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Soil microbial response to *Rhododendron* understory removal in southern Appalachian forests: Effects on extracellular enzymes



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ABSTRACT

Rhododendron maximum is a native evergreen shrub that has expanded in Appalachian forests following declines of american chestnut (*Castanea dentata*) and eastern hemlock (*Tsuga canadensis*). *R. maximum* is of concern to forest managers because it suppresses hardwood tree establishment by limiting light and soil nutrient availability. We are testing *R. maximum* removal as a management strategy to promote recovery of Appalachian forests. We hypothesized that *R. maximum* removal would increase soil nitrogen (N) availability, resulting in increased microbial C-demand (i.e. increased C-acquiring enzyme activity) and a shift towards bacterial-dominated microbial communities. *R. maximum* removal treatments were applied in a 2 × 2 factorial design, with two *R. maximum* canopy removal levels (removed vs not) combined with two O-horizon removal levels (burned vs unburned). Following removals, we sampled soils and found that dissolved organic carbon (DOC), N (TDN, NO₃, NH₄), and microbial biomass all increased with *R. maximum* canopy + O-horizon removal. Additionally, we observed increases in C-acquisition enzymes involved in degrading cellulose (β-glucosidase) and hemicellulose (β-xylosidase) with canopy + O-horizon removal. We did not see treatment effects on bacterial dominance, though F:B ratios from all treatments increased from spring to summer. Our results show that *R. maximum* removal stimulates microbial activity by increasing soil C and N availability, which may influence recovery of forests in the Appalachian region.

1. Introduction

In terrestrial ecosystems, plant-soil interactions regulate the structure of aboveground and belowground communities as well as rates of biogeochemical processes (Berg and Smalla, 2009; Ehrenfeld et al., 2005; Wardle et al., 2004). Plants influence soil microbial communities through their carbon (C) inputs via litterfall and root exudation (Berg and Smalla, 2009; Chapman and Newman, 2010; Wardle et al., 2006), while soil microorganisms influence plant productivity by mobilizing nutrients such as nitrogen (N), highlighting the potential for complex feedbacks between plants and belowground communities (van der Heijden et al., 2008). Such feedbacks are common in forest ecosystems, where different tree species are associated with distinct microbial communities that exhibit significant functional differences in terms of extracellular enzyme production and nutrient cycling (Ribbons et al., 2016; Weand et al., 2010). Similarly, forest understory shrubs and herbaceous vegetation can influence microbial community structure and function, even within the same forest type (Burke et al., 2011; Fu et al., 2015; Shen et al., 2018; Wurzburger and Hendrick, 2007).

In moist cove and riparian habitats in southern Appalachian forests of the eastern US, the dominant understory species is rosebay rhododendron (Rhododendron maximum L.), a native evergreen shrub. R. maximum dominates plant-soil interactions in these forests by suppressing decomposition rates (Ball et al., 2008; Hunter et al., 2003; Strickland et al., 2009) and immobilizing N and other nutrients in complex organic compounds that are preferentially utilized by R. maximum's own mycorrhizal symbionts (Wurzburger and Hendrick, 2009, 2007). This immobilization of nutrients, along with attenuation of light, inhibits recruitment of hardwood tree seedlings, thereby influencing forest dynamics (Beckage et al., 2000; Clinton, 2003; Nilsen et al., 2001). Further, in the past century R. maximum has experienced a habitat expansion, due to the die-off of American chestnut (Castanea dentata (Marsh) Borkh) in the early 20th century (Elliott and Vose, 2012), and more recently it has increased its growth following the decline of eastern hemlock (Tsuga canadensis (L.) Carrière) due to hemlock wooly adelgid (Adelges tsugae Annand) infestation (Ford et al., 2012). Landscape-level studies also show that where R. maximum is present in the understory, forest trees are on average 6 m shorter than

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https://doi.org/10.1016/j.soilbio.2018.09.008 Received 14 June 2018; Received in revised form 6 September 2018; Accepted 9 September 2018 Available online 11 September 2018 0038-0717/ © 2018 Elsevier Ltd. All rights reserved. where it is absent (Bolstad et al., 2018). These studies suggest that riparian forest structure may be fundamentally altered in the wake of eastern hemlock decline. This has prompted forest managers to suggest aggressive management strategies involving the removal of *R. maximum* from areas impacted by hemlock die-off in order to promote forest recovery (Vose et al., 2013).

Proposed R. maximum management strategies include mechanical removal of the R. maximum understory and subsequent use of herbicides to suppress stump sprouting (Vose et al., 2013). Soil responses to understory vegetation removal are challenging to predict, with prior studies reporting positive, negative, and neutral responses of soil C and N, microbial biomass, fungal:bacterial (F:B) ratios, and extracellular enzyme activities in response to forest understory removal (Boerner et al., 2008; Giai and Boerner, 2007; Shen et al., 2018; Wu et al., 2011; Zhao et al., 2011). A prior R. maximum removal study in the southern Appalachian region showed modest increases in soil inorganic N with no evident effects on soil microbial biomass or invertebrate communities (Wright and Coleman, 2002; Yeakley et al., 2003). Though that study was not replicated and was confounded by a large disturbance event (hurricane) that affected the reference plot, it suggests that R. maximum canopy removal alone may not affect soil communities and processes in the short term.

Proposed R. maximum management strategies also involve the use of low-intensity prescribed fire to remove the thick soil O-horizon that develops in R. maximum thickets (Vose et al., 2013). Soil responses to prescribed fire in forests generally depend on vegetation type, fire frequency, and fire intensity (Certini, 2005). Though soil organic matter (SOM) often decreases following fires (Certini, 2005; González-Pérez et al., 2004), low intensity burns can increase SOM decomposability by heat-altering carbon polymers (Knicker, 2007), resulting in increased C available to soil microorganisms. Additionally, low-intensity burns can increase soil N availability by converting organic N to inorganic forms (Certini, 2005; Hernández and Hobbie, 2008). In southern Appalachian forests, low intensity prescribed fires have not significantly affected soil C and N stocks (Hubbard et al., 2004; Knoepp et al., 2009, 2004), but have increased inorganic-N transformation rates in some cases (Knoepp et al., 2004). In other forested regions, prescribed burns have resulted in increased N availability and altered activities of microbial extracellular enzymes (Boerner et al., 2008; Rietl and Jackson, 2012; Taylor and Midgley, 2018). Studies addressing the combined effects of forest understory removal and prescribed burns in eastern US forests are rare, though increased bacterial activity and altered fungal and bacterial catabolic function have been reported when understory removal and prescribed burning were combined (Giai and Boerner, 2007).

The objective of this study was to examine soil responses to *R. maximum* understory removal in combination with soil O-horizon removal via prescribed burning at the Coweeta Hydrologic Laboratory in the southern Appalachian mountains of North Carolina. We focused on responses of soil C and N pools, fungal vs bacterial dominance, and extracellular enzyme production by microbial communities following *R. maximum* removal. We hypothesized that (1) *R. maximum* + O-horizon removal would mobilize organic matter from recalcitrant *R. maximum* leaf litter, resulting in increased DOC and N availability in mineral soils and a shift towards bacterial-dominated microbial communities; (2) that increased N availability would increase microbial C demand, resulting in elevated production of extracellular enzymes associated with C acquisition; and (3) that reductions in lignin-rich *R. maximum* leaf litter in the O-horizon following burning would result in reduced activities of lignolytic enzymes.

2. Materials and methods

2.1. Site description

We conducted this study at the Coweeta Hydrologic Laboratory (CWT, latitude 35°03' N, longitude 83°25' W), a U.S. Forest Service experimental forest located in the Nantahala Mountains of western North Carolina within the Blue Ridge physiographic province in the southern Appalachians. Soils are deep sandy loams underlain by folded schist and gneiss. Two soil orders are found within the study sites, Inceptisols and Ultisols in the Cullasaja-Tuckasegee and Edneyville-Chestnut complexes, respectively (Thomas, 1996). Soils are characterized by high organic matter in the A horizon, a clay accumulating B horizon, and depth to saprolite of 80–100 cm.

We selected areas within the Coweeta Basin in mesic, riparian areas with low-to-moderate slopes (< 30%) and elevations ranging from 760 to 1060 m. All study areas had high abundance of *R. maximum*. Mean annual temperature at Coweeta is 12.6 °C and seasonally ranges from 3.3 to 21.6 °C. While annual rainfall is usually abundant in this region, averaging ca. 1800 mm, drought years are becoming increasingly common (Laseter et al., 2012).

2.2. Experimental design and sample collection

We applied four R. maximum removal treatments to sixteen $20 \text{ m} \times 20 \text{ m}$ (0.04 ha) plots located in the Coweeta Basin. Six of the sixteen plots have been monitored for vegetation dynamics, carbon and nutrient pools and fluxes, and soil solution chemistry since 2004 (Ford et al., 2012; Knoepp et al., 2011; Nuckolls et al., 2009). We established ten additional plots with similar characteristics, and then randomly selected among the sixteen plots to assign treatments, resulting in four replicates of each treatment. The four treatments were designed to remove the R. maximum canopy (hereafter, CR), remove the soil O-horizon (hereafter, FF), remove the R. maximum canopy and soil O-horizon (hereafter, CFFR), and no removal (hereafter, REF). The CR and CFFR treatments included cutting R. maximum, immediately followed by application of herbicide on cut stumps (Esen and Zedaker, 2004; Harrell, 2006; Romancier, 1971). The herbicide was a triclopyr amine (Garlon 3A[°], DOW Agrosciences) formulation with an aquatic label (50% triclopyr amine/50% water) to prevent stump sprouting. R. maximum cutting (CR, CFFR) occurred in March-May 2015. O-horizon removal in the FF and CFFR treatments involved low intensity prescribed fires, which temporarily removed the Oi (leaf litter) layer but did not consume the Oe+Oa layers (Elliott and Miniat, 2018). Fires were implemented in plots in March 2016 and were performed according to the USDA Forest Service, Nantahala National Forest Prescribed Burning Plan (USDA, 2011).

In April and July 2017, two years following *R. maximum* canopy removal and one year following partial O-horizon removal (Oi only), we took three A-horizon (0–10 cm depth) soil cores from each plot and composited samples by plot. We transported soils to the lab on ice and stored samples at 4° C until analysis.

2.3. Soil pH, soil C and N, microbial biomass C and N

Gravimetric soil water content was determined by mass loss after drying at 105 °C for 24 h. Soil pH was measured in a soil:water slurry, 1:1 by volume, using a Hach Sension + pH meter (Hach company, Loveland, CO, USA). Microbial biomass C and N were determined using a modified chloroform fumigation extraction procedure described by Fierer and Schimel (2003). Extracts were measured for extractable dissolved organic carbon (DOC), total extractable nitrogen (TDN), microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) on an Elementar vario cube TOC/TN (Elementar Americas Inc, Mt. Laurel, NJ, USA). Extracts were analyzed for extractable NH₄ and NO₃ on a Lachat QuikChem flow injection analyzer (Hach Company, Loveland, CO, USA). Dissolved organic nitrogen (DON) was calculated as TDN – (NH₄ + NO₃).

2.4. Extracellular enzyme assays

We measured activities of eight extracellular enzymes involved in C,

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