



# Influence of coarse wood and pine saplings on nitrogen mineralization and microbial communities in young post-fire *Pinus contorta*

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## ABSTRACT

Nitrogen (N) limits productivity in many coniferous forests of the western US, but the influence of post-fire structure on N cycling rates in early successional stands is not well understood. We asked if the heterogeneity created by downed wood and regenerating pine saplings affected N mineralization and microbial community composition in 15-yr old lodgepole pine (*Pinus contorta* var. *latifolia*) stands established after the 1988 fires in Yellowstone National Park (Wyoming, USA). In three 0.25-ha plots, we measured annual *in situ* net N mineralization in mineral soil using resin cores ( $n = 100$  per plot) under pine saplings, downed wood (legacy logs that survived the fire, and fire-killed trees that had fallen and were contacting or elevated above the ground), and in bare mineral soil. Annual *in situ* net N mineralization and net nitrification rates were both greater in bare mineral soil ( $8.4 \pm 0.6$  and  $3.6 \pm 0.3$  mg N kg<sub>soil</sub><sup>-1</sup> yr<sup>-1</sup>, respectively) than under pine saplings, contact logs, or elevated logs (ca.  $3.9 \pm 0.5$  and  $0.8 \pm 0.1$  mg N kg<sub>soil</sub><sup>-1</sup> yr<sup>-1</sup>, respectively). Net nitrification was positively related to net N mineralization under all treatments except for elevated logs. In laboratory incubations using <sup>15</sup>N pool dilution, NH<sub>4</sub><sup>+</sup> consumption exceeded gross production by a factor of two in all treatments, but consumption and gross production were similar among treatments. Contrary to our initial hypothesis, microbial community composition also did not vary among treatments. Thus, two- to three-fold differences in *in situ* net N mineralization rates occurred despite the similarity in microbial communities and laboratory measures of gross production and consumption of NH<sub>4</sub><sup>+</sup> among treatments. These results suggest the importance of microclimate on *in situ* annual soil N transformations, and differences among sites suggest that broader scale landscape conditions may also be important.

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## 1. Introduction

Wildfires have numerous direct effects on soil nitrogen (N) availability (Wan et al., 2001; Smithwick et al., 2005; Certini, 2005), which limits productivity in many northern coniferous forests (Vitousek and Howarth, 1991). Wildfires also initiate plant community dynamics and introduce a subsequent pulse of coarse

wood in burned forests (Clark et al., 1998; Ferguson and Elkie, 2003; Tinker and Knight, 2000), creating structural heterogeneity locally and across the landscape. This heterogeneity includes individual plants that accumulate nutrients and produce litter of varying quality, and physical formations such as coarse wood that modify the soil microenvironment and provide substrate for decomposers (Busse, 1994; Harmon et al., 1986). Previous studies showed that the amount, position and age of coarse wood influenced local litter decomposition rates within young post-fire stands of lodgepole pine (*Pinus contorta* var. *latifolia* [Engelm. ex Wats.] Critchfield), and these local differences scaled up to the landscape (Remsburg and Turner, 2006). However, whether the coarse wood also influences soil processes in young post-fire stands is not known. Downed wood has been shown to lower total and microbial N, increase microbial C:N ratios, and lower N<sub>2</sub>O production and denitrification enzymatic activity in mixed forests

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(Hafner and Groffman, 2005), but other studies in conifer forests show minimal effects (Spears et al., 2003; Laiho and Prescott, 2004; Spears and Lajtha, 2004; Brais et al., 2005). Given that forest fires are common and increasing in western US landscapes (Westerling et al., 2006), we were interested in whether the heterogeneity created by downed wood and pine saplings in post-fire stands might influence soil biogeochemistry. If so, such variation could suggest mechanisms that are important in the functioning of young post-fire forests, particularly with regard to spatial heterogeneity in process rates, and could potentially facilitate extrapolation to the broader landscape.

Extensive severe fires in Yellowstone National Park (YNP) in 1988 created ~25 million metric tons of standing dead wood (Tinker and Knight, 2001). Many of the trees killed by the fires have now fallen, and coarse wood is abundant in the post-fire forest. Because relatively little pre-fire coarse wood was consumed in the fires (~8%; Tinker and Knight, 2000), legacy coarse wood, i.e., downed wood from the previous stand also contributes to within-stand structure. In addition, post-fire regeneration of lodgepole pine has been extensive yet variable, with sapling densities ranging from 0 to >500,000 ha<sup>-1</sup> (Turner et al., 2004). Thus, coarse wood and pine saplings are the main structural components of these post-fire stands.

The presence of coarse wood and lodgepole pine saplings may potentially influence soil N dynamics in many ways. Coarse wood provides locations for N immobilization and fixation (Brunner and Kimmins, 2003) and serves as a substrate for decomposition (Busse, 1994; Fahey and Knight, 1986; Harmon et al., 1986). Newly introduced coarse wood begins as a net N sink due to initially high C:N ratios, whereas older, decayed coarse wood becomes a net N source (Holub et al., 2001; Laiho and Prescott, 2004; Spears et al., 2003). The position of coarse wood may also modify soil N dynamics; decomposition is slow for standing wood (Harmon et al., 1986) but accelerates once the wood establishes contact with the ground (Busse, 1994). As a result, standing versus fallen wood may affect nutrient input to underlying mineral soil differently with regard to leaching of dissolved organic carbon (C) (Spears et al., 2003) and subsequent formation of soil organic matter. Pine saplings may also modify soil N dynamics, primarily through plant nutrient uptake and litter production. In Rocky Mountain forests, lodgepole pine needles

decompose slowly (Fahey and Knight, 1986), and local accumulations of needle litter may slow net N mineralization rates (e.g., Stump and Binkley, 1993). In addition to effects on substrate quality and quantity, downed wood and pine saplings modify local microclimatic conditions, which can affect microbial community composition (Sinsabaugh et al., 1993) and subsequent N availability (Balser et al., 2001; Waldrop et al., 2000). However, it is not known whether microbial communities are sensitive to the variation in saplings and wood that is typical of post-fire forest stands.

The objective of this study was to determine whether the position and age of coarse wood ≥20 cm diameter and the presence of pine saplings influenced N mineralization rates and microbial communities in 15-yr old post-fire lodgepole pine stands in Yellowstone National Park (YNP), Wyoming, USA. With regard to downed wood, we expected that soils under legacy wood would have higher N mineralization relative to the other wood classes due to higher levels of labile C and N (Fahey, 1983) compared to soils under less decayed wood. We also expected N mineralization to be low under pine saplings because of the low quality of pine needle litter (Fahey and Knight, 1986; Stump and Binkley, 1993). Finally, we hypothesized that models to predict N mineralization would be improved by inclusion of metrics describing microbial community composition, substrate (initial NH<sub>4</sub><sup>+</sup> pool, extractable C) and percent cover of overlying vegetation. Because coarse wood and pine sapling densities vary so much across the burned landscape, our overarching goal was to determine whether these features might be associated with local differences in soil N dynamics in the young post-fire forests and, in turn, potentially be important across the landscape.

## 2. Study area and methods

### 2.1. Study sites

Yellowstone National Park (YNP), Wyoming, USA, encompasses approximately 9000 km<sup>2</sup> and is characterized by cold, snowy winters and dry, mild summers. Our study was conducted at three sites in the central and southern portions of YNP that experienced stand-replacing fires during 1988: Biscuit Basin, Lewis Canyon, and Riddle Lake (Table 1). The three sites were all on infertile soils

**Table 1**

Summary of general stand characteristics and soil properties in three 0.25-ha post-fire lodgepole pine sites

Site characteristic	Site		
	Biscuit Basin	Lewis Canyon	Riddle Lake
Sapling density (stems ha <sup>-1</sup> )	18,100	11,333	7,000
Elevation (m)	2,228	2,377	2,437
Lodgepole pine ANPP (mg ha <sup>-1</sup> yr <sup>-1</sup> ) <sup>1</sup>	11.5	6.6	2.2
Herbaceous ANPP (mg ha <sup>-1</sup> yr <sup>-1</sup> ) <sup>1</sup>	0.5	1.2	1.2
Basal area of fallen coarse wood (m <sup>2</sup> ha <sup>-1</sup> )	20.1	18.2	17.9
Soil properties			
pH	4.8 (0.04) <sup>a</sup>	4.3 (0.04) <sup>b</sup>	4.5 (0.03) <sup>b</sup>
K (kg ha <sup>-1</sup> ) <sup>2</sup>	424.2 (50.7) <sup>a,b</sup>	358.2 (23.4) <sup>b</sup>	442.7 (31.3) <sup>a</sup>
Ca (kg ha <sup>-1</sup> ) <sup>2</sup>	1411.2 (29.2) <sup>a</sup>	644.5 (29.4) <sup>c</sup>	1137.9 (32.7) <sup>b</sup>
P (kg ha <sup>-1</sup> ) <sup>3</sup>	24.0 (2.1) <sup>a</sup>	9.8 (0.7) <sup>c</sup>	18.0 (1.2) <sup>b</sup>
Mg (kg ha <sup>-1</sup> ) <sup>2</sup>	237.8 (7.6) <sup>a</sup>	106.9 (7.5) <sup>c</sup>	173.5 (10.3) <sup>b</sup>
Total N (%) <sup>4</sup>	0.07 (0.01)	0.07 (0.01)	0.07 (0.04)
Organic matter (%) <sup>5</sup>	2.8 (0.1) <sup>b</sup>	4.2 (0.1) <sup>a</sup>	3.9 (0.1) <sup>a</sup>
C:N ratio <sup>6</sup>	23.2 <sup>b</sup>	34.8 <sup>a</sup>	32.3 <sup>a</sup>

Soil and vegetation were sampled in 2002 (stand age = 14 yrs). Soil properties are average values from five composite samples. ±1 standard error is in parentheses. Significant differences among means by site were determined by Tukey's Studentized Range with  $\alpha = 0.05$ .

<sup>1</sup> See Turner et al. (2004) for methods.

<sup>2</sup> Atomic absorption after extraction with H<sub>2</sub>SO<sub>4</sub> (Schulte et al., 1987).

<sup>3</sup> Truog method.

<sup>4</sup> Micro-Kjeldahl procedure (Jackson, 1958).

<sup>5</sup> Dry combustion using the Tekmar-Dohrman 183 TOC Boat Sampler DC-190 (Tekmar-Dohrman, Mason, OH).

<sup>6</sup> Assuming a carbon-to-organic matter ratio of 0.58.

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