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.

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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 relatively 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.
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). The soils 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 to the experimental plots. For the ambient and high treatments, the contents of one and two collection tanks respectively were applied to 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: \( \text{NA g}^{-1} = \frac{(\text{number of individuals}) \times 10}{\text{g soil}} \). 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 Microlmaging, 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 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 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 Aphelenchoidae, 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 using the Tukey’s test (\( P < 0.05 \)). All statistical analyses were performed using SAS 9.2 (SAS Institute Inc., Cary, NC, USA), and

Results

Nematode abundances and community composition

Rainfall manipulations had significant effects on nematode abundances ($P = 0.0006$, Fig. 1). Abundances within drought treatments (13 g soil$^{-1}$) were significantly lower than in high and natural plots, which were similar (100 g soil$^{-1}$ and 106 g soil$^{-1}$ respectively, Fig. 1). In ambient plots (53 g soil$^{-1}$), there were four times as many nematodes as in drought plots, and about half the number of nematodes in comparison to high and natural rainfall plots (Fig. 1).

A total of 14 nematode families were represented in the samples, of which six comprised 97% of the nematode community. These were the Aphelenchoididae and Tylenchidae (fungal feeders), the Cephalobidae and Plectidae (bacterial-feeders), the Criconematidae (plant-parasite), and the Qudsianematidae (omnivores). Other families identified were the Hoplolaimidae, Pratylenchidae, Bunonematidae, Teratoccephalidae, Monhysteridae, Prismatolaimidae, Chrysonematidae and Thorneenematidae. The most commonly encountered morphospecies across the samples were an Aphelenchoides sp. (family: Aphelenchoididae, 23% to 62% of the community) and a Wilsonema sp. (family: Plectidae, 0.3–34%). All families were negatively impacted by drought as compared to high rainfall plots (Fig. 1).

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Nematode functional groups

Across all samples, 71% of the nematodes identified were classified as either fungal (42%) or bacterial-feeders (28%), with the remaining 29% classified as omnivores or plant-parasites (no predators were found). Bacterivores were negatively impacted by drought ($P < 0.09$, Fig. 3), whereas fungal-feeders, omnivores and plant parasites were unaffected by the precipitation manipulations ($P > 0.50$).
Discussion

Changes in precipitation intensity and temporal periodicity are aspects of global climate change that are not as frequently considered as changes in temperature. Yet, changes in precipitation that influence soil moisture status will profoundly impact soil biota and biogeochemistry. The objective of our study was to investigate the impact of altered annual precipitation patterns on nematode abundance and community composition in field plots where precipitation was either eliminated or doubled for one year.

Because we analyzed nematode communities during a single sampling event, it is difficult to assess how precipitation might affect nematode communities during other seasons. However, whereas no changes in microbial biomass or community composition were detected over six sampling events during this experiment (Landesman and Dighton 2010), the fact that we found a strong treatment response of nematode abundance during a single sampling event is highly significant. Furthermore, these treatment effects were detected despite the fact that no rain water was applied to ambient or high rainfall plots in the 26 days prior to sampling. Our results therefore demonstrate that nematodes not only responded to the long-term precipitation manipulations, but that the changes are not quickly reversed. A notable aspect of our results is that nematode abundances were reduced in ambient plots with precipitation exclosures versus natural plots without exclosures (Figs. 1 and 2). This result is likely due to the fact that total rainfall in natural plots was higher than rainfall in ambient plots and, furthermore, that nematodes are sensitive not only to changes in precipitation amount, but also to changes in precipitation frequency. In contrast, neither bacterial nor fungal biomass were impacted by differences in precipitation amount or frequency between ambient and natural plots (Landesman and Dighton 2010).

An increase in nematode abundances with precipitation (Fig. 1), but no change in microbial biomass, including during a sampling event only eight days prior to sampling for nematodes (Landesman and Dighton 2010), is consistent with a theoretical model proposed by Oksanen et al. (1981). According to this model, herbivores are expected to limit the increase in primary production that accompanies a rise in productivity (i.e., soil moisture). The additional primary production is instead transferred to the consumer trophic level (Oksanen et al. 1981). While predators would be expected to positively influence primary producers by suppressing grazer populations (Hairston et al. 1960), no nematode predators were observed in our samples. Interestingly, other long-term field experiments have reported only small or non-significant changes in microbial biomass or gene copy number in response to rain-fall manipulations (Jensen et al. 2003; Castro et al. 2010), and one experiment found that most bacterial families decreased in response to elevated rainfall (Cruz-Martinez et al. 2009). In light of our results, one potential explanation for these counterintuitive responses is that grazers, which were not measured in these other studies, played a role in regulating microbial growth. This potential regulatory role of nematodes was also seen in a study in which atmospheric CO2 levels were experimentally increased (Yeates and Newton 2009).

The sharp decrease in nematode abundance in response to the drought treatment is in contrast with experiments on silt–sand soil from an old field in which soil drying had almost no effect (Görres et al. 1999; Neher et al. 1999) or very little effect (Savin et al. 2001) on nematode abundances. Nematodes were also largely unaffected by soil drying in pasture soils with a variety of textures (Yeates et al. 2002). In these studies, it was concluded that water-filled soil aggregates provided habitable pore spaces in which nematodes were concentrated with their prey, prolonging survival (the “enclosure hypothesis”). Our observation of a reduction in nematode abundance with reduced precipitation is consistent with the “exclusion hypothesis” which predicts that survival decreases with decreasing soil moisture, due to restrictions in movement and nematode to access prey (Görres et al. 1999). The exclusion hypothesis explanation for the reduction in nematode abundances is supported by the fact that aggregation, while not directly measured, is very low in Pinelands soil. This is because these soils contain only very small quantities of clay (Douglas and Trela 1998), which are centers of aggregate formation (Jastrow and Miller 1998). On the other hand, in a silt-loam soil from another old field, Kardol et al. (2010) found that nematode abundance was negatively affected by reduced precipitation. While this result suggests that the protective role of soil aggregates during drought may be overstated, the experimental plots in Kardol et al. (2010) were subjected to considerable disturbance, including the application of herbicide and re-planting. These manipulations could have disrupted the aggregate structure of the soil.

In response to the drought treatment, nematodes could have survived by migrating below the sampling depth. This is unlikely, however, because our sampling design captured the entire organic horizon, which is a distinct habitat. Below the sampling depth, microbial biomass, nutrient pools and water holding capacity should be much lower, and less supportive of nematode communities. It is more likely that drought led to nematode mortality, and that surviving individuals from most, if not all families entered a state anhydrobiosis (Freckman et al. 1975; Townshend 1984; Treonis and Wall 2005). This ametabolic state is induced by desiccation and shields nematodes from environmental stress (Crowe and Madin 1975; Crowe et al. 1992; Wharton and Barclay 1993).

Although anhydrobiosis likely played a role in the differential survival of nematodes under drought conditions (Fig. 2), little is known about the comparative anhydrobiotic abilities among nematode taxa (Treonis and Wall 2005). Due to the extreme nature of the drought treatment, it is not surprising that abundances were reduced among all families. However, our results suggest that the Cephalobidae and the Qudsianematidae may have been most effective at entering anhydrobiosis because abundances of these families were not significantly affected by the drought treatment (Fig. 2). For the Cephalobidae, this conclusion is supported by observations from the polar desert soils of the Antarctic Dry Valleys, where the abundances of the endemic nematode Scottnema lindsayae (Cephalobidae) were negatively correlated with soil moisture (Treonis et al. 1999). By contrast, in the Pinelands soils, individuals from the Plectidae (primarily a Wilsonema sp.) experienced a significant decline in drought plots not only in total abundances (Fig. 2), but in proportional representation as well (data not shown). This suggests that they were least effective at employing anhydrobiosis. Consistent with these results, a Plectus species in the Antarctic Dry Valleys was found to be more abundant in moist, relative to drier habitats (Treonis et al. 1999). This implies that desiccation survival is different among nematode taxa, likely as a function of their relative ability to employ anhydrobiosis.

Given the high sensitivity of bacterial-feeding nematodes to drought (Fig. 3), relative to all other trophic groups, our results suggest that changing precipitation patterns may alter nitrogen mineralization rates by increasing bacterivorous grazing (Ingham et al. 1985; Hunt et al. 1987). Consistent with this hypothesis, nitrogen mineralization rates were positively correlated with soil moisture during July 2007 and July 2008 (Landesman and Dighton 2010). However, precipitation treatments had no effect on nitrogen mineralization rates during the sampling event that preceded the nematode sampling by only 8 days (Landesman and Dighton 2010). Due to extremely low precipitation in the month prior to sampling, both nematode and microbial activity were likely very low, and this may explain why the treatments had no effect on nitrogen mineralization during this period. However, a higher abundance of bacterial-feeding nematodes in ambient, high and natural plots,

relative to drought plots, may lead to altered nitrogen mineralization rates following individual rain events. The potential for such changes warrant further investigation.

Conclusions

Our results provide strong evidence that soil nematodes are highly sensitive to changes in annual precipitation amount and that nematode grazing may have prevented larger increases in microbial biomass in response to elevated precipitation. Our results further suggest that soil properties may influence the nematode response to soil drying. In light of similar studies, we conclude that the lack of aggregation in Pinelands soils might play an important role in the response of nematodes to changing soil moisture. The effect of rainfall may also be influenced by nematode community composition, at least to the extent that composition relates to anhdybiotic ability. A large body of research indicates that soil nematodes play an important role in nitrogen mineralization. The high sensitivity of nematode abundances, and especially bacterial-feeding nematodes, to changes in precipitation may be of great importance to the terrestrial nitrogen cycle in the NJ Pinelands.

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