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Soil chemistry and microbial community functional responses to invasive shrub removal in mixed hardwood forests

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ABSTRACT

Invasive woody plant species are a threat to biodiversity and ecosystem function in forests of the eastern U.S., due in part to their effects on soil properties and nutrient cycling. Controlling invasive shrubs can benefit the ecosystem at multiple scales, but these species tend to resprout when cut, and post-cutting flushes of root exudates have been linked to accelerated decomposition of soil organic matter (SOM), a rhizosphere priming effect. We removed the invasive shrub *Lonicera maackii* (Rupr.) Herder (Amur honeysuckle) from forested sites in central Indiana, USA, using cut-stump and forestry mulching head treatments. For two growing seasons after the initial removal treatments, we compared the soil chemistry and microbial community function of bulk and honeysuckle rhizosphere soils in shrub removal areas to those in invaded reference areas. Microbial activity measured using multiple substrate induced respiration (MSIR) in bulk soils was generally lower in removal areas than reference areas the first year, coinciding with relatively elevated responses in the rhizosphere soils of resprouting shrubs. Elevated SOM and organic C in rhizosphere soils of resprouting shrubs suggested a flush of rhizodeposits from cutting and regrowth. However, bulk soil chemistry responses to shrub removal did not show any evidence of a rhizosphere priming effect, but instead reflected the reduced effects of honeysuckle on throughfall precipitation chemistry—higher ammonium and lower magnesium. Nonetheless, changes in bulk soil chemistry between years were driven by the chemical characteristics of rhizosphere soil associated with resprouting honeysuckle. This study is the first to document the potential for invasive shrub control to affect soil properties through rhizodeposition by the target species.

1. Introduction

Exotic invasive species represent a threat to global biodiversity, and the eastern U.S. is among the most invasion-vulnerable regions in the world (Early et al., 2016). Throughout forests of the eastern U.S., numerous invasive shrub species pose a threat to understory biodiversity and forest regeneration, often forming monotypic thickets in the understory and even becoming the dominant species in some forest systems (Gorchov and Trisel, 2003; Mascaro and Schnitzer, 2007; Miller and Gorchov, 2004). One of the ways in which invasive plant species frequently affect their invaded habitat is through altered carbon and nitrogen pools and fluxes (Ehrenfeld, 2003). Invasive species often possess different resource use strategies than the native community that allow them to take advantage of alterations in soil resource availability (Fridley, 2012; Jo et al., 2015).

Like many invasive plants, a common characteristic of invasive shrubs in eastern forests is litter that decomposes more rapidly than that of native species, increasing available soil N (Elgersma and Ehrenfeld, 2011). These faster decomposition rates are associated with lower lignin concentrations and lower C:N ratios than litter of native deciduous tree species (Arthur et al., 2012). In addition to faster decomposition rates of their own litter, invasive shrubs can accelerate the decomposition of litter from native species (Blair and Stowasser, 2009; Elgersma and Ehrenfeld, 2011; Trammell et al., 2012). Coupled with the extended leaf phenology of many invasive shrub species (i.e., earlier leaf-out in spring; later leaf-drop in autumn), rapid N release from litter may represent a feedback strategy that allows the invader to synchronize high soil N availability with its own N demand before other species break dormancy (McEwan et al., 2009; Schuster and Dukes, 2014; Trammell et al., 2012).

Abbreviations: MSIR, multiple substrate induced respiration; RPE, rhizosphere priming effect; LDA, linear discriminant analysis; DF, discriminant function; RDA, redundancy analysis; PERMANOVA, permutational analysis of variance

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Lonicera maackii (Rupr.) Herder (Caprifoliaceae; Amur honeysuckle, henceforth "honeysuckle") is an exotic invasive shrub introduced in 1897 both for its ornamental value and for soil stabilization (Luken and Thieret, 1997). In addition to accelerated litter decomposition, honeysuckle invasion has been implicated in changes to throughfall chemistry, increased soil pH, changes in the structure of soil microbial communities, and higher potential activity of β-glucosidase, an extracellular enzyme involved in the decomposition of plant material (Kuebbing et al., 2014; McEwan et al., 2012; Poulette, 2012). Despite a large body of work examining how honeysuckle and other invasive shrubs influence soil properties, there has been far less research on how soil properties change following management efforts to remove them. Shrub invasions can cause lasting legacies in the soil, which can influence the composition of recovering plant communities (Grove, 2014; Jordan et al., 2011).

The well-documented impacts of honeysuckle and other invasive shrubs on forest understory plant and wildlife communities have prompted land managers to prioritize their control as a means to improve forest health at multiple scales (Madritch and Lindroth, 2009; McNeish and McEwan, 2016). However, the dense thickets characteristic of mature shrub invasions can require expensive and time-intensive control strategies (e.g., the cut-stump technique; Bailey et al., 2011; Webster et al., 2006), and small-scale control efforts can leave sites prone to re-establishment from nearby invaded areas due to dispersal by wildlife (Bartuszevige and Gorchov, 2006; Castellano and Gorchov, 2013). Forestry mulching heads (e.g. Fecon® Bull Hog, henceforth "Fecon heads") are toothed, rotary drums mounted to skidsteers, tractors, or excavators that masticate shrubs and woody vegetation. Utilization of Fecon heads may accelerate the control of invasive shrubs over wide areas, but their effectiveness for invasive shrub control is understudied, and no studies to date have examined how their use may affect soil properties in eastern hardwood forests. Notably, Fecon head control deposits a layer of masticated woody debris (mulch) on the forest floor. Existing work indicates that mulch deposition from mastication treatments used for fuel reduction in the southern Rocky Mountains and Colorado Plateau reduced mean temperature and temperature variability, increased soil moisture, and had system-specific effects on soil nitrate and ammonium (Rhoades et al., 2012). The variability in mulch effects on inorganic soil N even among relatively arid systems prevents us from drawing conclusions as to how mulch deposition will affect available soil N in eastern forests.

The effects of invasive plants on belowground processes rarely result solely from aboveground characteristics, but rather from the combined effects of litter and of organic deposits from plant roots (Weidenhamer and Callaway, 2010). These rhizodeposits are capable of affecting both the microbial communities and chemistry of surrounding bulk soil (Kourtev et al., 2002; Morris et al., 2016), and may be particularly important in the context of invasive shrub control. Amur honeysuckle and many other invasive shrubs resprout readily when cut in initial control efforts (Hanula et al., 2009; Love and Anderson, 2009; Luken and Mattimiro, 1991; Ward et al., 2013). Evidence from work on grass herbivory suggests that physical wounding aboveground leads to temporary increases in root exudation and greater quantities of organic acids in root exudates (Bardgett et al., 1998; Dyer and Bokhari, 1976; Paterson et al., 2003). These pulses of exudates can elevate soil microbial activity and lead to the loss of existing soil organic matter (SOM) via a rhizosphere priming effect (RPE; Kuzyakov, 2002). Reduced organic compounds from rhizodeposition provide a readily-available energy source for the decomposition of native soil carbon and/or organic acids liberate SOM from organo-mineral complexes (Keiluweit et al., 2015). In intentionally coppiced *Quercus cerris* (European turkey oak) stands, cutting and subsequent regrowth led to decreased soil organic C and increased soil pH, in conjunction with higher microbial activity, suggesting a possible RPE from the flush of readily-available rhizodeposits after cutting (Pignataro et al., 2012).

In this study, we examined how two control techniques (use of a Fecon head and cut-stump treatment) for invasive honeysuckle affected soil chemistry and microbial community function and how changes observed in bulk soils related to differences between rhizosphere soils of resprouting and untreated honeysuckle shrubs. We expected that honeysuckle control would cause a temporary reduction in microbial community function in bulk soil, associated with lower SOM, and that these changes would coincide with higher microbial community function in the rhizosphere of resprouting shrubs. We also expected that mulch deposited by honeysuckle control with the Fecon head would lead to higher concentrations of P, K, and available N, but that any effects of this mulch deposition would be more apparent in the second year post-treatment.

2. Materials and methods

2.1. Site description

Study sites were established across two locations in Indiana's Central Till Plain Region near the city of West Lafayette—1) Purdue University, Richard G. Lugar Forestry Farm (40°25′25″N 86°57′43″W; hereafter LF) and 2) Purdue University, Wildlife Area (40°27′22″N 87°03′33″W; hereafter PWA). Both locations consist of natural forest tracts intermixed with tree plantations and/or tallgrass prairie and are surrounded by an agricultural matrix. All study sites at these locations were in mature, secondary mixed-hardwood forests, each with components of *Quercus* L. spp. (oaks), *Carya* Nutt. spp. (hickories), *Acer* L. spp. (maples) and *Prunus serotina* Ehrh. (black cherry) in the overstory and dense *L. maackii* thickets throughout the understory. Growth ring counts from the five largest *L. maackii* individuals at each site indicated that the shrub established ca. 30, 37, 33, and 25 years prior to the commencement of the study at three sites at LF (LF1, LF2, LF3), and the site at PWA, respectively. Though both PWA and LF locations include areas with past invasive shrub control efforts, sites selected for this study had no history of invasive plant control. All sites were generally flat. Soils are glacial in origin; those at LF sites are primarily Miami silt loams with some Kalamazoo and Ockley silt loams; PWA soils are Miami and Rainsville silt loams (NRCS Soil Survey Staff).

2.2. Experimental design

At each of the four sites, we established a grid of 24 plots, organized into six blocks of four plots (Fig. 1). Two of these blocks (eight plots) were maintained as an untreated reference condition and were intentionally kept adjacent to one another to minimize possible edge effects, but were randomly placed on one side or the other of the other four blocks containing treatment plots. We randomly assigned one of two honeysuckle removal treatments—either "cut-stump" or "Fecon" removal—to the four remaining treatment blocks (16 plots) such that each site contained eight plots of each removal treatment. Within each block, plot center points were placed 8 m apart. Between separate blocks, the closest adjacent plot center points were placed 11 m apart to provide a buffer between blocks with different honeysuckle removal methods. Overall placement of the plot grid was randomly selected within an area that would allow the entire grid to stay at least 10 m from any forest edge or previous honeysuckle removal areas.

The cut-stump treatment consisted of cutting shrubs at the base with a gas-powered clearing saw and treating the resulting stumps with an herbicide mix of 15% triclopyr (Garlon 4 Ultra®; DowAgroSciences), 3% imazypyr (Stalker®; Cyanimad), and 82% Ax-It® (Townsend Chemical) bark oil using a hand sprayer. We removed the resulting honeysuckle slash from each site to avoid altering the light environment or physically obstructing browsing by *Odocoileus virginiana* (white-tailed deer) and other herbivores. Fecon removal treatments were accomplished using a skidsteer-mounted forestry mulching head (Bull Hog®, Fecon, Inc.), attempting to clear honeysuckle shrubs as thoroughly as possible while avoiding incidental damage to native saplings and overstory