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Do plant species of different resource qualities form dissimilar energy channels below-ground?

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ABSTRACT

This study aimed at examining whether plant species of varying resource quality give rise to a fungal- or bacterial-based energy channel in the plants' rhizosphere, when planted in soil, in which the plant species naturally occur. In an 18-month large-scale laboratory mesocosm experiment, two plant species (*Holcus lanatus* and *Lotus corniculatus*) producing labile litter and two plant species (*Picea abies* and *Calluna vulgaris*) producing recalcitrant litter were placed in the same mesocosm. This allowed the decomposer biota (microbes, protozoa, nematodes, collembolans, and enchytraeid worms) to freely choose their preferred plant rhizosphere. Because a fungal-based energy channel is in theory regarded to retain nutrients better in the soil than a bacterial-based energy channel, water was collected underneath the plant species and analyzed for its nutrient (N and P) content.

In general, the number of soil biota groups responding significantly to the plant treatment increased with time. Soil microbes were the first group to react, but the ability of the plants to boost a clearly fungal- or bacterial-based energy channel was generally weak. However, at the end of the study, a higher fungal-to-bacterial biomass ratio was found beneath *Calluna* than beneath the other plant treatments. Of the secondary consumers, nematodes were the most responsive group, with total number and especially plant parasites being more abundant beneath *Lotus* than beneath *Picea* and *Calluna* indicating a root-based energy channel to persist under the legume. Protozoa, enchytraeid worms and collembolans responded weakly and inconsistently to plant treatment. Liberation of plant-available nutrients was plant-dependent. Towards the end of the study, less nitrate and phosphate leached through the *Picea* soils than through the control, which indicates a more effective nutrient retention to take place under this plant species. We found that plant species can, in a relatively short time, modify the composition of the soil decomposer community. However, no consistent evidence for the plant–soil systems developing to separated detritus energy channels emerged, we found a clearly separated root energy channel under the legume *L. corniculatus*.

1. Introduction

Primary producers, particularly vascular plants, are known to evolve reciprocal, mutualistic relationships with decomposer communities in the soil (Wardle, 2002). While activities of soil biota regulate plant growth (Bonkowski et al., 2000; Bever, 2003; Wardle et al., 2004), plants affect the soil and its organisms through, for instance, the uptake of water and nutrients. Evidence indicates, that plants influence the composition of the soil decomposer community through variation in the quantity and quality of litter (Wardle et al., 2006) and root exudates (Bais et al., 2006). Moore and Hunt (1988) proposed that the degradation of plant-derived material depends on the chemical nature of the resources (recalcitrant or labile), and that the decomposition (i.e. detritus channel, Moore and Hunt, 1988) is divided into two separate energy/nutrient channels: a bacterial-based channel and a fungal-based channel. A separate energy channel is characterized by living plant roots (i.e. the root channel).

Plant species identity seems to play a role in this (Wardle and Nicholson, 1996; Priha and Smolander, 1997; Bardgett et al., 1999a,b; de Deyn et al., 2004; Wardle, 2005). Slow-growing plants, such as conifers or hardy dwarf shrubs, produce poor-quality (recalcitrant) litters due to their high C:N ratio, high lignin content, and the presence of large amounts of phenolic compounds (Priha and Smolander, 1997; Wardle, 2002), slowing down the decomposition of such litters. Furthermore, secretion of root-derived compounds (root exudation) by conifers is hampered due to the ectomycorrhizal hyphal mantle around their roots. This can lead not only to reduced growth of bacteria (Olsson et al., 1996), but also of their predators, such as protozoa (Timonen et al., 2004).

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In contrast, fast-growing plants, such as grasses and herbs, produce labile, easily decomposable litter (Priha and Smolander, 1997; Bardgett, 2005). These plant species commonly exude plenty of resources to the soil through root exudation. The energy channel theory of Moore and Hunt (1988) predicts that plants producing recalcitrant resources and liberating reduced amounts of root exudates promote a fungal-based energy channel underneath, which is characterized by a higher amount of fungal than bacterial biomass. A decomposer food web with a relatively higher bacterial than fungal biomass is likely to exist beneath plant species that produce labile litters. The energy channel theory rests on the assumption that, of the two primary decomposer groups bacteria and fungi, only fungi are able to degrade recalcitrant resources efficiently (de Boer et al., 2005). Given that the consumers of fungi and bacteria differ in their diet, for example Collembola are regarded commonly as fungal feeders (Hopkin, 1997) while protozoa as bacterial consumers (Bonkowski et al., 2000), a cascading effect is expected to take place higher up in the soil food web. Consequently, more fungal feeding nematodes and microarthropods are anticipated to settle beneath plant species that produce recalcitrant material, whereas beneath labile plant species a food web rich in bacterivores is expected. According to Moore and Hunt (1988) the root channel is characterized by a high number of root feeding nematodes, followed by predatory nematodes and nematophagous mites.

The influence of different plant species or species communities on soil decomposers has been studied in various terrestrial ecosystems. For example, soil microbial biomass (Wardle and Nicholson, 1996; Priha et al., 2001; Innes et al., 2004), and its composition (Bardgett and McAlister, 1999; Priha et al., 2001) and activity (Bradley and Fyles, 1995) have been shown to vary beneath different plant species. Knapp et al. (2009) recently showed that different food recourses also influence the microflora through the gut microbes of earthworms. Furthermore, changes in plant species or species properties have been proven to affect the composition of soil microfauna (protozoa: Timonen et al., 2004; nematodes: Ingham et al., 1985; de Deyn et al., 2004; Saj et al., 2007) and of mesofauna (microarthropods: Petersen and Luxton, 1982).

Plant community composition can reflect the rate at which nutrients are cycled within a system and hence affect the fertility of the soil (Mulder et al., 2002; Bever, 2003). The fungal-based energy channel is assumed to be more conservative, being capable of retaining nutrients in the system better than a strongly bacterial-dominating system (Coleman et al., 1983; Wardle et al., 2004; van der Heijden et al., 2008). Recently de Vries et al. (2006) and Gordon et al. (2008) showed that fungal-dominated systems tend to loose less nitrogen by leaching than bacterial-dominated systems.

Despite the existence of distinct fungal-dominating (such as coniferous forests) and bacterial-dominating (such as grasslands) plant communities, we know little how responsive the various trophic levels of the below-ground decomposer community are to variation in single plant species or different plant community compositions (Wardle and Nicholson, 1996; Bardgett and Shine, 1999; Wardle et al., 2003; Wardle, 2005). In order to find out whether plant species have the ability to control the composition of decomposer community, we designed our experiment to test the following hypotheses:

(i) the perennial grass *Holcus lanatus* and the legume *Lotus corniculatus* promote a bacterial-dominating system beneath, while the dwarf shrub *Calluna vulgaris* and the coniferous tree *Picea abies* promote a fungal-dominating soil food web;
(ii) the divergent energy channels give rise to dissimilar higher level decomposer communities;
(iii) nutrients (N and P) leach out in higher amounts from soil beneath *Lotus* and *Holcus* and from the plant-free soil than from soil beneath *Calluna* and *Picea.*

To test these hypotheses, we used a novel laboratory experimental approach that allowed soil biota to freely choose and establish in their favored below-ground environment during an 18-month (three growth periods for the plants) experiment.

2. Methods

2.1. Mesocosms

Eight round plastic vats (Ø 50 cm, depth 40 cm) were prepared as experimental mesocosms. Each was divided into five sections by a 5-cm-high plastic wall glued to the bottom of the mesocosms to form one circular section (Ø 17 cm) in the center, and four outer trapeze-shaped sectors of similar area. A lysimeter system to collect water leachates was adjusted to the bottom of each section. The lysimeters consisted of a plastic funnel (Ø 5 cm) glued upside down on a conventional garden root mat (mesh size <0.5 mm). The root mat efficiently prevented root growth and particle flow into the funnel, when the system was irrigated with water. The mesocosms were filled with 30 kg (fresh mass) of soil, forming a 12-cm-deep layer, i.e. reaching 7 cm above the rims of the plastic walls on the bottom. The soil was the common test soil applied in the multinational project BIORHIZ (Biotic Interactions in the Rhizosphere as structuring forces for plant communities). It was collected in February 2005 at a re-established grassland area next to the CLUE site in the Netherlands (Planken Wambius, Ede, 52°04′N 5°45′E), where the last crop plant in 1995 was corn. The site is surrounded by heath, mixed forest, and abandoned arable land (van der Putten et al., 2000; Hedlund et al., 2003). The soil was transferred to Lahti, Finland, and stored at 4 °C in darkness until the experiment started. It had an organic carbon content of 21.3 g kg^{-1}, a total N content of 1.27 g kg^{-1}, a total P content of 0.33 g kg^{-1}, and a pH (water) of 6.3. Stones, soil macrofauna, and plant debris were sorted out by hand, and the soil was homogenized by gently mixing.

2.2. Plants and litter

As model plants we selected the perennial grass *H. lanatus*, the legume *L. corniculatus*, the hardy shrub *C. vulgaris* and the conifer *P. abies*. *Holcus* and *Lotus* occur naturally in the site of the soils origin and were used as model plants in the above-mentioned project BIORHIZ. They are regarded to produce easy decomposable litter (Bardgett, 2005), whereas *Calluna* and *Picea* produce recalcitrant litter (Wardle, 2002). All plants differ in their root symbionts: *Holcus*: arbuscular mycorrhiza (West, 1996), *Lotus*: nitrogen fixing bacteria (Bardgett, 2005) and arbuscular mycorrhiza (Scheublin et al., 2004), *Calluna*: ericoid mycorrhiza (Genney et al., 2000), and *Picea*: ectomycorrhiza (Bonkowski et al., 2001).

Before initiation of the experiment, 10 g of fresh litter, collected at the site where the soil originated, was placed on the surface of each mesocosm to ensure an effective inoculation of the systems with soil biota. This method is not sufficient to inoculate the experiment with the entire soil biota. Hence euedaphic life forms are not considered in this study. The litter was removed 1 week after placement. Each outer sector of the mesocosms received one plant species either as seedlings or as seeds. *P. abies* seedlings (five 3-month-old seedlings for each mesocosm) were pre-grown in quartz sand and provided with Ingestad nutrient solution (Ingestad, 1979) every month. *C. vulgaris* (five 8-cm-high seedlings for each mesocosm, with debris attached to the roots carefully removed) was collected from a road bank in southern Finland.