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Body size and population dynamics of enchytraeids with different disturbance histories and nutrient dynamics

Jouni K. Nieminen*, Jari Haimi

Department of Biological and Environmental Science, University of Jyväskylä, FI-40014 University of Jyväskylä, Finland

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Abstract

The population dynamics of the enchytraeid *Cognettia sphagnetorum* originating from an unmanaged forest (FP), a clear-cut area (CCP) or a plot treated with birch ash (APP) and the effects of population origin on labile C and N dynamics were investigated. Twenty individuals of *C. sphagnetorum* were introduced in microcosms containing humus from the unmanaged forest devoid of enchytraeids and amended with sucrose, and incubated for 14 weeks. Triplicate microcosms from FP, CCP and APP treatments were destructively sampled every second week and enchytraeid population density, individual length, nematode abundance and trophic structure, humus properties and dissolved organic C (DOC) and N (DON), and NH_4–N in soil were determined. The enchytraeid body size was initially smaller in CCP and APP than in FP. The enchytraeid propagation rate was lower and individual size less variable in APP than in FP or CCP, and although enchytraeid size increased in all treatments, exponential population models indicated that APP was less stable. Nematode community was dominated by bacterial-feeders especially in the microcosms with APP. N mineralization rate was lower and DOC decomposition rate greater in APP systems. The results show that *C. sphagnetorum* is more sensitive to wood ash than clear-cutting, and its altered body size distribution has the potential to affect the dynamics of soluble nutrients.

Zusammenfassung

Es wurden die Populationsdynamiken und der Einfluss der Herkunft der Populationen auf die labilen C und N Dynamiken bei Enchyträen der Art *Cognettia sphagnetorum* untersucht, die aus einem nicht bewirtschafteten Wald (FP), einem Kahlschlag (CCP) und aus einer Fläche stammten, die mit Birkenasche behandelt wurde (APP). Es wurden zwanzig Individuen von *C. sphagnetorum* in Mikrokosmen eingesetzt, die Humus aus einem nicht bewirtschafteten Wald enthielten, der frei von Enchyträen und mit Saccharose angerichtet war, für zwei Wochen inkubiert. Dreifache Mikrokosmen aus den FP, CCP und APP Ansätzen wurden jede zweite Woche destruktiv beprobt und die Populationsdichte der Enchyträen, die individuelle Länge, die Nematodenabundanz und die trophische Struktur, der gelöste organische C (DOC), N (DON) und NH_4–N im Boden bestimmt. Die Körpergröße der Enchyträen war anfangs bei CCP und APP geringer als bei FP. Die Fortpflanzungsrate der Enchyträen war geringer und die Variation der individuellen Länge war bei APP geringer als bei FP oder CCP. Und obwohl die Größe der Enchyträen bei allen Behandlungen zunahm, zeigten exponentielle Populationsmodelle, das APP weniger stabil war. Die Lebensgemeinschaft der Nematoden wurde von Bakterienfressern dominiert, vor allem in den Mikrokosmen mit APP. Die Rate der N-Mineralisation und die Zersetzungsrate von DOC war in den APP-Systemen größer. Die Ergebnisse zeigen,

*Corresponding author. Tel.: +358 14 2604182; fax: +358 14 2602321.
E-mail address: jouni.k.nieminen@jyu.fi (J.K. Nieminen).

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dass *C. sphagnetorum* empfindlicher auf Holzasche als auf Kahlschlag reagiert und die veränderte Verteilung der Körpergröße hat das Potenzial, die Dynamik der gelösten Nährstoffe zu beeinflussen.

Keywords: *Cognettia sphagnetorum*; Size distribution; Nematodes; Dissolved organic carbon; Nitrogen

Introduction

Human activity is changing both biotic and abiotic components of terrestrial ecosystems and creating new selection pressures for organisms driving vital ecosystem processes (Wardle, Verhoef, & Clarholm 1998; Van der Putten et al. 2004). Our ability to predict the responses of soil organisms and processes to environmental changes is limited because the population dynamics and resource-consumer interactions of soil animals are poorly understood (Hedlund et al. 2004).

Because of their high biomass (up to 30% of soil animal biomass in spruce forests, Huhta & Koskenniemi 1975), enchytraeids have long been considered an important component of the soil food web in boreal forests. Soil animals excrete mineral N (Setälä, Tyynismaa, Martikainen, & Huhta 1991), which can enhance plant growth in nutrient-limited conditions (Laakso & Setälä 1999). Soil animals also affect labile DON (Briones, Carreira, & Ineson 1998) and DOC pools (Briones, Ineson, & Poskitt 1998; Cole, Bardgett, & Ineson 2000; Van Vliet, Beare, Coleman, & Hendrix 2004), which are rate-limiting steps in N and C mineralization.

The harvesting of round timber, logging residues and stumps is the most important human activity impacting on enchytraeids in managed boreal forests. Conventional harvesting with logging residues left on site increases enchytraeid populations probably because logging residues provide resources for microbes and because the physical cover by woody debris indirectly enhances the growth of soil organisms and decomposition processes (Lundkvist 1983; Siira-Pietikäinen, Pietikäinen, Fritze, & Haimi 2001). However, harvesting may affect the reproductive strategy of enchytraeids, their vulnerability to parasitism (Lundkvist 1983) or destabilize their size distributions (Nieminen 2009a).

Another aspect of intensive forestry is that the wood ash resulting from burning logging residues should be returned to harvested sites so as to prevent the loss of mineral nutrients. Enchytraeid worms are sensitive to loose wood ash in microcosms (e.g. Nieminen 2008) and in the forest (Haimi, Fritze, & Moilanen 2000). As reviewed by Aronsson and Ekelund (2004) wood ash effects on enchytraeids can be attributed to both direct mechanisms such as elevated pH, or heavy metal biotoxicity, and indirect mechanisms such as a shift to bacteria-dominated microbial community.

The interpretation of the experimental results is, however, complicated by the fact that the dominant enchytraeid, *Cognettia sphagnetorum* reproduces asexually by fragmentation (Standen 1973), and the poorly known size-specific fragmentation and mortality rates may be affected by the disturbance. Lundkvist (1982) suggested increased mortality during fragmentation and Salminen and Haimi (2001) reported increasing survival with age. By combining several field data, Nieminen (2009b) detected a relationship between the stability of enchytraeid size distribution and environmental variability. Although both clear-cutting (Nieminen 2009a) and wood ash (Nieminen 2008) are known to alter enchytraeid size distributions, the relationship between size-structured population dynamics and nutrient cycling has not been studied independent of indirect disturbance effects through soil properties and microbes.

We compared the body size and population dynamics of replicated experimental populations of *C. sphagnetorum* originating either from an unmanaged Norway spruce forest, a clear-cut area, or a plot treated with birch ash, when growing in the same undisturbed organic soil. We hypothesized direct impacts on the enchytraeid population structure, and in particular, that the small, disturbed enchytraeid populations would have lower propagation rates and unstable size distributions when growing on a new, unlimited resource for longer than one generation. On the other hand, any changes in the soil or in the nematode community in the microcosms, which were never exposed to disturbance, must be indirect effects of altered enchytraeid populations. Further, we expected that the residence time of food in the enchytraeid gut would increase with body size, and as a consequence of this, large body size would enhance C and N mineralization. Thus, we hypothesized that the undisturbed populations would be associated with higher C and N mineralization rates than the disturbed ones.

Materials and methods

Twenty soil cores (diam. 57 mm) were taken from the humus layer (thickness 55 ± 16 mm, mean $\pm$ standard deviation (S.D.)) of a plot (1.5×1.5 m) 2 months after treatment with birch ash ($2.4\ \mathrm{Mg\ ha^{-1}}$), 20 samples from a site clear-felled in the preceding winter (logging residues were also harvested), and 20 samples from the untreated Norway spruce forest (age ca. 80 years) in which the ash plot was located. The soil cores were put individually into marked 1 l polyethylene bags and stored in a 20 l polyethylene bag at +3 °C until extraction. Enchytraeids were extracted from the humus layer (96 ± 1% organic matter (OM), pH(H_2O) 4.6 ± 0.27) using the Baermann wet funnel technique (O'Connor 1957).