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Soil nematode community structure as affected by temperature and moisture in a temperate semiarid shrubland

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ABSTRACT

Nematodes are key agents in important soil processes, such as decomposition, mineralization and nutrient cycling. Therefore, alterations of the nematode community structure induced by global change may have a considerable influence on ecosystem functioning. However, it is not clear whether minor changes in soil temperature and/or moisture have any significant effect on nematode community structure. A field experiment was performed in a mosaic of open sand grassland and Juniper–Poplar woodland (VULCAN Project). Soil temperature and moisture were modified to the extent expected for the near future due to global changes. Community diversity and multivariate structure of the nematode community proved to be more sensitive to minute changes in soil temperature and moisture than different indices, such as specific richness (SR), maturity index (MI), plant parasite index (PPI), enrichment index (EI), channel index (CI), fungal feeder to bacterial feeder ratio (F/B) and nematode channel ratio (NCR). Nematode genera with high densities (>0.1 individual g^{-1} soil) were better indicators of the temperature and moisture changes than those of low density (<0.1 individual g^{-1} soil) in this sandy soil. Both drying and warming had significant influence on low density (Wilk's lambda: 0.02) and high density (Wilk's lambda: 0.002) genera according to canonical variate analysis. *Cephalobus* and *Plectus* were associated with the dried plots, while *Cervidellus*, *Ditylenchus*, *Eudorylaimus*, *Seinura* and *Thonus* were favoured by warming. Drying induced the development of a more structured nematode community in the bare soil compared to the control. Drying and warming effects on the soil nematode community were most pronounced in bare soil, less so in soil under poplar, while no significant effect was found in the fescue grass soil.

1. Introduction

Moderate, but continuous warming and/or drying in some areas of the Earth is a common phenomenon whose occurrence is supposed currently being enhanced (IPCC, 2001). This will have effects on community structure of different groups of organisms, including soil animals (Adams and Wall, 2000; Shaver et al., 2000) and as a result on different soil processes like nitrogen cycling (Swift et al., 1998).

Soil temperature and moisture content are usually the main abiotic factors to determine nematode distribution and abundance. The effects may be direct and/or indirect and these two factors are strongly interdependent. Local climate, soil type and plant community, all modify temperature and

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moisture effects. Many nematode species are able to survive under extreme abiotic conditions at very low or high soil temperatures (McSorley, 2003; Treonis and Wall, 2005) or at 0% relative humidity (Wall and Virginia, 1999). Therefore, it is not expected that nematode communities will react sensitively to low and minute global changes. However, temperature seems to be an important factor determining nematode community structure in different areas, such as subarctic (Ruess et al., 1999), Antarctic (Freckman and Virginia, 1997), Alpine summit (Hoschitz and Kaufmann, 2004) and arid regions (Pen-Mouratov et al., 2004). Moisture effects seem to be especially important under dry conditions as in the case of deserts (Noy-Meir, 1974). Positive effects of soil moisture on total nematode density and feeding group composition have been shown in the northern Negev Desert (Liang and Steinberger, 2001) and in the Judean Desert (Steinberger et al., 2001). However, Papatheodorou et al. (2004) did not find any notable moisture effect on a grassland nematode community structure in a small-scale manipulation experiment in Greece.

Nematode community structure can react to changes in soil temperature and moisture even within weeks under temperate climatic conditions (Bakonyi and Nagy, 2000). Reactions of the different taxa are various. Sohlenius and Boström (1999) demonstrated that Rhabditida and Tylenchida were sensitive to cold. Papatheodorou et al. (2004) found in a small scale experiment that the density of *Acrobeles* and *Cephalobus* increased in warm plots, but that of *Chiloplacus* increased in cold plots.

There are two important points to consider when soil temperature and/or moisture effects on nematode communities are investigated. First, microclimatic conditions are particularly important in determining nematode community structure (Hoschitz and Kaufmann, 2004) especially in natural ecosystems where the spatial heterogeneity of microhabitats is high. Therefore, careful analysis of different microhabitats is necessary to discover temperature and moisture effects on the whole ecosystem. Second, the thickness of water films on soil aggregate surface rather than gravimetric soil water content (Yeates et al., 2002; Strong et al., 2004) determines aspects of nematode biology, such as activity, feeding or population growth.

It is well known that nematode community structure is sensitive to environmental disturbances (e.g. Bongers and Bongers, 1998). Therefore, the aim of this experiment was to study some effects of locally simulated climate change involving slight but long-lasting drying and warming of soil on the nematode communities. The questions addressed were whether: (i) minor changes in the long-term soil temperature and soil moisture content have any effect on nematode community structure and, if so (ii) which components of the community were influenced. Heterogeneity of the vegetation was also taken into account.

2. Methods

2.1. The study site and experiment

The study was conducted within the framework of the VULCAN project funded by the EC (www.vulcanproject.com). The Hungarian experimental field is located in the Danube-Tisza Interfluve (geographical coordinates are 46°53′N and 19°23′E). The mean annual temperature is 10.5 °C, and the mean monthly temperature ranges from −1.9 to 21.0 °C. The mean annual precipitation is 550–600 mm. The soil of the site is a coarse textured sandy soil with high calciumcarbonate and low organic matter content. The average carbon and nitrogen content was 0.74%C (0–10 cm), 0.32%C (10–20 cm), 0.03%N (0–10 cm) and 0.028%N (10–20 cm), respectively. The vegetation of the site is characterised by a mosaic of open sand grassland, Juniper–Poplar woodland and shrubland.

Soil warming and drying were manipulated according to Beier et al. (2004). Briefly, warmed plots were covered at night by IR-reflective curtain. Drying of soil was achieved by covering the plots during certain periods of the growing season (May–June). For that, a polyethylene plastic cover was automatically extended over the plots when any rain was detected and removed afterwards. Treatments were applied during the years between 2002 and 2004. Three replications were set up. The experimental plots had an area of 20 m^2. The vegetation of each plot was quite heterogeneous. Therefore, three microhabitat types were distinguished and designated as (i) poplar trees (*Populus alba*), (ii) fescue grass (*Festuca vaginata*) and (iii) bare soil. The vegetatively emerged poplar sprouts formed little shrubs with a maximum height of 0.6–0.7 m at the time of sampling. Fescue stems were located in small groups of 8–10 in the area sampled. Gaps between higher plants were covered with moss and lichen in a very patchy distribution.

2.2. Nematode sampling and processing

Nematode samples were taken from the soil between sprouts and close to stems, after removing litter, moss or lichen if present.

Samples were taken for nematode community analysis under poplar tree sprouts (P), under fescue grass (F) and bare soil (B) and all of these within control (C), dried (D) and warmed (W) plots. As a result, nine combinations (PC, PD, PW, FC, FD, FW, BC, BD and BW) were sampled. All combination had three replicates, as treatments were set up in triplicate. Therefore, 27 samples were collected in total (3 treatments × 3 microhabitats × 3 replicates). Each bulk sample comprised 10 soil cores taken with an auger 2 cm in diameter to a depth of 10 cm on 15 June 2004. The soil temperature was measured continuously at 10 cm depth and soil moisture content at 20 cm depth. Data are expressed on a dry soil basis as v/v%. Daily average values were calculated for temperature and moisture data. Results obtained between 1 May 2004 and 15 June 2004 are presented.

Treatment of nematode samples consisted of extraction with Cobb's sieving and decanting technique (s'Jacob and van Bezooijen, 1984), counting and fixing in 3–4% formaldehyde. Subsequently, glass slides were prepared and processed under a compound microscope. An average of 150 nematodes were identified per sample to genus level.

2.3. Data analysis

Data were analyzed by ANOVA (split-plot design) with a General Linear Model using the Minitab Statistical Program

(Minitab Release 15, Minitab Inc., USA). Responses of nematode richness (number of taxa), total nematode density and density of each genus to the treatments (control, drying, warming) and microhabitats (poplar tree, fescue grass, bare soil) were tested. This analysis was followed by post hoc comparisons using Tukey's HSD test. The data for total nematode density and density of genera were $\log_{n+1}$ transformed before analyses. Only results for genera having an average density higher than 0.1 individual per gram of soil are presented.

Nematode community structure was characterised by specific richness (SR) (Yeates and Bird, 1994), genus dominance, maturity index (MI), plant parasite index (PPI) (Bongers, 1990), enrichment index (EI), structure index (SI), channel index (CI) (Ferris et al., 2001), nematode channel ratio (NCR) (Yeates, 2003) fungal feeder to bacterial feeder ratio (F/B). Nematode feeding group composition (Yeates et al., 1993) and functional group distribution on the c-p scale (Bongers and Bongers, 1998) were also compared according to the treatments. Significance was tested by Chi^2 analysis for each microhabitat type separately.

Nematode diversity in the plots was compared by diversity profile analysis (Patil and Taillie, 1979). This method has the advantage of being free from bias which arises from the fact that the other diversity measures are sensitive in different ways to the density changes in the rare or common species (Tóthmérész, 1995). The result of the diversity profile analysis is a curve rather than a single number. The left part of the curve reflects rare species diversity, while the right half shows the diversity of common species. It is possible to compare the significant difference of two curves as well. The DivOrd 1.50 statistical program package was used for the diversity profile analyses (Tóthmérész, 1993). Significance of the curves was tested between the scale parameter 0.01 and 15.0. Evenness of the communities was calculated as $\sum p_i^2$ where p_i is the relative density of the species i.

Two types of ordination, namely principal components analysis (PCA) and canonical variate analysis (CVA) were performed. Centered PCA was conducted on the average density data for the genera in the three replicate plots. The resulting PC scores were analysed by ANOVA. The structure of the low (less than 0.1 individual g^{-1} soil) and high (more than 0.1 individual g^{-1} soil) density genera were analysed separately by CVA. The objects of the basic matrix were (i) the different treatments and (ii) the microhabitat types in both cases of the analyses. The results of the two ordinations were superimposed in a biplot (Podani, 2000). All ordinations were carried out with the use of the SynTax2000 software (Podani, 2001).

3. Results

Soil temperature was consistently higher in warmed than in control plots in May. On average, a difference of approximately 1.5 °C was observed (Fig. 1). As the air temperature increased, this difference disappeared gradually. No difference in temperature between treatments was seen in June. By contrast, clear differences in soil moisture content were obtained between the control and dried plots during the 6 week period immediately before nematode sampling (Fig. 1). Continuously, lower soil moisture values were found in the dried than in the control plots, the difference being up to 30% on average. The soil moisture content in bare soil was significantly higher than in the poplar and fescue soils ($P < 0.01$ and 0.002, respectively).

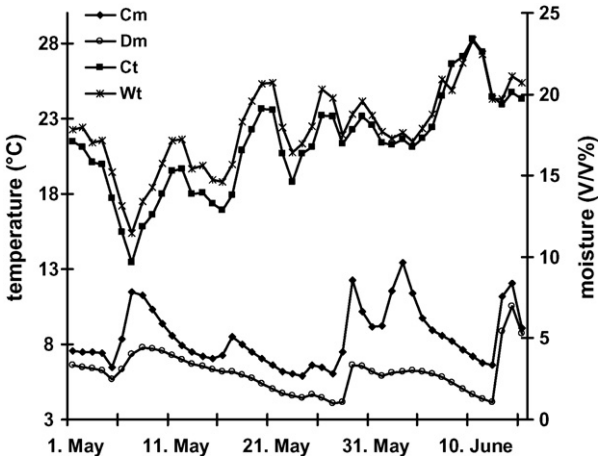

Fig. 1 – Soil temperature at 10 cm depth and soil moisture at 20 cm between 1 May 2004 and 15 June 2004 before nematode sampling. Cm: control plot moisture content, Dm: dried plot moisture content, Ct: control plot temperature, Wt: warmed plot temperature.

The density data for the 22 most abundant nematode taxa in the different treatments and microhabitats are presented in Table 1. The nematode fauna of the experimental field was relatively rich, with 45 genera being found in the plots. The treatments did not show any effects on nematode richness (average ± S.D.: 22.6 ± 2.7, 23.7 ± 3.1 and 22.3 ± 1.9 for control, dried and warmed plots, respectively) or total nematode density (average g^{-1} soil ± S.D.: 0.40 ± 0.12, 0.36 ± 0.10 and 0.41 ± 0.11 for control, dried and warmed plots, respectively). Treatment effects were found at the genus level in the cases of *Acrobeloides*, *Aphelenchus* and *Plectus* (Table 2). Results of the post hoc tests show that drying decreased significantly the density of *Acrobeloides* ($P < 0.032$) and enhanced the density of *Aphelenchus* ($P < 0.029$) and *Plectus* ($P < 0.046$). Moreover, the density of *Acrobeloides* decreased as a result of warming ($P < 0.044$).

No microhabitat effect was found on nematode richness (average ± S.D.: 24.1 ± 2.8, 22.9 ± 2.2 and 21.6 ± 2.3 for poplar soil, fescue soil and bare soil, respectively) or total nematode density (average g^{-1} soil ± S.D.: 0.45 ± 0.10, 0.33 ± 0.07 and 0.39 ± 0.12 for poplar soil, fescue soil and bare soil, respectively). However, microhabitat influenced the density of the *Acrobeles* ($P < 0.007$), *Aphelenchoides* ($P < 0.008$), *Cervidellus* ($P < 0.004$), *Eudorylaimus* ($P < 0.014$), *Leptonchus* ($P < 0.010$), *Microdorylaimus* ($P < 0.030$), Monhysteridae ($P = 0.000$), *Plectus* ($P < 0.026$), *Prismatolaimus* ($P < 0.033$), *Thonus* ($P < 0.028$) and *Wilsonema* ($P = 0.000$). Treatment and microhabitat only had significant interaction effects in the case of *Aporcelaimellus* density (Table 2).

PCA results show that the first two axes explained 83.9% of the total variance in the data (first axis 56.5%, second axis

Table 1 – Nematode density (individual g^{-1} soil) in samples taken from three microhabitat types (only genera with mean density > 0.1 individual g^{-1} soil are included)

Treatment	Nematode (ind. $(g\ soil)^{-1}$)								
	PC	FC	BC	PD	FD	BD	PW	FW	BW
Acrobeles	5.06 ± (0.64)	2.30 ± (0.58)	4.42 ± (3.35)	3.42 ± (0.99)	1.24 ± (0.43)	2.59 ± (0.85)	4.03 ± (1.79)	2.21 ± (0.90)	2.78 ± (0.92)
Acrobeloides	1.31 ± (0.42)	0.96 ± (0.53)	1.38 ± (1.15)	0.80 ± (0.08)	0.45 ± (0.32)	0.30 ± (0.38)	0.71 ± (0.38)	0.67 ± (0.49)	0.30 ± (0.27)
Aphelenchoides	0.55 ± (0.30)	0.50 ± (0.26)	0.16 ± (0.14)	0.35 ± (0.15)	0.37 ± (0.16)	0.05 ± (0.09)	0.34 ± (0.30)	0.31 ± (0.31)	0.12 ± (0.05)
Aphelenchus	0.04 ± (0.06)	0.03 ± (0.05)	0.11 ± (0.05)	0.12 ± (0.04)	0.16 ± (0.08)	0.43 ± (0.31)	0.19 ± (0.25)	0.08 ± (0.07)	0.15 ± (0.09)
Aporcelaimellus	0.60 ± (0.27)	0.12 ± (0.14)	0.14 ± (0.05)	0.27 ± (0.06)	0.35 ± (0.37)	0.50 ± (0.19)	0.52 ± (0.08)	0.53 ± (0.29)	0.25 ± (0.09)
Cephalobus	0.04 ± (0.06)	0.09 ± (0.09)	0.18 ± (0.12)	0.19 ± (0.27)	0.21 ± (0.09)	0.16 ± (0.08)	0.05 ± (0.09)	0.12 ± (0.21)	0.03 ± (0.04)
Cervidellus	2.83 ± (0.30)	3.20 ± (1.07)	6.89 ± (2.22)	2.40 ± (0.66)	3.80 ± (0.92)	5.52 ± (2.40)	3.94 ± (3.34)	4.92 ± (2.70)	7.08 ± (0.53)
Discolaimium	0.11 ± (0.19)	0.23 ± (0.14)	0.32 ± (0.14)	0.16 ± (0.14)	0.27 ± (0.12)	0.30 ± (0.20)	0.26 ± (0.22)	0.19 ± (0.07)	0.22 ± (0.24)
Ditylenchus	0.15 ± (0.15)	0.19 ± (0.17)	0.17 ± (0.29)	0.09 ± (0.08)	0.05 ± (0.09)	0.07 ± (0.06)	0.80 ± (1.16)	0.59 ± (0.57)	0.10 ± (0.09)
Eudorylaimus	0.51 ± (0.46)	0.36 ± (0.40)	0.26 ± (0.16)	0.72 ± (0.47)	0.35 ± (0.12)	0.15 ± (0.20)	1.86 ± (1.37)	0.40 ± (0.26)	0.44 ± (0.30)
Heterocephalobus	0.41 ± (0.54)	0.34 ± (0.29)	0.11 ± (0.05)	0.23 ± (0.26)	0.16 ± (0.21)	0.00 ± (0.00)	0.11 ± (0.12)	0.34 ± (0.22)	0.00 ± (0.00)
Leptonchus	0.75 ± (0.61)	0.62 ± (0.24)	1.60 ± (0.94)	0.44 ± (0.23)	0.24 ± (0.16)	1.78 ± (0.71)	1.02 ± (0.62)	0.99 ± (0.84)	1.17 ± (0.51)
Microdorylaimus	2.44 ± (1.05)	1.77 ± (1.02)	1.58 ± (0.31)	4.13 ± (3.59)	1.57 ± (0.83)	1.96 ± (0.32)	3.19 ± (1.14)	2.22 ± (0.81)	1.36 ± (0.97)
Microlaimus	0.64 ± (0.62)	0.33 ± (0.33)	0.54 ± (0.79)	0.79 ± (0.51)	0.08 ± (0.14)	0.13 ± (0.12)	0.30 ± (0.51)	0.27 ± (0.14)	0.44 ± (0.40)
Monhysteridae	1.22 ± (0.42)	0.66 ± (0.58)	0.21 ± (0.24)	0.66 ± (0.18)	0.76 ± (0.54)	0.08 ± (0.13)	0.96 ± (0.68)	0.58 ± (0.22)	0.31 ± (0.08)
Plectus	0.30 ± (0.27)	0.40 ± (0.13)	0.11 ± (0.13)	0.48 ± (0.17)	0.97 ± (0.22)	0.48 ± (0.23)	0.14 ± (0.24)	0.25 ± (0.31)	0.17 ± (0.07)
Prismatolaimus	0.20 ± (0.16)	0.03 ± (0.05)	0.05 ± (0.09)	0.28 ± (0.17)	0.16 ± (0.14)	0.00 ± (0.00)	0.04 ± (0.07)	0.14 ± (0.08)	0.04 ± (0.07)
Pungentus	0.15 ± (0.17)	0.14 ± (0.09)	0.05 ± (0.09)	0.18 ± (0.14)	0.03 ± (0.05)	0.08 ± (0.14)	0.19 ± (0.21)	0.10 ± (0.12)	0.08 ± (0.14)
Seinura	0.15 ± (0.13)	0.05 ± (0.09)	0.13 ± (0.04)	0.14 ± (0.25)	0.11 ± (0.09)	0.16 ± (0.09)	0.46 ± (0.48)	0.15 ± (0.26)	0.17 ± (0.09)
Thonus	0.12 ± (0.13)	0.06 ± (0.10)	0.27 ± (0.25)	0.12 ± (0.04)	0.11 ± (0.09)	0.31 ± (0.13)	0.22 ± (0.19)	0.24 ± (0.10)	0.40 ± (0.29)
Tylenchorhynchidae	0.88 ± (0.23)	0.44 ± (0.31)	1.03 ± (0.76)	0.67 ± (0.55)	0.60 ± (0.27)	0.79 ± (0.46)	0.73 ± (0.40)	0.64 ± (0.33)	0.50 ± (0.35)
Wilsonema	0.57 ± (0.14)	1.02 ± (0.27)	0.37 ± (0.23)	1.19 ± (0.56)	1.43 ± (0.42)	0.13 ± (0.16)	1.17 ± (0.50)	1.25 ± (0.29)	0.13 ± (0.16)

Data represent means ± S.D. Soil sample under poplar tree seedlings (P), under fescue (F) and bare soil (B) and from control (C), dried (D) and warmed (W) plot. PC: poplar soil, control; PD: poplar soil, dried; PW: poplar soil, warmed; FC: fescue soil, control; FD: fescue soil, dried; FW: fescue soil, warmed; BC: bare soil, control; BD: bare soil, dried; BW: bare soil, warmed. n.s.: not significant.

Table 2 – Results of ANOVA for overall effects of treatments and microhabitats on the densities of the more abundant genera as defined in Table 1, total nematode density and nematode richness

Nematode genus	Microhabitat		Treatment		Interaction	
	F values	*P* values	*F* values	*P* values	*F* values	*P* values
Acrobeles	6.85	0.007**	3.09	0.074	0.28	0.890
Acrobeloides	0.74	0.491	4.99	0.021*	0.53	0.717
Aphelenchoides	6.59	0.008**	1.65	0.223	0.21	0.930
Aphelenchus	2.75	0.094	4.11	0.036*	1.41	0.274
Aporcelaimellus	1.86	0.188	1.32	0.294	3.53	0.030*
Cephalobus	0.25	0.778	1.98	0.170	0.58	0.678
Cervidellus	7.83	0.004**	1.30	0.301	0.22	0.921
Discolaimium	1.04	0.376	0.06	0.940	0.64	0.640
Ditylenchus	0.86	0.441	3.01	0.078	0.88	0.500
Eudorylaimus	5.60	0.014*	2.92	0.083	1.62	0.217
Heterocephalobus	2.62	0.103	1.02	0.383	0.38	0.816
Leptonchus	6.23	0.010**	0.41	0.672	1.21	0.344
Microdorylaimus	4.38	0.030*	0.53	0.583	0.60	0.671
Microlaimus	2.10	0.155	0.57	0.576	1.12	0.380
Monhysteridae	13.87	0.000***	0.98	0.395	1.17	0.362
Plectus	4.60	0.026*	11.91	0.001***	1.20	0.349
Prismatolaimus	4.24	0.033*	1.25	0.314	2.29	0.105
Pungentus	1.42	0.270	0.11	0.896	0.29	0.880
Seinura	1.16	0.337	1.23	0.318	0.56	0.694
Thonus	4.49	0.028*	2.01	0.167	0.06	0.992
Tylenchorhynchidae	0.89	0.431	0.39	0.682	0.76	0.565
Wilsonema	20.02	0.000***	1.32	0.294	1.54	0.237
Nematode density	2.69	0.098	0.64	0.538	0.36	0.832
Nematode richness	2.05	0.161	0.64	0.540	0.35	0.838

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

27.4%). Fig. 2 indicates a relatively strong microhabitat effect on the nematode community structure, while the treatment effect was less pronounced than the microhabitat effect. According to the results of the ANOVA analysis on the PC scores, warming had an effect in fescue soil on axis 1 and warming and drying had an effect in bare soil on axis 2. It is also apparent that dried plots differed on axis 2 from the corresponding control plots. *Cervidellus* and *Microdorylaimus* are responsible for warmed plots separation, while *Acrobeles* discriminated between dried and control plots. Besides, these are the three dominant genera having average densities (individual g^{-1} soil ±S.D.) of 4.51 ± 1.2, 3.12 ± 1.7 and 2.25 ± 9.0 for *Cervidellus*, *Acrobeles* and *Microdorylaimus*,

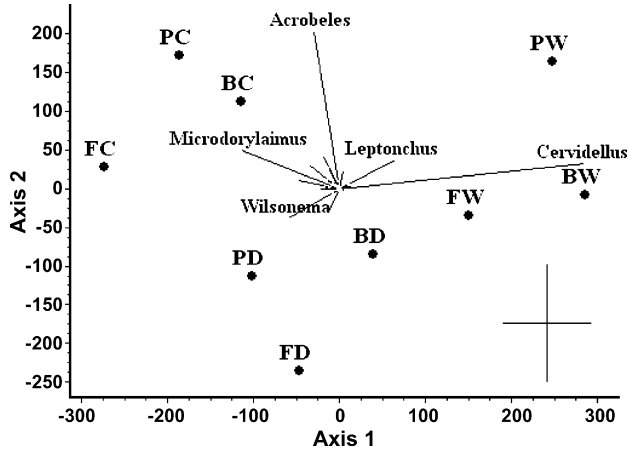

Fig. 2 – Treatment–species biplot based on the results of the centered PCA. Lines indicate species responsible for separating sampling points. Points (and letters) indicate the mean PCA scores for sampling points (three replicates). Bars are the least significant difference ($P < 0.05$). PC: poplar soil, control; PD: poplar soil, dried; PW: poplar soil, warmed; FC: fescue soil, control; FD: fescue soil, dried; FW: fescue soil, warmed; BC: bare soil, control; BD: bare soil, dried; BW: bare soil, warmed.

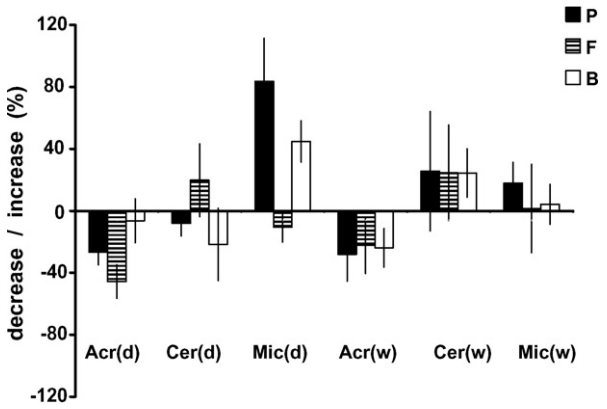

Fig. 3 – Increase or decrease in dominance (%) of the three most common genera in the dried (d) and warmed (w) plots comparing to the control. Mean of three replicates ± S.E. P: poplar soil, F: fescue soil, B: bare soil; Acr: *Acrobeles*, Cer: *Cervidellus*, Mic: *Microdorylaimus*.

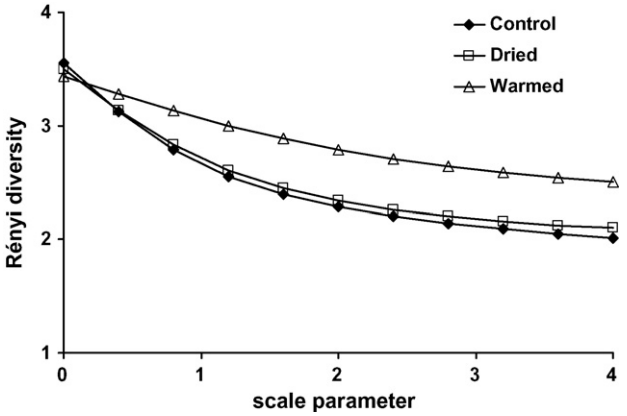

Fig. 4 – Diversity profiles of the nematode communities in poplar soil (mean of three replicates). Letters indicate control (C), dried (D) and warmed (W) plots.1

respectively. Comparing the percentage increases or decreases in the densities of these genera relative to the control, no consistent result is seen in the case of the dried treatment (Fig. 3). However, *Acrobeles* and *Cervidellus* showed clearly opposite trends in the warmed plots (Fig. 3). These trends were independent of the microhabitat effect.

The diversity of the genera responded to warming regardless of the microhabitat type. In spite of the fact that total diversity did not differ significantly according to the treatments, diversity profile analysis showed that warmed plots had significantly higher diversity of high density species (the right side of the graphs) than the control (Figs. 4–6). Drying did not influence the diversity of the nematode communities. The evenness of the communities was higher in warmed (average ± S.D.: 0.128 ± 0.01, 0.131 ± 0.03 and 0.237 ± 0.06 for poplar soil, fescue soil and bare soil, respectively) than control plots (average ± S.D.: 0.118 ± 0.02, 0.123 ± 0.01 and 0.198 ± 0.03 for poplar soil, fescue soil and bare soil, respectively) in all microhabitat types. However, these differences were not statistically significant.

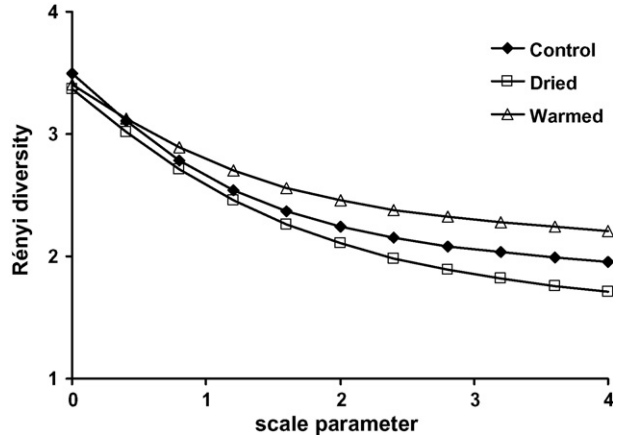

Fig. 5 – Diversity profiles of the nematode communities in fescue soil (mean of three replicates). For explanation of abbreviations, see Fig. 4.

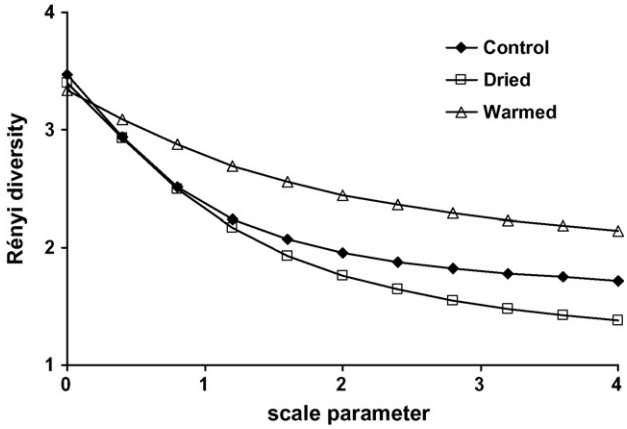

Fig. 6 – Diversity profiles of the nematode communities in bare soil (mean of three replicates). For explanation of abbreviations, see Fig. 4.

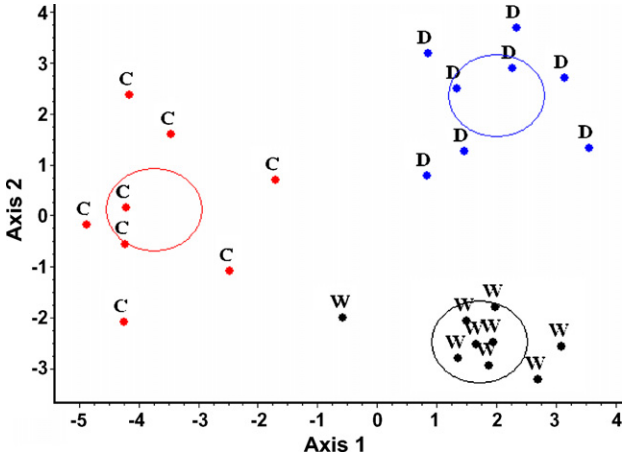

Fig. 7 – CVA of the treatments calculated on the basis of the genera (less than 0.1 individual g^{-1} soil). Points and letters indicate the mean CVA scores for sampling points (three replicates). Ninety-five percent confidence circles are shown. Wilk's lambda is 0.02. For explanation of abbreviations, see Fig. 4.

The most obvious treatment effect was found when low density and high density genera were analysed separately by CVA. The treatments differed significantly both in the case of the low density (Wilk's lambda: 0.02) and high density (Wilk's lambda: 0.002) genera (Figs. 7 and 8), showing that both drying and warming had a detectable influence on nematode community structure. Superimposing the CVA results for the high density genera (Fig. 8), it becomes clear that several genera were responsible for treatment effects. Control plots were characterised by high densities of *Acrobeles* and *Acrobeloides* and low densities of *Aphelenchus*, while *Cephalobus* and *Plectus* were prominent in the dried plots. Warmed plots were separated from unwarmed plots by five genera (*Cervidellus*, *Ditylenchus*, *Eudorylaimus*, *Seinura*, *Thonus*). Two of them (*Eudorylaimus* and *Thonus*) are omnivorous, having relatively persistent life history (belonging to the c-p group 4).

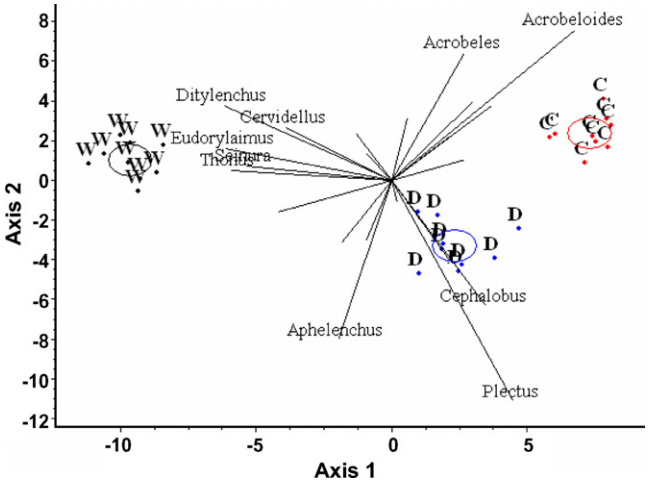

Fig. 8 – Treatment–species biplot based on the results of the CVA. CVA of the treatments was calculated on the basis of the high density genera (>0.1 individual g^{-1} soil). Lines indicate species responsible for separating sampling points. Points and letters indicate the mean CVA scores for sampling points (three replicates). Ninety-five percent confidence circles are shown. Wilk's lambda is 0.002. For explanation of abbreviations, see Fig. 4.

Feeding group composition was influenced significantly by drying under poplar and on bare soil (Table 3). The effect was straightforward, with percentages of the bacterivorous genera decreasing and those of omnivorous genera increasing in both cases. No such effect was detected under fescue. The percentages of plant feeding nematodes were extremely low, between 4.1 and 6.4%. The c-p structure changed significantly only in one case (Table 4). Drying of the bare soil decreased the ratio of the c-p 2 and c-p 3 groups, whereas that of the c-p 4 and c-p 5 groups increased.

No statistically significant effects were observed in the case of SR, MI, PPI, EI, CI, F/B and NCR, either due to the treatments or due to the microhabitats. SI was significantly enhanced only in the bare soil due to drying. Simultaneous graphical representation of CI and SI clearly shows that drying enhanced SI in poplar and bare soils and warming enhanced both CI and SI in all soils (Fig. 9). Changes in these indices were minor in the case of fescue, but well-defined in the poplar and bare soils.

4. Discussion

Recent experiments suggest that the method used in this study is a useful tool for manipulating soil temperature and moisture with minimal disturbance of other factors (Beier et al., 2004). Temperature and moisture differences between control and treated plots were in the range reported by Beier et al. (2004) and as experienced in earlier studies (Kertész, 1991).

Generic level response analysis of nematode communities to soil temperature and moisture changes based on field data is very difficult because of the possible differences in species composition of the genera in different experimental fields. Sohlenius and Boström (2001) pointed out that nematode species respond differently to changes in temperature and moisture. This is a prerequisite for species coexistence. Consequently, it is difficult to explain the responses of any genera to warming and/or drying of field experimental soils. Besides, it is seldom possible to separate the direct and indirect effects of soil temperature and moisture on the nematode community (Yeates et al., 2002).

Papatheodorou et al. (2004) found a positive temperature effect on *Acrobeles* and Bakonyi and Nagy (2000) on *Acrobeloides*

Table 3 – Effects of treatments on the feeding-group distribution patterns

Feeding group	PC	PD	PW	FC	FD	FW	BC	BD	BW
Ba	68.6	60.7	55.9	69.3	69.7	63.5	74.6	61.0	71.3
Fu	8.3	6.5	11.5	10.3	7.9	12.8	10.9	15.1	9.9
Ca	6.0	3.6	7.1	3.2	6.8	6.2	3.1	7.5	4.3
Om	17.2	29.2	25.5	17.3	15.6	17.5	11.5	16.5	14.6
Chi^2		0.05	n.s.		n.s.	n.s.		0.05	n.s.

Data are given as percentages. Treated plot values are compared to the appropriate control in every case. Ba: bacterivorous, Fu: fungivorous, Ca: carnivorous, Om: omnivorous, n.s.: not significant. For microhabitat abbreviations, see Table 1.

Table 4 – Effects of treatments on the c-p group distribution patterns

c-p	PC	PD	PW	FC	FD	FW	BC	BD	BW
1	1.8	1.3	0.5	0.2	0.2	0.0	0.2	0.2	0.0
2	66.5	57.4	60.7	72.0	74.0	68.6	74.3	64.5	71.6
3	5.3	6.0	2.4	3.0	2.0	2.4	3.1	0.8	3.3
4	21.4	32.5	31.4	22.0	18.4	23.7	20.1	28.3	21.9
5	5.1	2.8	5.0	2.8	5.4	5.3	2.4	6.1	3.2
Chi^2		n.s.	n.s.		n.s.	n.s.		0.02	n.s.

Data are given as percentages. Treated plot values are compared to the appropriate control in every case. n.s.: Not significant. For microhabitat abbreviations, see Table 1.

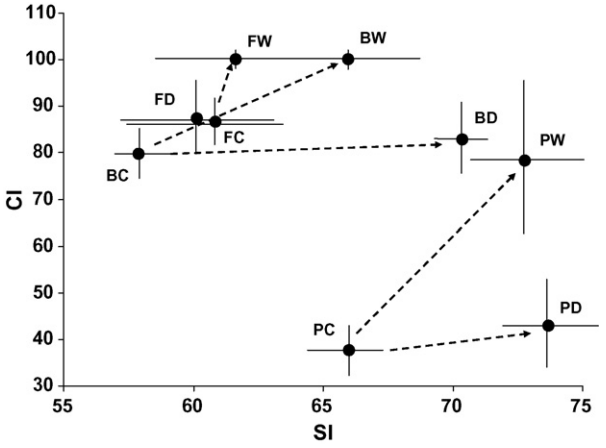

Fig. 9 – SI and CI values for the different treatments. Arrows show the direction of changes due to the treatments. Mean of three replicates ± S.E. For explanation of abbreviations, see Fig. 2.

in comparable manipulation experiments. In contrast to these results, the density of *Acrobeloides* decreased due to warming in the present experiment. *Acrobeloides* was shown to have a relatively wide temperature niche breadth in laboratory tests (from 12 to 35 °C) which is suitable to sustain population development (Anderson and Coleman, 1982). Therefore, it is reasonable to suppose that antagonism or competition between the genera and indirect, not direct temperature and/or moisture effects may be reasons for the contradictory results. Antagonism or competition occurs frequently between nematode taxa (Sohlenius, 1985). Opposite changes in the relative densities of *Acrobeles* and *Cervidellus* in warmed plots compared to the control, may be an example of this phenomenon because both species are bacterivorous and belong to the same c-p group.

In a laboratory soil incubation experiment, Sohlenius (1985) found a high density of *Acrobeloides nanus* and a low density of *Aphelenchoides* under wet conditions. He assumed that this was due to competition between the two taxa. However, since *A. nanus* is a bacterial feeder and *Aphelenchoides* a fungal feeder, a change in the food supply could also be responsible for this result. Bakonyi and Nagy (2000) did not find any effect of moisture on *Acrobeles* and *Acrobeloides* in the field. Moreover, Griffiths et al. (1995) found that the population of *Acrobeloides* spp. developed better under dry conditions. Variable water conditions enhanced the abundance and proportion of *Acrobeloides* in another experiment (Griffiths et al., 2003). *Plectus* density was enhanced by drying in this experiment, the opposite to the findings of Porazinska et al. (1999), who found more *Plectus* in wet soils and explained these results by the aquatic origin of the genus. The effects on nematodes of irrigation, a common agricultural practice, were investigated by Porazinska et al. (1998). They did not find density responses in most cases, except for *Aporcelaimellus* and *Eudorylaimus* whose densities correlated positively with irrigation rate. No such effect was found in this experiment in the case of *Eudorylaimus*. The variable responses of *Aporcelaimellus* to drying and warming under poplar, fescue and in bare soil support the findings of Porazinska et al. (1998) and confirm the importance of vegetation in relation to temperature and moisture effects. All these contradictory results may be attributed to the different experimental circumstances, differences in the nematode species, soil type and indirect effects of the soil moisture on soil biota.

Soil temperature and moisture either may influence density of plant feeding nematodes in a positive way (Verschoor et al., 2001; Todd et al., 1999) or may have no effect (Smolik and Dodd, 1983). There are clear differences between the responses of individual species. *Tylenchorhynchus acutoides* and *Xiphinema americanum* densities are affected by soil temperature and moisture changes more than *Pratylenchus neglectus* (Griffin et al., 1996). No differences were found in the density of the plant parasitic genera in the present study, but no detailed analysis of this feeding group was possible because of their low density. Plant effects as demonstrated in this study can be attributed to microclimatic conditions, but may also indicate resource preference. Kovács and Szigetvári (2002) found that 76–100% of the root length of *P. alba* and *F. vaginata* is colonized by endo- and ectomycorrhiza. This corresponds with the abundance of fungivorous and omnivorous groups in *Populus* and *Festuca* samples.

Our data show that enhanced soil temperature during the plant-growing season (spring) can enhance community diversity due to higher evenness. This was the finding in the case of the high density species. Higher diversity in warmed plots than in control plots during a hotter period in summer was found by Bakonyi and Nagy (2000). Soil temperature was also identified as a driving force for nematode community organization under hot conditions by Pen-Mouratov et al. (2004).

More structured communities developed due to drying in bare soil than in the control. The ratio of the bacterivorous nematodes (belonging to the c-p 2 group) decreased and that of the omnivorous and predatory nematodes (belonging to the c-p 4 and 5 groups) increased. SI and fungal biomass (unpublished data) increased significantly. Enhanced density of *Leptonchus* (probably due to the elevated fungal biomass) and *Microdorylaimus* correspond to the predictions of Ferris et al. (2001). The reason for this finding is not clear. Nematodes are in fact aquatic animals. Therefore, decreasing soil moisture content is expected to be a detrimental factor. However, this effect was counterbalanced by the fact that bare soil was significantly wetter than poplar and fescue soil. A small quantity of water-filled pores in the soil is enough to maintain nematode activity (Griffiths et al., 2003).

It is often the case that no statistically significant responses of nematode population or community parameters to subtle changes in soil temperature and moisture can be found in field experiments because of the high variance of the data and limited replication. The coefficient of variation in nematode density within treatments was higher than 30% in several cases in this experiment. It is quite probable that this is why we did not find statistically significant effects on SR, MI, PPI, EI, CI, F/B and NCR. In these circumstances, diversity and/or ordination analyses can provide valuable information on community structure by combining small differences in various parameters (Podani, 2000). Thus, when temperature and soil moisture cause small, insignificant effects on several

parameters (e.g. species number, density, species composition, dominance) which all point in the same direction, as occurred in the present case, these methods can effectively demonstrate differences between treatments (Bakonyi and Nagy, 2000; Griffiths et al., 2003).

Temperature was a more important factor influencing nematode community structure than soil moisture in this experiment. This finding is in accordance with data of Bakonyi and Nagy (2000) and Griffiths et al. (2003). It seems likely that if there is a minimum level of soil water available to cover the soil aggregates with water film or small water filled pore are available (Yeates et al., 2002; Strong et al., 2004), this circumstance is necessary and adequate for nematode activity. That is why higher soil moisture content has only a minor influence on nematode community structure. However, normal temperature regime has a direct influence on nematode growth, reproduction, feeding and activity as well as on soil bacterial and fungal biomass. Increasing temperature enhances all these parameters in a species specific way which may results in changes in the structure of the nematode community.

Acknowledgements

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