Soil Biology & Biochemistry 108 (2017) 78–83

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Nematode exclusion and recovery in experimental soil microcosms

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ARTICLE INFO

Article history:
Received 2 December 2016
Accepted 1 February 2017
Available online 6 February 2017

Keywords:
Nematode removal
Soil defaunation

ABSTRACT

Experimental manipulations of soil fauna are a powerful tool for assessing causal relationships between belowground biodiversity and key ecosystem properties. However, preparing soil microcosm treatments without soil fauna for ecological experiments can be problematic. Methods to exclude nematodes, a ubiquitous and functionally important component of terrestrial ecosystems, have been developed for a few specific ecosystems, some of them involving the application of nematicides that may have interactive effects throughout the soil food web. Our goal was to develop a method to remove nematodes from soils of three Long Term Ecological Research (LTER) grassland sites, ranging from desert to moist, without use of chemicals and with moderate disturbance. Moreover, we aimed at testing whether the nematode removal would remain effective up to several weeks later. The following treatments were applied to ~3-kg soil microcosms in the laboratory: (1) a 72 h heating (65 °C) - freezing (−20 °C) - heating (65 °C) cycle using soil maintained at its original water content, and pre-wetting soil 24 h before heating (65 °C) for either (2A) 48 h or (2B) 24 h. We measured treatment effects on total abundance and trophic structure of the nematode community. To investigate whether nematodes would recolonize eight weeks after treatments, we conducted a greenhouse experiment where individual seedlings of the dominant grass species for each ecosystem were transplanted to treated and non-treated (control) soils. A heat-freeze-heat cycle of 72 h using soil in its original field water content killed 60, 95, and 99% of the nematodes for the desert, semi-arid, and moist tallgrass prairie soils, respectively. Pre-wetting soil before heating increased mortality to 99% for all ecosystems after only 24 h at 65 °C. Root-feeders were the most resistant nematode trophic group. Eight weeks after treatments, there was no significant nematode recolonization for the pre-wetted 48 h heated soils from the three sites, while for the semi-arid and moist sites there was a slight recovery in abundance in soil from the 24 h heating treatment. Therefore, a treatment at 65 °C for 48 h using pre-wetted soil is recommended for eight-week long manipulative experiments in order to assure the effectiveness of the nematode removal throughout the experiment.
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1. Introduction

Nematodes are among the most abundant and diverse multicellular organisms inhabiting soils (Bongers and Ferris, 1999) and represent key connections across soil food webs through their remarkable range of feeding strategies as herbivores, bacterivores, and fungivores, to omnivores and predators (Yeates et al., 1993). Although the understanding of how nematodes interact within extremely complex soil food webs has rapidly grown (Ferris, 2010; Cesarz et al., 2015), there is an immediate need for further experiments studying their responses to global change, and possible consequences for soil and ecosystem function. The manipulation of nematode functional diversity in soil is key to answering such questions (Xiao et al., 2010; Gebremikael et al., 2015).

Experimental manipulation of soil fauna is a powerful tool for assessing causal relationships between belowground biodiversity and key ecosystem properties (Bardgett and van der Putten, 2014; Wagg et al., 2014). However, one of the biggest challenges lies in establishing treatments without nematodes (Ingham et al., 1985), which are used in laboratory or field microcosm manipulations to contrast responses of an ecosystem process with the native nematode community. Exclusion of nematodes and other soil fauna

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http://dx.doi.org/10.1016/j.soilbio.2017.02.001
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groups has usually been performed by physical or chemical methods, with the latter becoming less frequently used because of well documented, non-target effects of biocides or nematicides on the soil food web (Wall and Reichman, 2000). Physical exclusion methods incorporate variations of timing of temperature extremes to kill nematode communities in soil (e.g. freeze/thaw cycles and heating treatments), and are generally developed for the specific ecosystem to be studied (Bruckner et al., 1995; Bardgett et al., 1998; Jaffee, 2006; Lopez et al., 2009). Examples of distinct exclusion methods tested in a particular ecosystem range from deep-freezing soil using dry ice at −78.5 °C (Bruckner et al., 1995), to heating for 24 h at 80 °C followed by freezing for another 24 h at −80 °C (Bardgett et al., 1998). These methods provide a useful guide for work within a specific ecosystem but are of limited value for experiments across several ecosystem types and at broader geographic scales. Physical exclusion can also occur by autoclaving or use of gamma irradiation (Wall and Reichman, 2000). An issue with autoclaving is that it may produce high nutrient release and loss of soil structure (Trevors, 1996), potentially compromising the representativeness of microcosm experiments to actual field conditions, while gamma irradiation becomes costly for experiments using large amounts of soil.

Here we performed a series of temperature extremes experiments in order to develop a single physical method for soil nematode exclusion that could be applied across ecosystems varying in climate (annual precipitation), soil types, and productivity, thus providing a tool for soil ecologists conducting manipulative experiments. Soils from three different grassland ecosystems, ranging from desert to humid, were used to test for water content influences on nematode exclusion efficiency. We hypothesized that soil nematodes from ecosystems with contrasting water regimes would respond differently to nematode exclusion treatments. Nematodes live in water films around soil particles and thus changes in soil water (chemicals, freezing, desiccation, seasonality) affect survival (Sylvain et al., 2014). At present there is no nematode exclusion technique tested in ecosystems across a spatial gradient of water availability. We also expected that nematode trophic groups would respond dissimilarly to exclusion treatments, with higher trophic levels being most sensitive to treatments as predaceous nematodes have been shown to be more sensitive to disturbance (Bongers, 1999).

Specifically, this study aimed to: (i) test nematode exclusion methods by examining its effect on total nematode abundance and the trophic structure of the nematode community; (ii) determine whether exclusion effectiveness varies among ecosystems across a gradient of water availability; (iii) determine how long a treated soil remains nematode-free by investigating temporal patterns in nematode community recovery; and (iv) investigate the effect of exclusion treatment intensity on nematode community recovery.

2. Materials and methods

2.1. Site description and soil collection

Soil was collected during summer 2015 in three types of US grassland ecosystems: desert grassland, semiarid shortgrass, and mesic tallgrass. The desert grassland site was located in the Jornada Basin Long-Term Ecological Research site (JRN), in New Mexico. This site receives on average, 247 mm of precipitation annually, and vegetation is dominated by *Bouteloua eriopoda*, with the presence of *Prosopis glandulosa* (Havstad and Schlesinger, 2006). The semiarid shortgrass site was located at the Semiarid Grasslands Research Center (SGRC), Colorado, formerly Shortgrass Steppe LTER. Mean annual precipitation is 321 mm, and vegetation is dominated by *Bouteloua gracilis* (Lauenroth and Burke, 2008). The tallgrass prairie site was located in Kansas at the Konza Prairie LTER (KNZ). Average annual precipitation is 835 mm, and vegetation is dominated by *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium* (Knapp, 1998). At each site three soil blocks measuring 20 × 20 cm were taken from the top 20 cm soil from directly beneath the dominant vegetation type. Soil was returned to laboratories at Colorado State University, stored at 4 °C and used within 7 days.

2.2. Nematode exclusion - experiment 1

Experiment 1 tested the exclusion of nematodes from soils of the three grassland ecosystems with heating/freezing cycles. Samples from each site were homogenized by a coarse-mesh sieving (6.25 mm), and a portion of each sample was placed into aluminum dishes (33 × 23 cm) to a depth of 5 cm. One dish was obtained per soil block, yielding a total of 3 dishes per site. Due to differing soil bulk densities among sites, the total weight of soil in the aluminum dishes used for nematode exclusion differed (e.g. ~4 kg of JRN soil per dish, compared to 2.5 kg of SGRC soil, and 2.2 kg of KNZ soil). The aluminum dishes were then subjected to three days of treatment: 24 h at 65 °C, followed by 24 h at −20 °C, then a further 24 h at 65 °C. Soil in the aluminum dishes was subsampled (100 g for nematode analyses, 50 g for soil moisture) four times from different quadrants of the dish at the following time intervals: control (T = 0 h), after heating (T = 24 h), after heating and freezing (T = 48 h) and after heating, freezing and heating (T = 72 h). Nematodes in soil subsamples were extracted using Baermann funnels (Hooper, 1970), and nematodes removed daily for 3 days, and stored at 4 °C. Nematodes were counted and identified using an inverted microscope (Olympus CKX41, 200X magnification) within 3 days of extraction. The first 150 nematodes per sample were identified to five different trophic groups: bacterial-feeders, fungal-feeders, root-feeders, omnivores, and predators (Yeates et al., 1993), and total numbers per feeding group were extrapolated based on full sample counts. Standardized nematode population abundances were calculated as individuals per kg of soil (corrected to oven dry weight equivalent). Gravimetric soil water content (w/w) and oven dry weight equivalents were determined from mass loss of soils heated to 105 °C for 48 h (Barrett et al., 2004).

2.3. Nematode exclusion - experiment 2

Experiment 2 aimed to reduce any nematode survival rates observed in experiment 1. Sieved soil (6.25 mm) was placed into aluminum dishes as in experiment 1. Soil was then pre-wetted and left at 4 °C for 24 h. To wet the soil, water was gently sprayed over the soil surface until it passed through small holes on the bottom of the dishes and wet an absorbent paper placed beneath the dishes. Then, samples were transferred to an oven at 65 °C for either 24 or 48 h (experiment 1 results showed that the freezing step was redundant). Soil subsamples (100 g for nematode analyses, 50 g for soil moisture and 100 g for experiment 3) were taken from different quadrants of the tray at the following time intervals: control (T = 0 h) and after heating for 24 and 48 h. Nematode and soil moisture samples were processed identically to experiment 1.

2.4. Nematode community recovery – experiment 3

A greenhouse experiment was design to examine the longevity of the exclusion treatments effects observed in experiment 2 and temporal patterns of nematode recovery. The environmental conditions in the greenhouse were 15–21 °C, 30%–50% humidity, and photoperiod of 16 h light / 8 h dark. To replicate a potential

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