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Extracellular enzyme activity in the mycorrhizospheres of a boreal fire chronosequence

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ABSTRACT

Saprotrophic microbes are typically credited with producing extracellular enzymes that recycle organic matter, though roots and mycorrhizal fungi also can contribute and may compete with the saprotrophs. We examined extracellular enzyme activity associated with the mycorrhizospheres of arbuscular mycorrhizal, ectomycorrhizal, dual-colonized (arbuscular and ectomycorrhizal), and ericoid mycorrhizal plants in a fire chronosequence in Alaska. Bulk soil and soil from beneath host plants were gathered in July 2004 and assayed for five enzymes that target organic C, P, and N substrates. Compared to bulk soil, activities of the C-targeting enzymes β-1,4-glucosidase and peroxidase were lower in arbuscular mycorrhizospheres and ericoid mycorrhizospheres, respectively. Moreover, extracellular enzyme activity varied among mycorrhizosphere types. Specifically, N-targeting leucine aminopeptidase was highest in arbuscular mycorrhizospheres, followed by ericoid and ectomycorrhizal/dual-colonized mycorrhizospheres; β-1,4-glucosidase had the reverse pattern. In addition, enzymatic stoichiometry suggested that extracellular enzyme producers invested more in C-acquisition than in N-acquisition in recent fire scars compared to mature forests. These data extend previous findings that roots and mycorrhizal fungi compete with saprotrophs by showing that the strength of this effect varies by mycorrhizal host. As a result the community composition of mycorrhizal host plants might mediate enzymatic activity in boreal soils.

Introduction

Mycorrhizospheres of plants consist of plant roots and their associated mycorrhizal structures, plus the surrounding soil and microbes directly influenced by them (Rambelli 1973). Numerous studies have established that ecological processes such as decomposition, N mineralization, and microbial community composition can be altered by the presence of plant roots; this phenomenon is referred to as the “rhizosphere effect” (e.g., Hiltner 1904; Katznelson 1946; Cheng et al. 2003). Frequently, roots decrease turnover rates of litter C and increase turnover rates of soil organic C (Cheng and Kuzyakov 2005). Traditionally, mycorrhizal fungi have not been explicitly incorporated within the rhizosphere concept (Timonen and Marschner 2006), even though mycorrhizal fungi colonize the roots of most terrestrial plants (Newman and Reddell 1987; Allen et al. 1995). The most common mycorrhizal groups are arbuscular mycorrhizal fungi, ectomycorrhizal fungi, and ericoid mycorrhizal fungi. They differ in their morphology, taxonomy, and physiology (Smith and Read 2008), so mycorrhizosphere effects on nutrient cycling could likewise vary depending on the mycorrhizal group involved (Linderman 1988). Nevertheless, few field studies have contrasted mycorrhizosphere effects associated with these three major groups.

Fungi and bacteria conduct nutrient transformations by secreting extracellular enzymes that break down soil organic matter (SOM) and release C, N, and P. Mycorrhizal fungi rely primarily on host plant C, so their contribution to SOM degradation is generally considered modest relative to that of the asymbiotic microbial community (Dighton 2003). However, there is accumulating evidence that mycorrhizal fungi produce a greater variety of enzymes than originally thought, including enzymes that target recalcitrant organic C (reviewed in Cairney and Burke 1998; Burke and Cairney 2002; Read and Perez-Moreno 2003). Thus, mycorrhizal fungi may also directly contribute to SOM decomposition (Talbot et al. 2008).

The extent to which plants and their mycorrhizal fungi contribute to extracellular enzyme production and decomposition in natural systems, however, remains unclear. Plant roots can directly release extracellular phosphatases for P acquisition (Duff

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et al. 1994) and proteases for N acquisition (Godlewski and Adamczyk 2007), but are not generally considered important producers of extracellular enzymes targeting lignocellulosic compounds. Culture-based studies have indicated that the enzyme capacity of mycorrhizal fungi is rarely as high as that of fungal saprotrophs. Specifically, white-rot fungi frequently display higher capacities than ericoid fungi, followed by ectomycorrhizal fungi, and then arbuscular mycorrhizal fungi (Read and Perez-Moreno 2003).

Fires are becoming more frequent in boreal forests, with potential consequences for nutrient dynamics. For instance, annual totals of burned area in Alaska increased 50% in the last decade, ostensibly due to a warmer, drier climate in this region (Kasischke et al. 2010). Fires can alter the nutrient availability of soils, directly via volatilization and mineralization of nutrients, and indirectly via changes in plant community composition and litter quality (Kasischke and Stocks 2000). Specifically, N availability can either increase or decrease following a fire, depending on fire severity and changes in plant community composition; organic material is often burned off and re-accumulates over time; and P availability tends to be greatest in young burn scars (Van Cleve et al. 1983, 1993, 1996; Smith et al. 2000; Treseder et al. 2004; Harden et al. 2006; O'Neill et al. 2006).

These shifts in nutrient availability during ecosystem recovery might alter the nutrient status of plants, mycorrhizal fungi, and other organisms. According to economic principles, plants and mycorrhizal fungi are expected to invest more in the production of a particular extracellular enzyme when the nutrient targeted by that enzyme is limiting to growth (Allison et al. 2010). Furthermore, enzymatic stoichiometry indicates the relative degree to which organisms are investing in acquisition of various nutrients. Previous studies have indicated that ratios of β-1,4-glucosidase:N-acetyl-glucosaminidase assess acquisition of C versus N (Sinsabaugh et al. 2008, 2009). As ecosystems recover from fire, we might expect that ratios of β-1,4-glucosidase:N-acetyl-glucosaminidase should be relatively high in fairly young sites, since soil organic C is scarce; and also relatively low where N availability is high. Any shifts as ecosystems recover from fire may have consequences for large-scale nutrient dynamics, since younger ecosystems are becoming more common in the boreal landscape owing to shortening fire-return intervals (Kasischke et al. 2010).

We examined extracellular enzyme activity associated with the mycorrhizospheres of arbuscular mycorrhizal, ectomycorrhizal, and ericoid plants in a fire chronosequence of upland boreal forests of Alaska. Our hypothesis focused on the activities of enzymes in soil associated with the different mycorrhizal plants. Based on laboratory findings (e.g., Read and Perez-Moreno 2003), we hypothesized that enzyme activity would increase in the order of arbuscular mycorrhizal mycorrhizospheres < ectomycorrhizal (or dual-colonized arbuscular mycorrhizal + ectomycorrhizal) mycorrhizospheres < ericoid mycorrhizospheres. In addition, we hypothesized that investment in C versus N acquisition should vary with site age as described above.

Materials and methods

Sites

We selected three study areas in upland boreal forests near Delta Junction in the interior of Alaska (63° 55′ N, 145° 44′ W). All of the sites were on alluvial flats, located within a 100-km^2 area. They represented boreal ecosystems at different successional stages (5, 17, and ~80 years) following severe forest fire. Soils in the sites were predominantly silt loams with underlying deposits of sand and gravel. Permafrost is discontinuous in this region and was not present in any of these sites. Arbuscular mycorrhizal fungi are most abundant in the younger two sites: arbuscular mycorrhizal hyphal length averages 30–116 km m^{-2} in the 5-year old site, 24–134 km m^{-2} in the 17-year old site, and 8–16 km m^{-2} in the 80-year old site; root length colonized by arbuscular mycorrhizal fungi is 0.69 km m^{-2} in the 5-year old site, 0.21 km m^{-2} in the 17-year old site, and 0.31 km m^{-2} in the oldest site (Treseder et al. 2007). Conversely, ectomycorrhizal fungi are most abundant in the older two sites, with root length colonized by ectomycorrhizal fungi averaging 0.20 km m^{-2} in the 5-year old site, 0.51 km m^{-2} in the 17-year old site, and 0.30 km m^{-2} in the 80-year old site (Treseder et al. 2007). Nitrogen availability (as potential net N mineralization and nitrification) is highest in the 17-year old site (Treseder et al. 2007). Soil organic matter content increases with site age (Harden et al. 2006; Treseder et al. 2007). In this immediate area, P availability (as extractable P) is greater in soils of recently-burned areas than in those of mature forests (O'Neill et al. 2006).

Plant community composition varies among the sites, and standing biomass increases with successional stage (Mack et al. 2008). Herbaceous plants are common at the 5-year old site, particularly arbuscular mycorrhizal-colonized northern rough fescue (*Festuca altaica*). Quaking aspen (*Populus tremuloides*) dominates the canopy of the 17-year old site; this species is dual-colonized by arbuscular mycorrhizal and ectomycorrhizal fungi (Neville et al. 2002). Black spruce (*Picea mariana*), which is colonized by ectomycorrhizal fungi, is the most abundant canopy species at the 80-year old site; ericoid shrubs dominate the understory.

Sample collection

For each site, we selected the most common arbuscular mycorrhizal host and most common ericoid host in the plots (Table 1). In addition, *Betula glandulosa* was the most common understory ectomycorrhizal host at the 80-year old site, so it was selected. In the two youngest sites, the most common ectomycorrhizal host plant (quaking aspen) was also dual-colonized by arbuscular mycorrhizal fungi. Conversely, no ectomycorrhizal-only host plants were abundant enough to use as study plants in the two youngest sites. Thus, we selected quaking aspen as a representative of a dual-colonized host. The ectomycorrhizal-only mycorrhizospheres did not differ significantly from the dual-colonized rhizospheres in enzyme activities (see Results). Likewise, in no case were plant species within the same mycorrhizal type significantly different from one another (see Results). In other words, the two AM plant hosts used in the study did not significantly differ from one another in extracellular enzyme activities, and neither did the two ericoid plant hosts. To simplify our analyses, we grouped the dual-colonized mycorrhizospheres with the ectomycorrhizal-colonized rhizospheres, and grouped plant species within mycorrhizal type.

Soil samples were gathered in July 2004, at peak growing season. Each plant was partially uprooted, and then soil from the top 15 cm of the mycorrhizosphere immediately within the root system of that plant (determined visually) was transferred to a plastic bag. Roots of other plants could have intermingled with the target plant to some extent, but we expect that the majority of the roots and associated hyphae were from the target plant. The sample was homogenized by hand mixing, placed on ice for transport back to the field laboratory, and then frozen at −20 °C. We collected four replicates of each mycorrhizosphere type from each site, for a total of 12 replicates per mycorrhizosphere type. Samples were collected in a blocked design, with four blocks per site, and each mycorrhizosphere type represented within each block. We also collected a sample of bulk soil from each block as a reference. For each bulk soil sample, two soil cores (15 cm deep by 5 cm diameter) were taken randomly within 10 m of one another and compiled to represent bulk soil (four replicates per site). Once frozen, the samples were