APPLIED SOIL ECOLOGY 38 (2008) 152–160

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/apsoil

Response of soil microorganisms and endogeic earthworms to cutting of grassland plants in a laboratory experiment

Olaf Butenschoen[a,*], *Sven Marhan*[b], *Stefan Scheu*[a]

[a] *Darmstadt University of Technology, Institute of Zoology, Schnittspahnstr. 3, 64287 Darmstadt, Germany*

[b] *University of Hohenheim, Institute of Soil Science, Department Soil Biology, Emil-Wolff-Strasse 27, 70599 Stuttgart, Germany*

ARTICLE INFO

Article history:
Received 22 May 2007
Received in revised form
4 October 2007
Accepted 4 October 2007

Keywords:
Defoliation
Rhizodeposition
Microbial biomass
Lumbricidae
Exudates

ABSTRACT

It has been hypothesized that defoliation and herbivory alter the availability of soluble carbon in the rhizosphere and thereby the biomass and activity of soil microorganisms, and presumably higher trophic levels as well. To test this hypothesis, we established a laboratory experiment investigating effects of shoot cutting of white clover (*Trifolium repens* L.) and perennial ryegrass (*Lolium perenne* L.) on soil microorganisms and juvenile endogeic earthworms of the species *Octolasion tyrtaeum* (Savigny), and *Aporrectodea caliginosa* (Savigny). Plants were grown in microcosms for 4 weeks, cut 5 cm above the soil surface and left to regrow until microcosms were destructively sampled after another 4 weeks.

Defoliation decreased total shoot biomass of *T. repens* but had no significant effect on shoot biomass of *L. perenne*. Root biomass of *L. perenne* significantly exceeded that of *T. repens*, but defoliation reduced root biomass of *L. perenne* and *T. repens* by 48.6 and 67.3%, respectively. Microbial biomass per gram of soil in treatments with *L. perenne* exceeded that in treatments with *T. repens*, but when calculated per gram of roots, microbial biomass in treatments with *T. repens* exceeded that in treatments with *L. perenne*. Defoliation of both plant species significantly increased microbial biomass. Microbial activity differed between treatments and was higher in the grass than in the clover treatment in the beginning, but the reverse was the case later. The biomass of both earthworm species decreased and was only slightly affected by the treatments. In addition, neither earthworm species affected plant growth, microbial biomass or the production of CO_2.

Our results suggest that defoliation of perennial ryegrass and white clover increased the availability of carbon in the rhizosphere as indicated by the increase in microbial biomass, but that quality and quantity of rhizodeposits differed over time and between plant species. Furthermore, endogeic earthworms were unable to exploit the microbial biomass pool in soil, rather, rhizosphere microorganisms appeared to have effectively competed with endogeic earthworms and exploited root exudates.

1. Introduction

Plants allocate considerable amounts of carbon belowground for the growth of roots to acquire nutrients and water. In addition, large amounts of carbon are either actively secreted into the rhizosphere, or passively diffused in response to the root-soil concentration gradient. The carbon input into the rhizosphere soil is estimated to account for 5–30% of the net assimilation of plants (Johansson, 1992; Swinnen et al., 1995). Most of this plant-derived carbon enters the soil at the sub-

* *Corresponding author*. Tel.: +49 6151 16 4114; fax: +49 6151 16 6111.
E-mail address: o.butenschoen@gmx.de (O. Butenschoen).
0929-1393/$ – see front matter
doi:10.1016/j.apsoil.2007.10.004

apical and the root-hair zone (Curl and Truelove, 1986). This deposition of carbon affects microorganisms in the rhizosphere, as the compounds are readily assimilated (Grayston et al., 1998). Thus, the carbon released into the rhizosphere soil affects microbial biomass, activity and community composition, and therefore several soil ecosystem processes such as soil organic matter decomposition and nutrient mineralization.

Defoliation through aboveground herbivory alters the allocation and release of carbon into the rhizosphere and may affect microbial community structure and organic matter dynamics in the rhizosphere; however, the effects of defoliation appear to be variable. Defoliation increased the exudation of carbon into rhizosphere soil in some studies (Paterson and Sim, 1999, 2000), whereas in others effects were neutral (Bazot et al., 2005) or negative (Miller and Rose, 1992). In addition, the response of the microbial community in the rhizosphere soil to defoliation is variable. For instance, Holland (1995) and Mawdsley and Bardgett (1997) found microbial biomass in the rhizosphere to be increased after defoliation, whereas others did not find any changes (Mikola et al., 2001; Kuzyakov et al., 2002). Microorganisms are the primary decomposers in the soil and the nutritional basis for a large number of soil invertebrates including amoebae, flagellates, nematodes and potentially also for earthworms (Hunt et al., 1987; De Ruiter et al., 1995; Berg et al., 2001). Hence, in response to defoliation subsequent alteration in carbon rhizodeposition, microbial biomass and community composition is likely to propagate to higher trophic levels. However, information on the effect of defoliation on the biomass of invertebrates in the rhizosphere is sparse and limited to certain groups such as nematodes (Bazot et al., 2005; Ilmarinen et al., 2005).

The responses of major groups of decomposer invertebrates such as earthworms have not been investigated in a rigorous way. Although endogeic earthworms are known to primarily consume soil and associated humified organic residues it is still uncertain as to whether microorganisms significantly contribute to earthworm nutrition (Edwards and Fletcher, 1988; Kristufek et al., 1992; Lattaud et al., 1997; Horn et al., 2003). Endogeic earthworms primarily feed in the rhizosphere (Spain et al., 1990), thereby they are expected to ingest roots (Cortez and Bouche, 1992). Predominantly, however, they are consuming rhizodeposits, and rhizobiota such as mycorrhizas, saprophytic fungi, nematodes and protozoa (Bonkowski and Schaefer, 1997; Doube and Brown, 1998). Hence, if defoliation alters the amount of rhizodeposits and thereby the microbial biomass and community composition in the rhizosphere, it likely also affects endogeic earthworms.

Commonly, earthworm nutrition is considered to depend on the input of resources from above ground, i.e. plant residues, in particular leaf litter. However, a large amount of carbon enters the soil via plant roots suggesting that endogeic earthworms may also benefit from belowground resource input. A large fraction of resources entering the soil via roots constitutes sugars which form a major component of root exudates. In fact, it has been documented that earthworms are limited by the availability of carbon resources and benefit from, e.g. the addition of glucose to the soil (Tiunov and Scheu, 2004). Root exudates, on the other hand are readily consumed by microorganisms. Therefore, endogeic earthworms and rhizosphere microorganisms likely interact and compete for carbon resources in the rhizosphere and these interactions may vary with the amount of exudates produced.

Earthworms form a major part of the soil decomposer macrofauna in temperate ecosystems (Edwards and Bohlen, 1996). They are regarded as ‘‘ecosystem engineers’’ directly or indirectly affecting below- and aboveground ecosystem processes such as organic matter processing and nutrient cycling (Jones et al., 1997; Lavelle, 1997). As saprophagous animals endogeic earthworms rely on organic matter entering the soil, but only little of the organic matter ingested is assimilated and incorporated into the biomass of earthworms (Whalen and Parmelee, 1999); the main part re-enters the soil system enclosed into casts. Fresh cast aggregates of endogeic earthworms are hotspots of microbial activity due to increased nutrient availability (Devliegher and Verstraete, 1997). During aging of casts, however, organic matter enclosed in casts becomes protected against microbial attack (Tiunov and Scheu, 1999; Marhan and Scheu, 2006). Hence, if endogeic earthworms and microorganisms interact and compete for carbon resources in the rhizosphere, earthworms may also affect carbon allocation in the soil.

The aims of the study were to determine (1) if plant defoliation affects microbial biomass and activity in the rhizosphere, (2) if endogeic earthworms benefit from the defoliation of plants, and (3) if the mineralization of soil carbon is affected by the defoliation of the plants and the presence of endogeic earthworms.

2. Material and methods

2.1. Soil, earthworms and plants

In September 2004 arable soil was collected from the upper 10 cm of the long-term fertilization experiment in Bad Lauchstädt (Saxony-Anhalt, Germany) and sieved (4 mm mesh size) to remove stones and coarse plant residues. The soil is a Haplic Chernozem loam (FAO classification) with a particle size distribution of 11.9% sand, 70.5% silt and 16.1% clay. Water holding capacity and pH of sieved soil, determined according to Dunger and Fiedler (1997), were 52% and 7.0, respectively. Total carbon and nitrogen concentrations as measured by an elemental analyzer (NA 1500, Carlo Erba, Milan, Italy) were 1.70 and 0.16%, respectively. For defaunation the soil was stored at −20 °C for 1 week and kept at 4 °C for 1 week before the experiment was set-up. Prior to adding to microcosms chemical and physical characteristics and microbial biomass of the soil were determined ($n = 4$). Microbial biomass as determined by the substrate-induced respiration method (SIR) (Anderson and Domsch, 1978; Scheu, 1992) was 210 $\mu g\ C_{mic}\ g^{-1}$ dry weight soil.

In September 2004, juvenile earthworms were collected in a 130-year old beech forest on limestone near Göttingen (Southern Lower Saxony, Germany). Details of the site are given in Schaefer (1991). Earthworms were transferred into the laboratory and identified. The endogeic earthworm species *Aporrectodea caliginosa* (Savigny) and *Octolasion tyrtaeum* (Savigny), both dominant in the beech forest, were chosen