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Original article

Effects of low quantities of added labile carbon on soil nematodes in intact forest soil microcosms

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ABSTRACT

Labile carbon compounds, such as root exudates, can have significant effects on soil communities even in low concentrations. Previous studies have shown that adding labile carbon can significantly affect the abundance and biomass of various groups of soil animals, including nematodes. However, many studies have used excessive quantities of added carbon and homogenised soil with artificial soil communities. I therefore set up a microcosm incubation experiment with intact soil cores and a natural composition of soil biota to determine the role of low quantities of labile carbon in soil nematodes. Different levels of carbon flow were simulated by a repeated pulse of three glucose concentrations (70, 140 and 350 μg C g^{-1} dry soil $week^{-1}$), which were comparable with the labile carbon supply to the plant rhizosphere. Pure water was added as control. Significant effects were observed in total abundance, microbivorous trophic groups and four nematode genera (*Acrobeloides*, *Plectus*, *Aphelenchoides* and *Filenchus*). Despite only four genera being affected, their total relative abundance was high and varied from 40% to 70% depending on treatments. The nematode abundance increased in the microcosms, where root exudation was simulated by glucose addition but decreased in the control. Moreover, no major differences in nematode abundance were found among the different quantities of added glucose except for the control. Results demonstrate that easily available carbon in an amount comparable with that found in root exudates is a significant factor that drives soil nematodes, although it has high taxon specificity. Only some genera are sensitive to such carbon applications. The data also suggest that variations in the carbon flow within estimates of root exudation do not cause substantial changes in the number of nematodes.

1. Introduction

Labile carbon represents a small but functionally important fraction of soil organic matter [1]. These compounds have low concentrations in soil, but they are involved in the regulation of microbial pool, plant litter decomposition and stability of soil organic carbon, among others [2–4]. Despite the many studies on the significance of labile carbon in the overall soil ecosystem, especially in soil microorganism communities, the role of low quantities of easily available carbon in soil invertebrates remains little understood. Root exudates, which consist of oligosaccharides and other low-molecular compounds, are one of the main sources of labile carbon in soil [5–7]. According to some estimates, about 10–100 μg C g^{-1} dry soil day^{-1} can be excreted into the soil via the roots [8–10]. Labile carbon represents a high-quality nutrient source for microbes, stimulating their growth and thereby increasing prey availability for their consumers, such as nematodes and protozoa. Therefore, a supply of easily available carbon to soil by root exudates can be one of the drivers of soil invertebrate communities. Thus, recent studies using isotope tracers have demonstrated that the majority of soil animal taxa acquire belowground carbon from living roots (e.g. rhizodeposits) [11–13].

A series of experiments have shown that the addition of labile carbon has a significant affects the abundance and biomass of various groups of soil animals, such as collembolans, enchytraeids and earthworms [14–17]. However, the responses of soil nematodes to labile carbon in previous studies were mixed, with some experiments finding no effect of labile carbon addition on soil nematodes [18–21] and others finding that it increased the abundance of bacterivorous or/and fungivorous nematodes [22–26].

Some limitations of the previous studies, however, do not allow a full evaluation of the role of low amounts of labile carbon in soil nematode communities. In most cases, the quantity of carbon used is unrealistic compared with carbon concentrations usually

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calculated for rhizosphere soil. For example, Nieminen [16] used a single application of 4000 μg C g^{-1} dry soil, Mikola and Setälä [26] used a weekly addition of 2500 μg C g^{-1} dry soil, Freckman and Virginia [23] and Ruess et al. [27] used a single pulse of 144 g C m^{-2} and 105 g C m^{-2}, respectively. While Mikola and Saj [20] found no effect on microbivorous nematodes using small amounts of labile carbon (8–175 μg C g^{-1} dry soil) as a single pulse in microcosms with homogenised soil.

Previous laboratory studies did not accurately reflect natural conditions that could yield inaccurate results. Thus, these studies were limited to simplified experiments in which few selected species of nematodes and microbes were applied or used soil that was disturbed by sieving and sterilisation [16,26,28]. The problems of these experiments lie not only in the difficulties of extrapolating the results to the actual field conditions but also in the actual interactions omitted [29]. Moreover, soil nematodes are a heterogeneous group that depends on environmental conditions and food sources [30–32]. However, earlier studies on the effects of labile carbon were based on assessments of the total and trophic groups abundance [16,22,25,28]. It is unknown whether or not all taxa within a specific trophic group are sensitive to the addition of labile carbon remains unknown. Finally, a range of abiotic and biotic factors, such as climate change, parasite attacks and soil nutrient availability, affects the intensity of root exudation (i.e. labile carbon availability) [33,34]. Variations in root exudation may serve to govern nematode fluctuations in natural habitats. However, to date, data on the effect of various labile carbon concentrations on the nematode community are lacking. Only Mikola and Saj [20] used a labile carbon gradient (18, 44 and 175 μg C g^{-1} dry soil) but found no significant differences among treatments under a microcosm condition with soil homogenisation.

Considering some of the limitations of previous experiments (e.g. using excessive quantities of added C and homogenised soil with artificial soil communities), I set up a microcosm incubation experiment with intact soil cores and a natural composition of soil biota to determine the role of low quantities of labile carbon on soil nematodes. Specifically, I addressed two questions: (1) Does the supply of labile carbon in quantities comparable with those found in root exudates significantly affect soil nematodes? (2) Are all taxa within a specific trophic group sensitive to the addition of labile carbon? Moreover, I aimed to obtain information on the effect of various labile carbon flows on soil nematodes.

2. Materials and methods

2.1. Field sampling and microcosm preparation

Undisturbed cores were collected in autumn from a spruce forest in an albeluvisol in the taiga zone of northwestern Russia (N 61°38.988, E 50°43.988). The stand was dominated by Norway spruce (*Picea abies*), interspersed with other species, including *Betula pubescens* and *Populus tremula*. The herbaceous layer is dominated by *Oxalis acetosella* and *Vaccinium uliginosum*. Less abundant herb species are *Maianthemum bifolium, Pyrola rotundifolia*, and mosses *Hylocomium splendens, Pleurozium schreberi, Rhytidiadelphus triquetrus*. Within the plot, 60 undisturbed cores were collected under spruce trees from the upper 7 cm using a soil core sampler (diameter of 10 cm), and carefully inserted in polypropylene containers. Cores were collected as far as possible without understory vegetation and containing only a small amount of moss. Each core was weighed. The average fresh weight was 140 ± 5 g (mean ± SE). Eight samples (5 × 5 × 7 cm) were collected to determine the baseline values of the nematode community and soil moisture content (61.3 ± 2.1%, mean ± SE) in the study plot (ca. 100 m^2).

2.2. Experimental setup

In the experiment, a glucose solution was used as the labile carbon source. Four treatments were used with 15 replicates each, namely, a control (pure water) and three levels of labile carbon addition (70, 140 and 350 μg C g^{-1} dry soil $week^{-1}$, which corresponded to 3.8, 7.6 and 18.9 mg C $core^{-1}$ $week^{-1}$). The glucose gradient corresponded with the estimate of carbon quantities, which were excreted into the soil via the roots [8–10]. Hereafter, the treatments are referred to as control, C_{70}, C_{140} and C_{350}. In the microcosm experiment, a glucose solution or water (1.20 ± 0.04 ml, mean ± SE) was added to eight locations through the top of the soil core (four at a depth of 5 cm and four at a depth of 2 cm) using a syringe. For acclimatisation, the microcosms were stored in a climate chamber for 10 days at 15 °C and relative humidity of 85% in the dark. The microcosms were then injected with the glucose solution or water. In addition, water was added to compensate for the weight loss of each microcosm through evaporation. Five microcosms from each treatment were analyzed after 10, 30 and 60 days of incubation, excluding acclimatisation. At each sampling event, five randomly selected cores per treatment were removed, gently homogenised and sampled for the determination of the nematode community.

2.3. Nematode analyses

The nematodes were extracted as above from 100 g of soil from each core using the modified Baermann method [35]. After extracting for 48 h, the nematodes were killed at 60 °C and then preserved in 4% formaldehyde. In each soil sample, at least 100 individuals were identified, where possible to the genus level, using a Leica DM4000 B inverted microscope. The nematodes were identified using established taxonomic keys [36–38]. The abundance of nematodes was measured as individuals per 100 g of dry soil. The nematodes were assigned to five trophic groups (bacterivorous, fungivorous, herbivorous, omnivorous or predators) according to Yeates et al. [39]. However, *Filenchus* was considered fungivorous as suggested by different authors [29,40,41], and the remaining genera of the Tylenchidae family were considered herbivores. Nematode taxon was assigned using a colonizer–persister (cp) scale [42]. Cp values describe the nematode life strategies and range from 1 (r-selected or colonizers with short generation times, large population fluctuations, high fecundity and tolerance to disturbance) to 5 (K-selected or persisters, produce few offspring, appear later in succession and sensitive to disturbance). To further assess whether the experimental treatments affected the overall functional diversity of the nematode communities, several ecological indices were calculated, including the maturity index (MI) as the successional stage of the nematode community (high values indicate the dominance of K-strategists and low values denote the dominance of r-strategists) [30], enrichment index (EI) as the rate of soil enrichment (high values indicate high abundance of available recourses) [32] and structure index (SI) as the connectedness of the nematode community (high values indicate high food web diversity and structure) [32]. We also calculated Shannon's diversity index (H') to reflect diversity through abundance as well as the number of taxa [43] and genera richness (S), the number of taxa.

2.4. Statistical analyses

The main and interactive effects of the addition of labile carbon (control, C_{70}, C_{140} and C_{350}) and incubation time (10, 30 and 60 days) on the soil's nematode abundance and ecological indices were determined using a two-way analysis of variance (ANOVA). If