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Effects of a one-year rainfall manipulation on soil nematode abundances and community composition

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ABSTRACT

Soil nematodes play a crucial role in the terrestrial nitrogen cycle by accelerating the release of ammonium from microorganisms (bacteria and fungi). As aquatic organisms, nematodes are likely to be affected by predicted changes in precipitation patterns and soil moisture during the 21st century. The objective of this study was to measure the response of soil nematodes to a one-year rainfall manipulation in the sandy, forest soils of the New Jersey Pinelands (USA). We excluded all rain from four replicate field plots and applied double the amount of natural rainfall to four additional plots. We then assessed the impact of these precipitation treatments on nematode abundance and community composition. We found that total nematode abundance increased with more precipitation, and were highly sensitive to annual precipitation amount. This is in contrast to microbial biomass which was previously found to be insensitive to precipitation change. We suggest that any increased microbial growth in high rainfall plots was consumed by microbivorous nematodes. We further suggest that nematodes in the freely draining, sandy soils we studied may be unsuccessful at surviving drought because few water-filled pore spaces remain, as compared to more aggregated soils. All nematode families were sensitive to drought, but the effect was greatest on the Plectidae, while no significant effects were found for the Cephalobidae and Qudsianematidae. While not directly measured, these results provide insight into the relative anhydrobiotic abilities of these families. We found that bacterial-feeding nematodes were most sensitive to drought, suggesting that grazer-induced alterations to the nitrogen cycle are possible if precipitation patterns change in the future.

Introduction

The study of soil microbial communities is often conducted without concern for the role of microbial grazers, despite the fact that grazers are intimately associated with microbes and play an important role in regulating microbial community composition and the terrestrial nitrogen cycle (Clarholm 1985; Ingham et al. 1985). Soil nematodes are one of the most important groups of microbivores responsible for stimulating microbial activity (Fu et al. 2005) and nitrogen mineralization (Woods et al. 1982; Ingham et al. 1985; Fu et al. 2005). Many species of nematodes are classified as either bacterial- or fungal-feeders, and while both groups can increase nitrogen mineralization rates (Ingham et al. 1985; Chen and Ferris 1999), the stimulatory effect is much stronger among the bacterial-feeders (Ingham et al. 1985; Hunt et al. 1987).

In the northeastern United States, climate models project that the amount and/or intensity of precipitation may increase during the 21st Century (Christensen et al. 2007; Tryhorn and DeGaetano 2010). Such changes could impact soil nematode abundance and community composition because nematodes depend upon water for movement and to migrate towards their prey (Griffiths and Caul 1993). Soil bacterial and fungal populations (soil microbial biomass), which comprise a large proportion of nematode food resource, may also be impacted by changes in precipitation and soil moisture which could, in turn, alter nematode abundances. Bacterivorous nematodes may be particularly sensitive to altered precipitation patterns because their bacterial prey depend on a continuous film of water for resource acquisition (Harris 1981). In contrast, soil fungi can extend hyphae through air-filled pore spaces (Jennings 1990) and, consequently, might remain more stable under shifting precipitation and soil moisture patterns. Furthermore, soil fungi are believed to be more drought tolerant than bacteria. Fungivorous nematodes may therefore be less impacted by altered precipitation patterns because their fungal prey should remain relatively more stable under both elevated and reduced precipitation.

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During a two-year rainfall manipulation study in the New Jersey (NJ) Pinelands, in which experimental plots were subjected to a 100% rainfall exclusion or a doubling of rainfall, no changes in soil microbial biomass, community composition or nitrogen mineralization rates were detected (Landesman and Dighton 2010). The lack of a response among the microbial community to drought was attributed to a resistant microbial community capable of multiple physiological modifications. NJ Pinelands soils are very sandy and susceptible to rapid leaching, which may have reduced the impact of a doubling of rainfall on microbial biomass and community composition. However, it is also possible that any changes in the microbial community resulting from elevated precipitation were moderated by concurrent changes in the grazer community. Specifically, an increase in microbial production would have represented an increase in grazer prey densities. Furthermore, grazer access to prey would have been facilitated by elevated soil moisture.

The objective of the current study was to evaluate the response of soil nematode abundances and community composition to changes in annual precipitation in the NJ Pinelands. We hypothesized that total nematode abundance would increase under elevated precipitation and decrease in response to drought conditions. We further predicted that bacterial-feeding nematodes would be most sensitive to changes in annual precipitation, relative to the fungal-feeders. Such changes in nematode abundance and community composition would have important implications for nitrogen cycling in the NJ Pinelands, as nematode grazing is known to stimulate nitrogen mineralization.

Methods

Study site and experimental design

Our field site was in the NJ Pinelands (USA), a forest ecosystem that is characterized by sandy, acidic soils with a history of wildfires and prescribed burning (Little 1998). The site is dominated by a mix of *Quercus* sp. and pitch pine (*Pinus rigida*) with an understory of ericaceous shrubs (*Gaylussacia* sp. and *Vaccinium* sp.). The soils are classified as Entisols from the Evesboro series (Markley 1998) with a pH ranging from 4.1 to 4.7 (Tedrow 1998). They contain a well-defined organic horizon to an average depth of 2.3 cm.

Rainfall was manipulated using twelve rain exclosures (2.5 m × 1.9 m × 0.7 m) within an approximately 25 m × 25 m area of uniform shrub density. The shelters were covered with clear PVC panels that diverted natural rainfall into collection tanks. Using a pump connected to a garden hose, rainfall was simulated by sprinkling collected rain water onto plots. Treatments included a complete rain exclosure ("drought" treatment), a 100% rainfall addition ("ambient" treatment) and a 200% rainfall addition ("high" treatment). For the ambient and high treatments, the contents of one and two collection tanks respectively were applied the experimental plots. Four additional "natural" treatments were established in which no manipulations were performed (i.e., no exclosures). Details of the experimental design are described in Landesman and Dighton (2010).

Total rainfall during the study period (September 2006–September 2007) was 1344 mm, which we estimate to be the equivalent of 6295 L reaching natural plots. Ambient treatments received 4708 L of rainwater, and high rainfall plots received 9197 L. The discrepancy between the volume of rain applied to natural and ambient plots resulted from slight inefficiencies in the water collection system, in which small amounts of rainwater often remained in the collection tank or in the water pump. On three occasions, significant precipitation events (>50 mm) caused the tanks to overflow. While the overflow did not reach any of the experimental plots, it contributed to the smaller amount of water being applied to ambient plots relative to natural plots. High rainfall plots always received twice the amount of rain in ambient plots, and drought plots never received any rainfall. During the week prior to sampling for this study, only 8 mm of natural rainfall rain was recorded, and this rainwater was not applied to ambient and high rainfall plots until after sampling. No other rainfall was recorded in the 26 days prior to sampling. As a result, natural plots received very little rain, and ambient and high rainfall plots received no water applications in the three weeks leading up to the sampling event.

Sampling procedure

Samples were removed in September 2007, 14 months after the start of the experiment. During sampling, three cores per plot (approximately 50 g in total) were removed for the organic horizon (0–3 cm depth) and pooled and homogenized through a 2 mm sieve. The sampling depth of 0–3 cm incorporated the entire organic horizon. Below the sampling depth, the soil rapidly transitions into almost 100% sand and therefore represented a distinct habitat. Nematodes were extracted from soil using a modified Cobb's decanting and sieving method (s'Jacob and van Bezooijen 1984). During this procedure, nematodes were separated from soil by submerging samples in deionized water and sieving with 422 μm, 125 μm, 75 μm and 43 μm sieves. Nematodes were separated from the remaining soil particles using deionized water and a cotton milk filter and concentrated into 100 mL of deionized water. Nematode abundance (NA) was calculated by counting all individuals in a 10 mL subsample: $\mathrm{NA\,g\,soil^{-1}} = [(\text{number of individuals}) \times 10]/\mathrm{g\,soil}$. After counting, nematodes were concentrated into 10 mL of water and mixed with 10% hot formalin. A minimum of 250 nematodes per sample were identified to the family level (genus where possible) using a Zeiss Axiovert 40 CFL inverted microscope (Carl Zeiss MicroImaging, Inc., Thornwood, NY, USA). The exception was one drought treatment sample, for which only 15 individuals were present in the entire sample. The proportional representation of each family was estimated by dividing the total number of nematodes assigned to a particular family in a given subsample by the total number of nematodes identified in the subsample. Abundances of nematodes from each family (number of individuals $\mathrm{g\,soil^{-1}}$) were estimated by multiplying these proportional estimates by total nematode abundance.

Nematode community composition was assessed by assigning families to trophic groups based on Yeates et al. (1993), allowing for an assessment of the abundances (number of individuals $\mathrm{g\,soil^{-1}}$) of bacterial-feeders, fungal-feeders, omnivores and plant-parasites. There is uncertainty with respect to the feeding behavior of some groups of nematodes, especially for the Tylenchidae and Aphelenchoididae, species of which may be fungivores, plant-parasites or both (Yeates et al. 1993). Because soil fungi tend to dominate the soil microbial community in acidic soils (van der Heijden et al. 2008), all nematodes from these families were assumed to be fungivores.

Statistical analyses

Total nematode abundance, family-level nematode abundances, proportional representation of nematode families and trophic groups were analyzed with a one-way analysis of variance (ANOVA). Significance was determined at the $P < 0.05$ level and $P < 0.10$ was considered to be strongly suggestive of a significant effect. Significant differences among treatment means were assessed with the Tukey's test ($P < 0.05$). All statistical analyses were performed using SAS 9.2 (SAS Institute Inc., Cary, NC, USA), and