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Climate change and *Cognettia sphagnetorum*: effects on carbon dynamics in organic soils

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Summary

1. A microcosm experiment was performed to test the impacts of *Cognettia sphagnetorum* on carbon leaching in a cambic stagnohumic gley soil.

2. Leaching of dissolved organic carbon (DOC) was significantly enhanced by *C. sphagnetorum*, with the greatest effect being found in the upper, 0–6 cm, soil layers. The ratio of DOC to dissolved organic nitrogen (DON) in the leachate decreased in faunated systems, indicating that the enchytraeids were mobilizing carbon from organic matter with a low C to N ratio.

3. The vertical distribution of the enchytraeids had an effect on the production of DOC, and this vertical distribution is affected strongly by climate. It is proposed that increases in DOC found in a field soil-warming experiment with the same soil are largely a result of changes in the vertical distribution of these organisms.

Key-words: Dissolved organic carbon, enchytraeids, microcosm

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Introduction

Soil organic matter is an important component of terrestrial ecosystems, representing a carbon (C) pool three times larger than that of the atmosphere (GCTE 1996). Soils in upland ecosystems contain the majority of terrestrial C in the UK (Howard *et al*. 1995), with the accumulation of soil organic matter resulting largely from climatic limitations on decomposition processes (Swift, Heal & Anderson 1979).

It has been suggested that the C stores in these systems will be responsive to climate change, with temperature and moisture controlling the activity of the soil biota, and therefore the dynamics of the soil organic matter. In order to determine the influence of climatic change on the C dynamics of hill soils, a field experiment at the Moor House Nature Reserve (northern Pennines) was performed as part of the NERC Terrestrial Initiative in Global Environmental Research (TIGER). A full description of the experimental design is given in Ineson *et al*. (1998).

Preliminary data showed that the mineralization of organic matter and the release of elements, particularly dissolved organic carbon (DOC), can be stimulated as a result of increasing temperatures (Ineson *et al*. 1995). However, to predict the effects of climate change on ecosystem functioning it is necessary to know how ecosystem processes relate to the underlying changes in microbial and faunal populations and activity.

Enchytraeids are a major component of the fauna in UK upland systems, where *Cognettia sphagnetorum* (Vejdovsky) 1877 may represent up to 95% of soil animal biomass (Coulson & Whittaker 1978). This species is frequently concentrated in the upper horizons of these soils, where organic matter is accumulated (Nielsen 1955a; Peachey 1963; Springett 1963), but they also occur in deeper layers where temporary increases in their numbers are attributed either to vertical migration in response to adverse conditions (Nielsen 1955a; Nurminen 1967; Abrahamsen 1972) or to differential mortality and reproduction rates (Nielsen 1955b; O'Connor 1957, 1967; Nurminen 1967). Increasing temperatures have been shown to have a marked effect on reproduction and vertical distribution of these organisms, indicating that temperature is the main factor influencing reproduction (Briones, Ineson & Piearce 1997).

Enchytraeids have also been reported to have a strong influence on both respiration and nutrient leaching in microcosm studies (Setälä *et al*. 1991; Haimi & Boucelham 1991). However, we have very little information about the role of these saprovores in the release of dissolved organic carbon and nutrients, yet there is a growing realization that plant uptake of inorganic nutrients as components of dissolved organic matter may be of importance in nutrient-poor systems (see, for example, Michelsen *et al*. 1996).

The aim of the current project was to investigate the effects of enchytraeids on DOC leaching in these

soils, together with the implications of potential climate change for this process. The work consisted of two main components: a field study investigating the responses of enchytraeids and DOC production to climate manipulation and a laboratory microcosm study to relate DOC production to DOC leaching in the same soil.

Materials and methods

SITE DESCRIPTION

The studies described here were conducted using soil and vegetation from the Moor House National Nature Reserve (NGR 710322), the principal UK ecosystem study site in the IBP tundra biome project (Heal & Perkins 1978). The specific soil used was a cambic stagnohumic gley (peaty gley) from near the summit of Great Dun Fell and the soil is more fully described in Hornung (1968). The vegetation on the peaty gley was dominated by *Juncus squarrosus* L., with *Festuca ovina* L., *Deschampsia flexuosa* (L.) Trin. and *Polytrichum commune* L.

Two sites along a climatic gradient were selected for establishment of the experiment; the first was close to the summit of Great Dun Fell (GDF) at an elevation of 845 m and the second near Sink Beck (SNK) at 480 m. The sites have a mean monthly temperature difference of 2·5 °C, and are located within the Moor House National Nature Reserve, less than 1 km apart.

CLIMATOLOGICAL MONITORING

Temperature probes at two soil depths (2 and 10 cm) and at 0·5 cm above the soil surface were established at GDF and SNK. Each was constructed from thermistor beads (Betatherm 2252 ohms at 25 °C; P/N 151–588: Farnell Components Ltd, Leeds, UK) soldered to round, screened, twin wire microphone cable and sleeved with adhesive-lined heat shrink sleeving. Data were logged using a Type DL2 automatic weather station (AWS; type WS01, Delta-T, Cambridge, UK), which also monitored rainfall, radiation air temperature and wind speed at each site.

FIELD EXPERIMENTS: LYSIMETER STUDIES

Twelve, intact undisturbed soil cores were taken using 15-cm diam. × 28-cm deep acrylic cylinders from a cambic stagnohumic gley with the associated vegetation described above and near to the summit of GDF. These were used to construct zero-tension lysimeters by the addition of an acrylic baseplate and PVC drainage tube. A lysimeter trench was constructed at each of the two sites, GDF and SNK, to accommodate the lysimeters and to facilitate collection of leachates from the lysimeters.

The lysimeters were randomized, with six lysimeters being inserted at each of the two sites. They were placed adjacent to the lysimeter trenches in 20 m × 20 m fenced sheep exclosures. At both sites soil leachates were collected in bottles located in the bottom of the trench, with each lysimeter draining to a separate bottle. The bottles were fitted with a waterproof cap with air vent, and they were covered with black plastic bags to prevent algal growth. The bottles were replaced every 2 weeks, and the contents returned to the laboratory for determination of volume and subsequent chemical analyses of dissolved organic carbon (DOC) as described below for microcosm leachates.

FIELD EXPERIMENTS: FAUNAL EXTRACTIONS

Additionally, undisturbed cores, 171, taken using 15-cm diam. × 28-cm deep acrylic cylinders from the same site, were used to establish parallel lysimeters for periodic destruction and analysis of enchytraeid population changes. Because of the high numbers of cores necessary to determine soil faunal population changes, these lysimeters were not monitored for leachate chemistry. Fifteen cores were used to assess initial faunal populations, with the remainder being inserted at each of the two sites. Cores, intact within the acrylic cylinders, were placed near the lysimeter trenches at GDF (78 cores) and SNK (78) where they were reinserted into the ground, ensuring that the surface was level with the surrounding soil.

Fifteen cores were sampled from each site every 2 weeks, from 13 June 1994 to 25 July 1994, and only nine cores on 15 August 1994 and 22 August 1994 using a randomized block design. Cores were sliced horizontally into five 2-cm layers to a depth of 10 cm and a subsample (≈ 20 cm^2) of each layer was placed separately in plastic bags and transported to the laboratory in a cool box. Animals were extracted within 48 h using a modified wet funnel method (O'Connor 1955) and preserved in 70% alcohol. Numbers of the enchytraeid *Cognettia sphagnetorum* in each layer at each site were counted.

PREPARATION AND WATERING OF MICROCOSMS

An additional laboratory microcosm experiment was established using cores taken from the site used to provide the lysimeter cores used in the field experiments. Eight intact soil cores with associated vegetation were taken from the cambic stagnohumic gley near to the summit of Great Dun Fell using 5-cm diam. × 10-cm deep acrylic cylinders.

The cores were returned immediately to the laboratory and all cores were defaunated by placing in liquid nitrogen for 1 h. After thawing, each of the eight cores was sliced into three layers, each of 3 cm, to a total depth of 9 cm using a sharp knife. Each layer was placed into a separate microcosm inner container (Anderson & Ineson 1982), resulting in a total of 24 experimental units (eight cores, three layers per core).

Half of the microcosms were allocated to the control treatments (C), and were not inoculated with enchytraeids, while the remaining 12 were designated as +animal treatments (A) and subsequently inoculated with *Cognettia sphagnetorum* (see below). The microcosms were incubated at 15 °C for 8 weeks, using a randomized block design, in which each shelf of the incubator acted as one block.

Cognettia sphagnetorum was extracted from an additional series of cores taken from the same site using a modified wet funnel method (O'Connor 1955), and they were placed, 350 individuals per microcosm, with a minimum of disturbance onto the soil surface in each of the four replicates of every soil layer. This produced a population density similar to that seen under optimal conditions, as observed from the field experiment ($\approx 180 \times 10^3$ m^{-2}, see also Fig. 2).

Subsequently, all the microcosms were leached with 200 cm^3 of distilled water, with leachates being retained for chemical analyses. Leaching was performed by gentle immersion of the soil layer in the distilled water, draining under gravity, and reapplication of the leachate to the surface of the soil twice. Every soil layer was therefore leached three times on each sampling occasion, which ensured thorough equilibration of mineralized nutrients between the soil and the leachate (Anderson & Ineson 1982). This procedure was slightly modified in following samplings by leaching with 100 cm^3 of distilled water and allowing to soak for 1 h, draining under gravity, and reapplication of the leachate to the surface of the soil twice. This procedure was repeated every 2 weeks over the experimental period of 8 weeks.

At the end of the experiment, the soil remaining in the microcosms was removed, weighed and the animals extracted using the modified wet funnel method (O'Connor 1955), preserved in 70% alcohol and counted under the microscope. Following extraction the soil remaining in the microcosms was dried to constant mass and final water content assessment.

CHEMICAL ANALYSES OF LEACHATES

All leachate samples were stored at 2 °C and analysed for dissolved organic carbon (DOC) using continuous flow auto-analysis by decolorization of phenolphthalein after UV/persulphate digestion (Skalar method).

STATISTICAL ANALYSIS

The leachate concentrations from the lysimeter leachates at sites GDF and SNK were compared using repeated measures ANOVA (SAS 1989). Total DOC fluxes for each lysimeter for 1994 were calculated by summing the total DOC flux (volume × concentration) for each sampling occasion. These total fluxes were compared using one-way ANOVA with no transformation of the data since they were normally distributed.

Similarly, DOC fluxes in the microcosm experiment were converted to mg per microcosm and mean values and standard errors of the means for the faunated and defaunated treatments calculated. Comparisons of means were made using analyses of variance (ANOVA), with one-way ANOVA to compare DOC fluxes for the whole experimental period.

Additionally, the relationships between the DOC fluxes from the lysimeters and the numbers of *C. sphagnetorum* recorded during the field experiment, at both sites, were analysed by means of canonical correspondence analysis.

One-way ANOVA was also used to compare water contents of the soil layers and numbers of enchytraeids at the end of the experiment. Similarly, total *C. sphagnetorum* numbers per core from the field experiment were analysed to test whether they were influenced by treatment. Because the abundance data of enchytraeids were not normally distributed, the logarithmic transformation of the total numbers of individuals within each core was performed in this case, followed by ANOVA to quantify interactions between sampling date, treatment and depth.

Results

FIELD EXPERIMENTS: LYSIMETER STUDIES

Figure 1 shows the concentrations of DOC in lysimeter leachates at both sites for the years October 1992 to July 1995. A significant increase ($P < 0{\cdot}05$) in dissolved organic carbon (DOC) concentrations was observed during the summers at SNK; after the warmer months this difference decreased and became less consistent. This indicates that warmer conditions under field experiments can affect C dynamics and, therefore, losses of C as DOC can be stimulated as a result of increasing temperatures (see also Ineson *et al*. 1995).

FIELD EXPERIMENTS: FAUNAL EXTRACTIONS

Cognettia sphagnetorum was concentrated in the upper two layers at both sites in early summer. In July, coincident with rising temperatures (mean soil temperature at 2-cm depth: 13 °C at GDF and 15·5 °C at SNK, rainfall 1·9 mm and 1·4 mm, respectively), the population decreased in the top soil layers and increased in the deeper layers (Table 1). At GDF this increase occurred in the layers at depths of 2–4 cm and 4–6 cm, with the two remaining layers being unaffected. At SNK, all four deeper layers showed a parallel increase in numbers of *C. sphagnetorum* and 10% of the total population remained in the 0–2 cm layer in July (25 July).

This increase in the number of individuals in deeper layers, and the decrease in the top soil layers, suggests vertical migration rather than mortality in response to the higher temperature and/or lower

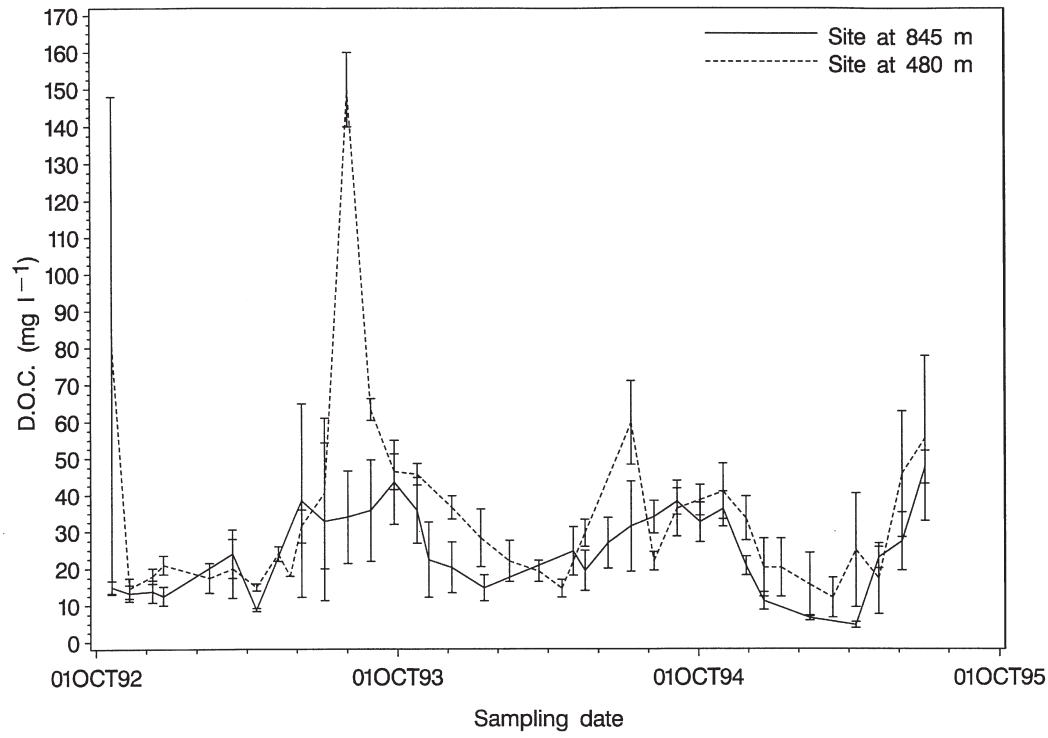

Fig. 1. Concentrations of dissolved organic carbon (mg DOC l^{-1}) in lysimeter leachate for the peaty gley soil between October 1992 and July 1995. Values represents the means, $n = 7$.

Table 1. Results from the analysis of variance (ANOVA) for abundance data (as number $\times 10^3$ m^{-2}) of *Cognettia sphagnetorum* at the different depths and at both sites. Significant differences are expressed as different letters, $P < 0{\cdot}05$, Tukey's HSD comparison of means. Lower case indicates depth comparisons and upper case site comparisons

	25 May 94	13 June 94	27 June 94	11 July 94	25 July 94	15 August 94	22 August 94
GDF							
0–2 cm	106·74^{a}	90·30$^{a\,A}$	82·63$^{a\,A}$	72·00$^{a\,A}$	66·53$^{a\,A}$	107·29$^{a\,A}$	114·99$^{a\,A}$
Standard error	10·11	10·47	8·99	7·45	11·11	10·99	10·94
2–4 cm	13·72^{b}	25·47$^{a\,A}$	31·35$^{a\,A}$	26·52$^{a\,A}$	73·63$^{a\,A}$	50·10$^{a\,A}$	43·16$^{ab\,A}$
Standard error	2·74	5·35	5·76	5·19	3·46	14·52	9·16
4–6 cm	1·63^{c}	9·81$^{b\,A}$	9·14$^{b\,A}$	6·32$^{b\,A}$	39·23$^{a\,A}$	9·00$^{b\,A}$	10·97$^{b\,A}$
Standard error	0·72	4·50	3·08	1·76	4·32	3·26	3·83
6–8 cm	0·17^{d}	1·32$^{c\,A}$	1·83$^{c\,A}$	2·41$^{bc\,A}$	11·82$^{b\,A}$	5·23$^{b\,A}$	2·82$^{c\,A}$
Standard error	0·06	0·77	0·53	0·79	2·95	3·02	1·51
8–10 cm	0·10^{d}	0·14$^{d\,A}$	0·85$^{c\,A}$	1·12$^{c\,A}$	4·18$^{c\,A}$	0·70$^{c\,A}$	1·01$^{c\,A}$
Standard error	0·05	0·06	0·24	0·21	1·09	0·20	0·34
SNK							
0–2 cm		92·10$^{a\,A}$	91·36$^{a\,A}$	69·99$^{a\,A}$	19·43$^{a\,B}$	64·74$^{a\,B}$	93·41$^{a\,A}$
Standard error		9·11	10·64	9·13	4·71	22·06	20·03
2–4 cm		56·85$^{ab\,B}$	40·07$^{a\,A}$	37·36$^{ab\,A}$	51·11$^{b\,B}$	67·35$^{a\,A}$	76·26$^{a\,A}$
Standard error		6·49	7·61	3·94	9·31	14·56	15·87
4–6 cm		21·77$^{b\,B}$	17·12$^{b\,A}$	18·64$^{bc\,A}$	60·59$^{b\,A}$	60·26$^{a\,A}$	42·56$^{ab\,A}$
Standard error		5·75	4·36	4·26	8·67	13·43	10·25
6–8 cm		3·63$^{c\,B}$	4·14$^{c\,A}$	14·57$^{d\,A}$	47·24$^{b\,A}$	36·22$^{ab\,A}$	31·39$^{b\,B}$
Standard error		0·95	1·58	4·88	9·18	21·27	11·99
8–10 cm		0·75$^{d\,B}$	1·05$^{d\,A}$	8·12$^{cd\,A}$	17·76$^{a\,A}$	23·34$^{b\,B}$	10·01$^{c\,A}$
Standard error		0·25	0·22	3·08	4·13	17·47	5·00

water content. Additionally, by the end of August, upward migration occurred in response to changing weather (at GDF the mean soil temperature was 10 °C and the rainfall 5·8 mm; at SNK the values were 13 °C and 5·3 mm, respectively), resulting in a recolonization of the upper layers at both sites accompanied by a decrease in numbers in the deeper layers (Table 1).

When comparing total abundance per core it can be seen that a higher number of *Cognettia* was recorded at SNK than at GDF across the entire experiment (Fig. 2). The differences were significantly different ($P < 0{\cdot}05$), except for 27 June and 25 July, coincidental with increasing temperatures.

MICROCOSM EXPERIMENT

The mean final numbers of enchytraeids per layer at the three different soil depths were 450 for the layer at 0–3 cm, 465 for that at 3–6 cm and 305 for that at 6–9 cm. This indicates that there was a significant increase in the final numbers in the upper two layers ($P < 0{\cdot}05$), with 28% and 32% increases with respect to the initial inoculum for the layers at 0–3 and 3–6 cm, respectively. Therefore, it can be concluded that reproduction was occurring in these layers whereas, in the layer at 6–9 cm, a population decrease of 13% was observed.

DOC released from the microcosms containing enchytraeids increased during the course of the experiment (Fig. 3a). This contrasted with the defaunated systems, in that they maintained relatively constant releases of DOC throughout the experimental period, with a greater DOC release from the top soil layer.

Increasing DOC release with decreasing depth was observed in the presence of *Cognettia* ($P < 0{\cdot}01$), with the greatest values being observed for the layer at 0–3 cm at week 4. In contrast, at depths of 3–6 cm and 6–9 cm DOC concentrations gradually increased during the course of the experiment, with values becoming significantly greater for the soil layer at 3–6 cm soil after 4 weeks ($P < 0{\cdot}01$), and even exceeded the amounts released from the layer at 0–3 cm by the end of the experimental period ($P < 0{\cdot}01$).

The final water contents at the various soil depths showed a positive interaction with the animals, with an increase in the final moisture content in the refaunated systems being observed. However, this effect was only significant for the layer at 6–9 cm ($P < 0{\cdot}05$).

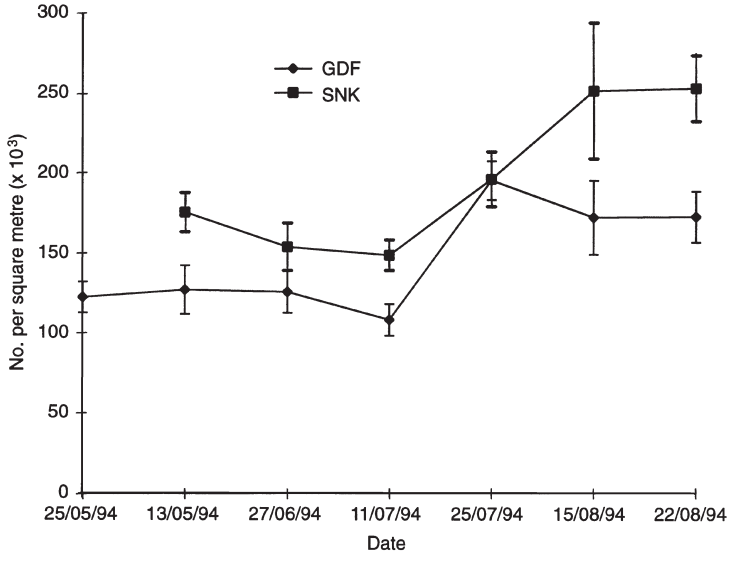

Fig. 2. Total numbers (as number × 10^3 m^{-2}) of *Cognettia sphagnetorum* at both sites. Values are means with standard errors, $n = 15$.

RELATIONSHIPS BETWEEN ENCHYTRAEID NUMBERS AND DOC FLUXES

Canonical correspondence analysis applied to the abundance data of *C. sphagnetorum* (both total numbers per core and per layer), DOC leachate concentrations and climatic factors produced a first axis mainly explained by temperature (Fig. 4 and Table 2). The inertia percentage for the first axis was 97·2% and, after applying the Monte-Carlo test, was found to be significant at the 5% level.

Total numbers of *Cognettia* and its abundance in the two upper layers were correlated with low temperatures, high rainfall and high DOC release. In direct contrast, the deeper layers showed a strong relationship with high temperatures and low DOC concentrations.

Discussion

Soil organic matter is a sensitive indicator of climatic patterns (Franz 1990) and microbial activity in highly organic soils is depressed by constantly low temperatures, soil acidity and waterlogging. At the global scale, soil organic matter increases along gradients of increasing precipitation and decreasing temperature (Post *et al*. 1982, 1985) and, from this, it can be inferred that climate change would have a marked effect on the organic matter turnover.

DOC and dissolved organic nitrogen (DON) are important fractions of organic soils, and may play an important role in N mineralization and subsequent availability to plants (Hart *et al*. 1994). DOC has been reported as an important factor in controlling soil microbial composition (Wynn-Williams 1980).

Field data have shown that increasing temperatures have a major effect on DOC release. DOC concentrations were greatest at the warmer site (mean annual temperature is 2·5 °C higher), with maximum concentrations occurring during the summer (Fig. 1). This is in agreement with the results obtained in a previous experiment where the effect of global warming on C dynamics was investigated by a soil-warming system based on electronically controlled cables which maintained the soil surface at 3 °C above ambient in the heated treatments (Ineson *et al*. 1995).

These observed peaks in the warmer treatments are not fully explained by the direct effect of increasing temperatures alone. Furthermore, the numbers and vertical distribution of enchytraeids have been shown to be very responsive to changes in temperature and moisture regimes (Briones *et al.* 1997), with *Cognettia* being found to move to deeper soil layers than previously reported by Springett, Brittain & Springett (1970). Additionally, significant positive correlations were found between soil temperature and enchytraeid numbers, indicating that temperature is a main factor influencing cocoon formation/hatching. From this it is anticipated that under a warmer environment increases in enchytraeid numbers would be seen, together with changes in their vertical distribution. At present, the full implications for functioning of the ecosystem are not understood and are difficult to predict.

The results obtained, using canonical correspondence analysis, showed that the 'temperature-moisture' gradient explains the abundance of *Cognettia* at the different layers and DOC concentrations were strongly related to total numbers. Despite the fact that the SNK site showed the greatest values of DOC, the analysis shows a negative relationship between DOC fluxes and temperature. This can be partially explained by the fact that the maximum values of DOC release were recorded at the end of August at this site, coincidental with decreasing temperatures and increasing rainfall. In addition, the results for vertical distribution are better explained by temperature, which leads to the conclusion that climate and its effect on total abundance and vertical distribution is the main factor influencing DOC production.

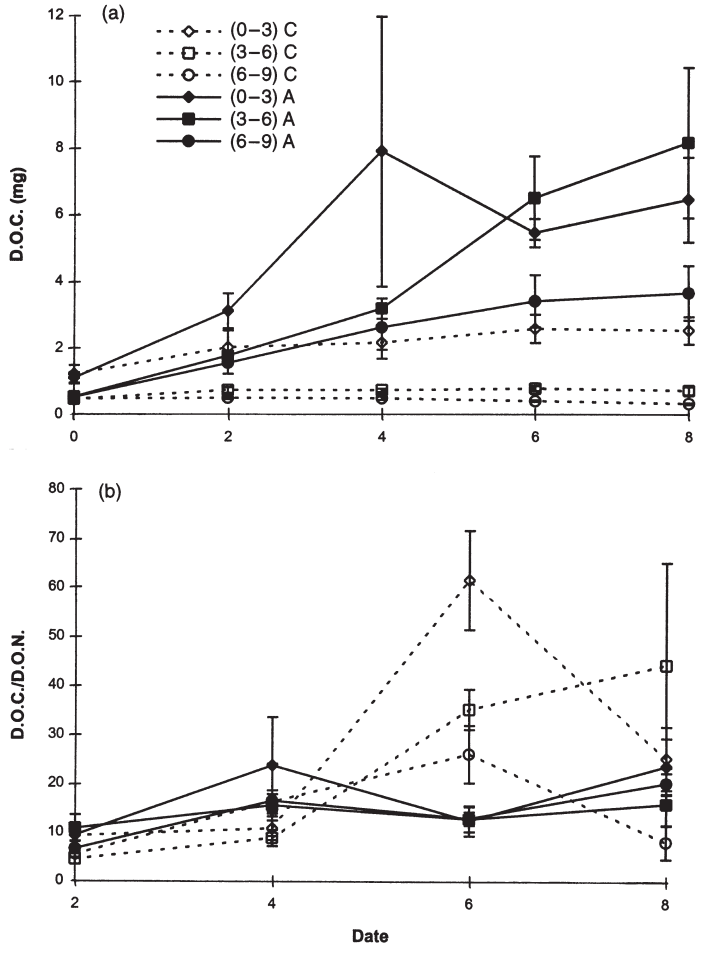

Fig. 3. Dissolved organic carbon release (mg DOC per 2 weeks) (a) and DOC to DON ratio (b) from microcosms containing soil from the different layers. Animal treatments are shown as solid symbols and controls as open symbols. Values are means (cm) with standard errors, $n = 4$.

In the current work rapid freezing with liquid nitrogen was used to defaunate the cores, with the assumption that other major groups of soil biota remained largely unaffected. Although this technique does not fully defaunate soil, it was recommended by Huhta, Wright & Coleman (1989) in a comparison of defaunation techniques because it minimizes unwanted side-effects on other organisms. However, the treatment will most certainly have resulted in damage to the microbial biomass, followed by a short-term flush of microbial growth associated with the rapid re-establishment after biocidal treatment (Powlson & Jenkinson 1976). Although all microcosms were subjected to the same pretreatment, interactions between the freezing and the inoculated fauna cannot be discounted; the reinoculation and mixing of soil microorganisms with the peat will have been accelerated in the presence of animals and may be a significant component of the effects resulting from animal addition.

Whatever the mechanisms involved, it can be concluded that enchytraeids exert a positive influence on DOC release from different soil layers and the effects on carbon dynamics vary with soil depth. These animals appear to have the greatest impact in the layers at 0–3 and 3–6 cm, indicating that organic matter turnover is accelerated by their presence. Furthermore, Briones, Carreira & Ineson (1998) found that the leaching of DON, ammonium and phosphorus was significantly enhanced in the presence of *C. sphagnetorum*, with the greatest effect in the top 6 cm. Figure 3(b) shows the trends in DOC to DON ratio using data reported before and those obtained here. From this it is clear that the presence of *Cognettia* resulted in a decrease of the DOC to DON ratio in the leachate, indicating that the enchytraeids appeared to affect the soil organic pool with the lowest C to N ratio.

Enchytraeids have a very low assimilation efficiency, and have to ingest large amounts of material, producing large amounts of undigested material characterized by increased microbial activity and nutrient availability (Martin & Marinissen 1993). In organic soils enchytraeids are frequently the key soil organisms in terms of carbon and nitrogen dynamics and, within the functional groups classification, could be defined as principal organic and inorganic substrate suppliers (GCTE 1996).

We can therefore expect the impacts of climate change in organic soils to result in an increase in the

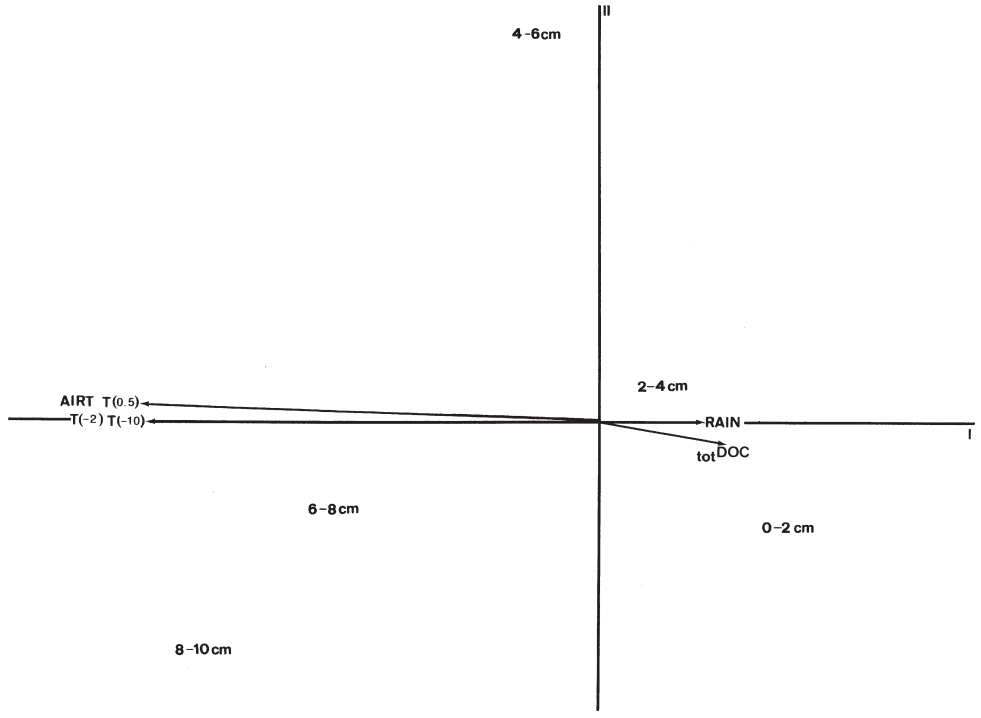

Fig. 4. Canonical correspondence analysis for total numbers (tot) and vertical distribution of *Cognettia* in relation to DOC leachate concentrations and five climatic factors (AIR T = Air temperature, T(0·5) = temperature at 0·5 cm above soil surface, T(– 2) = temperature at 2-cm soil depth, T(– 10) = temperature at –10-cm soil depth and RAIN = rainfall).

Table 2. Interset correlation coefficients between the first two axes and DOC and the climatic factors

	Axis I	Axis II
Air *T*	–0·8628	0·0467
T(+ 0·5 cm)	–0·8665	0·0420
T(– 2 cm)	–0·8600	0·0082
T(– 10 cm)	–0·8585	–0·0209
Rain (mm)	0·1891	0·0900
DOC	0·1739	–0·3635

abundance of enchytraeids and in the extent of their migration down the soil profile, resulting in an increase in organic matter turnover. These impacts of climate change on organic soils are of great potential importance in terms of carbon balance for the UK, since the majority of terrestrial C stored in the UK is in these soils (Howard *et al*. 1995).

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