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Alexei V. UVAROV^{1,2*}, Natalia KOLOSOVA³, Oleg KULINICH³

¹Institute of Ecology and Evolution, Russian Academy of Sciences; Leninisky prospect 33, 119071 Moscow, Russia

²Centre for Ecological Research, Polish Academy of Sciences; Konopnickiej 1, Dziekanów Leśny, 05-092 Łomianki, Polska, *av.uvarov@hotmail.com (corresponding author)

³Centre of Parasitology, Russian Academy of Sciences; Leninisky prospect 33, 119071 Moscow, Russia

COMBINED EFFECTS OF EARTHWORMS AND DIURNAL TEMPERATURE FLUCTUATIONS ON SUCCESSIONAL CHANGES OF LITTER NEMATODE COMMUNITY

ABSTRACT: Earthworm functioning and temperature regime are among the most important biotic and abiotic factors of soil environment; their combined action on soil nematode activities has not been studied. In a 4-month laboratory experiment, effects of the epigeic earthworm *Dendrobaena octaedra* on a succession of nematode community in litter of a mid-European birch/oak forest were tested in the gradient of an increase of diurnal temperature fluctuations from 0°C (constant 15°C; T₁₅) to 10°C (daily range between 10° and 20°C; T₁₀₋₂₀) and 20°C (daily range between 5° and 25°C; T₅₋₂₅). Earthworm and temperature effects were measured as differences in nematode community respiration rates between the experimental treatments. Nematode respiration rates were calculated on the basis of body size/weight/O₂ consumption relationships for individual species. Nematode community was dominated by bacterial feeders and changed in a characteristic successional pattern which, however, was markedly modified by temperature regime and earthworm activities. Dominant nematode taxa revealed specific patterns of temporal dynamics in connection with their responses to temperature and earthworm presence. Thus, metabolic activity of *Plectus acuminatus* was strongly reduced by *D. octaedra* but did not react to variation of temperature regime. In contrast, activity of *Panagrolaimus* sp. significantly responded to temperature but not to earthworm presence, whereas *Pl. thornei* reacted to both factors separately and in

combination. *Ceratoplectus armatus* was stronger affected by earthworm presence than by temperature; *Tylocephalus auriculatus* showed the opposite pattern. The variety of responses may explain the coexistence of several taxonomically related (Plectidae) and trophically similar species within the dominant group. Both earthworm presence and increase of the range of diurnal temperature fluctuations strongly affected the net of interspecific correlations within the nematode community. Earthworms strongly reduced total activities of nematode community at any temperature regime. T₁₅ regime showed markedly lower level of cumulative nematode respiration than both fluctuating regimes, irrespective of earthworm presence. In conclusion, combined effects of earthworms and temperature regime drastically changed patterns of relationships within the nematode litter community. The results of the experiments may have implications for the perspectives of global warming events at the study site: it is suggested that the ultimate vector of the changes in litter environment might be directed towards the conditions of the treatment [T₁₅ regime; earthworms present], with the corresponding trends in the development of the litter nematode community.

KEY WORDS: Nematodes, earthworms, temperature regime, community succession, global change

1. INTRODUCTION

Free-living nematodes are the most numerous metazoan microfauna group playing, together with protozoans, the major role in controlling microbiological activities in soil. Depending on their trophic preferences, nematodes strongly interact with bacteria and fungi, thus manipulating direction and rates of soil decomposition processes. Therefore, investigation of nematode community responses to biotic and abiotic factors affecting density, diversity and successional dynamics of this group may significantly contribute to the knowledge of regulatory mechanisms of the functioning of soil microorganisms and soil system as a whole.

Temperature regime is one of the most important abiotic factors of soil environment delimiting ranges of nematode activities and determining rates of their population dynamics (Sohlenius 1968, 1973, Procter 1984, Moorhead *et al.* 1987, Venette and Ferris 1997). There is some information on temperature niche differentiation (Anderson and Coleman 1982, Sohlenius 1985) or ecophysiological reactions to temperature, such as respiration rates (as summarized by Byzova 2007), of certain nematode taxa. Differential responses to temperature have been found in different trophic groups of nematodes (Schouten *et al.* 1998). Several field investigations have recently shown the significance of even minor changes in temperature regime for species composition and nematode community structure (Ruess *et al.* 1999, Sohlenius and Boström 1999, 2001, Bakonyi *et al.* 2007). However, temperature responses of soil nematodes are insufficiently studied; in particular, effects of the diurnal temperature fluctuations have not been investigated so far.

As keystone soil organisms earthworms exert strong and variously directed effects on diversity and abundance of nematodes. Earthworms are often reported as detrimentally affecting nematode populations in litter and soil, presumably due to environmental disturbance, depletion of food resources and grazing (Dash *et al.* 1980, Yeates 1981, Hyvönen *et al.* 1994, Huhta and Viberg 1999, Dominguez *et al.* 2003, Rätty and Huhta 2003). In contrast, a stimulation of nematode population density by earthworms

has also been documented in soil (and explained by earthworm nitrogenous excreta, mucus, dead tissue and physical effects; Senapati 1992) or in middens and drilosphere of *Lumbricus terrestris* L. representing patches of microbial food concentration and refuges (Görres *et al.* 1997, Maraun *et al.* 1999, Tiuonov 2007). Earthworm effects on nematodes can markedly vary with time, earthworm density and nematode ecological identity, showing a necessity of more detailed investigations on earthworm/nematode relationships. Thus, differential responses of nematode trophic groups to the presence of *Lumbricus rubellus* Hoffm. (*i.e.* a fast reduction of bacterial feeders with earthworm density increase but a stimulation of plant feeders after 2-3 months) were documented in a peat soil (Ilieva-Makulec and Makulec 2002, Makulec 2002).

The combined action of these principal factors of soil environment on nematode communities has not been studied. A special interest to investigation of earthworm/temperature effects on nematodes is connected with global change events, since: (1) warming by 1–6°C (as expected in the nearest century) will facilitate penetration of lumbricids into vast territories devoid or poor in earthworms and (2) terrestrial daily minimum temperatures are expected to increase twice as fast as daily maximum temperatures (IPCC, 1995, *cit.* after Beier *et al.* 2004). Consequently, the range of daily fluctuations will tend to decrease with likely changes in earthworm activities and presumably in their interactions with soil biota, in particular nematodes.

In the present study effects of an epigeic earthworm (*Dendrobaena octaedra* Savigny, Lumbricidae) on development of nematode community in leaf litter of a mid-European forest were tested in the gradient of an increase of diurnal temperature fluctuations: from a constant to a highly alternating regime. *D. octaedra* is a characteristic early colonizer of decomposing litter material, a species known for effects on soil microflora and nematodes (Hyvönen *et al.* 1994, McLean and Parkinson 1998) and for responses to temperature fluctuations (Uvarov 1995, 1998), and abundant at the study site. It was hypothesized that effects of *D. octaedra* on early succession of nematode community would be modified by the type of temperature regime.

2. MATERIALS AND METHODS

Experimental microcosms represented 150 mL plastic containers filled with 65.5 ± 0.5 g of sand covered with 2.5 ± 0.2 g (dry wt) of birch/oak overwintered litter, each layer occupying about 1/3 of the container's volume. The leaf material was collected in May, in F-horizon of a typical forest habitat of Kampinos National Park (20 km NW of Warsaw, Poland), and homogenized to pieces of 2–3 cm, twigs removed. The substrates were previously heat-sterilized (105°C, 24 h), and then reinoculated with litter microbiota in a water suspension prepared from the same intact litter. During the inoculation the suspension was thoroughly mixed, to achieve a homogeneous initial nematode community structure, and control samples (10) were periodically taken. The nematode community inoculated with the suspension was dominated by *Plectus acuminatus* Bastian ($45 \pm 0.4\%$), *P. thornei* Rühm ($8 \pm 0.8\%$), *Prionchulus* sp. ($8 \pm 0.9\%$), Plectidae spp. ($6 \pm 0.4\%$) and *Heterocephalobus latus* (Cobb) ($5 \pm 0.4\%$). The whole procedure of preparation followed the idea of creating initially identical microcosms and microcosm communities, as far as possible.

At the start of the experiment, the microcosms were distributed over 3 climatic chambers (HERAEUS-Votsch type) modeling 3 patterns of diurnal temperature regime: (i) constant 15°C (T_{15}); (ii) oscillations from 10° (“night”) to 20°C (“day”) (T_{10-20}); (iii) oscillations from 5° to 25°C at “night” and “day”, respectively (T_{5-25}). Fifteen days after the start, small litter earthworms – adults of *Dendrobaena octaedra* were collected in the same habitat and introduced individually into half of the microcosms in each chamber. Moisture content was favorable and was maintained constant by frequent weighing and water adding at the level of *ca* 75% of microcosm holding capacity. Gauze covers (0.1 mm mesh size) prevented rapid water evaporation and earthworm escape from the microcosms.

Microcosms were destructively sampled 16, 45, 77, 100, 118 and 124 days after the start of the experiment (June-October), in 4–8 replicates for each treatment/regime combination (overall, 204 microcosms were sampled). Nematodes were extracted from the litter samples

of *ca* 0.4 g using wet funnel (modified Baermann's) method (Ghilarov 1987), counted and determined to the species or genus level (50–100 animals per sample). Trophic group was assigned after Yeates *et al.* (1993). Total numbers of nematodes in the litter layer were calculated from the proportion [(density in the sample) \times (total litter weight) / (litter sample weight)]. This value was assumed as an approximation of the total nematode numbers in the whole microcosm; sand material had extremely small nematode density and was ignored.

Comparing the responses of nematode communities, energetic (respiratory) units were used instead of density, to stress the functional aspect of the analysis and reduce the bias of interspecific body size differences.

Individual biomass (W , μg) of nematode species was calculated on the basis of measurements of body length (L , mm) and maximum diameter (D , mm) (Uvarov and Novikova 1983, and unpubl. data of A.V. Uvarov), using Andrassy's (1956) equation:

$$W = 1.084 \times D^2 \times L / 1.7 \quad (1)$$

Respiration activity of nematode individuals ($\mu\text{L O}_2 \times 10^{-3} \text{ ind}^{-1} \text{ hr}^{-1}$) at 20°C was calculated after the equation of Klekowski *et al.* (1972) as $R_{\text{ind}} = 1.40 \times W^{0.72}$ and adjusted for the other temperature levels (5, 10, 15, 25°C) using temperature coefficient $Q_{10} = 2.5$ in the whole interval of 5–25°C (considering estimates of $Q_{10} = 1.6$ –3.5 by Santmyer 1956, Anderson 1978 and Laybourn 1979).

Daily respiration of nematode community in a microcosm ($\mu\text{L O}_2$ per 24 hrs) at any sampling was calculated as:

$$R_{\text{com}} = 12 \times \{ (Day_1 + Night_1) \times s_1 + (Day_2 + Night_2) \times s_2 + \dots + (Day_n + Night_n) \times s_n \} \quad (2)$$

where *Day* and *Night* are individual respiration rates of species 1, 2...*n* in the community during day and night, s_1, s_2, \dots, s_n are densities of corresponding species, and 12 is the duration of day or night period (hr). Cumulative respiration (R_{CUM} , $\mu\text{L O}_2$) for the whole duration of the experiment in each treatment was computed using average daily respiration rates of nematode communities in the *S* microcosms ($\Sigma R_{\text{com}} / S$) at each sampling

of the experiment, and time intervals (t , days) between the samplings (*e.g.* t_{12} means time interval between the 1st and 2nd samplings):

$$R_{\text{CUM}} = \frac{\sum R_{\text{com}1} / S_1 \times (t_{01} + t_{12}) / 2 + \sum R_{\text{com}2} / S_2 \times (t_{12} + t_{23}) / 2 + \dots + \sum R_{\text{com}5} / S_5 \times (t_{45} + t_{56}) / 2 + \sum R_{\text{com}6} / S_6 \times (t_{56} / 2)}{(3)}$$

Overall data on successional dynamics of nematode communities in the course of the experiment were statistically analyzed using 3-way ANOVA with the factors of E_WORM

(presence or absence of earthworms), T_REGIME (type of temperature regime) and SAMPLING DATE. Pearson correlation was used in the analysis of interspecific relationships within the nematode communities. The calculations were performed using "Statistica" program. The data were logarithmically transformed or arcsine transformed (when dealing with percentages), to fit the normality of distribution.

The taxa contributing $\geq 5\%$ of community respiration at least at one of the sampling dates were considered as dominants.

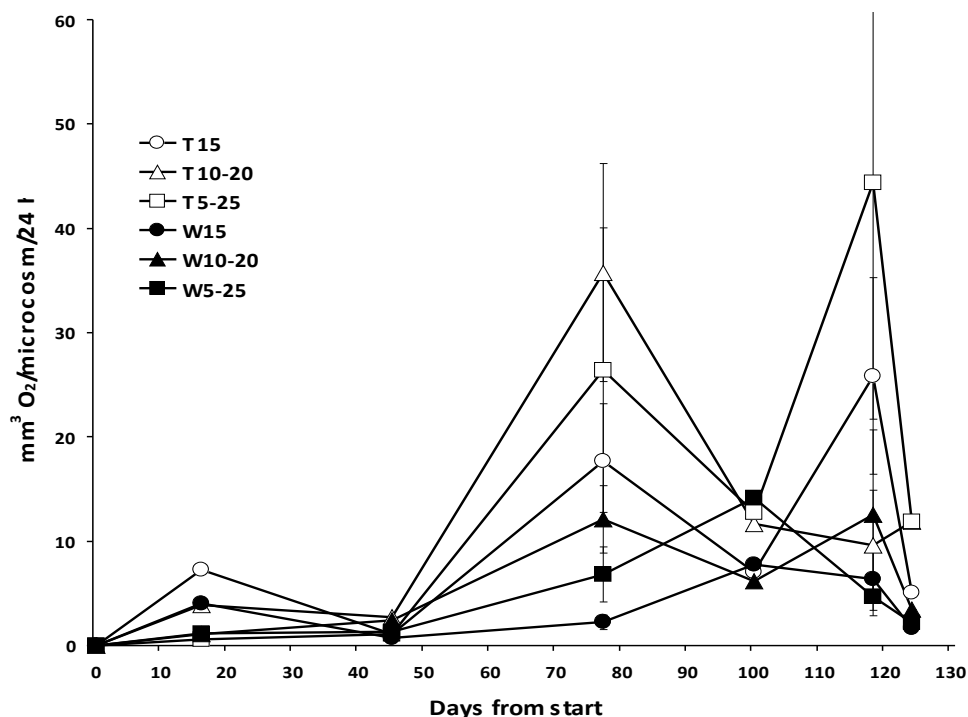


Fig. 1. Dynamics of nematode community respiration rates (equation 2) (means \pm SE) as affected by temperature regime (T_{15} , T_{10-20} and T_{5-25}) and presence of the lumbricid *Dendrobaena octaedra* (W_{15} , W_{10-20} and W_{5-25}). T_{15} and W_{15} – constant temperature regime of 15°C, T_{10-20} and W_{10-20} – diurnal temperature fluctuations from 10 to 20°C, T_{5-25} and W_{5-25} – diurnal temperature fluctuations from 5 to 25°C; T – earthworms absent, W – earthworms present.

Table 1. Significant ANOVA effects of earthworm presence (E_WORM), temperature regime (T_REGIME) and sampling date (SAM) on respiration rates of nematode community (equation 3) in litter microcosms. See text for the experiment design.

Factors & interactions	df	F	P
E_WORM	1,153	23.79	<0.001
SAM	5,153	18.53	<0.001
E_WORM \times SAM	5,153	3.21	0.009
T_REGIME \times SAM	10,153	1.84	0.057

Table 2. Cumulative respiration ($\text{mm}^3 \text{O}_2$) of nematode community (equation 3) for the period of the experiment (124 d), as affected by temperature regime and earthworm presence. See Fig.1 for the temperature regimes and text for the experiment design.

Temperature regime	Earthworm absent	Earthworm present
T ₁₅	1371	462
T ₁₀₋₂₀	1796	864
T ₅₋₂₅	2048	698

Table 3. Significant ANOVA effects of earthworm presence (E_WORM), temperature regime (T_REGIME) and sampling date (SAM) on respiration rates (see equation 2) of dominant nematode species in litter microcosms. See text for the experiment design.

Factors	Df	<i>Rhabditis</i>		<i>P. minimus</i>		<i>Panagrolaimus</i>		<i>T. auriculatus</i>		<i>C. armatus</i>		<i>Prionchulus</i>		<i>P. thornei</i>		<i>P. acuminatus</i>	
		F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
T_regime	2,153	7.87	***	3.29	*	4.26	*	8.33	***					3.80	*		
Sampling	5,153	6.95	***	15.36	***	9.32	***	24.17	***	24.66	***	6.14	***	26.76	***	15.94	***
E_Worm	1,153	8.28	**							10.69	***			5.08	*	18.15	***
T × Sam	10,153	2.49	**	1.98	*	2.36	**	3.02	**	5.92	***						
T × EW	2,153													3.94	*		
Sam × EW	5,153	4.14	***	6.01	***			3.18	**	4.47	***			2.25	*	3.90	**
T × S × EW	10,153							2.36	**	1.98	*						

3. RESULTS

During the earlier stage of community development (1st and 2nd samplings) daily respiration of nematode community (equation 2) was low and did not differ between the treatments (Fig. 1). Later respiration rate was markedly increased and significantly varied across treatments and sampling dates (Table 1). Presence of earthworms strongly reduced rates of nematode community respiration, starting from the 3rd sampling. There was a significant interaction between the both factors (E_WORM and SAMPLING DATE) revealing different trends in dynamics of nematode community respiration rates: stronger fluctuations and higher peaks in the absence of earthworms and more sweeping curves in their presence (Fig. 1). In contrast, temperature regime did not show consistent effects on total nematode community respiration rates. However, a close to significant interaction between T_REGIME and SAMPLING DATE (Table 1) indicated temporal differences in dynamics of respiration rate between the regimes.

In the absence of earthworms, dynamics of nematode metabolic activities followed different patterns: three smaller peaks at constant 15°C and one or two larger peaks at diurnally fluctuating regimes (Fig. 1). Whether the differences are explained by temperature regimes, remains unclear. However, presence of *D. octaedra* sharply (and in a various way) changed the patterns at all the regimes, thus indicating a marked earthworm influence on the metabolic activity of litter nematode community.

Calculation of cumulative respiration of nematode community (equation 3) confirmed a strong reduction of nematode metabolic activities by earthworms at all temperature regimes (Table 2). Interestingly, T₁₅ regime showed markedly lower level of cumulative respiration as compared with both fluctuating regimes, irrespective of earthworm presence.

Eight dominant taxa were represented by seven species from bacterivorous trophic group and a carnivorous species (*Prionchulus* sp.). Their respiration responses to the combinations of the factors studied individually varied (Table 3). Some species (*Plectus minimus* Cobb, *Pl. thornei*, *Panagrolaimus* sp., *Tyloceph-*

alus auriculatus Bütschli, *Ceratoplectus armatus* Buetschli) had the lowest metabolic activity at T_{15} regime; in contrast, *Rhabditis* spp. had the maximum activity at T_{15} and was absent at T_{5-25} , whereas *Pl. acuminatus* did not respond to temperature regime. Respiration activities of most of the dominants were reduced in the presence of *D. octaedra*, though the degree of reduction varied with temperature regime and sampling dates. This explains the fact that all the dominants highly significantly responded to SAMPLING DATE but exhibited specific

population dynamics in the course of the experiment.

Considering the succession of the dominant taxa, effects of both temperature regime and earthworms were evident (Fig. 2). At T_{15} regime and absence of *D. octaedra*, development of nematode community was started with *Rhabditis* spp. and *Panagrolaimus* sp., continued at the medium stage by *T. auriculatus* and *C. armatus* and followed by *Prionchulus* sp.; finally *Pl. acuminatus* became the main dominant. In the sequence of

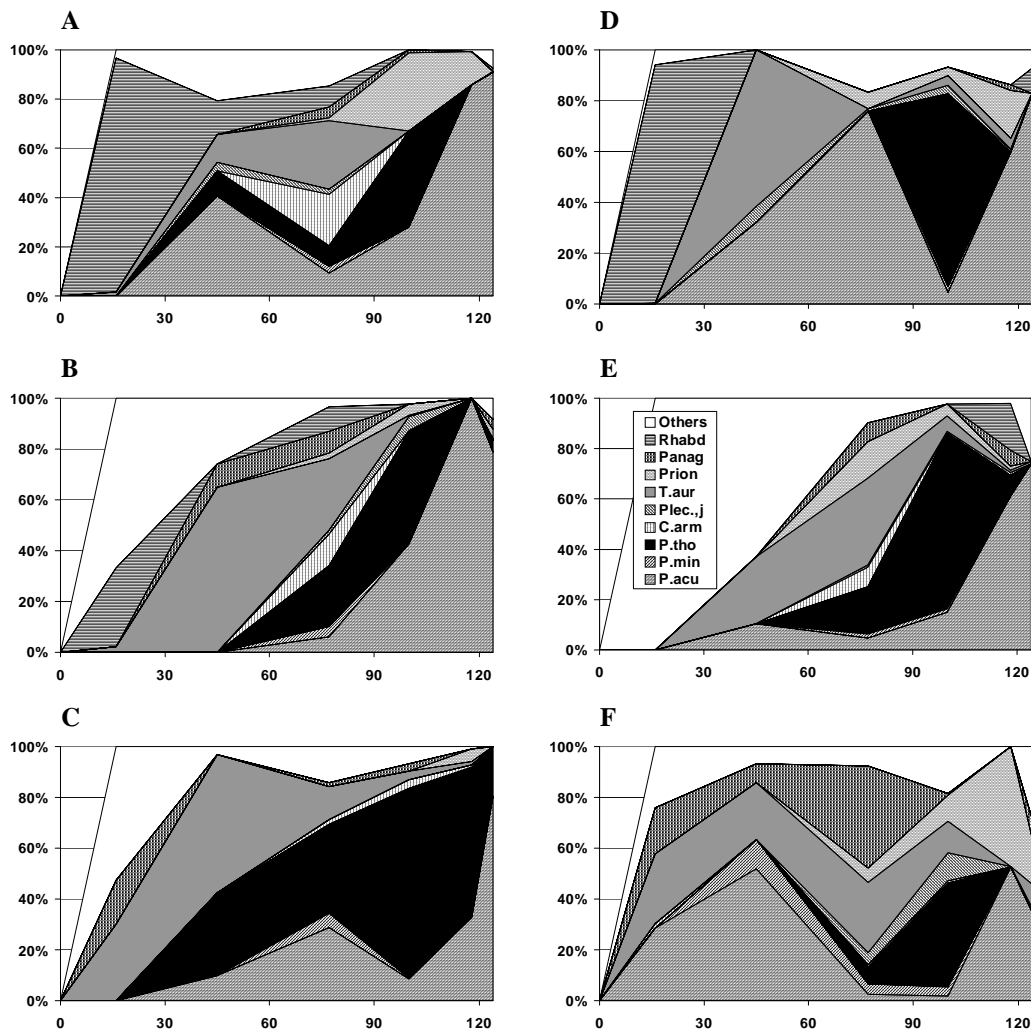


Fig. 2. Changes in dominance structure (expressed as % in total respiration rate, see equation 2) in the course of nematode community succession as affected by temperature regime (A, D = T_{15} ; B, E = T_{10-20} ; C, F = T_{5-25}) and absence/presence (ABC/DEF) of lumbricid *Dendrobaena octaedra*. See Fig.1 for the codes. Horizontal axis indicates days of the experiment. Taxa name abbreviations: Rhabd – *Rhabditis* spp., C. arm – *Ceratoplectus armatus*, T. aur – *Tylocephalus auriculatus*, Panag – *Panagrolaimus* sp., Prion – *Prionchulus* sp., Plec. j. – *Plectus juvs.*, P. min – *Plectus minor*, P. tho – *P. thornei*, P. acu – *P. acuminatus*.

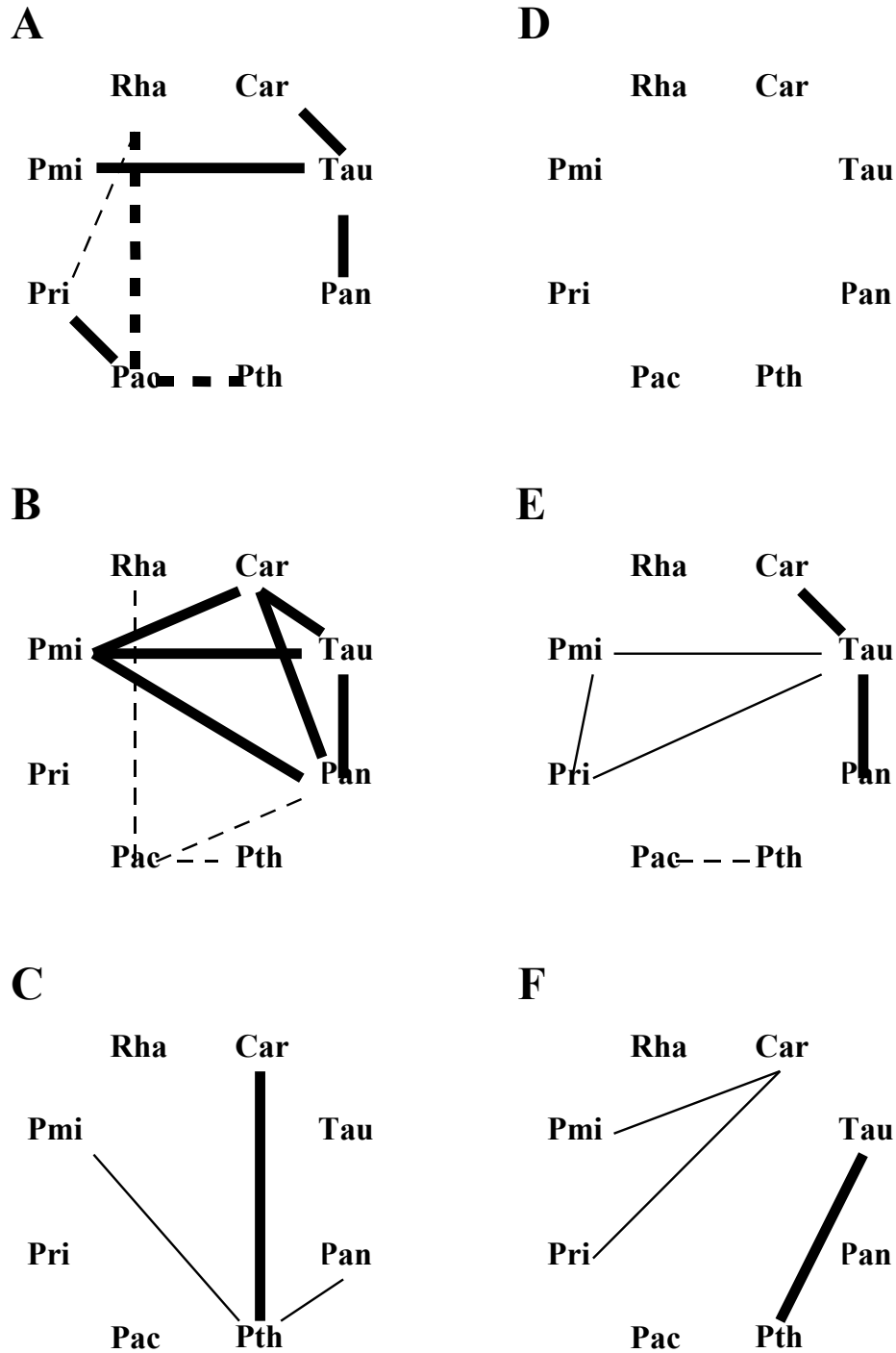


Fig. 3. Relationships between the dominant nematode species (shown as correlation values between the respiration activity rates, equation 2) at different experimental treatments: A, D = T_{15} ; B, E = T_{10-20} ; C, F = T_{5-25} ; ABC/DEF = absence/presence of *Dendrobaena octaedra*. See Fig.1 for codes. Bold and thin lines indicate r values significant at $P < 0.05$ and at $0.05 < P < 0.1$, respectively; solid and dashed lines – positive and negative correlations, respectively. Taxa name abbreviations: Rha – *Rhabditis* spp., Car – *Ceratoplectus armatus*, Tau – *Tylocephalus auriculatus*, Pan – *Panagrolaimus* sp., Pri – *Prionchulus* sp., Pmi – *Plectus minor*, Pth – *P. thornei*, Pac – *P. acuminatus*.

regimes T_{15} - T_{10-20} - T_{5-25} (reflecting the gradient of increase in the range of diurnal temperature oscillations) marked changes in relative significance of various nematode taxa may be followed (Fig. 2, left column). Thus, rhabditids decreased their respiration at T_{10-20} and completely disappeared at T_{5-25} . Under fluctuating regimes, in the course of the succession there was an increase in participation of *T. auriculatus* and (especially at T_{5-25}) of *Pl. thornei*, and a decrease in participation of *C. armatus* and of *Prionchulus* sp. However, final dominance of *Pl. acuminatus* was retained at all the regimes. Thus, temperature regime affected relative success of nematode species with similar trophic orientation.

In the presence of *D. octaedra* the general patterns of the succession were retained: early rhabditid development at T_{15} regime and their absence at T_{5-25} regime, dominance of *T. auriculatus*, *Pl. thornei* and *Prionchulus* sp. at the medium stage, character of dynamics and final dominance of *Pl. acuminatus* (Fig. 2, right column). However, the reduction of the metabolic activity of nematode community by earthworms was accompanied with changes in the proportions of the dominants: *e.g.*, a participation of *C. armatus* during the medium stage and of *Pl. acuminatus* during the final stage was reduced; some rhabditids appeared at the final stage of T_{15} and T_{10-20} treatments. Relationships between the dominant nematode species varied at different treatments (Fig. 3). At T_{15} and absence of earthworms (Fig. 3A), respiration activities of *Pl. acuminatus* and *Prionchulus* sp. were significantly negatively correlated with that of *Rhabditis* spp. ($r = -0.46$ and -0.35 , respectively), which was caused by their time separation during the succession. In contrast, strong negative correlation ($r = -0.57$) between metabolic activity of *Pl. acuminatus* (tending to a monodomination at the end of the experiment) and *Pl. thornei* (abundant at the late medium stage) may indicate competitive interactions between closely related species. Positive correlation between the activity of carnivorous *Prionchulus* sp. and microbivorous *Pl. acuminatus* ($r = 0.45$) may mean a predator/prey relationship. Positive correlations between the activities of *T. auriculatus*, *C. armatus*, *Pl. minimus* and *Panagrolaimus* sp. ($r = 0.49$ – 0.67) are due to their common presence at the medium succession stage.

Considering the latter treatment (T_{15} , earthworms absent) as a conventional control, marked differences can be followed in other treatments. In the absence of earthworms, at T_{10-20} similar relationships between the activities of *Pl. acuminatus* and *Rhabditis* spp. ($r = -0.36$) or *Pl. acuminatus* and *P. thornei* (-0.36), or between *T. auriculatus*, *C. armatus*, *Pl. minimus* and *Panagrolaimus* sp. ($r = 0.73$ – 0.92), were retained (Fig. 3B). However, at T_{5-25} regime a strong reduction of the number and different patterns of interspecific correlations were observed (Fig. 3C). Presence of *D. octaedra* strongly affected the net of relationships within the nematode community activity at corresponding temperature regimes. Thus, no significant interspecific correlations were revealed at T_{15} regime with *D. octaedra* (Fig. 3A, D). At T_{10-20} the number of significant connections was reduced in the presence of *D. octaedra*, though some principal correlations (*Pl. acuminatus* – *Pl. thornei*, $r = -0.33$; or *T. auriculatus* – *C. armatus* – *Pl. minimus* – *Panagrolaimus* sp., $r = 0.33$ – 0.71) were retained (Fig. 3B, E). Correlation patterns at T_{5-25} regime with and without earthworms had nothing in common (Fig. 3C, F).

4. DISCUSSION

Cumulative respiration of nematode community (equation 3) for the whole duration of the experiment (124 d) as expressed in energy units ($1 \text{ L O}_2 = 20.08 \text{ kJ}$), was 17.2 – 25.5 kJ m^{-2} in the absence and was reduced to 5.9 – 10.9 kJ m^{-2} in the presence of earthworms. These values are in the range of 5.9 – $138.2 \text{ kJ m}^{-2} \text{ yr}^{-1}$ for nematode respiration in temperate forests as revised by Sohlenius (1980). This suggests that the experimental results are comparable with natural conditions and also shows the substantial level of the reduction of nematode activities by earthworms. The latter fact is supported by a 2-year long experiment on decomposition of clover remains in soil (Uvarov 1989), where respiration of nematode community was reduced by 35% when earthworms interfered in the decomposition process (1st year) and by 50% when they became the dominant macrofauna group (2nd year).

A strong decrease in metabolic activity of nematode community in the presence of earthworms as found in the present study, is

corresponding to the majority of the published data and in particular to the reduction of bacterial-feeding nematodes by litter-dwelling *D. octaedra* (Hyvönen *et al.* 1994). Hyvönen *et al.* explained earthworm effects on bacterial feeders by predation rather than competition for microbial food, since bacterial numbers and biomass in their microcosms were not reduced by *D. octaedra*. In the present study, microbial activity (total microcosm respiration measured minus respiration calculated for earthworm, nematode and mesofauna populations; data not shown) was markedly reduced in *D. octaedra* treatments at all temperature regimes; thus, competition for microbial food between *D. octaedra* and nematodes can not be excluded.

At the start of the present experiment, nematode community in the suspension inoculated into the microcosms was dominated with *Pl. acuminatus*, *Pl. thornei* and other Plectidae, *Prionchulus* sp., *Heterocephalobus latus*. This explains the important patterns of nematode community in the present study: presence of the main dominants (in particular plectids), dominance of bacterial feeders and slight representation of fungal feeders and omnivores.

The metabolic responses of separate nematode species and whole nematode community to the combined effects of earthworms and variations of diurnal temperature regime were studied for the first time. In the absence of earthworms differences in nematode community respiration between the temperature treatments ($T_{5-25} > T_{10-20} > T_{15}$, Table 2) may in part be explained by the method of calculation (a constant Q_{10} value used throughout the whole range of 5–25°C); however, this bias should not be overrated (especially for T_{10-20}) due to very different dynamics of overall community and separate dominants (Figs. 1, 2). Effects of *D. octaedra* varied across the temperature regimes in the course of the experiment (Fig. 1); overall, cumulative community respiration was reduced markedly less at T_{10-20} than at other regimes (by 52 and 66%, respectively; Table 2). Eight dominant taxa of the nematode community showed individual patterns of temporal dynamics in connection with their responses to the factors studied (Table 3). Thus, metabolic activity of *Pl. acuminatus* was strongly reduced by *D. octaedra* but did not react to temperature regime. In contrast, activity

of *Panagrolaimus* sp. significantly responded to temperature but not to earthworm presence, whereas *Pl. thornei* reacted to both factors separately and in combination. *C. armatus* was stronger affected by earthworm presence than by temperature; *T. auriculatus* showed the opposite pattern. The variety of responses may explain the coexistence of several taxonomically related (Plectidae) and trophically similar species within the dominant group. This supports the assumption that differentiation in the reactions to soil climatic conditions is a prerequisite for species coexistence in nematode communities (Sohlenius 1985, Sohlenius and Boström 2001), with the addition that nematode reactions to earthworm activities are no less important. Interestingly, the predatory *Prionchulus* sp. did not significantly respond to any of the factors studied but often correlated with the activity of potential prey species (Table 3, Fig. 3). Thus, earthworm treatment/regime combinations specifically modified the successional trends of nematode community, with individual patterns for different species dynamics.

According to the Bongers' c-p scale ranging nematode species in the gradient from 'colonizers' to 'persisters' (c-p indices 1 to 5), or from *r*- to *K*-strategists *sensu lato* (Bongers 1990, Bongers and Bongers 1998), in the course of the succession studied two ecological groups of bacterial feeding nematodes participated. Both are considered as typical *r*-strategists; however, Rhabditidae and Panagrolaimidae are the first-rate 'colonizers' indicative of nutrient-enriched conditions (index 1 in the c-p scale), whereas plectids (index 2) replace less efficient rhabditids under lower food supply. After Porazinska *et al.* (1999), these groups markedly differ in their preferences to soil environment: rhabditids respond predominantly to sudden flushes of food resources, whereas Plectidae and Wilsonematidae (*T. auriculatus* in the present study) reflect some physico-chemical aspects of soil environment rather than food availability. Despite the presence of the predatory *Prionchulus* sp. (c-p index 4), no *K*-strategist species characteristic for the late stages of litter decomposition were present among the community dominants. Thus, the results of the present experiment refer to the early stages of forest litter decomposition and development of the nematode community.

Indeed, nematode succession started in the overwintered leaf litter material with a relatively fast rate of organic matter loss and a high level of microbial respiration, the conditions being favorable for rhabditid colonizers (*Rhabditis* spp. and *Panagrolaimus* sp.). By the end of the experiment the microbial activity was reduced by a factor of 5–8, with 19–25% of the organic matter in the microcosms being lost (Uvarov 1993 and unpubl. data) indicating a slow down of the rate of decay and changes in the resource supply for bacterial-feeding nematodes. This may explain the alterations in nematode community shifting to the dominance of *Plectus* spp., *C. armatus* and *T. auriculatus*; presence of *D. octaedra* in principle retained though modified patterns of this succession (Fig. 2).

Variations in temperature reactions of dominant nematode species may be responsible for some differences in community dynamics at temperature regimes studied. For a number of soil nematode species the lower temperature limits for reproduction and development are in the range of 5–10°C (as reviewed in Procter 1984); e.g. for *Panagrolaimus rigidus* a basal temperature of development was suggested to be 7°C. Sohlenius and Boström (1999) suggested that rhabditids are sensitive to cold; for a number of rhabditid species the upper temperature limits of egg laying and population growth are about 20–25°C; 5°C is also not favorable temperature for rhabditid egg laying (Sohlenius 1968, Venette and Ferris 1997). These data might explain the absence of *Rhabditis* spp. but the presence of *Panagrolaimus* sp. in the microcosms at T_{5-25} regime. In contrast, in a 28-wk incubation experiment of Sohlenius (1985) the peak densities of *Rhabditis* sp. were unexpectedly registered at the coldest/wettest regime (2–5°C and 100% moisture), which however was explained by their competitive exclusion in more favorable conditions. In the same experiment two *Plectus* species reached their highest densities within 10–20°C, though *Pl. acuminatus/parietinus* at lower and *Pl. longicaudatus* at higher part of this range. This might explain abundance of *Pl. acuminatus* at T_{10-20} and T_{15} regimes of the present study.

Duration of generation period and lifespan, rates of growth and population increase in nematodes show species-specific temperature responses; the duration of generation

period is generally negatively related to temperature (Sohlenius 1968, 1973, de Souza 1973, Laybourn 1979, Procter 1984, Moorhead *et al.* 1987; Ferris *et al.* 1996, Venette and Ferris 1997). However, there is no experimental data on responses of these parameters to diurnally alternating temperature. Approximate estimates of the rates of species generation turnover and nematode community succession at T_{15} , T_{10-20} and T_{5-25} regimes performed on the basis of constant temperature data (combination of the data for 5–10–15–20–25°C from the above citations; calculations not shown) result in contradictory estimates.

Temperature/earthworm effects as documented in the present study presumably have an ecological significance for the litter/soil nematode community of the forest sites in the Kampinos National Park near Warsaw. First, temperature regimes tested may be compared with temperature conditions in the natural birch/oak forest. According to Uvarov (1995, 2003), the long-term mean litter temperature of the vegetative season is around 15°C with mean daily temperatures mostly ranging between 12 and 20°C. The proportion of summer days with the range of diurnal fluctuations below 5°C (*i.e.* close to T_{15} regime) is 28%. Furthermore, the proportion of days with the diurnal range of 5–12°C is 68%; this situation is approximated by the T_{10-20} regime. Daily range of more than 12°C rarely occurs in summer (about 4% of days); hence, the T_{5-25} regime corresponds to temperature extremes of the summer season. In contrast, T_{5-25} regime is more typical for spring and autumn when the frequency of wide range of diurnal fluctuations is higher because buffering effect of the forest canopy on litter temperature is absent. Thus, trends of nematode succession in overwintered litter may change both within the vegetative season and between the seasons depending on more or less fluctuating weather conditions. It should be noted, however, that natural temperature fluctuations are irregular (in contrast to the experimental regimes tested) and therefore, extrapolation of the experimental results to the field conditions should be cautious. Second, reproduction of *D. octaedra*, a keystone species in the forest litter of the Kampinos National Park, is strongly mediated by the temperature regime and is growing with the decline of the range

of temperature oscillations ($T_{5-25} < T_{10-20} < T_{15}$) (Uvarov 1995, 1998). Thus, densities of *D. octaedra* would tend to be higher after summer seasons with less fluctuating temperature conditions. The frequency of such seasons might increase with global warming tending to narrow range of temperature fluctuations (see Introduction). Following this assumption, *D. octaedra* effects on litter nematode community would consequently grow with the global change events, and the ultimate vector of nematode community patterns might be directed towards the treatment [T_{15} regime; earthworms present] with the strongest reduction of metabolic rates and deterioration of interspecific connections as analyzed in the present study (Table 2, Fig. 3).

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