Soil Biology & Biochemistry 83 (2015) 76–83

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Fine root decomposition, nutrient mobilization and fungal communities in a pine forest ecosystem

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ARTICLE INFO

Article history:
Received 19 November 2014
Received in revised form
16 January 2015
Accepted 20 January 2015
Available online 30 January 2015

Keywords:
Basidiomycetes
Ectomycorrhizae
Nitrogen
Nutrient
Phosphorus
454 pyrosequencing

ABSTRACT

Despite its importance to energy flow and nutrient cycling the process of fine root decomposition has received comparatively little detailed research. Disruption of the fine root-soil interface during preparation of root litterbags for decomposition studies could affect decay rates and nutrient mobilization in part by altering the community of decay organisms. We compared rates of decomposition and nutrient release from fine roots of pine between litterbags and intact cores and characterized the fungal community in the decomposing roots. Fine root decomposition was about twice as fast overall for intact cores than litterbags, and rapid mobilization of N and P was observed for roots in cores whereas nutrients were immobilized in litterbags. Fungal communities characterized using 454 pyrosequencing were considerably different between decaying roots in intact cores and litterbags. Most interesting, taxa from ectomycorrhizal fungal orders such as Boletales, Thelephorales and Cantharellales appeared to be more common in decaying roots from cores than litterbags. Moreover, the rate of N and P mobilization from decaying fine roots was highly correlated with taxa from two orders of ectomycorrhizal fungi (Thelephorales, Cantharellales). Although we caution that DNA identified from the decaying roots cannot be conclusively ascribed to active fungi, the results provide tentative support for a significant role of ectomycorrhizal fungi in decomposition and nutrient mobilization from fine roots of pine.

1. Introduction

Root turnover and decomposition is a major pathway of carbon and nutrient flux to soil (Parton et al., 2007; Bird et al., 2008). At the global scale, fine root turnover has been estimated to account for over one-third of net primary productivity (Jackson et al., 1997). Inputs of organic matter from dead fine roots can result in more C stabilized in soil and more nutrients released than aboveground litter (Vogt et al., 1986). Despite the importance of fine roots to soil C sequestration and nutrient cycling, relatively little attention has been paid to root decomposition, and only a few principles have been established concerning factors that regulate the root decay process (Berg, 1984; Hobbie et al., 2010; Goebel et al., 2011). In a review of root decomposition data, Silver and Miya (2001) suggested that root chemistry indices, such as C:N ratio and Ca concentration, and climatic factors like actual evapotranspiration are the primary controllers of root decomposition. The possible roles of decay microorganisms and soil environment have not been thoroughly evaluated. Roots form complex associations with rhizosphere microbes throughout their life time (Singh et al., 2004). Root decay microorganisms are derived from both these pre-mortality rhizosphere microbes and the wider soil microbial community (Fisk et al., 2011). Some studies have shown that the rhizosphere organisms have a strong impact on root decay patterns following root senescence. In fact, Langley et al. (2006) suggested that fungal colonization, including its effect on root chemistry, could play a key role in regulating fine root decomposition. Studies of saprotrophic fungi on leaf litter indicate that an important component of the decomposition process is the formation of fungal hyphal networks, through which organic C and mineral nutrients are transported, thereby facilitating the utilization of heterogeneous soil organic matter substrates (Tlalka et al., 2008). Hyphal networks also could

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http://dx.doi.org/10.1016/j.soilbio.2015.01.019
0038-0717/

play an important role in root decomposition because of the highly heterogeneous distribution of dead fine roots in soil.

The role of soil heterogeneity in root decay has also received little study. In northern forest ecosystems, fine roots are distributed in both organic and mineral soil horizons, which differ in C availability, nutrient status, moisture, faunal abundance, microbial community, and edaphic conditions (Parmelee et al., 1993). Microbes living in surface organic horizons depend primarily on labile C supply from leaf litter and are often N limited, whereas microbes living in mineral soils derive much of their C and energy from recalcitrant soil organic matter and are limited primarily by C (Fontaine and Barot, 2005). Thus, dead roots of the same individual tree decay in very different physical and biotic environments, as shown previously for conifer needle litter (Osono et al., 2006). Also, fine roots in organic and mineral soil horizons differ significantly in organic matter quality and mineral nutrient concentrations (Fahey et al., 1988). These differences in root chemistry, decomposers, and environment between organic and mineral soils may lead to distinct patterns of fine root decomposition in the two soil horizons.

By far, most of our understanding of fine root decay comes from experiments using the litterbag approach (Silver and Miya, 2001), yet possible artifacts associated with this method have been suggested (Fahey and Arthur, 1994; Dornbush et al., 2002). During litterbag preparation, roots are separated from soil, washed and dried, and the rhizosphere associations that roots developed over their lifetime are disrupted (Bloomfield et al., 1993; Dornbush et al., 2002). This may influence microbial community development on decomposing fine roots (Fisk et al., 2011) and result in anomalously low decay rates (Dornbush et al., 2002). In contrast, the intact core technique developed by Dornbush et al. (2002) can largely avoid this problem by keeping the normal rhizosphere intact. For the present study we employed the intact core technique alongside root litterbags, and we compared decay rates and nutrient dynamics with the aim of evaluating the possible role of differences in fungal communities influencing the root decay process.

The specific objectives of the present study were to: (1) evaluate the role of fungal hyphal networks in regulating root decomposer community composition and root decay rates in organic and mineral horizons, (2) disentangle the interactive effects of substrate chemistry and soil environment on fine root decomposition, and (3) evaluate the possible role of fungal community composition in determining root decay and nutrient mineralization. We used 454 pyrosequencing to examine the fungal communities. We hoped that results from this study would enhance understanding of the factors that regulate the fine root decomposition process in forest ecosystems.

2. Materials and methods

2.1. Study area and field experiments

We conducted two parallel experiments. Experiment 1 was an *in-situ* root decomposition experiment with intact cores, designed to examine the impact of filamentous fungal network on fine root decomposition. Experiment 2 was a reciprocal fine root transplant experiment with litterbags, designed to compare the effects of root chemistry and soil environment on the root decay process. The fine root (<1 mm diameter) substrates in the two parallel studies were the same, permitting comparison of the two techniques. Both experiments were conducted at the Pack Demonstration Forest of SUNY-ESF located near Warrensburg in the southeastern Adirondacks, New York, USA (43.55°N, 73.82°W). The Pack Plantations are situated on a uniform, sandy outwash plain, and include several replicate monospecific plots of red pine (*Pinus resinosa* Sol. ex Aiton; Nowak et al., 1989). A thick organic horizon with abundant roots has developed on the surface of the mineral soil (Nowak et al., 1991) and root distribution is relatively homogeneous because of the regular tree spacing and the uniform mineral substrate (C. Nowak, pers. comm.) These characteristics are crucial for root decomposition experiments with intact cores (Experiment 1), which require relatively low spatial variation in fine root biomass (Dornbush et al., 2002).

For Experiment 1, we quantified fine root biomass in the field site immediately before the incubation experiment. On 6 May 2010, we collected twenty intact soil cores, 30 cm deep and 5 cm in diameter, from a red pine monoculture using PVC corers. The soil cores were separated into organic and mineral horizons based on color and texture, stored in a cooler, and returned to the laboratory on the same day. Fine roots (<1 mm diameter) were sorted manually from each soil horizon in each soil core, and ash-free dry mass was determined.

On 24 May 2010, sixty intact soil cores of the same size as in the preliminary survey were collected at the same site with PVC pipes. Each of these PVC pipes had been drilled with holes on the walls so that a total of 40% of surface area of each pipe was holes. Each core was covered with 53-μm pore size mesh to allow the passage of fungal hyphae but not roots, and was inserted back into the ground at the collection location to start the incubation. Visual inspection indicated that the coarse soil texture allowed for good contact between soil and cores. The cores were arranged in pairs; for each pair, one core remained static during the incubation period, and the other one was rotated every month to sever fungal hyphae.

For Experiment 2, we harvested roots from organic and mineral soil horizons at the same site on 6 May 2010 and brought them back to lab on the same day stored in a cooler. Fine roots (<1 mm) were sorted from soil, gently rinsed of adhering soil particles, and air-dried for 48 h. A precisely-measured weight of air dry roots was placed in 15 × 15 cm litterbags made of 53-μm pore size mesh and subsamples were retained for initial moisture and chemistry (see Chemical Analysis, below). On 24 May 2010, litterbags were buried at six plots, chosen randomly at the study site, in a reciprocal transplant design. Each plot consisted of four subplots, separated by 30 cm. In one subplot, one bag of organic soil fine roots was incubated in the organic horizon at 5 cm depth; in another subplot, one bag of organic soil fine roots was incubated in the mineral horizon at 15–20 cm depth. In the other two subplots, two bags of mineral soil fine roots were incubated in the same way in the organic horizon and mineral horizon, respectively.

Fifteen pairs of intact cores and twelve litterbags from the three plots were chosen randomly and harvested at 170 d from study initiation (10 Nov 2010), and the other half of samples were harvested at 395 d from decay initiation (23 Jun 2011). Soil cores were separated into organic horizon and mineral horizon in the field, and both soil cores and litterbags were stored in plastic ziploc bags, placed on ice in a cooler, transported to the laboratory within a few hours, and samples were frozen at −20 °C for later processing. After thawing, soil core samples were soaked in water to loosen adhering soil particles. Fine roots (<1 mm) were sorted and washed with dH_2O to remove soil.

2.2. Chemical analysis

After removing a small subsample for fungal analysis (see below), fine roots from each soil core and litterbag were oven-dried to constant weight at 55 °C for 48 h, and weighed. For chemical analysis, root samples from each collection date were pooled by soil horizon, treatment (i.e. fine roots from static cores or rotated cores, and original or transplanted soil horizons for litterbag roots) and thoroughly mixed. A subsample of each pooled sample was ground