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Soil Biology & Biochemistry 38 (2006) 1353–1363

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Soil fauna modifies the recalcitrance-persistence relationship of soil carbon pools

Oliver Fox *, Silke Vetter, Klemens Ekschmitt, Volkmar Wolters

IFZ-Department of Animal Ecology, Justus Liebig University, H.-Buff-Ring 26-32, D-35392 Giessen, Germany

Received 23 May 2005; received in revised form 29 September 2005; accepted 5 October 2005
Available online 29 December 2005

Abstract

Traditional models of soil organic matter decomposition predict that soil carbon pools with high chemical stability and large physical structure are more resistant against degradation than chemically labile and fine-grained material. We investigated whether soil fauna, by its direct and indirect effects on carbon turnover, would reinforce or counteract this general trend.

The effects of four major faunal groups on carbon pools of differing recalcitrance were studied in an extensive microcosm experiment. Ninty-six microcosms were inoculated with nematodes, enchytraeids, collembola, and lumbricids in three densities, including combinations of groups. Bare agricultural soil and soil covered with maize litter were used as substrates. The microcosms were kept under constant conditions at 12 °C and 50% water holding capacity for 60 days. At the end of the experiment, soil particles were separated into size classes (<63 μm, 63–250 μm, >250 μm) and carbon pools were separated into solubility fractions (K_2SO_4-soluble, pyrophosphate-soluble, insoluble), by means of ultrasonic dispersion and subsequent stepwise solubilisation.

Both in bare soil and in soil with litter, the carbon pools with the highest chemical stability (insoluble) and the larger particle sizes (>63 μm) were degraded more intensively than all other pools in the presence of lumbricids. The pools of intermediate chemical stability (pyrophosphate-soluble) underwent simultaneous degradation and neoformation brought about by different animal groups. The chemically most labile pool (K_2SO_4-soluble) remained largely unaffected by the fauna. Fixation of carbon in microbial biomass was increased by nematodes in bare soil and by enchytraeids in soil with litter. The results illustrate in detail how, under the influence of soil fauna, soil carbon pools are decomposed in a cascade-like process where carbon is transferred from the stable to the more labile pools, while simultaneously a proportion is fixed in microbial biomass and another part is lost as CO_2. Thereby, the relationship between a substrate's persistence and its chemical stability and physical size is substantially modified. We summarize the mechanisms that most likely are responsible for the different effects of the investigated faunal groups.

Keywords: Soil carbon pools; Recalcitrance; Soil fauna; Decomposition; Laboratory microcosms; Particle size

1. Introduction

Decomposition of soil organic matter is controlled by external factors such as climate and soil management, and by internal factors such as substrate quality and decomposer community structure (Swift et al., 1979; Raich and Tufekcioglu, 2000). To realistically assess the risks of climate change, a thorough understanding of the pools and fluxes of the global carbon budget is required to identify sources and sinks of carbon (Lal, 2004). Whether the soil acts as a relevant source for atmospheric CO_2 through decomposition of soil organic matter (King et al., 1997; Smith et al., 1997), or as a sink for CO_2 through stabilization and accumulation of soil carbon, depends on the relationship between carbon input and decomposition rate (Djajakirana and Joergensen, 1996). Decomposition rates are traditionally seen as being directly related to the chemical stability of organic substrates, in the way that more recalcitrant components are more resistant against microbial and enzymatic decomposition and therefore exhibit longer residence times in the soil (Swift et al., 1996; Krull et al., 2003). On the other hand, it has been repeatedly and consistently shown that soil fauna strongly regulates decomposition rates through direct effects on soil organic matter as well as through indirect effects mediated via the microflora. Direct faunal effects consist, e.g. in the crushing of larger organic structures and in the physical protection of organic particles in faeces (Lavelle and Martin, 1992; Brown et al., 2000; Bossuyt et al., 2005). Indirect faunal effects emerge, e.g. from selective feeding on the microbial biomass or from selective spreading of microbial propagules (Seastedt, 1984; Lussenhop, 1992;

* Corresponding author. Tel.: +49 641 9935713; fax: +49 641 9935709.
E-mail address: oliverfox@gmx.net (O. Fox).

0038-0717/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2005.10.014

Hedlund and Augustsson, 1995; Wardle, 1999; Brown et al., 2000). It has also been shown that the various soil faunal groups can exert opposing effects on decomposition that combine in a non-linear way (Vetter et al., 2004).

Because soil microflora and soil fauna ultimately depend on soil organic matter for energy and nutrient supply as their main resource (Lavelle, 1997), they principally act as competitors (Tiunov and Scheu, 2004). Therefore, the question arises whether (a) the soil fauna would follow the microbial strategy of an overall preferential use of labile organic substrates, thereby reinforcing the relatively faster decomposition of those substrates, or whether (b) the soil fauna would, in the sense of resource partitioning, specialise in the use of chemically and physically stable organic components, thereby compensating or even reverting the positive correlation between recalcitrance and persistence of organic compounds. To address this question, we performed a microcosm experiment, in which we introduced soil fauna of varying density and composition into bare soil and soil amended with litter. We separated soil carbon by particle size and by solubility fractionation into pools of differing physical and chemical stability, and we analysed the development of those pools under the influence of the fauna.

2. Materials and methods

2.1. Experimental design

Ninety-six treatments were established in three consecutive blocks of 32 microcosms. The blocks were inoculated and measured one after the other and each block was kept for 60 days under constant conditions in a climate chamber. The microcosms (height: 24 cm, diameter: 5 cm) were inoculated with lumbricids represented by *Aporrectodea caliginosa*, as well as with enchytraeids, collembola and nematodes represented by natural multispecies mixtures. Within the nematodes, microbivores were the predominant feeding group (47% bacterial feeders, 8% hyphal feeders). Plant feeding nematodes (41%) were almost exclusively unspecific ectoparasites. Obligatory root feeding nematodes were largely excluded from our experiment due to the lack of intact living roots in the sieved substrate (nematode classification after Yeates et al., 1993).

Inoculation densities amounted to 0, 1 and 2 earthworms per microcosm, and to 0, 1 and 3 times the average natural density in fallow of enchytraeids (mean density of 0.1, 23.7 and 76.7 individuals $100\,g^{-1}$ DM soil = dry mass soil), collembola (mean density of 0, 58.8 and 123 individuals $100\,g^{-1}$ DM soil) and nematodes (mean density of 681, 1709 and 3484 individuals $100\,g^{-1}$ DM soil). Treatments comprised inoculations with single faunal groups and with combinations of groups, according to a D-optimised design which was calculated using Fedorov's method (Cook and Nachtsheim, 1980). This design is targeted towards testing for correlations between carbon pool sizes and animal densities, at the expense of less statistical power in detecting differences in carbon pool sizes between groups of treatments. Treatments were randomised within blocks to avoid any correlation of treatments and the position of microcosms, as well as across blocks to avoid any correlation of treatment states and blocks. Ten microcosms were left as controls without addition of fauna. Each faunal treatment was established in two substrate treatments: (1) bare soil (175 g FM soil = fresh mass soil, equivalent to 160 g DM soil), containing mainly organic matter integrated into the mineral soil, and (2) soil covered with a layer of maize litter (175 g FM soil with 3.5 g FM litter), a constellation dominated by new plant material. The microcosms were kept under constant conditions at 12 °C and at 50% water holding capacity, equivalent to 16% soil water content.

The soil used derived from the experimental field 'Julius Kühn' held by the Agricultural Faculty of the Martin Luther University in Halle, Germany. The area belongs to the dryer zones of Central Europe with an average annual precipitation of 466 mm and an average annual temperature of 9.0 °C (Schliephake et al., 1999). The site is located on a 10–15 km wide sandy loess stripe at an altitude of approximately 110 m ASL. The soil is classified as black earth with sandy loess (FAO: luvic phaeozem) and is composed of 29.9% sand, 58.2% silt and 11.8% clay. The organic carbon content amounts to 2.5%, the C/N ratio to 15.6 and pH ($CaCl_2$) to 7 (Schliephake et al., 1999). Soil was sampled on October 18, 2000, from an experimental plot held under continuous cropping and no fertilisation. Samples were taken between the rows. They did not contain visible plant residues and proved almost free of fauna. The soil was carefully sieved (2 mm mesh) and filled into the microcosm tubes. In half of the microcosms, maize litter was added on top of the soil column. The maize had been previously harvested in the same area and was shredded to less than 1 cm.

Before establishing each of the three experimental blocks, soil fauna was extracted from a bulk sample of 100 kg undisturbed soil taken from a set-aside field near Giessen, Germany. Earthworms were collected by hand-sorting, identified to species and weighed. Live enchytraeids were extracted using a modified O'Connor wet funnel technique. Live microarthropods were expelled from soil using high gradient canister extraction (MacFadyen, 1953; Wolters, 1983). During the three weeks of microarthropod extraction, specimens were collected every 2 days and samples were cycled to achieve a homogeneous distribution of species and developmental stages across replicates. Acari and collembola were counted separately. Extracted numbers of acari were low, and tests did not yield significant effects of acari. Therefore, we restrict the presentation of results on microarthropods to the collembola. Nematodes were elutriated using Cobb's method modified according to s'Jacob and Van Bezooijen (1984), counted and concentrated in tap water, then aliquots of the suspension were added to the microcosms. Additional soil samples were taken from the soil substrate after sieving and analysed for soil fauna in order to determine the initial animal density of the untreated microcosm substrate, as well as from selected microcosms at the end of the experiment in order to check for population development during the experiment.