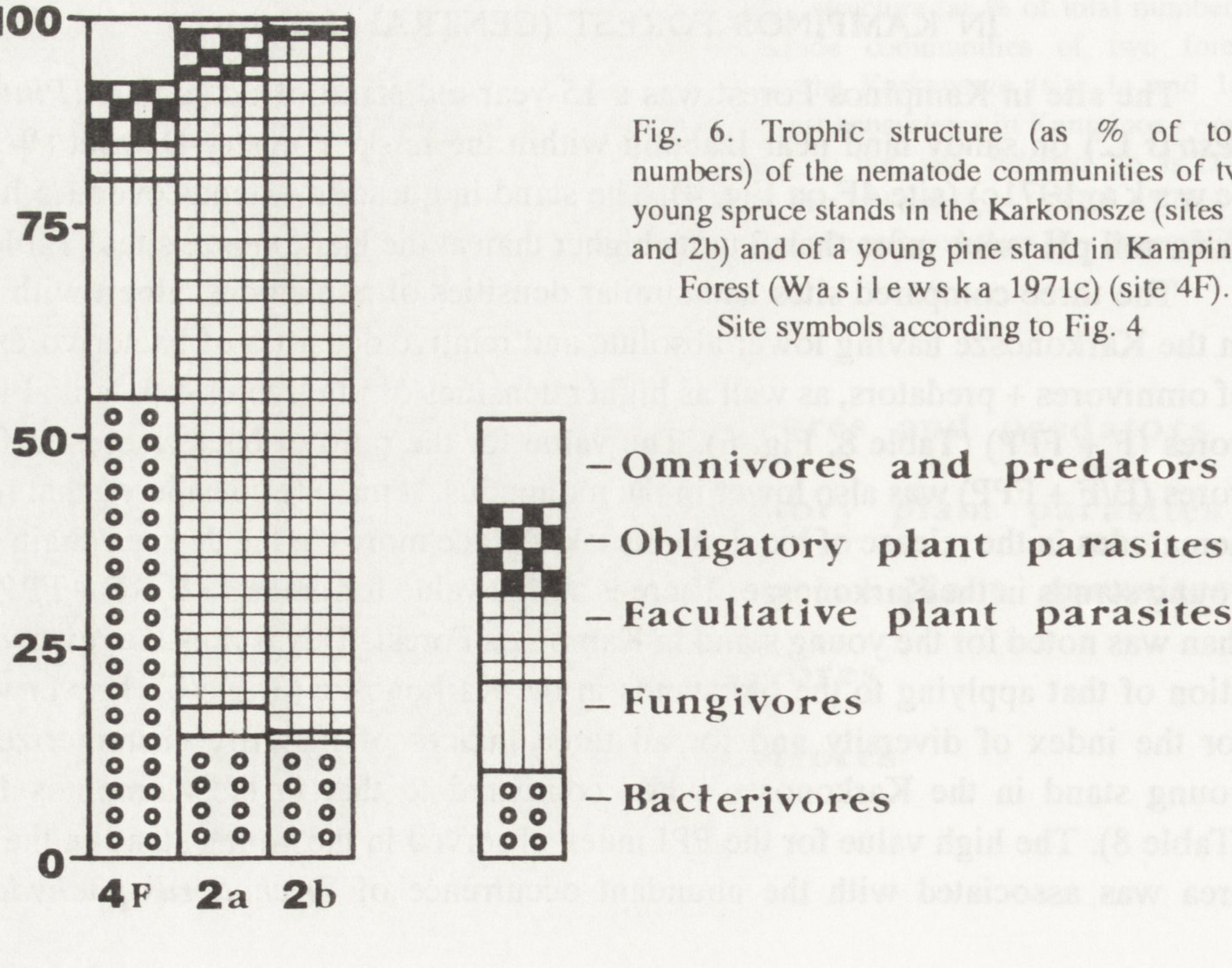

Fig. 6. Trophic structure (as % of total numbers) of the nematode communities of two young spruce stands in the Karkonosze (sites 2a and 2b) and of a young pine stand in Kampinos Forest (Wasilewska 1971c) (site 4F). Site symbols according to Fig. 4

(Seinhorst 1954) and *Xiphinema americanum* (Cobb 1913). These are species of the highest rank where the colonizer-persister (c-p) scale of Bongers (1990) is concerned. In comparisons with Kampinos Forest, the young Karkonosze tree stand resembled its mature counterpart (Table 7) in having a greater proportion of taxa of higher life strategy rank (higher values on c-p scale) among the bacterivores (Table 9).

Table 9. Percentage share of nematode taxa with different life strategies (colonizer-persister (c-p) values after Bongers 1990) in the group of bacterivores of young forest stands in the Karkonosze and Kampinos Forest (central Poland). Site symbols are as given in Table 8 and Fig. 4)

c-p value	Site		
	4F	2a	2b
	Kampinos Forest	Karkonosze	
1	9	9	
2	88	50	70
3	3	32	25
4		9	5

5.4. COMPARISON OF THE GRASS-HERB COMMUNITIES AT HALA IZERSKA WITH UNUSED PASTURE IN THE CARPATHIAN FOOTHILLS OF SOUTH POLAND, AND WITH PERMENENT MEADOW IN THE SUWAŁKI REGION OF NORTH-EAST POLAND AND WITH UTILIZED HAY MEADOW IN CENTRAL POLAND

Selected intentionally for the comparison were permanent grasslands with limited human intervention, as well as an intensively-managed meadow for the sake of contrast. The first of the sites was an unused (i.e. unfertilized, ungrazed and uncut) pasture dominated by the Lolio Cynosuretum R. Tx. association and located within the Pieniny Range of the Carpathians (Wasilewska 1974a) (site 3G in Fig. 4). The second comparison was made with a permanent multispecies meadow of the Anthyllidi Trifolietum montani association, in a varied landscape, ungrazed in the period of research and located at the side of the Szeszupa Valley in the Suwałki region of the North-Eastern Lakeland (Wasilewska 1994b) (site 2G in Fig. 4). The third site was a hay meadow near Warsaw featuring Arrhenatheretum medioeuropaeum developed by succession from a mixture of meadow grasses sown ten years before on light brown soil and given moderate applications (280 kg NPK/ha) of mineral fertilizer (Wasilewska 1976) (site 4G in Fig. 4).

The most characteristic differences between the Karkonosze sites and those in other regions include the higher densities of fungivores (obligate and potential treated together) and of obligate plant parasites (Table 10).

The appraisal of relative abundance confirmed the above situations and also made clear the limited numerical role of bacterivores and omnivores + predators at Hala Izerska sites (Fig. 7).

Table 10. Abundance ($N \cdot 10^3 \cdot m^{-2}$) and biocoenotic parameters for the soil nematodes in the two meadow areas at Hala Izerska (sites 3a and 3b), unused pastureland in the Carpathians (Wasilewska 1974a) (site 3G), a permanent meadow in the Suwałki region (Wasilewska 1994b) (site 2G) and an intensively-cultivated meadow in central Poland (Wasilewska 1976) (site 4G). Site symbols according to Fig. 4

Parameter		Site				
		4G	2G	3G	3a	3b
		Central Poland (Warsaw region)	NE Poland (Suwałki region)	S Poland (Carpathian region)	Hala Izerska	
pH (H_2O) in the 0–10 cm soil layer		5.7–6.0[1)]	7.1[2)]	~ 6.7[3)]	3.9	4.1
N	Total	2473	6950	5224	9825	5775
	Bacterivores – B	1079	1500	748	1525	400
	Fungivores – F	199	350	462	700	375
	Facultative plant parasites – FPP	267	1450	748	3400	1450
	Obligatory plant parasites – OPP	517	1950	1228	3625	3475
	Omnivores	378	1700	1668	550	75
	Predators	33		370	25	
Ratio	B/F + FPP	2.3	0.8	0.6	0.4	0.2
	B + F + FPP/OPP	3.0	1.7	1.6	1.5	0.6
Number of genera		41	29	30	21	20
Shannon generic index (H’)		4.6	4.4	4.0	3.5	2.8
Maturity indices: MI		2.3	3.0	3.4	2.6	2.3
Σ MI		2.4	2.6	3.1	2.5	2.2
PPI		2.7	2.2	2.6	2.5	2.2

[1)] According to Traczyk et al. (1976), concerning the 0–20 cm layer; [2)] According to Jankowski (1991), concerning the 0–20 cm; [3)] According to Czerwiński and Tatur (1974).

The value for the ratio of bacterivores to fungivores is lowest at Hala Izerska, while the proportion of nematodes in the detritus chain to those making direct use of primary producers (B + F + FPP/OPP) is also lower (Table 10). In turn the site in question also had the lowest number of taxa and the lowest index of diversity (H’). Indices of maturity (MI and Σ MI) were highest in grasslands with the most limited cultivational intervention (sites 2G and 3G), and a little lower value characterized the non-dried grass-herb communities of Hala Izerska (site 3a). In contrast, the drier site (3b) there joined the managed meadow (site 4G) in displaying the lowest values for these indices. Finally, values for the PPI indicator would seem to be difficult to interpret (Table 10).

The nematode communities of Hala Izerska resembled those of the Karkonosze sites in maintaining lower proportions of low-ranking (r-strategist) nematodes among its bacterivores, and higher proportion of high-ranking (K-strategist) species (Table 11).

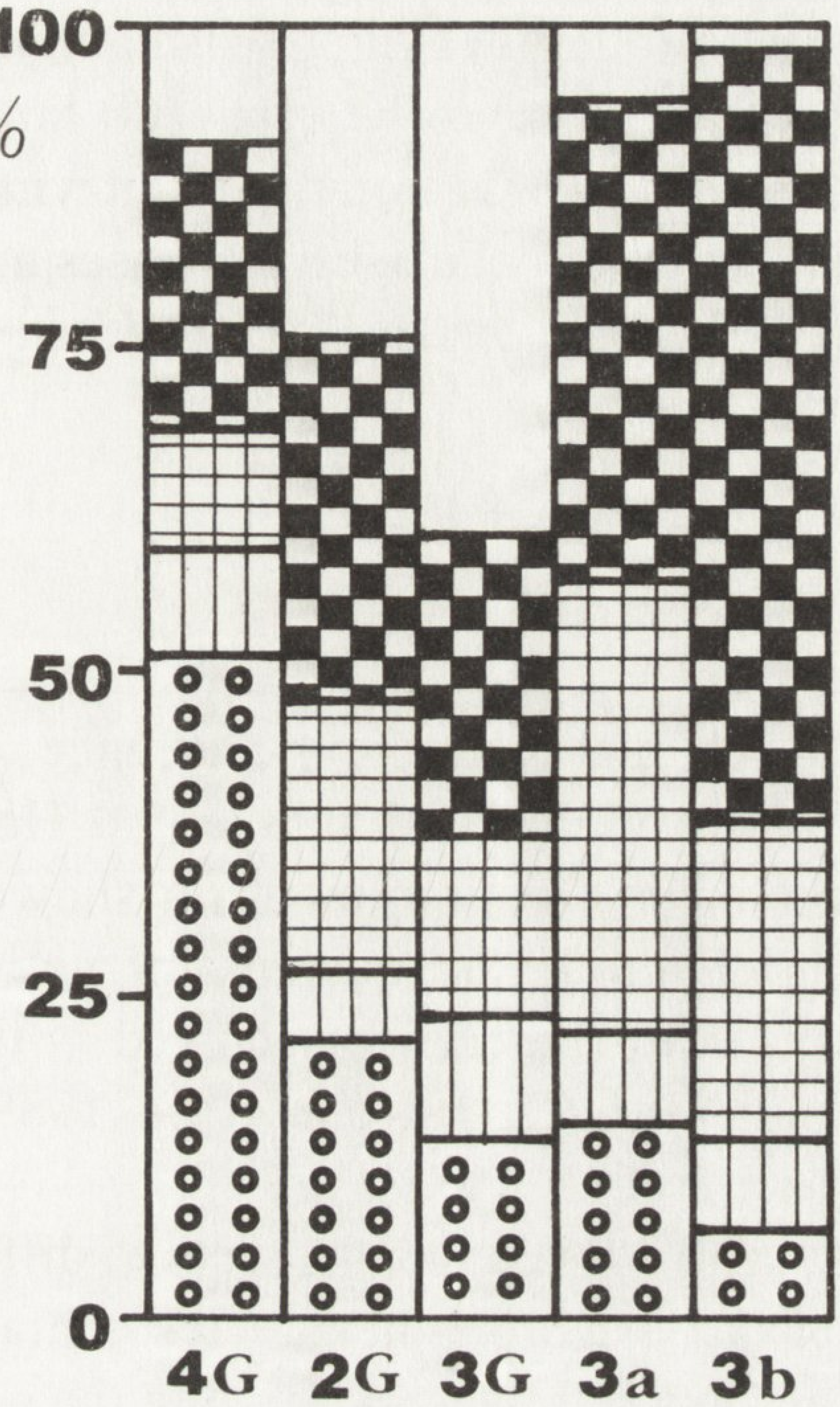

Fig. 7. Trophic structure (as % of total numbers) of the nematode communities of two grass-herb ecosystems at Hala Izerska (sites 3a and 3b), as well as unused pasture in the Carpahian region (W a s i l e w s k a 1974a) (site 3G), permanent meadow in the Suwałki region (W a s i l e w s k a 1994b) (site 2G) and meadow in central Poland (W a s i l e w s k a 1994 b) (site 4G). Site symbols according to Fig. 4

Table 11. Percentage share of nematode taxa with different life strategies (colonizer-persister (c-p) values after B o n g e r s 1990) in the group of bacterivores of meadows at Hala Izerska and in three other regions of Poland. Site symbols are as given in Table 10 and Fig. 4

c-p value	Site				
	4G	2G	3G	3a	3b
	Central Poland	Suwałki region	Carpathian region	Hala Izerska	
1	51	33	12	10	7
2	49	47	84	64	60
3		17		21	33
4		3	4	5	

6. DISCUSSION

6.1. MICROFLORAL ACTIVITY

The results of most experiments resemble theoretical knowledge on soil processes in indicating reduced decomposition of organic matter as acidification of soil proceeds (C o l e m a n 1983, H å g v a r 1994). It is well-known that increased acidity favours fungi over bacteria and strong experimental acidification of soils has been shown to reduce the abundance and biomass of bacteria (B å å t h et al. 1980, P e r s s o n 1988). The poverty of the bacterial microflora of Karkonosze soils has been demonstrated by P i e t r et al. (1993), who found dehydrogenase activity (an indicator of the physiological activity of the microflora) to be even 100 times lower than in the mineral soils of lowland areas of Poland. The activity of enzymes associated with the breakdown of organic matter – such as cellulases, proteases and phosphatases – is depressed, while the activity of phenolic oxidases (considered to indicate the rate of humification) is practically undetectable.

6.2. BACTERIVORES

Certain specific attributes were found to characterize the occurrence of bacterivorous species in the nematode communities of the Karkonosze and Hala Izerska. Above all, the group of nematodes feeding in the detritus chain showed a shift in the direction of fungivorous feeding. Even if the quantity of active fungal hyphae falls after acidification – as one field experiment showed – the fungivorous nematodes still maintain their populations (P e r s s o n et al. 1989), albeit with compositional changes noted (B å å t h et al. 1984).

The acid rain-stressed sites in the Karkonosze and at Hala Izerska seem to differ from other areas of Poland in having groups of bacterivorous nematodes characterized by a significant reduction in the number of taxa of lowest rank along the r-K continuum (i.e. those with c-p value of 1 and 2 in the classification devised by B o n g e r s (1990)), and an increase in the number of taxa of higher ranks (c-p values 3 and 4) (Table 7, 9 and 11). The functional group of bacterivorous nematodes are the first to colonize in large numbers, rapidly breaking down organic matter (e.g. W a s i l e w s k a 1992). This particularly applies to nematodes with high reproductive rates like rhabditids, panagrolaimids, diplogastrids and monhysterids, which are generally insensitive to pollutants (B o n g e r s 1990). This group is thus linked with the bacteria responsible for the earliest stages of decomposition, creating a certain feeding guild and – together with other bacterivores (such as protozoa) – a grouping to which the term "league" *sensu* F a b e r (1991) might reasonably be applied. As mentioned above, protozoa are very much reduced in numbers in the soil of the Karkonosze (S z t r a n t o w i c z 1994). The absence or reduced presence of this group of bacterivores (primary "colonizers") may result either from enhanced sensitivity to the acidification of soil or from the lack of a previously prepared broken-down organic substratum. This could thus be a reduction of the specific microflora and perhaps of the fauna as well. Decomposition is modified by the very activity of feeding, which changes the composition of the bacterial assemblage. G r i f f i t h s and C a u l (1993) cited example supporting the contention that the feeding of protozoa favours fast-growing species of bacteria. They further considered that the bacterial grazers influence the microbiological type and activity, and that there is thus a feedback process.

The lack of colonizers among bacteriophagous nematodes may also result from their greater sensitivity to acidification. Indicative of this are experiments with liming (and hence the counteraction of acidification). These brought about an increase an the proportion of bacteriophagous nematode taxa with low ranking on the colonizer-persister scale (d e Goede and Dekker 1993). The strong colonizers among bacterivores (*Rhabditis* s.l.) are distinguished by intrinsic rates of natural increase that are high (and higher than in the family Cephalobide). This quickly leads to a situation in which the increase becomes limited by the availability of food. Their greater susceptibility to drought (Bouwman and Zwart 1994) may also be of significance. Members of the Rhabditidae did not occur in the soils of the Karkonosze and Hala Izerska sites, but were numerous in artificially acidified soils studied near Warsaw (Dmowska 1993). Furthermore, *Rhabditis* species were noted in areas of the Czech Republic contaminated by industrial emissions (Háněl 1993b). However, the proportions of bacterivores in the nematode communities of the Karkonosze and Hala Izerska sites were found to be 1.5 to 3 times lower than those in the spruce forests of contaminated parts of the Czech Republic and Germany (Háněl 1993b and Ruess 1995).

The prevalence of more K-selective bacterivorous species in all three types of Karkonosze and Hala Izerska environments could point to the more mature successional stage of this functional group of nematodes. However, the characteristic "dissimilarity" of this group may equally be evidence of disturbance to the breakdown of organic matter, and more specifically of reduced bacterial decomposition.

6.3. FUNGIVORES

The group F + FPP was not reduced by the impact of acid rain and even increased in abundance in the young spruce stands of the Karkonosze and in the meadow ecosystems at Hala Izerska. However, the significant increase in the FPP group is characteristic.

Various opinions are to be found in the literature when it comes to the reaction of fungivores to acid rain. This is especially the case if reference is made to experimental studies (Hyvönen and Persson 1990, Háněl 1993b). Ruess (1995) reported an increase in fungivores (of the kind presented in the present paper), while Háněl (1993b) observed lower representation in more-degraded sites. Hánel supposed that this decline could be linked with the degradation of mycorrhizae. The disparity between these different sets of results attests to the irrefutable complexity of the problem. Above all, there is only incomplete knowledge regarding the mutual impacts of nematodes and the different types of fungi, namely saprophytic, ectomycorrhizal and endomycorrhizal species. Examples of the differential effects of acid rain on these groups are known (Myrold 1990), while the consequences of the trophic links of mycophagous nematodes are mainly known from laboratory or microcosmic studies (e.g. Walker 1984, Wasilewska et al. 1975). It is known that total plant mycorrhization increases with elevated CO_2 levels and that VAM fungi increase proportionately with increases in fine roots or mass. However, EMC fungi exhibit greater colonization per unit length or mass at elevated concentrations of CO_2 than at current atmospheric levels (O'Neill 1994). This would explain the increase in fungivorous nematodes. However the complexity of the interactions between mycorrhizal fungi and other organisms (including nematodes) is very great (Fitter and Garbaye 1994). It has long been known that the fungivorous species *Aphelenchus avenae* feeds and reproduces when mycorrhizal fungi are available as food, and thus brings about a significant reduction in the quantity of mycorrhizae inhabiting the root systems of seedling pines (Sutherland and Fortin 1968). Fungivorous nematodes apply a brake to the development, and/or weaken the formation, of mycorrhizae, and thus obstruct contacts between mycorrhizal hyphae and symbiotic plant. In addition, mycorrhizal fungi protect roots from invasion by certain pathogenic fungi. Known from the literature are some examples of negative correlations between the colonization of plant roots by mycorrhizae and the density of populations of pathogenic nematode species (Winkler et al. 1994). It is not therefore possible to exclude the idea that the weakening of mycorrhizal associations with plants in the Karkonosze and at Hala Izerska can also be explained by reference to antagonism between parasitic nematodes and mycorrhizal fungi. The reduction of mycorrhizae by nematodes thus requires special recognition and is particularly important in situations relating to acid rain.

6.4. OBLIGATE PLANT PARASITES

Nematodes of this group are very abundant in the degraded spruce stands of the Jakuszyce area of the Karkonosze Mountains, as well as in the grass-herb communities of Hala Izerska (a similar situation did not however apply to the young spruce stands studied). The numbers observed were significantly greater than those for the same group in the non-agricultural ecosystems studied by the author in other regions of Poland, and in the mixed coniferous forest of Kampinos Forest studied by Domurat et al. (1975). The greater numerical representation of this group in grasslands than in forest ecosystems is a known phenomenon (Wasilewska 1979, Háněl 1993a), but the results presented here for Hala Izerska make clear that it is dominant. It would seem that the supposition of Stachurski et al. (1993) regarding the impairment of plant chemical defences against phytophages and pathogens does hold true in conditions of probable high nitrogen-trophy in an environment stressed by acid rain. This would account for the greater abundance of pathogenic nematodes and also for the increase noted for the group in question when mineral (especially nitrogenous) fertilizers have been applied (Wasilewska 1989, Sohlenius and Wasilewska 1984, Sohlenius et al. 1987).

6.5. RELATIONSHIPS BETWEEN THE PROPORTIONS OF NEMATODES IN THE DETRITUS-BASED AND GRAZING FOOD CHAINS

In the situation of the greater abundance of phytophages observed in the Karkonosze and Hala Izerska, there is a reduction in the ratio of detritus-chain nematodes to those linked closely to a living plant host (i.e. in the value of B + F + FPP/OPP). Such a case was noted for both the spruce stands of the Karkonosze and the meadow sites at Hala Izerska. Differences between sites within and beyond the region studied were greater for the forest environment than for the meadow environment.

In the consideration of these relationships, the facultative plant parasites (group FPP) pose considerable difficulties. In the present work the role of potential fungivores has been ascribed rather arbitrarily to the members of this group, which was more abundant at the Karkonosze and Hala Izerska sites than at the majority of the other sites. In spite of this fact (FPP only in the numerator of the ratio), the index was lower in sites contaminated by acid rain (excluding the young spruce stands where the FPP group made up about 80% of the total and the OPP group represented less than 5%). By sucking, phytophages release nutrients from plants in the most direct way and thus increase the speed with which bioelements are cycled (Odum and Biever 1984). A similar mode of feeding and impact on the release of elements is indicated for mycetophagous (fungivorous) nematodes, which do however differ from phytophages in the trophic level exploited. If a bioindicative role of nematodes is thus to be recognized, then it indicates the hindered release of elements from the detritus chain in favour of their more rapid release from the primary producer level in an environment stressed by acid rain.

6.6. PREDATORS AND OMNIVORES

Representing the highest trophic level among the soil microfauna, predacious nematodes are considered indicators of biological conditions (Arpin et al. 1984, Wardle and Yeates 1993). The predatory nematodes were sometimes strongly related to the microbial trophic level because their juvenile stages feed on bacteria. The group in question was more or less absent from the Karkonosze and Hala Izerska sites.

It is reasonable to consider proven the hypothesis that predators and occasional predators (i.e. omnivores) disappear from nematode communities influenced by stress (Wasilewska 1995b), including the stress exerted in forests and their soils by acid rain (Háněl 1993a, Ruess 1995) or heavy metals (Popovici 1992). The behaviour of the group in question at the Karkonosze sites may thus be considered typical. A question should therefore be asked at this point regarding the reasons for the disappearance of K-strategists, which this group may be considered to include. The experiments of Wright and Coleman (1993) suggested that the limitation of resources results first in the disappearance of predatory nematodes (Mononchidae), with those small, numerous and hence opportunistic species occupying lower trophic levels coming to predominate, as O d u m (1985) predicted.

H o w a r t h (1991) was of the opinion that ecosystems dominated by opportunistic species are more resistant to stress than those dominated by more-specialized organisms. Emerging in turn in relation to aquatic ecosystems was a hypothesis that those with more open cycling of elements (more generalists and insensitive species) are more resistant to toxic chemical stress than those that are to a greater extent closed. However, O d u m (1985) maintained that it is in fact the more mature, closed ecosystems that are more resistant to stress, because of their greater functional complexity.

The acid rain-stressed nematode communities of the Karkonosze and Hala Izerska display certain unique features – they lose characteristic K-strategists on the scale of the community as a whole (i.e. predators), while losing r-strategists (to the benefit of K-strategists) from among the bacterivores. At the same time, the abundance of obligate plant parasites increses and the total populations reach high levels. There was thus no evidence to support the supposition that this type of chemical stress is a factor likely to lead to a reduction in numbers of these animals without integument to prevent direct contact with acid rain.

6.7. DIVERSITY AND MATURITY INDICES

It had been expected that both the H' diversity index and the maturity indices (MI, Σ MI and PPI) would allow for an evaluation of the degree to which the nematode communities of the Karkonosze and Hala Izerska had been modified. However, this was not the case as the indices did not show a clear downward trend (or an upward trend in the case of PPI) when the sites in question were compared with areas uncontaminated by acid rain. It is possible that Y e a t e s and B i r d 1994) were right in concluding from their research that comparison of these indices may relate only to the local scale and are not useful in regional comparisons.

7. CONCLUSIONS

The communities of soil nematodes were studied at selected sites in the acid rain-contaminated region of the Karkonosze Mountains and Hala Izerska (SW Poland). Comparisons with other, not contaminated regions of Poland did not reveal any decrease in total numbers but did indicate that the contaminated sites had greater numbers of fungivores and parasites of higher plants, as well as a lack of predators. The group of nematodes feeding on reducers was characterized by a shift in the direction of those feeding on fungi. The loss of characteristic K-strategists (namely predators) on the scale of differentiated trophic levels was a feature specific to the sites studied, as was the replacement of r-strategist bacterivores by more K-strategic representatives of this group.

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8. SUMMARY

It has recently been considered in the literature that nematode communities may be used as bioindicators of the contamination and degradation of the environment. Parameters have been derived for the description of these communities and their bioindicative significance has been established.

The influence of acid rain on soil nematode communities was considered in relation to 6 sites in the south-western part of the Karkonosze Mountains and in the eastern range of the Izerskie Mountains (Fig. 1). The contamination-related dieback of tree stands has been noted in this area. Two sites each were selected to represent spruce forest (more degraded and less degraded), young spruce stands and grass-herb vegetation (Fig. 1, Table 1). The composition of genera found was presented, and the level of representation and dominance determined (Table 2 and 3), along with the trophic structure (Table 4, Fig. 2), the Shannon diversity index and indices of maturity of the community (Maturity Index, Σ Maturity Index and Plant Parasite Index) (Fig. 3). The intensification of environmental degradation (as evaluated by reference to treefall) was associated with lower diversity and maturity of the nematode communities as well as by increased abundance of fungivorous nematodes. It was found that dryness enhanced these trends.

Comparisons were made between the nematode communities of the acid rain-contaminated area of the Karkonosze and Hala Izerska, and other areas of Poland which had been studied by the author about 20 years previously and which may reasonably be considered uncontaminated (Fig. 4). Use was made of the same parameters in each case, with comparisons relating to mature tree stands (Table 6, Fig. 5), young tree stands (Table 8, Fig. 6) and grasslands (Table 10, Fig. 7). The groups of bacterivorous nematodes in the compared sites were studied in relation to the percentage role of taxa with different life strategies (i.e. different c-p values on the scale devised by Bongers 1990) (Table 7, 9 and 11). It was noted that the communities from the contaminated areas did not display lower total numbers of nematodes (Table 5). They did however differ in their greater abundance of fungivores and parasites of higher plants, as well as in their lack of predatory species. The group of nematodes feeding on reducers was characterized by an apparent shift in the direction of fungus-feeders. The loss of characteristic K-strategists (namely predacious trophic group) was a feature specific to the sites studied, as was the replacement of r-strategist bacterivores by representatives of this group closer to the K end of the continuum. It was assessed that the indices of diversity and maturity were more suitable for estimating the level of degradation on the local scale than on the regional scale.

9. POLISH SUMMARY

Przedstawiono stanowisko znane od niedawna w literaturze, iż zespoły nicieni glebowych można wykorzystać jako bioindykatory skażeń i degradacji środowiska. Wytypowano parametry do opisywania tych zespołów i uzasadniono ich znaczenie dla bioindykacji.

Wpływ kwaśnych deszczy na zespoły nicieni glebowych przedstawiono dla 6 stanowisk usytuowanych w płn-zach. części pasma górskiego Karkonoszy i we wschodnim paśmie Gór Izerskich (rys. 1), gdzie obserwuje się wymieranie drzewostanów w wyniku skażeń. Wybrano dwa stanowiska borów świerkowych (zróżnicowane stopniem degradacji), dwa młodniki świerkowe oraz

dwa stanowiska ziołoroślowe (rys. 1, tab. 1). Przedstawiono zestaw rodzajów, określono nasilenie ich ilościowego występowania oraz dominację (tab. 2 i 3), określono strukturę troficzną (tab. 4, rys. 2) oraz wskaźnik różnorodności Shannona i wskaźniki dojrzałości zespołu nicieni (Maturity Index, Σ Maturity Index oraz Plant Parasite Index) (rys. 3). Nasilenie degradacji ocenione wypadaniem drzew, obniżyło różnorodność i dojrzałość zespołu nicieni i spowodowało wzrost liczebności nicieni grzybożernych. Posuszność nasila te zmiany.

Dokonano też porównania zespołów nicieni ze skażonego kwaśnymi deszczami terenu Karkonoszy i Hali Izerskiej z innymi terenami Polski, badanymi przez autorkę około 20 lat temu, które można uznać za nieskażone (rys. 4). Posłużono się tymi samymi parametrami jak poprzednio. Porównania dotyczyły drzewostanów (tab. 6, rys. 5), młodników (tab. 8, rys. 6) oraz grasslandów (tab. 10, rys. 7). W obrębie grupy nicieni bakteriożernych porównywanych stanowisk wyznaczono udział procentowy taksonów o różnych strategiach życiowych (wartości na skali c-p według Bongersa 1990) (tab. 7, 9 i 11). Stwierdzono, iż zespoły z terenów skażonych nie wykazały obniżonej ogólnej liczebności nicieni (rys. 5). Wyróżniały się wyższą liczebnością grzybożerców i pasożytów roślin wyższych oraz brakiem drapieżców. Wśród nicieni spasających reducenty nastąpiło przesunięcie w kierunku spasania grzybów. Utrata charakterystycznych K-strategów w skali zróżnicowanego troficznie zespołu (a mianowicie drapieżców) oraz r-strategicznych bakteriożerców na rzecz bardziej K-strategicznych przedstawicieli grupy bakteriożernej, stanowi swoistą specyfikę tych zespołów. Oceniono, że wskaźniki różnorodności i dojrzałości okazały się bardziej przydatne do oceny degradacji w skali lokalnej niż w skali regionalnej.

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