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Plant-microbe interactions regulate carbon and nitrogen accumulation in forest soils

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ABSTRACT

Understory removal is a common practice in forest plantations, which is aimed at reducing competition for resources and increasing the productivity of target tree species. Recent studies have shown, however, that the presence of understory vegetation can increase soil carbon and nutrient content, especially where N-fixing species are present. To investigate whether this response can be attributed to changes in soil microbial communities, we conducted experiments with isotopically-labeled litter in *Pinus ponderosa* stands where N-fixing understory species were present (UP) or absent (UA). We measured carbon and nutrient stocks and monitored changes in soil microbial biomass and composition. Field and laboratory experiments strongly suggest that understory suppression and relatively small changes in litter quality can yield significant changes in soil C and N stocks, which are critical to maintaining forest productivity. We detected a greater accumulation of carbon and nitrogen (relative to controls) when mixtures of pine and N-rich litter were applied to the soil. In contrast, soils amended only with pine litter showed a net loss of carbon and nitrogen stocks. Soil microbial biomass was significantly higher in UP than in UA stands and microbial community composition varied with type of litter inputs and incubation time (0–180 days), but not as a function of understory management. Similar results were obtained from field experiments, in which mesocosms were incubated for ~2.5 years with pine and N-rich understory litter mixtures. The suppression of understory species caused a decline in litter-derived carbon and nitrogen in the soil, even when the microbial community was resilient to the imposed treatments.

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1. Introduction

The growing emphasis on tree plantations as a primary source of forest products requires that managers boost timber yields through intensive management (Wyoming State Forestry Division, 2009; Hartmann et al., 2010; Powers and Reynolds, 2000). Control of understory vegetation to facilitate stand establishment and increase tree growth is a common practice in forestry, which is intended to reduce competition between target tree species and understory shrubs for water and nutrients (Hartmann et al., 2010; Powers and Ferrell, 1996). However, studies of management practices in plantations have suggested that removal of competing vegetation may in fact result in significant

reductions of soil organic matter (SOM) and levels of soil nutrients (Thomsen et al., 2008; Merino et al., 2004; Munson et al., 1993; Burgess et al., 1995). Studies of mature natural forests have also suggested that understory vegetation and mixtures of tree species play a more beneficial role in maintaining long-term productivity by enhancing soil nutrient accumulation and stabilization of carbon (C) and nitrogen (N) in SOM (Silva and Anand, 2011; Chen et al., 2004).

Positive effects of species mixtures on soil C and N accumulation appear to be particularly strong where N-fixing species are present, especially in soils with low intrinsic fertility (Johnson and Curtis, 2001; Binkley, 2003). A number of mechanisms have been proposed to explain these effects, ranging from shifts in soil water availability to changes in community composition and interspecific competition, associated with variation in quantity and quality of litter and root inputs (Silva et al., 2016; Silva and Anand, 2011; Busse et al., 1996). Post-depositional drivers of

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organic matter stabilization, such as those involving complex interactions between soil minerals, microbial biomass, free amino acids, and NH_4 released from litter and roots of the N-fixer, are also of fundamental importance (Rasmussen et al., 2008; Throckmorton et al., 2012; Silva et al., 2015b). Studies of species mixtures with N-fixing plants in forest plantations have also shown that enhanced accumulation of new C from recent litter inputs is often coupled with conservation of older C in SOM (Drinkwater et al., 1998; Kaye, 2000). Curiously, these effects are generally not apparent when N is supplied as fertilizer (Binkley et al., 2004), which implies that factors associated with litter quality and decomposability, apart from N supply, are responsible for the effects of N-fixation on soil C accumulation and retention.

These results suggest that litter inputs from N-fixing plants exert a negative priming effect on C mineralization. Unlike positive priming effects, which commonly occur when the addition of fresh substrate induces a transient nutrient limitation and results in a short-term increase in mineralization of existing soil C, negative priming effects occur when plant-derived (fresh) materials reduce the mineralization of SOM (Bader and Cheng, 2007). The mechanisms are not yet clear, but enhanced size and metabolic efficiency of the microbial biomass, which depend on the stabilization of labile C and N on soil mineral colloids, are thought to be the cause of this phenomenon (Rasmussen et al., 2008; Kuzyakov et al., 2000). If confirmed, this would mean that soil-plant-microbe feedbacks controlling N-fixation, as well as interspecific competition, can be more important in regulating soil C and N dynamics than total nutrient inputs.

Here we explore this hypothesis by combining results from laboratory incubations with data gathered from a long-term field experiments, describing patterns of litter decomposition and microbially-mediated soil C and N dynamics. Specifically, we tested whether (i) suppression of understory species reduces levels of soil C and N derived from litter inputs; (ii) application of N-rich litter exerts a negative priming effect on SOM, i.e. leading to accumulation of C and N relative to controls; and (iii) microbial biomass and community composition are affected by understory suppression and influence soil C and N dynamics. We discuss the rationale and possible involved in these hypotheses and present results that will improve our understanding of fundamental processes controlling responses to management practices in forest ecosystems.

2. Methods

2.1. Field site

Our field site is a ponderosa pine plantation at the USDA Forest Service Challenge Experimental Forest, situated in the northern Sierra Nevada in California (39°29'N, 121°13'W, elevation 790 m). The plantation was established in 1965 to determine the effects of ponderosa pine density and understory competition on timber production (Oliver, 1990). Understory suppression treatments have been maintained since then. Precipitation at this site averages 1730 mm annually with about half falling as snow. In all plots, the soil is fine textured and derived from volcanic parent material, with a clay mineralogy dominated by iron and aluminum oxides and low-activity kaolinite (clayey, mixed, Typic Palexerults - Challenge Series). The understory is dominated by species of the genera *Arctostaphylos*, *Ceanothus*, and *Lithocarpus*, which are ubiquitous in the region unless understory suppression treatments are imposed. Control of understory shrubs in stands where understory is absent (UA) was obtained in the first and third year by herbicide application (primarily atrazine) and by manual removal thereafter. Stands where understory is present (UP) were not manipulated in any way following the plantation of pine trees.

2.2. Hypotheses testing

The effect of understory suppression on soil C and N deriving from litter inputs (hypothesis i), reflects the integrated effect of changes in plant species composition, herbicide application, and soil disturbance associated with manual removal of shrubs.

To test the effect of litter from N-fixing shrubs (hypothesis ii), we used laboratory incubations with *Ceanothus integerrimus* (ceanothus) residue, which is the most abundant N-fixer species in UP stands. To differentiate the effect of N-rich litter from that of pine litter, we used a combination of pine needles and ceanothus residues, enriched in ^{13}C and ^{15}N isotopes. Briefly, we performed in situ decomposition experiments by isotopically labeling litter residues obtained from *P. ponderosa* trees grown by the USDA Forest Service (Placerville, CA, nursery). One year-old pine seedlings were uniformly labeled weekly for one growing season in the greenhouse with $^{13}\text{CO}_2$ (8 atom%; or $\delta^{13}\text{C}$ 6739.1‰) and ^{15}N (4 atom%; or $\delta^{15}\text{N}$ 10334.78‰) applied as KNO_3 (Qiao et al., 2014). Unlabeled plants were grown under the same conditions and received the same amount of ^{14}N - KNO_3 . In both cases litter was collected upon senescence and air-dried before application. Pine senescence was induced by water stress. Ceanothus leaves senesced naturally. The application of labeled litter allowed us to partition litter- and soil-derived C and N pools.

We further tested hypothesis ii under field conditions, using the same experimental design used in laboratory incubations, with litter from *Arctostaphylos viscida* (manzanita) instead of ceanothus. Manzanita residues were not labeled and this species is not an N-fixer. Nevertheless, manzanita leaves contains more N than pine litter and commonly occurs at the study site. Thus, application of labeled pine residues allowed us to partition manzanita-, pine- and soil-derived C and N pools in the field. For details see Qiao et al. (2014) and discussion below. Manzanita residues were collected from the site as dead leaves, still attached to the plant and air-dried to constant weight before application.

To evaluate changes in microbial community (hypothesis iii) we collected soils from surface horizons (0–15 cm deep) in four randomly-selected locations in UP and UA stands. The soils were incubated for 180 days with 3 litter-amendment treatments consisting of no amendment (control), a 1:1 pine-ceanothus mixture, and pine only treatment. Each litter \times soil treatment was replicated 4 times for each of 7 sampling dates and included 4 sets of paired pine-ceanothus replicates, constructed such that one replicate contained labeled pine and unlabeled ceanothus, and the other replicate contained labeled ceanothus and unlabeled pine. A ceanothus-only treatment was omitted because it would not be representative of field conditions since pines are dominant in both UP and UA stands. The microbial analysis is described below.

2.3. Field experiment

We used a randomized block design with 6 plots (4 m² each) distributed on elevated flat areas in three plantation at the study area, each consisting of adjacent UP and UA stands. In each plot, we installed 4 mesocosms, one for each of the 4 litter treatments, namely a 1:1 mixture of labeled pine and manzanita, labeled pine litter only, a 1:1 mixture of unlabeled pine and manzanita, and unlabeled pine litter only. The latter two treatments served as controls for stable isotope measurements of soils taken over the course of the experiment. Each mesocosm consisted of a plastic cylinder, 30-cm in diameter and 20 cm long, that was pushed into the soil to a depth of 15 cm. During installation, care was taken to not disturb the existing litter and soil surface horizons. Plastic mesh that allows for passage of soil fauna (2 \times 2 cm) was placed over each mesocosm to prevent the litter from being blown or washed out of the mesocosm. As with the laboratory study, the mass of each

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