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Effects of seasonal and diurnal temperature fluctuations on population dynamics of two epigeic earthworm species in forest soil

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ABSTRACT

Temperature fluctuations are a fundamental entity of the soil environment in the temperate zone and show fast (diurnal) and slow (seasonal) dynamics. However, responses of soil ecosystem engineers, such as earthworms, to annual temperature dynamics are virtually unknown. We studied growth, mortality and cocoon production of epigeic earthworm species (*Lumbricus rubellus* and *Dendrobaena octaedra*) exposed to temperature fluctuations in root-free soil of a mid-European beech–oak forest. Both earthworm species (3 + 3 individuals of each species) were kept in microcosms containing soil stratified into L, F + H and A_h horizons. In the field, earthworm responses to smoothing of diurnal temperature fluctuations were studied, simulating possible global change. In the laboratory, earthworm responses to seasonal (±5 °C of the annual mean) and diurnal temperature fluctuations (±5 °C of the seasonal levels) were analyzed in a two-factorial design. Both experiments lasted 12 months to differentiate between seasonal and diurnal responses. In the third experiment overwintering success of both earthworm species was investigated by comparing effects of constant temperature regime (+2 °C), and daily or weekly temperature fluctuations (2 °C ± 5 °C).

Temperature regime strongly affected population performance of the earthworms studied. In the field, smoothed temperature fluctuations beneficially affected population development of both earthworm species (higher biomass, faster maturity and reproduction, lower mortality). Consequently, density of both species increased faster at smoothed than at ambient temperature conditions. In the laboratory, responses of *L. rubellus* and *D. octaedra* to temperature treatments differed; however, in general, earthworms benefited from the absence of diurnal fluctuations. Total earthworm numbers were at a maximum at constant temperature and lowest in the treatment with both diurnal and seasonal temperature fluctuations. However, after one year *L. rubellus* tended to dominate irrespective of the temperature regime. In the overwintering experiment *L. rubellus* sensitively responded to even short-term winter frost and went extinct after one week of frost whereas *D. octaedra* much better tolerated frost conditions. Earthworms of both species which survived frosts were characterized by a significant body weight decrease during the period of frosts and fast recovery in spring suggesting a different pattern of individual resource expenditure as compared with constant +2 °C winter regime. Contrasting trends in the population dynamics of *L. rubellus* and *D. octaedra* during the frost-free period and during winter suggest that in the long-term temperature fluctuations contribute to the coexistence of decomposer species of similar trophic position in the forest litter. The results are discussed in context of consequences of climate change for the functioning of soil systems.

1. Introduction

Temperature is one of the principal environmental agents determining activity of biota and rates of decomposition processes in the soil (Swift et al., 1979). Temperature effects on a number of soil functions have been investigated, including activities of soil invertebrates (Byzova, 1973, 2007; Petersen and Luxton, 1982), soil microorganisms (Insam et al., 1989), and interrelationships among soil biota (Wolters and Ekschmitt, 1995). However, responses of soil organisms and communities to temperature have been investigated almost exclusively by using constant temperature regimes. Yet, rhythmic temperature fluctuations are a fundamental entity of soils

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in temperate and other biomes. These fluctuations show fast (diurnal) and slow (seasonal) dynamics and represent the natural environmental background which needs to be considered if we are to understand the functioning of soil systems. As stressed by Cossins and Bowler (1987), studies on temperature effects disregarding temperature fluctuations are of "questionable ecological significance".

Earthworms are among the most functionally important components of soil biota, acting as ecosystem engineers (Jones et al., 1994) strongly modifying soil structure, processes, biota community composition (Brown, 1995; Doube and Brown, 1998; Kretzschmar, 1998; Scheu et al., 2002; Tiunov, 2007; Eisenhauer, 2010) and ecosystem functions, which may result in shifting the functioning of soils from a sink to a source of carbon (Frelich et al., 2006; Hale et al., 2006; Eisenhauer et al., 2007).

Effects of temperature on earthworm activities have been extensively studied (Lee, 1985; Edwards and Bohlen, 1996); however, few studies investigated earthworm responses to temperature fluctuations. Most of the information available comes from short-term experiments investigating earthworm respiration and reproduction (Byzova, 1977, 2007; Uvarov, 1995, 1998; Uvarov and Scheu, 2004, 2005). However, the role of seasonal and/or diurnal temperature fluctuations on the performance of earthworm populations in the long-term remains virtually unknown. As well, effects of freeze/thaw fluctuations on overwintering success of earthworms have been studied only for cocoons (Jensen and Holmstrup, 1997). Knowledge on the response to temperature fluctuations is particularly important for epigeic earthworm species which are most exposed to short-term and seasonal climatic changes.

In one year long experiments we studied effects of seasonal and/or diurnal temperature fluctuations on the functioning of a forest litter–soil system (Uvarov et al., 2006). In the field, effects of natural and reduced temperature fluctuations were compared and in the laboratory effects of presence/absence of seasonal and diurnal fluctuations were investigated. It was shown that both seasonal and diurnal fluctuations significantly affect soil respiration and biomass and activity of soil microorganisms. In particular, reducing diurnal fluctuations resulted in a significant increase in CO_2 production and microbial activity. Seasonal temperature fluctuations significantly changed the dynamics of carbon loss from the soil system, as compared with the constant temperature regime. Considering earthworms and microorganisms as major and closely interconnected components of soil food webs, effects of temperature fluctuations on the performance of earthworm populations are necessary to be studied to understand how climatic changes will affect the functioning of soils.

In the present study we investigated the response of two epigeic earthworm species abundant in European forests to short-term (diurnal) and long-term (seasonal) changes in temperature. In an additional experiment significance of temperature fluctuations during winter for overwintering success of both earthworm species was investigated. The two species studied, *Lumbricus rubellus* and *Dendrobaena octaedra*, dominate the macrofauna in the litter horizon of acidic deciduous forests in Europe as the studied beech–oak forests near Darmstadt, Germany. *D. octaedra* is a small strictly epigeic species with relatively small impacts on the structure and microbial community of the forest floor, whereas *L. rubellus* is larger and colonizes the litter and upper mineral soil (epi-endogeic species) thereby strongly impacting soil structure, organic matter distribution, soil bulk density and nutrient mineralization (Scheu and Parkinson, 1994; McLean and Parkinson, 1997, 2000; Frelich et al., 2006). According to Satchell (1980) these species differ by their position in r/K gradient with *D. octaedra* being more r-strategist than *L. rubellus*. This suggests differences in energy budget and consequently in temperature sensitivity between the two earthworm species. We hypothesized that (1) both diurnal and seasonal temperature fluctuations affect population performance of both earthworm species; (2) *L. rubellus* and *D. octaedra* differentially respond to changes in temperature fluctuations; (3) winter temperature regime differentially affects overwintering success of *L. rubellus* and *D. octaedra* thereby shifting the dominance ratio between the both species.

2. Materials and methods

2.1. Study site

Earthworms, litter (L and F/H) and soil (A_h) materials were collected in the Kranichsteiner Wald, close to Darmstadt, Germany, in April and May 2000 and stored at 4 °C. The site is a 50–70 y old beech and oak forest on a gentle slope of southern exposition. The soil is characterized as orthic luvisol (FAO–UNESCO classification) with moder humus, with pH (KCl) values in the F/H and A_h horizon of 4.4–4.9 and 3.5–4.3, respectively. The climate in the Darmstadt region is subcontinental (warm summers and mild winters) with a precipitation of ca. 700 mm y^{-1} (Müth, 1990). The annual mean long-term minimum (January) and maximum (July–August) air temperatures are 10.7, 1.4 and 19.9 °C, respectively (Fuchs, 1999). In 2000–2003 the temperature in the humus layer of the forest studied ranged between 0 and 20 °C, only occasionally and shortly exceeding these limits. The winter 2000/2001 was mild with only two periods of frost lasting for 1–3 days; frost did not extend deeper into the soil than to the F layer. However, occasional frosts down to −15°C are also common during winters in the Kranichsteiner Wald.

The earthworm community in the litter of the study site was dominated by *L. rubellus* Hoffmeister and *D. octaedra* (Savigny), with a small admixture of *Dendrodrilus rubidus* (Savigny).

2.2. Microcosms

Microcosms consisted of plastic cylinders of 15 cm inner diameter and 35 cm height, with air/water-tight bottom and lid; the lid had a 2 cm round hole (sealed with gauze to prevent earthworms from escape) for air exchange. In the microcosms, soil columns were established resembling the soil structure in the field: 1 kg A_h material was covered by 150 g F/H and 15 g L litter materials (equivalent to 35.2, 16.3 and 5.1 g C, respectively). After 5 months fresh L material equivalent to 8.5 g C was added to the microcosms simulating autumn litterfall. The substrates were sorted to remove earthworms and large predators. The soil was sieved (4 mm) for homogenization and removal of roots. Chambers were switched to day and night temperature at 5 h and 17 h, respectively. Due to buffering capacity of the soil, the change to the day (or night) temperature regime in the microcosms after the switch lasted 7–8 h; then temperature level was constant for 4–5 h before the next switch. Temperature regime was monitored at the litter/soil interface by data loggers (Gemini Ltd., UK) at hourly intervals. Soil moisture was kept at a constant level by regular watering (every 2 weeks; in winter once per month) with 180 ml and subsequent drainage at −0.5 MPa. Despite the same procedure, the moisture content of substrates in some microcosms in the absence of (laboratory) and at smoothed (field) diurnal fluctuations was slightly increased (by 0–7%). Therefore, when evaluating effects of temperature regime, soil moisture content was used as a covariate.

2.3. Field experiment

The field experiment investigated effects of temperature fluctuations (natural or smoothed) on the population development of earthworm species. Microcosms were dug into the soil of