



Soil microbial community resilience with tree thinning in a 40-year-old experimental ponderosa pine forest



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ABSTRACT

Establishment of native grasses is a primary objective of restoration in *Pinus ponderosa* var. *scopulorum* (P. & C. Lawson) forests in the southwestern United States. Interactions among native grasses and soil microorganisms generate feedbacks that influence the achievement of this objective. We examined soil chemical properties and communities of plants and soil microorganisms in clear-cuts and *P. ponderosa* stands thinned and maintained at low and medium tree densities for over 40 years along with high density (unthinned) stands. Phospholipid fatty acids (PLFA) in soils were analyzed to examine arbuscular mycorrhizal (AM) fungi and microbial communities in the three thinning treatments and the unthinned stands with and without a recent broadcast burn. Additionally, two native bunchgrasses, *Festuca arizonica* and *Muhlenbergia wrightii* were grown in containers filled with intact soil cores collected from each field plot to more thoroughly compare the abundance of AM fungi and microbial communities across different stand densities and burn treatments. Tree thinning decreased litter cover and increased the abundance and diversity and altered community composition of both herbaceous vegetation and AM fungi. In the mineral soil layer, the pH, total carbon, nitrogen, phosphorus and PLFA profiles did not differ significantly among the four stand density or burn treatments. Mycorrhizal colonization of the container grown grasses did not significantly differ with tree density or burn treatments; however, *F. arizonica* roots had a strong trend for decreased colonization when grown in soil from high density (unthinned) tree cover. Soil from the containers with *F. arizonica* had a greater abundance of AM fungal spores. Furthermore, bacterial community composition varied with grass species. Concentration of biomarkers for bacteria were higher in soil that supported *F. arizonica* compared to soil in which *M. wrightii* was grown. Our results indicate that the creation of clear-cut openings in forests may increase the abundance and richness of AM fungal propagules and soil bacterial communities were surprisingly resilient to tree thinning and low-intensity fire treatments. These results suggest managing forests to create clear-cut openings generate conditions that favor understory native grasses and AM fungi that are linked to soil bacterial communities.

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1. Introduction

Restoration of overly-dense ponderosa pine (*Pinus ponderosa*) forests to more fire-resilient grass-dominated savannas similar to pre-Euro-American conditions is a primary management goal in

the southwestern United States. The overly-dense stand structure of the largest contiguous stand of ponderosa pine in the United States, exacerbated by almost a century of fire suppression, poses a threat to both the ecosystem and human populations in close proximity due to large, often catastrophic wildfires. Reducing tree densities and creating canopy openings can lessen the threat of stand-replacing fires and encourage the establishment of native understory vegetation (Graham et al., 1999; Laughlin et al., 2010). Plant community structure and native plant succession are strongly influenced by communities of soil organisms and plant symbionts such as mycorrhizal fungi (reviewed in Kulmatiski et al.,

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2008; Pringle et al., 2009). Thinning of overstory trees can influence both understory plants and soil microbial communities (Jones et al., 2003; Owen et al., 2009; Pickles et al., 2010).

Structural changes following thinning in ponderosa pine forests have been shown to alter soil microbial communities that in turn influence plant diversity and composition (Kaye et al., 2005; Laughlin et al., 2010; Pringle et al., 2009; Schnitzer et al., 2011). Reducing densities of ectomycorrhizal (EM) trees helps arbuscular mycorrhizal (AM) grasses thrive by opening the canopy to provide greater light penetration, reducing competition for resources, and increasing microbial populations that are beneficial to herbaceous plants (Korb et al., 2003; Laughlin et al., 2008). Microbial populations influence ecosystem processes that, in turn, affect plant populations, creating feedbacks between aboveground and belowground communities (Bardgett, 2005; Hart et al., 2005). These feedbacks between plants and soil organisms are important determinants of plant community structure (Klironomos, 2003). Host plants benefit when mycorrhizas acquire nutrients that heterotrophic soil microorganisms mobilize from complex substrates in the soil (Aert, 2002; Talbot et al., 2008; Hodge and Fitter, 2010). Mycorrhizas are typically mutually beneficial, but their influence varies with species of plants, fungi and environmental conditions (Johnson and Graham, 2013). Depending on the manner in which woody debris is treated following tree thinning, AM fungi have been shown to either be more abundant with tree thinning (Korb et al., 2003), or have reduced propagule abundance and richness (Korb et al., 2004; Owen et al., 2009) compared to untreated areas with high tree density.

Changing the plant community from a high density forest to an open canopy forest with an herbaceous community is expected to alter the soil microclimate and chemical properties (DeBano et al., 1998; Waldrop et al., 2003; Grayston and Renneberg, 2006). Following tree thinning, decomposition and N mineralization rates have been shown to increase in the short-term in southwestern *P. ponderosa* (Kaye and Hart, 1998a,b; Grady and Hart, 2006). This increase was assumed to be the result of decreased canopy allowing greater soil insolation to warm the soil surface and increase available soil moisture (Kaye and Hart, 1998a,b). Even with increased soil microbial activity immobilization of N can occur (DeLuca and Zouhar, 2000). If prescribed burning is combined with thinning, lethal temperatures ($>100^{\circ}\text{C}$) can negatively affect microbial populations with a disproportionate decrease in fungi especially in the O horizon (DeBano et al., 1998; Hart et al., 2005; Cairney and Bastias, 2007). Additional negative impacts include limiting water infiltration and available soil moisture from the formation of hydrophobic surface conditions and reduced microbial activity (DeBano et al., 1998). Yet increased soil insolation and soil moisture (Hart et al., 2005; Simonin et al., 2007), available N (Covington and Sackett 1992; Kaye and Hart, 1998b; Frey et al., 2004; Kaye et al., 2005), surface soil pH (cation deposition), and the addition of charcoal (Hart et al., 2005) from surface fires has been shown to enhance microbial activity (Pietikäinen and Fritze, 1995; Pietikäinen et al., 2000). To date the majority of studies that have altered ponderosa pine densities for restoration have focused on short-term responses following thinning treatments.

The goals of our study were to examine the long-term (>40 years) influences of varying levels of tree density and a low intensity prescribed fire on understory plant communities, soil chemical properties, microbial biomass, and the abundance and composition of AM fungi. We expected that long-term maintenance of varying stand densities would influence the composition of soil microbial communities. Because AM fungi are obligate symbionts of herbaceous plants including grasses, their abundance and diversity were hypothesized to be lowest in untreated, high-density stands. In clear-cuts we expected abundance and diversity to be the highest due to greater

diversity of potential host plants (Korb et al., 2003). Low intensity fire was expected to reduce the amount of litter in the organic horizon, but have only a short-term influence on mineral soil pH, nutrients or microbial community composition as heat penetration should be minimal. We tested four hypotheses: (H_1) long-term *P. ponderosa* stand density reductions should increase the abundance, diversity, and alter the community composition of herbaceous plants, AM fungi, and other soil microorganisms; (H_2) long-term *P. ponderosa* stand density reductions will reduce litter mass and litter C concentration, but increase available N and P; (H_3) low intensity fire would decrease litter mass and possibly increase soil pH, but not influence other plant, microbial or soil variables; and (H_4) different communities of heterotrophic soil organisms would develop from the interaction of varying stand densities and host plants.

2. Materials and methods

2.1. Study sites

In 1962 the United States Forest Service established and has maintained to date an experimental gradient of mechanically-thinned stands of *P. ponderosa* at Taylor Woods, a subdivision of the Fort Valley Experimental Forest. Taylor Woods is approximately 14.5 km northwest of Flagstaff, Arizona, at an elevation of 2266 m (Ronco et al., 1985). Study plots are within a 36.4-ha area on a gentle (4%), southwest-facing slope, in the *P. ponderosa*/Arizona fescue (*Festuca arizonica* Vasey) habitat type. Mean annual air temperature is 6.1°C ; mean daily air temperatures range from -3.9°C in January to 17.2°C in July. Mean maximum air temperatures in January and July are 5.6°C and 27.2°C , respectively. Mean annual precipitation is 55.9 cm, of which approximately 29% falls in July and August, the wettest months of the year. The summer rainy season is bracketed by spring and fall droughts. Mean annual snowfall from 1950 to 2006 was 246 cm (all climate data from: <http://www.wrcc.dri.edu/summary/climsmaz.html>). The soil at Taylor Woods is derived from flow and cinder basalt and is classified as Brolliar stony clay loam, a fine, smectic, frigid Typic Argiboroll (Meurisse, 1971). The A horizon is rather shallow, extending to only 10 cm, but the remainder of the soil profile reaches a depth of 114 to more than 152 cm before bedrock of fractured basalt is encountered.

This study examined four tree density treatments: clear-cut (0 trees ha^{-1}), low (145 trees ha^{-1}), medium (471 trees ha^{-1}), and unthinned high density ($3200\text{ trees ha}^{-1}$). Each treatment was replicated three times, with plots ranging in size from 0.30 to 0.50 ha (Ronco et al., 1985; McDowell et al., 2007). The plots were initially thinned to specified stand densities in 1962 and these stand densities maintained by thinning as needed in 1972, 1982 (Ronco et al., 1985), 1992, and 2003 (C. Edminster, Personal Communication, 2003, Rocky Mt. Research Station, U.S. Forest Service, Flagstaff, AZ). During the fall of 1998, the plots were split, and one half of each plot burned during the fall and winter of 1998–1999 creating a replicate split-plot design. Very low fire intensities were applied to burn understory and surface litter, and no tree mortality occurred within the plots. The high density (unthinned) plots were not burned because it was impossible to perform prescribed burns in a controlled manner.

2.2. Plot vegetation and microbial communities

Plant cover was measured within the different tree density plots to determine if understory plant abundance and diversity would be greater at higher levels of forest thinning. In August, 2003, herbaceous plant canopy cover and frequency

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