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SOIL NEMATODE RESPONSE TO ROOT PRODUCTION IN GRASSLANDS ON FEN PEAT SOILS

ABSTRACT: The density of soil nematodes was examined in relation to root production in peat grasslands that differed in the origin of peat and, consequently, in moisture and in physical and chemical soil properties. Root production was estimated by using the root ingrowth technique, and expressed in g dry wt m^{-2}, over the period April-October. Total nematodes, bacterivores, fungivores, and facultative plant feeders were not correlated with root production. Obligate plant feeders and the number of taxa forming this group were negatively correlated with root production. The ratio of numbers of bacterivorous + fungivorous to obligate plant feeding nematodes was highly positively correlated with root production.

Based on earlier publications, the author argues that the specific character of drained peat soils, that is, intensified N and C mineralization, obstructs full understanding of the relationship between root production and nematode abundance, especially in the case of nematodes from the detritus food web.

KEY WORDS: drainage, fens, grasslands, nematode density, root production.

1. INTRODUCTION

A positive relationship between primary and secondary production was found for animals of different trophic groups (Begon *et al.* 1986). But, as indicated by Elliott *et al.* (1988) and Hendrix *et al.* (1990), soil animals perform the dominant role in energy flow through grasslands. This is also true of soil nematodes. They use plant primary production directly (phytophages) and indirectly (bacterivores, fungivores, and predators). If they feed on living plants, they belong to the grazing food web, and if they feed on dead plant material, they are in the detritus food web. Consequently, soil nematodes can have a negative effect on primary production if they are phytophages (reduction of plant biomass, growth rate, etc.) or a positive effect when bacterivores and fungivores stimulate decomposition and mineralization of organic matter (Coleman *et al.* 1983, Ingham *et al.* 1985, Walter and Ikonen 1989). It should also be remembered that the feeding by phytophages accounts for a rapid flow of matter and energy. The efficiency of energy transfer from primary producers to consumers differs markedly depending on whether the pathway is from living primary producers to herbivores or from dead primary producers through decomposers

to detritivores (Hairston and Hairston 1993).

The relationship between plants and phytophagous nematodes has a complex character. It depends on the biomass of young and old roots, including the current-year production, their quality (chemical composition, physical structure), and also on the degree to which they transform the habitat by developing rhizosphere. In turn, grazing by herbivorous nematodes on roots can affect the whole plant or only some parts of it, depending on the species of both plant and nematodes. Grazing by plant-feeding nematodes also releases nutrients that are a potential source of food for soil microorganisms that occur at high densities in the rhizosphere (Yeates et al. 1998).

A question arises whether a higher plant production, and consequently also a higher level of organic substances (including root excretions stimulating growth of bacteria), promote the development of nematodes, especially bacterivores and fungivores. Several authors have shown a positive correlation between the total abundance of nematodes, in terms of numbers or biomass, and the primary production (or standing biomass) of aboveground parts or roots of herbaceous plants (Yeates 1979, 1987a, 1987b, Yeates and Coleman 1982, Dash and Prad-

han 1984, Sohlenius et al. 1987, Stanton 1988). These findings mostly concern natural ecosystems or extensively exploited ones. No data are available for organic soils, like fen peat.

The objective of this paper is to examine the relationship between the standing crop (density) of soil nematodes and the net primary production of roots on peatlands that differ with respect to peat origin, the time after drainage and subsequent management as meadows. This analysis involves both nematodes of the grazing food web and nematodes of the detritus food web, thus plant feeding nematodes as well as bacterivorous and fungivorous nematodes. As a result, it is possible to compare a natural fen with habitats subject to heavy human impact arising from the drainage of peat soils. Drainage was followed by changes that depended on the origin of peat and on the time after drainage (secondary succession). Consequences of these changes for nematodes have already been described (Wasilewska 1991a, 1991b, 1991c, and 1991e). The present paper describes the continuation of the study at the same sites, and it is focused on the correlation of nematodes with root production, this analysis being possible as the net primary production of roots was estimated in the same habitats (Andrzejewska 1991).

2. MATERIALS AND METHODS

2.1. STUDY SITES

The study sites were located in grasslands of the Biebrza and Narew icemarginal valleys, north-eastern Poland. This region of Poland is distinguished as the Biebrza Basin.

The climate of this region is moderately continental, with a mean annual tem-

perature of about 6°C and precipitation ranging from 400 mm to 600 mm.

Among nine study sites, one was natural, not drained sedge-moss fen (DA) and the remaining eight (WA, LB, WB, TB, MB, WC, TC, MC) were drained peatlands (Table 1). All of them were situ-

Table 1. Characteristics of the study sites and sampling

Site symbol[*]	Geographical name	Nematode sampling		Root production[**] g dry wt m^{-2} per 7 months (Apr–Oct)[***]	Years after drainage	Soil moisture in 0–10 cm layer, % by weight	Plant community
		Year	Month				
DA	Dobarz	1981	Jun, Jul, Oct	892.3	not drained	85.0	*Peucedano-Caricetum paradoxae*
		1983	Jul, Oct	1302.9	not drained	82.8	*Peucedano-Caricetum paradoxae*
WA	Wizna	1981	Jul	831.6	15	79.9	*Festuca rubra, Carex rostrata*
		1983	Jul, Oct	576.6	17	76.6	*Festuca rubra, Carex rostrata*
LB	Lipniki	1983	Oct	173.0	5	69.2	Mixture of meadow grasses,
WB	Wizna	1981	Jul	420.8	15	77.5	*Festuca rubra, Dactylis glomerata*
		1983	Jul, Oct	230.0	17	73.0	*Festuca rubra, Dactylis glomerata*
TB	Toczyłowo	1982	Dec	366.5	50	69.5	Mixture of meadow grasses
		1983	Jul, Oct	232.9	51	69.5	Mixture of meadow grasses
MB	Modzelówka	1982	Sep	219.6	100	65.6	*Deschampsia coespitosa, Potentilla anserina*
		1983	Jul, Oct	257.6	101	66.7	*Deschampsia coespitosa, Potentilla anserina*
WC	Wizna	1983	Jul, Oct	278.0	17	69.1	*Festuca rubra*, herbs and weeds
TC	Toczyłowo	1982	Dec	259.4	50	62.1	Mixture of meadow grasses
		1983	Oct	439.0	51	63.7	Mixture of meadow grasses
MC	Modzelówka	1982	Sep	276.7	100	–	*Festuca rubra*, herbs, weeds

[*]The final letter indicates type of peat: A – sedge-moss fen peat soils, B – sedge fen peat soils, C – alder fen peat soils;

[**] After Andrzejewska (1991);

[***] Years of study as for nematode sampling.

More details in Wasilewska (1991a, b, c) and Andrzejewska (1991).

ated on fen peat soils. Differences among sites were mostly concerned with the origin of peat and years from the time of drainage and management of the peatlands (Table 1). The intensity of peat moorshing (mucking), speeded up by drainage, showed differences in relation to peat origin. It was weak on peats of type A, forming "fibric soils" derived from weakly decomposed sedge-moss peat, medium on peats of type B, forming "hemic soils" derived from moderately decomposed sedge peat, and strong on peats of type C, forming "sapric soils" derived from highly decomposed alder peat (Kajak and Okruszko 1989). As a result, physical, chemical, and biotic soil properties and plant communities developed on these soils showed marked differences, as indicated in earlier publications (Wasilewska 1991a, 1991b, Wasilewska *et al.* 1985) and partly in Table 1.

Time after drainage (from 5 to about 100 years) can be considered as a period of successional changes (Table 1).

The drained meadows were mown twice a year and moderately treated with mineral fertilizers.

Nematode abundance and root production were estimated on nine plots at a similar time (Table 1).

2.2. ROOT PRODUCTION

Data concerned root production were taken from Andrzejewska (1991). According to the terminology proposed by Coleman and Crossley (1996), the method used by Andrzejewska can be classified as the "Root Ingrowth Technique". Framed mesh bags of a size of $3 \times 15 \times 40$ cm with a mesh size of 2×2 mm were filled with sieved sand and burried at the study sites. After the required time, they were removed, roots were isolated by using sieves, dried, and weighed. The results are calculated per m^2 of meadow area, down to 40 cm of soil depth over the period April-October. Measurements were taken twice (in 1981 and 1983 or in 1982 and 1983) at each site, except for three sites where they were taken only once (Table 1).

2.3. SOIL NEMATODES

Soil samples were taken using a steel soil corer (with 2 cm^2 opening and 50 cm^3 capacity) to a depth of 25 cm. On each site and sampling time, the soil from 20 cores taken at random was bulked. Four 25 cm^3 subsamples of this mixed soil were extracted by a modified Baermann funnel technique (Wasilewska 1979) and preserved in a 5% formalin solution. In each subsample, nematodes were counted and identified to the genus (taxon) level.

Taxa were allocated to trophic groups according to Wasilewska (1971) and Yeates *et al.* (1993). The following categories were distinguished: bacterivores (B), fungivores (F), obligate plant feeders (OPF), and facultative plant feeders (FPF). The last group is fungivorous in part. Also omnivores (O) and predators (P) are included in Table 2.

The following parameters and indices were used to estimate numbers of nema-

todes and the diversity and maturity of their communities:

• Numbers (indiv. m^{-2}) for total nematodes and each trophic group separately;

• Taxon (genus) number for total nematodes, obligate plant feeders (OPF), bacterivores (B), and bacterivores + fungivores + facultative plant feeders (B + F + FPF);

• Shannon-Wiever Diversity Index – H' (Shannon and Wiever 1949);

• Maturity Index – MI (Bongers 1990) . Different nematode taxa are given values (c-p values) based on their position on the colonizer-persister spectrum, which is based on reproduction rate and other correlated characteristics. The MI is the weighted mean of the c-p values for the nematode taxa in a sample: $MI = v_i \, p_i$, where p_i is the proportion of individuals in the i-th taxon, v_i is the c-p value of the i-th taxon, and c-p values of 1–5 denote the position of the taxon on the r-K continuum (Bongers 1990, Bongers et al. 1995).

MI is based on the free-living taxa of nematodes. Lower values of MI indicate an earlier stage of succession or a disturbance to environmental conditions, whereas higher values refer to a later successional stage or less disturbed environment;

• Bacterivore Maturity Index – BaMI (Bongers 1990, Wasilewska 1997).

BaMI is the MI for only bacterivorous nematodes, and indicates the life strategy within this trophic group;

• Plant Parasite Index – PPI (Bongers 1990).

It is constructed as MI, but using only phytoparasitic nematodes (c–p values 2–5). It seems to be correlated with primary production, and its higher values would thus indicate nutrient enrichment;

• The ratio in numbers of bacterivores plus fungivores plus facultative plant feeders (as potentially facultative fungivores) to obligate plant feeders (B + F + FPF)/OPF.

This ratio is indicative of differences in the mineralization of dead and live plant tissues, that is, between the "detritus food web" and the "grazing food web" (Wasilewska 1997).

Correlation coefficients between root production and nematode parameters were calculated.

3. RESULTS

Table 2 shows the densities of the nematode taxa with indication of their trophic groups and c-p values for estimating maturity indices. These data were used to calculate the parameters listed above.

Correlations of the total nematode numbers, and of facultative plant feeders (FPF), bacterivores (B), fungivores (F), (B + F) and (B + F + FPF) with root production were not significant (Table 3).

Numbers of obligate plant feeders (OPF) were negatively correlated with root production (Table 3). A similar correlation was found for all phytophages (OPF + FPF). Also the number of OPF taxa was negatively correlated with root production (Table 3).

When the peat origin was ignored in pooling the data, the OPF group, as noted earlier, was negatively correlated with root production (r = – 0.502, P = 0.05, n = 15) (Fig. 1). At four sites on the sedge-moss fen peats negative correlation was also obtained. At sites on alder fen peats

Table 2. The average density for the study period (indiv. 10^3 m^{-2}) of nematode taxa in grasslands developed on fen peat soils differing in root production; B – bacterivores, F – fungivores, OPF – obligate plant feeders, FPF – facultative plant feeders, O – omnivores, P – predators; c–p value explained in the text. See Table 1 for site symbols

Trophic group	c–p value	Taxon	Site: DA 1981	DA 1983	WA 1981	WA 1983	LB 1983	WB 1981	WB 1983	TB 1982	TB 1983	MB 1982	MB 1983	WC 1983	TC 1982	TC 1983	MC 1982
B	1	Rhabditis s.l.	10	3920	60	1150	200	50	1760	250	4300	180	10050	300	300	3800	900
B	1	Panagrolaimus	0	45	130	3900	1200	590	2655	520	2500	120	1950	2600	400	3400	400
B	2	Acrobeloides	80	670	400	450	2200	530	1305	210	1400	80	700	3600	1200	2200	200
B	2	Heterocephalobus	3	0	0	50	400	20	0	10	0	20	100	0	0	200	0
B	2	Cervidellus	0	200	0	0	0	0	0	0	0	0	0	0	0	0	0
B	2	Plectus	57	845	50	500	200	50	570	30	200	80	750	500	100	200	100
B	2	Wilsonema	0	5	0	0	0	10	5	0	50	0	200	1500	0	200	0
B	2	Monhystera	10	70	40	0	0	0	5	0	0	50	50	0	0	0	300
B	3	Prismatolaimus	40	560	0	0	200	70	105	10	50	0	0	1200	0	0	400
B	3	Teratocephalus	17	150	60	50	0	80	10	0	100	0	100	300	0	0	0
B	3	Rhabdolaimus	23	300	0	600	400	90	365	10	50	150	300	100	100	0	400
B	3	Chronogaster	3	0	20	0	0	0	0	0	0	0	0	0	0	0	0
B	4	Alaimus	0	10	0	0	0	0	10	0	0	20	100	0	0	200	200
F	2	Aphelenchoides	7	885	120	1050	400	270	900	100	950	380	1700	700	100	1200	700
F	2	Aphelenchus	7	0	20	100	600	40	950	90	850	30	850	200	300	800	100
F	2	Nothotylenchus	0	5	0	0	0	0	10	0	0	0	50	100	0	0	0
OPF	3	Tylenchorhynchus	13	150	120	100	1000	50	80	510	1000	120	250	600	3900	4400	700
OPF	2	Paratylenchus	3	0	0	0	5400	220	1500	0	800	20	500	9900	0	800	0
OPF	3	Hirschmaniella	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OPF	3	Hemicycliophora	13	10	80	0	0	30	65	0	0	0	0	0	0	0	0
FPF	2	Tylenchus	120	795	160	1850	3200	280	400	610	4250	580	1550	1400	600	6000	1400
FPF	2	Aglenchus	37	115	400	50	0	340	115	40	400	200	150	500	200	1000	100
FPF	2	Coslenchus	0	25	0	50	0	0	5	0	0	0	0	0	0	0	100
FPF	2	Ditylenchus	0	355	0	250	0	0	0	0	400	0	550	100	100	200	100
FPF	2	Tylenchida others	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
B	3	Cylindrolaimus	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	3	Prodesmodora	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	3	Aphanolaimus	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0
O	4	Eudorylaimus	30	375	30	200	200	60	60	130	200	90	450	100	20	400	600
O	5	Mesodorylaimus	17	40	20	100	0	0	150	30	200	30	150	100	20	600	200
O	5	Aporcelaimellus	0	20	0	50	0	0	5	0	100	0	0	0	0	200	0
O	4	Dorylaimida others	3	5	0	0	0	0	10	0	0	0	0	0	0	0	0

Lucyna Wasilewska

			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
P	5	*Actinolaimus*	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	4	*Mononchus* s.l.	0	5	0	50	0	0	5	0	50	0	0	0	0	0	0
B	3	*Ethmolaimus pratensis*	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	3	*Tobrilus*	13	10	0	0	0	0	0	0	0	0	0	0	0	0	0
B	2	*Cephalobus*	0	0	50	300	0	100	115	360	550	30	50	0	300	200	600
B	2	*Eucephalobus*	0	0	30	350	200	30	140	20	600	40	200	0	0	400	200
B	2	*Anaplectus*	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0
B	2	*Euteratocephalus*	0	0	0	50	0	0	0	0	0	0	100	100	0	0	0
OPF	3	*Helicotylenchus*	0	0	0	300	3800	270	215	710	2250	280	2100	200	1100	1800	1000
OPF	3	*Rotylenchus*	0	0	0	300	400	140	105	160	150	120	500	200	400	200	100
OPF	3	*Pratylenchus*	0	0	110	50	0	0	50	40	250	60	500	0	0	2600	200
F	4	*Tylencholaimus*	0	0	0	150	200	20	215	0	0	220	450	0	0	800	100
B	3	*Chromadoridae*	0	0	0	50	0	0	0	0	0	0	100	0	0	0	0
P	2	*Seinura*	0	0	0	50	0	20	15	10	0	10	0	100	0	0	0
B	2	*Acrobeles*	0	0	0	0	200	0	0	0	0	0	0	100	0	0	0
F	2	*Paraphelenchus*	0	0	0	0	200	0	100	80	150	0	200	300	0	0	300
OPF	4	*Trichodorus*	0	0	0	0	200	0	0	0	0	0	0	0	0	0	0
F	3	*Diphtherophora*	0	0	0	0	200	0	0	0	0	0	0	100	0	0	100
F	2	*Deladenus*	0	0	0	0	0	0	100	0	0	0	0	200	0	0	0
O	4	*Eudorylaimus* „1"	0	0	0	0	0	0	0	10	200	0	0	0	0	0	0
P	4	*Ironus*	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0
OPF	3	*Criconemoides*	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0
OPF	3	*Meloidogyne* juv.	0	0	0	0	0	0	0	0	0	560	600	0	0	0	0
OPF	3	*Heterodera* juv.	0	0	0	0	0	0	0	0	0	0	50	0	0	0	0
FPF	2	*Basiria*	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0
P	3	*Tripyla*	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0
B	2	*Chiloplacus*	0	0	0	0	0	0	0	0	0	0	0	0	0	200	0
OPF	2	*Gracilacus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	800
O	4	*Enchodelus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
		Total	538	9590	1930	12150	21000	3360	12100	3950	22100	3490	25350	25100	9140	32000	10400

Soil nematode response to root production in grasslands

alone and sedge fen peats the correlations were not significant (Fig. 1).

The relationship between two trophic groups was analysed, of which one (OPF) represented the grazing food web, and the other (B + F + FPF) the detritus food web (FPF is considered here as fungivores). A significant positive correlation was found for all data combined (r = 0.650, P = 0.01) (Fig. 2). Thus, if the number of obligate phytophages was increasing per g dry wt of roots, also the total number of nematodes feeding on bacteria and fungi was increasing (P = 0.01) (Fig. 2). This relationship was also found separately for the sedge-moss peat (r = 0.954, P = 0.05) (Fig.2).

The ratio of numbers of bacterivores plus fungivores plus facultative plant feeders to obligate plant feeders, (B + F + FPF)/OPF, varied in relation to root production, and a positive correlation was found (r = 0.838, P = 0.001) for all data combined (Fig. 3). The values of this ratio ranged from 0.7 to 56.1. This relationship indicates that the increase in root production enhances the proportion of nematodes of the detritus food web, and that the lower is the root production, the higher is the proportion of nematodes of the grazing food web. This relationship was also marginally significant in case of the sedge-moss peat (r = 0.839, P = 0.1) (Fig. 3).

The remaining parameters such as the number of taxa (except for already mentioned OPF), the index of diversity (H'), and maturity indices were not significantly related to the root production (Table 3).

Table 3. Correlation (n = 15) coefficients (r) between root production (g dry wt m^{-2} per 7 months (Apr–Oct)) and trophic group numbers (indiv. m^{-2}), indices of nematode fauna and moisture content in grasslands on fen peat soils

| Parametr	r
Nematode total	– 0.38
Obligate plant feeders (OPF)	– 0.50**
Facultative plant feeders (FPF)	– 0.25
(OPF + FPF)	– 0.45*
Bacterivores (B)	– 0.20
Fungivores (F)	– 0.40
(B + F)	– 0.24
(B + F + FPF)	– 0.26
Total number of taxa	– 0.07
Number of taxa of obligate plant feeders (OPF)	– 0.52**
Number of taxa of bacterivores (B)	0.32
Number of taxa of (B + F + FPF)	0.08
Shannon-Wiever Diversity Index (H')	– 0.17
Maturity Index (MI)	0.07
Bacterivore Maturity Index (BaMI)	0.21
Plant Parasite Index (PPI)	– 0.27
Soil moisture to depth of 10 cm, % by weight	0.80***

***P = 0.001, **P = 0.05, *P = 0.1.
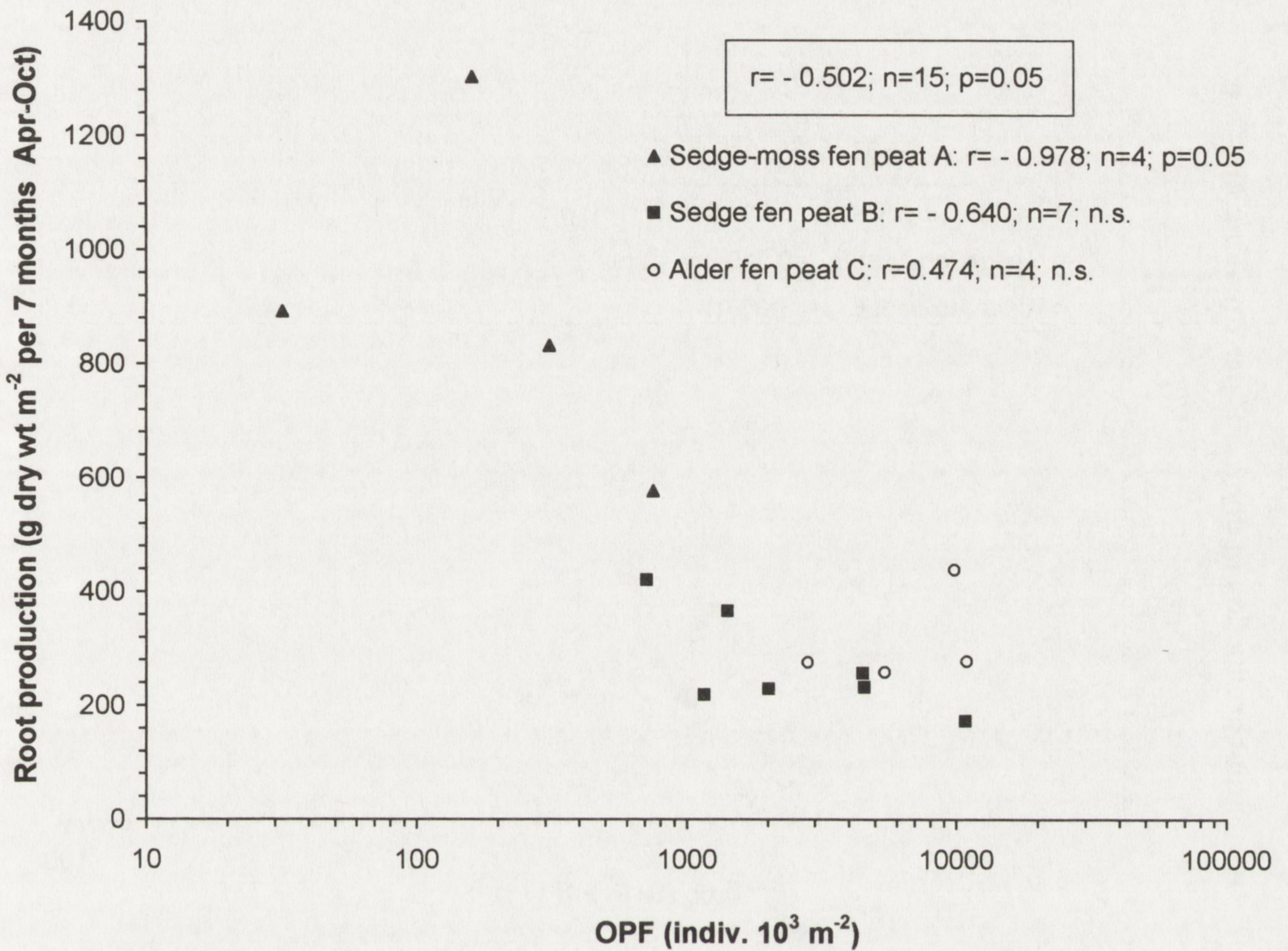
Fig.1. The average density of obligate plant feeders (OPF) in relation to root production for all the sites combined (in frame) and for each peat type separately.
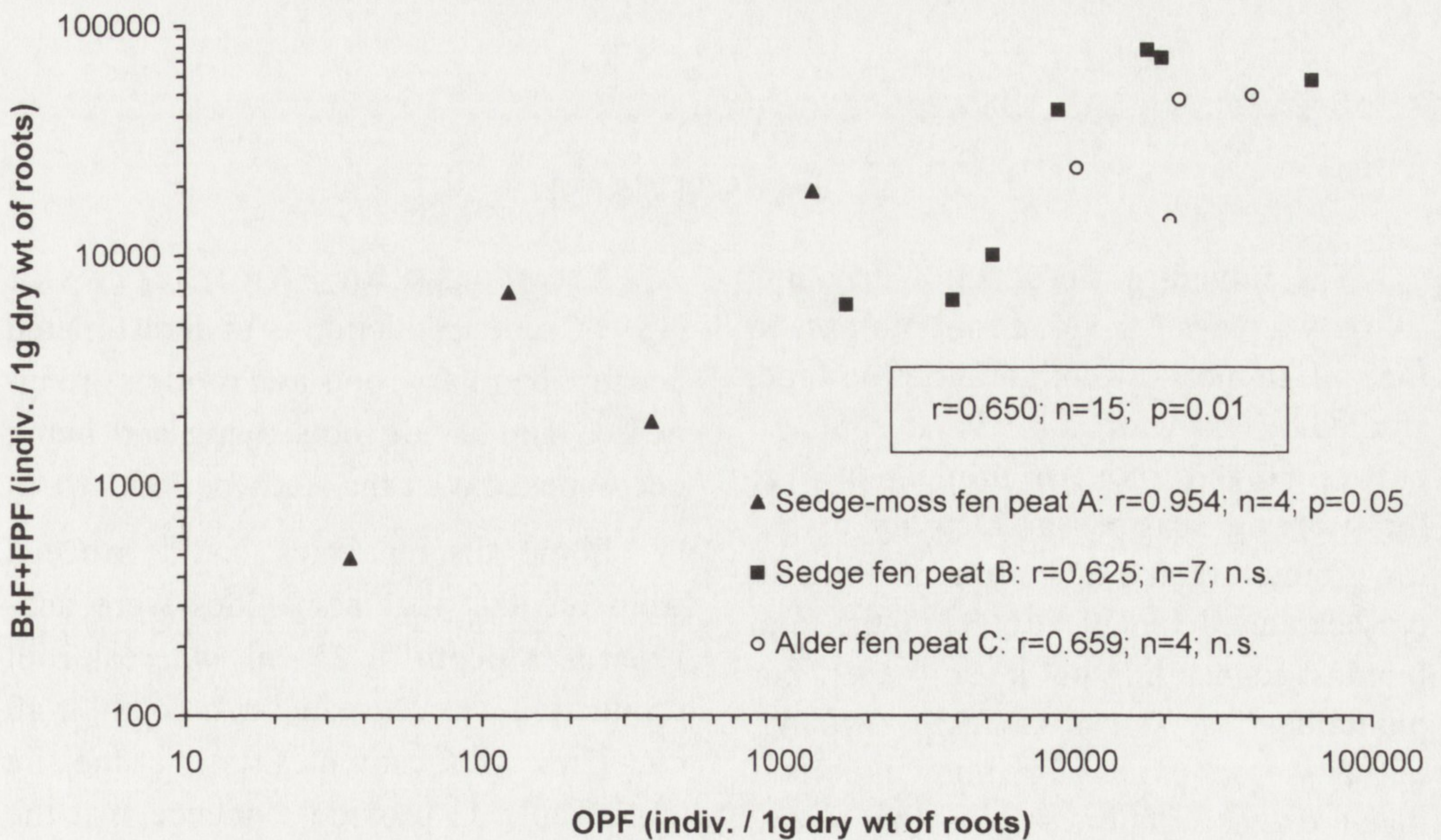

Fig. 2. The relation of the density of obligate plant feeders (OFP) per g dry wt of roots to the density of bacterivores, fungivores, and facultative plant feeders jointly (B + F + FPF) per g dry wt of roots for all the sites combined (in frame) and for each peat type separately.
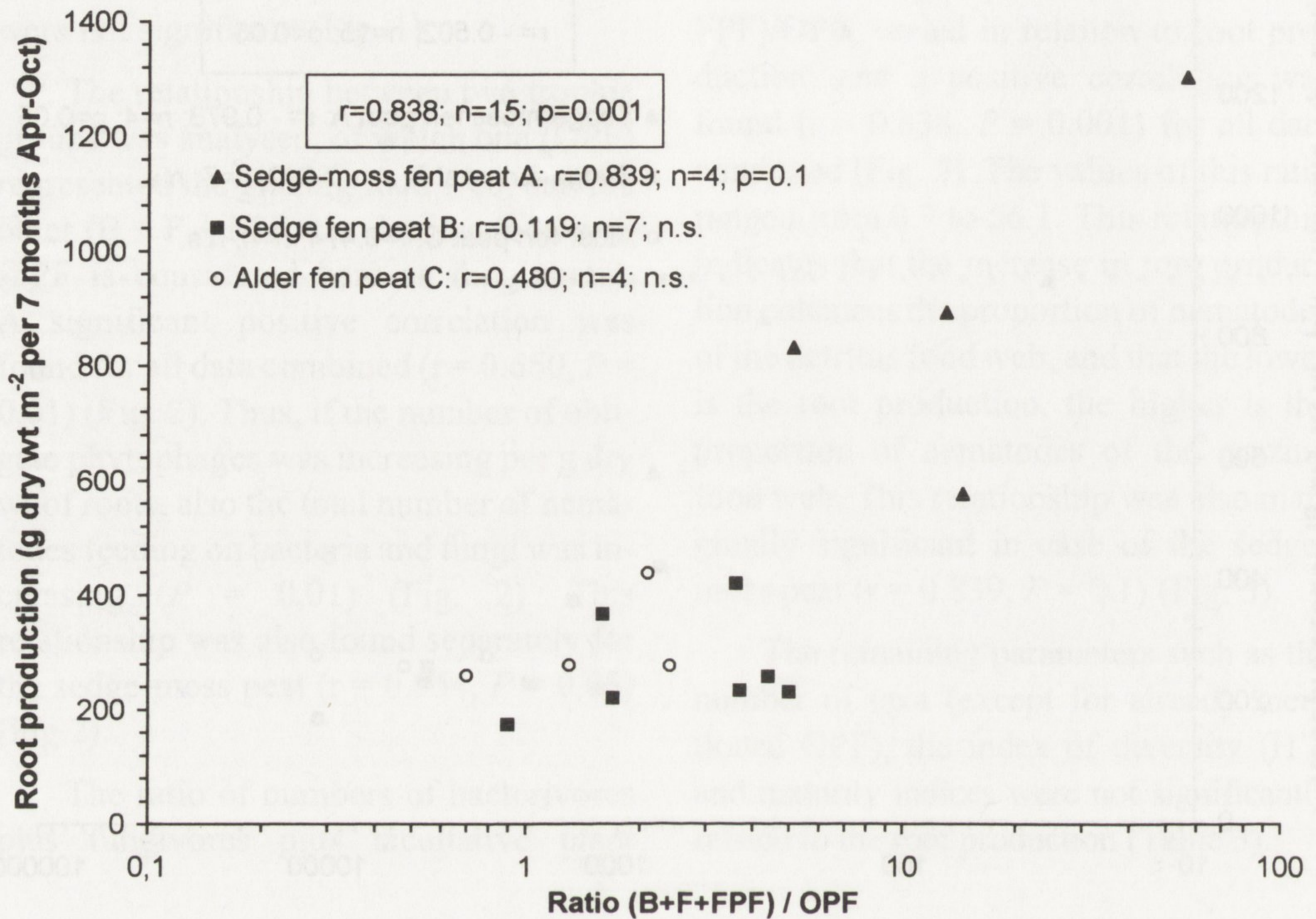
Fig. 3. The ratio of numbers of bacterivores + fungivores + facultative plant feeders (B + F + FPF) to obligate plant feeders (OPF), in relation to root production for all the sites combined (in frame) and for each peat type separately.

4. DISCUSSION

The annual root production accounts for only a part of the total root biomass in the soil. In meadow communities on lime, studied by Kotańska (1970) in southern part of Poland, biomass production over the growing season (productivity of belowground organs) down to a depth of 30 cm accounted for 30 to 60% of the total biomass, depending on the soil layer. For phytophagous nematodes, young, current-season roots are more important than the total root biomass, and that is why the parameter of production (rather than standing crop) was used for correlations with nematode abundance.

According to Andrzejewska (1991), root production is underestimated because capillary roots and rootlets are ignored, along with roots dying and being decomposed over the study period.

Some discrepancies could proceed from the fact that nematodes were analysed to a depth of 25 cm, whereas root production was estimated to a depth of 40 cm. The earlier estimates (only at the site WA, Table 1) provide evidence that the nematode populations occurring to a depth of 25 cm contribute to about 90% of their populations occurring to a depth of 50 cm

(Wasilewska 1991b). In turn, Andrzejewska (1991) estimated that root production to a depth of 30 cm accounted for about 90% of root production to a depth of 40 cm.

To estimate the effect of a single factor such as root production, the effects of other co-existing factors should be excluded or at least recognized. In this case it was peat origin: sedge-moss, sedge, and alder peat, and the related differences in physical and chemical soil properties such as soil moisture.

Root production was clearly correlated with soil moisture, as estimated to a depth of 10 cm ($P = 0.001$) (Table 3). Typically, higher production was noted on wet and less fertile meadows (sedge-moss peat) (Andrzejewska 1991). Similarly, Finér and Laine (1998) found on a drained peatland in southern Finland that Scots pine root production was somewhat greater on nutrient poor site than on the richer site. On the other hand, it was found earlier that the total number of nematodes and the number of plant feeders and the group of bacterivores plus fungivores were negatively correlated with soil moisture that differed from year to year (Wasilewska 1991e, Andrzejewska and Wasilewska 1991, Ciesielska et al. 1991). In the present study, negative correlation between nematode numbers and root production was found only for the group of obligate plant feeders or for the group of obligate and facultative plant feeders jointly.

Thus, the lower the soil moisture, the lower was root production and the higher the abundance of phytophagous nematodes inhabiting peat soils under study.

Plant and soil nematodes are fundamentally dependent on the energy input to the ecosystem by plants. According to Yeates (1987b), the greater the plant growth at a site, the greater the total nematode population. Roots are the source of sloughed root tissues, soluble materials, and exudation of organic and inorganic components (Coleman 1976). The primary input of reduced carbon from vegetation growth senescence and death processes is the major source of energy to primary decomposers and subsequently to saprophagic food chains (Coleman et al. 1983). Many authors confirmed the positive role of live root inputs or root biomass as important substrates for maintaining biological activity in the mineral soil horizons, enhancing nematode densities (Sohlenius et al. 1977, Giddens and Todd 1984, Parmelee et al. 1993).

In this study, total nematodes and saprophagous nematodes were not correlated with root production in meadow peat soils. In grasslands, belowground net primary production can be several times higher than aboveground production, and a large part of its energy is processed by nematodes (Coleman et al. 1976). At the sites on organic soils analysed in this paper, as well as at other sites in this area where root production was not analysed (Wasilewska 1991a), low nematode densities were interspersed with very high densities, not noted in mineral soils (Wasilewska 1996). High densities occur mostly in alder and sedge peats, especially on newly-established meadows with a low root production, as found in this study, but with high level of peat decomposition and N and C mineralization (Kajak and Okruszko 1989). It has been found that the mineralization rate increases from sedge-moss peat, through sedge peat, to alder peat (Szymanowski 1997). In alder peat and to a lesser extent in sedge peats, decomposers (mainly bacteria) and subsequently bacterivorous nematodes use energy from the mineralized peat. The dependence of nematode numbers and

structure of their communities on root production is certainly much lower than their dependence on the released products of peat mineralization. There is evidence for differential nematode activity with respect to the rate of peat mineralization (Wasilewska 1991c).

The rule that the plant subsystem is related to the herbivore subsystem and decomposition subsystem (Hutson 1989) holds in the peat soils under study, but it is modified by the fact that the decomposition subsystem is significantly supplied by the mineralization of plant material that was accumulated centuries ago. Thus, the group of bacterivorous and fungivorous nematodes occuring in meadow peat soils use not only the annual input of primary production but also the mineralized peat. The resulting decline in peat mass is estimated as a loss of peat surface area by 0.5 to 1 cm a year on the average. It was calculated, that the amount of nitrogen released from the organic matter of peat soils over the year can vary from 325 kg ha^{-1} to 825 kg ha^{-1} (Kajak and Okruszko 1989).

In terrestrial ecosystems, phytophage populations can consume from 0.5 to 20.4% (7% on the average) of plant production (Pimentel 1988). Plant feeding nematodes may have large effects on plant production through feeding on roots (Stanton 1983, Freckman and Virginia 1989). According to Ingham and Detling (1984), consumption of roots by root-feeding nematodes ranges from 6 to 13% of annual root production in grasslands. At three sites of the study fen (sites WA, WB, WC), this consumption was estimated at 2.8 to 19.6% of root production depending on peat origin (Wasilewska 1991c). There is also evidence, though less frequent, that feeding stimulates plant growth (Ingham et al. 1985, Freckman and Virginia 1989, Urbanek 1989). The results of the present study,

showing a negative correlation between plant feeding nematodes and root production, imply that this group of nematodes is partly responsible for a decrease in root production.

In stressed environments, plants are more susceptible for parasitic and pathogenic nematodes (Wasilewska 1989). In the case of nitrogen excess in the soil, defense mechanisms of plants are likely to be impaired. According to Wasilewska (1996) this could have been a cause of high abundance of plant feeding nematodes in the environment stressed by acid rain. I suppose a similar situation is in moorshing, mainly alder fen peat soils, where the response of plant feeding nematodes to plant-root resources appears to be "undetectable", because of a quite different order of these two simultaneous processes. The much stronger is the moorshing process.

It is known that herbivores can significantly alter productivity (Huntly 1991). It has recently been found that a disproportion in plant supply with N and K, which occurs when the rate of N mineralization in the soil is high (alder peat and to a lesser extent sedge-moss fen peat soils), leads to reduced biomass production and reduces utilization of the available nitrogen supply by plants (Stachurski and Zimka 1998).

Positive correlation between the density of plant feeding nematodes per g dry wt of roots, and the density of saprobiotic nematodes is supported in different studies. Based on the experimental data, Yeates et al. (1998) show that plants infected with Heterodera trifolii released more C-compounds into the rhizosphere, resulting in increased microbial biomass and C-turnover. This implies that an increase in the activity of plant feeding nematodes can account for an increase in

the activity of bacterivorous nematodes. The activity of phytophages, including plant feeding nematodes, not only limits plant growth but also contributes to soil fertilization and promotes the detritus food web (e.g. Wasilewska 1998). Site enrichment with nitrogen, in turn, stimulates the growth of plant feeding nematodes (Wasilewska 1989, 1991d).

The ratio of the two trophic groups discussed above, (B + F + FPF)/OPF, is positively correlated with root production if all sites are combined and differences in peat origin are ignored (Fig. 3). When analysed for each peat type separately, this correlation was statistically significant only for sedge-moss peats, thus for soils with low fertility, high moisture content, and the lowest degree of nitrogen mineralization. To give an example, nitrogen mineralization at site WA (Table 1) was about one-fifth of that at Wizna C (Wasilewska 1991c). In sedge-moss peats, the ratio (B + F + FPF)/OPF varied between 5.1 and 56.1, implying that decomposition was caused primarily by bacteria and fungi, that is in the detritus food web (Fig. 3). High root production was not markedly reduced by phytophages. A different situation was observed in alder and sedge peats where the value of the index ranged from 0.7 (newly drained site) to 5.0. This suggests that in these peats, nutrients were more rapidly released by phytophage feeding, that is, through the grazing food web (among others, by plant sucking nematodes), this being indicative of the most rapid turnover of organic matter in the habitat. This takes place, therefore, in soils derived from alder and sedge peats, decomposed after drainage at a higher rate. Root production was considerably lower in these two types of peat. It should be added that not only the activity of phytophagous nematodes but also the activity of phytophagous insects feeding in masses on roots of plants in alder peats could contribute, among other factors, to site degradation (Andrzejewska and Wasilewska 1991).

On the natural, not drained sedge-moss fen peat (site DA, Table 1), where root production was highest, the parameters had extreme values as compared with those at other sites. Thus, at this site the number of obligate phytophages was the lowest (Fig. 1) and the ratio of numbers (B + F + FPF)/OPF was the highest (Fig. 3).

5. CONCLUSIONS

The densities of the all nematode community as well as the bacterivorous + fungivorous group were not correlated with root production estimated over the growing season. Only the group of obligatory plant parasites was negatively correlated with root production. An estimate of the correlation between root production and nematodes, especially with reference to the nematodes of the detritus food web, is distorted by a specific character of drained peat soils, arising from the release of mucking processes and mineralization of N and C. The ratio of bacterivorous and fungivorous nematodes to plant feeding nematodes was positively correlated with root production over the growing season. This implies that in the situation when root production is high, as in wet and less fertile peat soils, organic matter is processed mostly through the nematodes of the detritus food web. Nematodes belonging to the grazing food web (plant feeding nematodes) intensify their activity in fertile but degraded peat soils derived from alder and sedge peats, where root production is considerably lower.

It seems that the relationship between net primary root production and nematode abundance can be estimated more accurately in mineral soils that do not contain organic matter other than recently produced plant material.

6. SUMMARY

In 1981–83, root production and nematode abundance were estimated in organic soils of fens at the sites drained and managed as meadows. The study was performed in the river Biebrza and river Narew ice-marginal valleys (north-eastern Poland). The study sites were located on nine meadows with different peat origin (sedge-moss, sedge, and alder peat). They also differed with respect to the time after drainage (Table 1). The study sites were described in more detail in earlier papers (Wasilewska 1991a, 1991b, 1991c, 1991e). Root production was estimated by Andrzejewska (1991) and expressed in g dry wt m^{-2} over the April–October period. The method of inserting framed mesh bags filled with sand into the soil was used. Roots that grew into the sand were weighed (Table 1). Nematodes were sampled with a soil corer on 1–3 occasions. Twenty soil cores were combined to obtain a mixed sample. Nematodes were extracted by a modified Baermann's technique using four subsamples of 20 cm^3 each, and they were identified to genus. Trophic groups were distinguished, and the diversity index, the number of taxa and maturity indices were calculated (Table 2).

The densities of the total nematode population and bacterivorous + fungivorous nematodes were not correlated with root production (Table 3, Fig. 1). The density of obligatory plant parasites was negatively correlated with root production (Table 3, Fig. 1). It was concluded that the estimate of this correlation is distorted by a high amount of organic matter other than root biomass which was accumulated in the drained peat soils. This is the specific character of these peat soils due to mucking and mineralization of N and C.

The density of plant feeding nematodes per g dry wt of roots was positively correlated with the density of bacterivores and fungivores (Fig. 2).

The ratio of bacterivores and fungivores to obligatory plant feeders was positively correlated with root production (Fig. 3). This implies that in the situation when root production is high, as in wet and less fertile sedge-moss peat soils, organic matter is consumed and bioelements released mostly by nematodes of the detritus food web. Nematodes of the grazing food web (phytophages) intensify their activity in fertile but degraded peat soils derived from alder and sedge peat, where root production is considerably lower.

Diversity index, total nematodes, numbers of bacterivores and fungivores, as well as maturity indices of nematode communities were not correlated with root production (Table 3).

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