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Root-induced decomposer growth and plant N uptake are not positively associated among a set of grassland plants

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ABSTRACT

It is known that plant species can induce development of different soil decomposer communities and that they differ in their influence on organic matter decomposition and N mineralization in soil. However, no study has so far assessed whether these two observations are related to each other. Based on the hypothesis that root-induced growth of soil decomposers leads to accelerated decomposition of SOM and increased plant N availability in soil, we predicted that (1) among a set of grassland plants the abundance of soil decomposers in the plant rhizosphere is positively associated with plant N uptake from soil organic matter. To test this, we established grassland microcosms consisting of two plant individuals, a natural soil decomposer community and ^{15}N-labelled plant litter as organic N source, and compared the rhizosphere decomposer communities and litter-N uptake of a grass *Holcus lanatus*, an herb *Plantago lanceolata* and a leguminous herb *Lotus corniculatus*. We further predicted that (2) in terms of litter-N uptake those plant species that induce lower abundance of decomposers benefit from sharing soil with species inducing higher decomposer abundance. To test this, we grew the three plant species in two-species combinations and compared the ability of each species to acquire litter-N when living in the monoculture and in the species combinations. We found that the three plant species induced development of different soil decomposer communities and that they acquired different amounts of litter-N. However, while *L. corniculatus* induced the highest abundance of decomposers, *H. lanatus* had the highest uptake of N from the litter, which refuted our first prediction. Since this prediction was falsified, we could not properly test the second one, but we found that litter-N uptake of *H. lanatus* and *P. lanceolata* were not significantly affected by the presence of *L. corniculatus* and the higher abundance of decomposers induced by *L. corniculatus* roots. Our results show that among the three plant species tested root-induced decomposer growth and plant N uptake from soil organic matter were not positively associated. It appears that plant traits such as competitive ability for soil mineral N were more important for plant uptake of litter-N than those that directly affected the growth of soil decomposers.

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1. Introduction

Nitrogen (N) availability limits primary production in most terrestrial ecosystems (Vitousek and Field, 1999), which keeps plants under selection for developing features that enhance their N acquisition ability. In terrestrial ecosystems, soil organic matter is a large N pool that accounts for more than 90% of the total ecosystem N content (Knops et al., 2002) and the availability of this pool for plant uptake is largely regulated by decomposer organisms (Lee and Pankhurst, 1992; Sparling, 1994). One way for plants to enhance their N acquisition therefore is to affect soil decomposers in a way that leads to faster decomposition of soil organic matter and better availability of mineral N in soil (Paterson, 2003). It is known that part of the carbon (C) allocated to roots is released into soil as exudates, secretions and sloughed off cells, jointly called rhizodeposition (Paterson et al., 1997), and that this C pool can maintain abundant populations of microbes (i.e. bacteria and fungi) and microbial-feeding animals in the plant rhizosphere (Christensen et al., 1992; Griffiths, 1994). Results from empirical (Clarholm, 1985) and modelling (Raynaud et al., 2006) studies further indicate that activation of soil microbes and their grazers through C exudation can lead to increased mineralization of N from soil organic matter. However, this issue remains controversial, since some models indicate that root-induced N mineralization is not quantitatively significant in relation to plant requirements (Griffiths and Robinson, 1992). Recently, it was also proposed that although simple C compounds released from living roots often have a positive effect on microbial growth, they may not induce production of microbial enzymes needed for enhanced decomposition of soil organic matter (Fontaine et al., 2003). It is as well becoming clear that many plants can acquire N in organic form, especially in low-N ecosystems, and may therefore be less dependent on N mineralization than previously anticipated (Schimel and Bennet, 2004). Finally, the effects of living plants on soil organic matter decomposition and N mineralization appear to vary between plant species (van der Krift et al., 2001; Fu and Cheng, 2002), and although the abundance, activity, and composition of soil decomposer communities also differ between plant species (Bardgett and Shine, 1999; Westover et al., 1997; Wardle et al., 1999, 2003), so far no study has tested whether the observed differences in N mineralization between species are directly linked to differences in decomposer abundance in the rhizosphere of different plant species.

Grasslands make up 25% of all terrestrial ecosystems (Bardgett and Cook, 1998) and much interest is devoted to developing sustainable management strategies that could, for instance, reduce the dependence of grassland production on fertilizer inputs (Yeates et al., 1997). Acquiring more information on whether plant species differ in their ability to induce mineralization of soil organic matter and to enhance N availability in soil is therefore of great importance (Paterson, 2003). In this study, we use a set of grassland plant species – including among them a leguminous herb, since legumes also take up mineral N from the soil despite being able to fix atmospheric nitrogen (Munoz and Weaver, 1999) – to test the hypothesis that root-induced growth of soil decomposers leads to accelerated decomposition of soil organic matter and increased plant N uptake (Clarholm, 1985; Raynaud et al., 2006). Based on the above assumption, we predict that the abundance of rhizosphere decomposers (i.e. microbes and microbial feeders) is positively correlated with the amount of N plants are able to acquire from soil organic matter. Secondly, we predict that a plant species that induces lower abundance of decomposers benefits from sharing soil with a species that induces higher decomposer abundance due to an increased N availability in the rhizosphere soil of the latter species.

2. Materials and methods

2.1. Microcosms and growth conditions

We performed a greenhouse experiment involving 65 microcosms. Each consisted of a plastic pot (height 15 cm, diameter 10–15 cm, drainage holes in the bottom), 934 g soil (dry weight equivalent) and two plant specimens. The soil was collected from a grassland in the Netherlands (Planken Wambuis, 52°04′ 5°04′) in February 2005. 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. The soil was transferred to Jyväskylä, Finland, stored at 3–6 °C and sieved (1 cm) before added to the pots in mid-June 2005. The microcosms were placed in a greenhouse, on a plastic tray within five replicate blocks. The microcosms were watered regularly with tap water and supplementary light was provided via 400 W daylight lamps for 16 h per day. The density of photosynthetic photon flux varied between 150 and 300 $\mu mol\ m^{-2}\ s^{-1}$ at the height of plant shoots depending on outdoor weather and position on the tray. To equalize the amount of radiation for each microcosm, the blocks were relocated and the microcosms rearranged within the blocks each week. Temperature varied in the greenhouse from 14 °C at night to 32 °C in the daytime.

2.2. Experimental set-up

The plant species used were the grass *H. lanatus*, the herb *P. lanceolata* and the leguminous herb *L. corniculatus*. The three plant species co-exist in the site of the soil origin. Plants and soil are used as common test material in a multi-national project ‘‘Biotic interactions in the rhizosphere as structuring forces for plant communities’’ of which this study is a part. Plant seedlings were raised from seeds sown in vermiculite. Three weeks old pairs of seedlings were planted into each pot to produce three different monocultures and three different two-species combinations. Each of the six types of microcosms was set up in five replicates. In addition, five microcosms were set up without plants to be able to test the general plant effect on soil decomposers. After five weeks of plant growth, ^{15}N-labelled *Lolium perenne* shoot litter was added into half of the replicates of each of the six microcosm types. The ^{15}N-litter was produced in quartz sand culture of *L. perenne* seedlings using $^{15}NH_4{}^{15}NO_3$-enriched nutrient solution prepared according to Ingestad (1979). The litter had a ^{15}N atom% of 21.45 and a total N concentration of 1.21% of the dry mass. To add the litter, three cores of soil (diameter 1 cm, depth 10 cm) were pulled out of the microcosm along a line between the two seedlings of the microcosm. The removed