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Above- and below-ground plant inputs both fuel soil food webs

Nico Eisenhauer*, Peter B. Reich

Department of Forest Resources, University of Minnesota, 1530 Cleveland Avenue N., St. Paul, MN 55108, USA

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ABSTRACT

Soil food webs depend almost exclusively on plant derived resources; however, it is still subject to debate how plants affect soil biota. We tested the effects on soil decomposers of three components of soil inputs of plant species identity: presence of live plants (representing rhizodeposits), identity of shoot litter input and identity of root litter input; using all combinations of these for *Trifolium pratense* and *Plantago lanceolata*. We assessed impacts on soil microorganisms, Collembola, Oribatida and earthworms in a full-factorial greenhouse experiment. Species identity of shoot litter input had greatest effect on decomposers, following by species identity of live plant. Microbial carbon use efficiency and Oribatida density were significantly higher in the presence of *T. pratense* shoot litter input than in that of *P. lanceolata* shoot litter input, while earthworm body mass ratio was significantly higher in the presence of *P. lanceolata* plants than in that of *T. pratense* plants. Oribatida density was at minimum in the presence of *P. lanceolata* plants, shoot and root litter input, resulting in a significant three-way interaction and pointing to the relevance of all investigated plant input pathways. Live plant identity effects were not due to differences in living root biomass among species and treatments. Detrimental *P. lanceolata* effects may have been due to significantly lower N concentrations than in *T. pratense* tissue. Our results indicate that both above- and below-ground plant inputs into soil determine the performance of decomposers, and thus suggest due consideration of both types of inputs fueling soil food webs in future studies.

1. Introduction

Aboveground–belowground interactions are key to the functioning of terrestrial ecosystems (Scheu, 2001; Wardle et al., 2004; Bardgett and Wardle, 2010). Although soil food webs depend almost exclusively on plant-derived resources, it is still subject to debate how plants affect soil biota (Pollierer et al., 2007; Keith et al., 2009). There is a growing number of studies showing distinct plant community/identity effects on soil biota (De Deyn et al., 2004; Keith et al., 2009; Viketoft et al., 2009; Bezemer et al., 2010; Eisenhauer et al., 2011a). Many previous studies assumed plant surface litter to be the most relevant carbon input for the soil food web, whereas some recent papers point at the relevance of root-derived inputs (Albers et al., 2006; Pollierer et al., 2007; Keith et al., 2009). However, the relative importance is likely dependent upon the ecosystem type (Bardgett and Wardle, 2010).

Using an elegant labeling experiment in a temperate forest, Pollierer et al. (2007) found that the majority of soil invertebrates obtain their carbon from roots. Similarly, primarily root presence rather than shoot litter addition affected nematode trophic group composition in a mesocosm experiment with birch and pine (Keith et al., 2009). The authors suggested that, in the short term, belowground rather than aboveground tree inputs have strong impacts on soil food web structure. Short-term greenhouse experiments using grassland plant species support this view by showing distinct live plant community/identity effects on soil biota, by manipulating plant community/identity but using uniform (standardized) soil surface litter (e.g., Milcu et al., 2006; Eisenhauer et al., 2009). Milcu et al. (2006) and Eisenhauer et al. (2009) found positive effects of legumes on earthworm performance without legume leaf litter entering the soil. Eisenhauer et al. (2009) reported detrimental effects of the forb *Plantago lanceolata* on earthworm biomass. By contrast, a recent microcosm study showed the opposite pattern for Collembola: while Collembola densities were significantly lower in the presence of the legume species *Trifolium pratense*, they were increased in the presence of *P. lanceolata* (Eisenhauer et al., 2011b). In both cases plant identity effects likely materialized through belowground plant inputs, though it remains unclear if observed effects were due to root litter material and/or rhizodeposits entering the soil. To our knowledge, no study has experimentally manipulated identity effects of live plants, shoot litter inputs and root litter inputs so far to investigate

* Corresponding author. Tel.: +1 612 624 6709; fax: +1 612 624 5212.
E-mail address: nico.eisenhauer@web.de (N. Eisenhauer).

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(i) the relevance of the identity of shoot litter inputs and (ii) the relative importance of root litter identity and rhizodeposit identity for the performance of decomposers. However, this information is essential since short-term microcosm experiments are increasingly utilized to study specific ecological mechanisms [see Fründ et al. (2010) for examples on earthworm studies]. More detailed knowledge on the relative importance of varying plant input pathways is thus crucial for the interpretation of such experiments as well as their transferability to natural conditions. For instance, if the identity of plant shoot litter inputs significantly affects decomposers, many previous studies may have underestimated plant identity effects by using uniform surface litter material.

We addressed these issues by performing a full-factorial greenhouse experiment, manipulating three aspects of potential plant species identity effects: identity of live plants, identity of shoot litter input, and identity of root litter input of *T. pratense* and *P. lanceolata*. Thus, the experiment was a $2 \times 2 \times 2$ factorial of live plant presence (*T. pratense* and *P. lanceolata*) × shoot litter inputs (*T. pratense* and *P. lanceolata*) × root litter inputs (*T. pratense* and *P. lanceolata*). Due to the short-term character of the experiment we assumed plant presence to largely represent the effect of rhizodeposits (e.g., Milcu et al., 2006), as very little tissue inputs occurred during the experiment and because specific microbial rhizosphere communities might not have developed. The objective of the present study was to investigate plant input effects on three functionally important groups of soil biota, namely microorganisms, detritivore microarthropods and earthworms. According to recent field studies (e.g., Albers et al., 2006; Pollierer et al., 2007) and pronounced plant identity effects in greenhouse studies using uniform soil surface litter (e.g., Milcu et al., 2006; Eisenhauer et al., 2009), we expected root-derived inputs (rhizodeposits and root litter) to be more important for the performance of soil biota than shoot litter material.

2. Materials and methods

2.1. Experimental setup

We grew separate trays of *P. lanceolata* L. and *T. pratense* L. to produce root and shoot litter material. After ca. 8 weeks we harvested shoot and root litter material, dried and chopped it (<20 mm). This was done in the same soil used in the subsequent experiment (pH 5.76, carbon concentration 1.57%, nitrogen concentration 0.091%, C-to-N ratio 17.2; water content 15%), taken at the Cloquet Forestry Center (Cloquet, Minnesota, USA; 46 31′ N, 92 30′ W). It should be noted that the litter produced was less senesced than typical detritus, but for brevity we will call it litter hereafter.

Microcosms were set up consisting of PVC tubes (inner diameter 100 mm, height 250 mm) covered by a 5 mm mesh at the bottom to allow drainage of water. A plastic barrier (100 mm height) at the top the microcosm prevented the escape of soil animals from experimental containers. A total of 40 microcosms were filled with 50 mm of Perlite at the bottom to allow drainage of water and prevent the escape of animals and then topped with 2 kg (fresh weight; total height of the soil column 200 mm) of sieved (with 10 mm mesh) and homogenized soil (see above for details on soil characteristics). We added 600 mg of root litter of *P. lanceolata* (C concentration 39.33%, N concentration 0.88%, C-to-N ratio 44.85; $n = 5$) or *T. pratense* (C 37.80%, N 1.93%, C-to-N ratio 19.71) in each case to half of the microcosms and mixed it thoroughly with the upper 50 mm of the soil to create two root litter treatments. Then, we planted four individuals of one of the two plant species in each case into half of the microcosms to create two live plant species treatments. Subsequently, 600 mg of shoot litter (chopped, <20 mm; *P. lanceolata*: C 37.65%, N 0.75%, C-to-N ratio 50.38, *T. pratense*: C 39.30%, N 1.97%, C-to-N ratio 19.97) was placed on the soil surface to create two shoot litter treatments. This resulted in $2 \times 2 \times 2 = 8$ treatments, each replicated five times (40 experimental units in total).

The microcosms were placed in a temperature controlled growth chamber at a day (16 h, 16 ± 1 °C)/night (8 h, 12 ± 1 °C) regime (mean temperature 14.67 °C). This corresponds to the mean temperature of the growing season (~April to October) close to the Cloquet Forestry Center from 2008 to 2010 (R. Rich, unpubl. data). One species of each Collembola (*Onychiurus* sp.) and earthworms (*Aporrectodea caliginosa* Savigny) were purchased from commercial suppliers and kept in the experimental soil for two weeks prior to transfer to the microcosms (Fründ et al., 2010). We added 20 Collembola individuals and two sub-adult individuals of *A. caliginosa* ($\sum 0.79 \pm 0.03$ g fresh weight with gut content) to each microcosm. The experiment lasted 12 weeks. Light intensity varied between 580 and 900 μmol m^{-2} s^{-1} depending on the location in the growth chambers. To avoid edge effects, microcosms were randomized every week. The microcosms were irrigated four times per week with deionized water and the volume was increased from 50 mL (weeks 1–6) to 100 mL (weeks 6 through 12).

2.2. Harvest and measurements

After twelve weeks we stopped the experiment and harvested the shoot material by cutting shoots at the soil surface level. There was no shoot litter left on the soil surface. One soil core per pot (50 mm diameter, 50 mm depth) was taken and extracted by heat to determine soil microarthropod densities (Kempson et al., 1963). Soil microarthropods were collected in glycerol, transferred into 70% ethanol, identified and counted. Similarly, five soil samples of the same volume were extracted prior to the experiment to determine soil microarthropod densities at the start of the experiment. On average, there were 2.4 ± 2.3 (overall mean ± standard deviation) Oribatida and no Collembola individuals in each sample at the beginning of the experiment, which likely was due to the pretreatment of the soil (sieving with 10 mm mesh).

Three soil cores (20 mm diameter, 50 mm depth) were taken, pooled and homogenized to determine soil microbial respiration and biomass using an O_2 microcompensation apparatus (Anderson and Domsch, 1978; Scheu, 1992). Microbial respiration was measured at hourly intervals for 20 h at 22 °C. Basal respiration was determined without addition of substrate; C_{mic} was calculated from the respiratory response to D-glucose (substrate-induced respiration method; Anderson and Domsch, 1978). The average of the lowest three readings within the first 10 h was taken as "maximum initial respiratory response" (MIRR) and C_{mic} was calculated as $38 \times$ MIRR (μl O_2 h^{-1} g^{-1} soil dw; Beck et al., 1997). Glucose was added in appropriate amounts to saturate the catabolic enzymes of the microorganisms (20 mg g^{-1} soil dw). Despite some criticism (Wardle and Ghani, 1995), the metabolic quotient is regarded as an indicator of change in microbial metabolism in response to disturbance, i.e., microbial C use efficiency (Anderson and Domsch, 1985). Gravimetric soil water content was determined for each sample by comparing soil fresh and dry weight ([%]; dried for two days at 70 °C).

The remaining soil was thoroughly checked for earthworms. Earthworms were weighed immediately before and after the experiment (body fresh weight including gut content) and we calculated the logarithmic relative biomass ratios (biomass at the end/biomass at the beginning). Roots were washed out of the soil using a 1 mm mesh and shoot and root material was dried at 70 °C for three days and weighed.