

# Influences of thinning, prescribed burning, and wildfire on soil processes and properties in southwestern ponderosa pine forests: A retrospective study

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## Abstract

Following Euro-American settlement in the late 1800s, fire suppression and livestock grazing in ponderosa pine-bunchgrass ecosystems of the southwestern US resulted in the replacement of grass openings with dense stands of ponderosa pine. This, in turn, has led to apparent decreases in decomposition, net N mineralization, and soil respiration (i.e., net soil CO<sub>2</sub> efflux) rates, losses of floral and faunal diversity, and greater risk of the occurrence of stand-replacing wildfire. Alterations in ecosystem structure and function have prompted the implementation of restoration treatments throughout the region. Using a retrospective approach, we investigated the effects of thinning, thinning plus prescribed fire, and wildfire, 6–15 years following treatments, on ecosystem processes and properties across a 750-km<sup>2</sup> area in northern Arizona. We found that stands that had thinning or thinning plus burning treatments had lower *in situ* annual rates of net N mineralization in the mineral soil than unmanaged stands. However, stands burned by high-severity wildfire had net N mineralization rates that were about 60% higher than unmanaged stands. Because of similarities in net N mineralization rates among treatments under laboratory conditions, we speculate that variation in *in situ* net N transformation rates among stands were due to differences in C inputs (thinned and thinned plus burned) and soil microclimate (wildfire) among the stands. Size of the soil microbial C and N pools generally declined with decreases in litterfall (highest in unmanaged, intermediate in thinned and thinned plus burned, and lowest in wildfire stands); however, *in situ* rates of net soil CO<sub>2</sub> efflux did not follow this pattern. Our results contrast with some previous studies in southwestern ponderosa pine forests where restoration treatments (both thinning and thinning plus burning) increased net N transformation rates. We hypothesize that the dissimilarity in responses to treatments across studies is due to differences in the relative effect of these treatments on the quantity and quality of C inputs. Large increases in easily decomposable understory biomass following restoration treatments appear to result in increases in N cycling rates, whereas treatments that result in either no change or minimal increases in understory biomass, accompanied by a long-term decrease in pine needle input to the forest floor, lead to reductions in N cycling rates. We recommend that restoration and fire-hazard reduction treatments be applied preferentially to stands that currently have low understory production.

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**Keywords:** Microbial biomass; Microbial respiration; Nitrogen availability; Restoration; Soil respiration; Substrate quality

## 1. Introduction

Following Euro-American settlement in the late 1800s, fire suppression and livestock grazing in ponderosa pine-bunchgrass ecosystems of the southwestern US resulted in the replacement of grass openings with dense stands of ponderosa pine (*Pinus ponderosa* var. *arizonica* (Engelm.) Shaw and var. *scopulorum* Engelm.; Cooper, 1960; Covington and Moore, 1994a). This change in forest structure has increased forest

floor biomass (Covington and Sackett, 1984), reallocated biomass from herbaceous plants to trees (Covington et al., 2001), and reduced herbaceous diversity (Fulé et al., 1997). These alterations in stand structure and species composition, in turn, have decreased rates of litter decomposition (Welch and Klemmedson, 1973; Hart et al., 2005), net nitrogen (N) mineralization (Kaye and Hart, 1998a), and soil net carbon dioxide (CO<sub>2</sub>) efflux (i.e., soil respiration; Kaye and Hart, 1998b). Increased tree density and fuel loading have also resulted in greater risk and occurrence of stand-replacing wildfires (Covington et al., 1994, 1997; Allen et al., 2002).

Alteration of ecosystem structure and function, potential loss of biodiversity, and the increased risk of wildfire associated

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with increased aboveground fuels have prompted restoration efforts (Covington and Moore, 1994b; Covington et al., 1997, 2001; Allen et al., 2002). Restoration treatments include the thinning of a majority of the mostly small-diameter, post-settlement trees and prescribed burning; the goal of these treatments is to re-establish stand structure and a fire regime of frequent, low-intensity surface fires characteristic of ponderosa pine forests prior to Euro-American settlement. The likely consequence of leaving dense pine stands unmanaged would be the occurrence of a stand-replacing wildfire (Covington et al., 1994, 2001). Indeed, the area burned by wildfires in ponderosa pine forests of the southwestern US has been increasing over the past three decades, largely due to the buildup of aboveground fuels (Swetnam and Betancourt, 1998).

Currently, there is a paucity of information on the longer-term effects of restoration treatments on soil processes in southwestern US ponderosa pine forests. Short-term studies (i.e., 1–2 years) that have evaluated the responses of ponderosa pine forests to thinning alone and thinning combined with prescribed burning have generally shown increases in rates of N cycling and soil net CO<sub>2</sub> efflux following treatment (Covington and Sackett, 1992; Kaye and Hart, 1998a,b). These increases in ecosystem process rates have been attributed to increased soil temperature, increased decomposition of roots following bole removal, decreased competition between microbes and plants for soil resources, and nutrients released through oxidation and mineralization of organic matter during and following prescribed burns. Wildfires affect soils in the short-term by reducing microbial biomass through direct heating and lysing of microbial cells (Choromanska and DeLuca, 2002; Hart et al., 2005), by increasing pool sizes of inorganic N released from these cells and from organic matter during combustion (Prieto-Fernandez et al., 1998; DeLuca et al., 2002), and by increasing soil temperature post-fire through increased solar radiation input to the surface with overstory removal (O'Neill et al., 2002; Treseder et al., 2004; Wolfson et al., 2005). Compared to prescribed burns, high-severity wildfires can result in the mortality of a majority of aboveground biomass, causing reduced plant uptake of nutrients. In wildfires, loss of plant uptake coupled with large inputs of detritus available for microbial metabolism may accelerate leaching losses of N (Prieto-Fernandez et al., 1993), whereas, following low-severity prescribed burning, increased nutrient availability would not lead to greater nutrient loss (Kaye et al., 1999). While the short-term effects of restoration treatments and wildfire on soil processes are likely driven by changes in microclimate and the quantity of organic matter inputs, longer-term effects may be more influenced by changes in the quality of organic matter inputs (Hart et al., 2005).

The longer-term impacts of thinning and burning on ecosystem processes in ponderosa pine forests appear idiosyncratic. For instance, at Gus Pearson Natural Area (GPNA) near Flagstaff, Arizona, Boyle et al. (2005) found that 8 years after thinning and thinning plus burning soil net CO<sub>2</sub> efflux was higher than untreated controls during dry periods but similar during wet periods. They also found that microbial N was not affected by either treatment. However, in ponderosa

pine forests in Montana, DeLuca and Zouhar (2000) reported that thinning plus burning decreased N availability, soil net CO<sub>2</sub> efflux, and microbial N for up to 11–12 years, while thinning without burning decreased only microbial N. Other research in ponderosa pine forests has also shown decreases in N availability 5–12 years following thinning plus burning in Montana (Sala et al., 2005) and 8–9 years following prescribed burn treatments in Central Oregon (Monleon et al., 1997). The longer-term effects of wildfire on N transformation rates, microbial biomass, and soil net CO<sub>2</sub> efflux in western pine forests are not well documented; however, in general, they seem to depend to a large degree on the recovery of vegetative inputs and hence of carbon (C) and N substrates for microbial growth (DeLuca et al., 2002; Litton et al., 2003; Hart et al., 2005).

Our research was conducted to help elucidate the longer-term changes (6–15 years after treatment) in ecosystem processes and properties following thinning, prescribed burning, and wildfires in southwestern ponderosa pine forests. We evaluated these treatments across a landscape area of 750 km<sup>2</sup> near Flagstaff, Arizona, USA. We used a retrospective approach for our experimental design by selecting stands treated by standard silvicultural methods and exposed to wildfire prior to initiation of our research. Although the silvicultural treatments were not originally designed as restoration treatments, the techniques used (thinning and prescribed burning) were similar; hence, investigating the ecosystem effects in these stands should provide insight to the longer-term changes in ecosystem processes across a large and heterogeneous landscape following restoration treatments. We developed three hypotheses for our study based on prior research of the longer-term effects of thinning and burning in ponderosa pine forests: (1) aboveground C inputs (i.e., litterfall) will decrease across treatments in the following order: unmanaged, thinned, thinned plus burned, and wildfire; (2) soil microbial biomass will also decrease along this gradient of C input; (3) soil processes mediated by the soil microbial biomass (rates of soil net N mineralization and net soil CO<sub>2</sub> efflux) will also decrease along this gradient.

## 2. Methods

### 2.1. Study site, stand conditions, and sampling protocol

Our research was conducted across 750 km<sup>2</sup> of the Coconino National Forest of northern Arizona, USA, near the city of Flagstaff (35°8'N, 111°39'W; Fig. 1). Elevations ranged among stands from 2000 to 2500 m. Meteorological data were taken from the Fort Valley Experimental Station located within a 30 km distance and 280 m of elevation of all stands (Fort Valley Arizona Meteorological Data (FVAMD), 2005). Precipitation during the 1-year study period (15 May 2003 to 15 May 2004) was 44.4 cm (Fig. 2; FVAMD, 2005). Mean annual air temperature was 6.9 °C with 119 days having daily low temperatures greater than 0.0 °C over this same period (FVAMD, 2005). Drought conditions occurred in the early summer months (15 May to 23 July 2003) with less than 1 cm of precipitation over this time period. Historically (1909–2000), annual precipitation averages 56.6 cm, and mean annual air

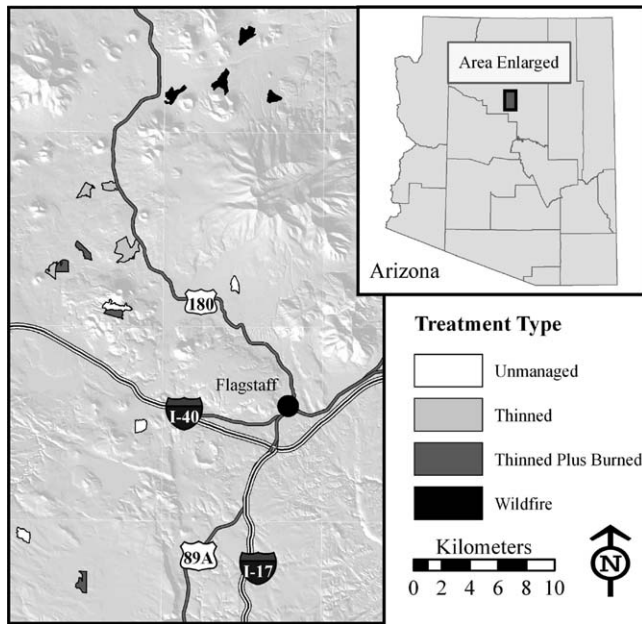


Fig. 1. Locations of unmanaged, thinned, thinned plus burned, and wildfire stands in the Coconino National Forest of northern Arizona.

temperature averages 6.3 °C (FVAMD, 2005). The dominant overstorey vegetation in all stands (except wildfire stands) was southwestern ponderosa pine (*Pinus ponderosa* var. *arizonica* (Engelm.) Shaw and var. *scopulorum* Engelm.). The understory community was dominated by Arizona fescue (*Festuca arizonica* Vasey) and mountain muhly (*Muhlenbergia montana* Hitch.) in unmanaged, thinned, and thinned plus burned stands, and by squirreltail (*Elymus elymoides* (Raf.) Swezey), foxtail (*Hordeum jubatum* L.) and cheatgrass (*Bromus tectorum* L.) in wildfire stands (Sabo, 2006).

The Stand Treatment Impacts on Forest Health (STIFH) study was initiated in 1997 by researchers at Northern Arizona

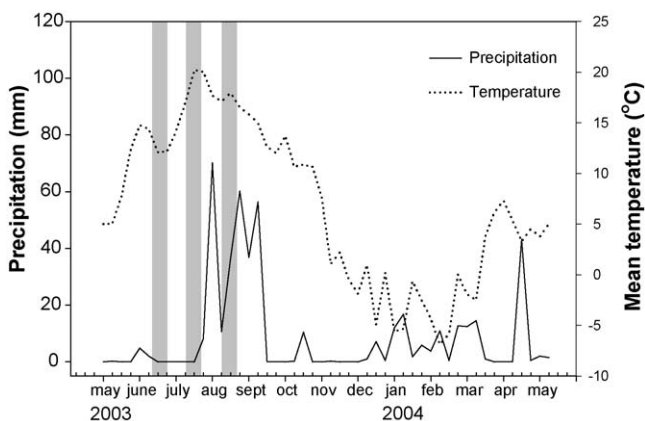


Fig. 2. Weekly precipitation and mean daily air temperature in a representative southwestern ponderosa pine forest for the period 1 May 2003 to 7 May 2004. This time frame coincides with the duration of the *in situ* net N transformation rate measurements. The shaded areas (vertical gray bars) denote the time period during which all other *in situ* measurements were taken. These data were collected from a weather station at Fort Valley Experimental Station located within approximately 30 km and 280 m of elevation from all stands used in this study (Fort Valley Arizona Meteorological Data, 2005).

University to evaluate the effects of thinning, prescribed burning, and wildfire on ecosystem structure and function (Bailey et al., 2001). This project was designed using a retrospective approach so that long-term effects of silvicultural treatments (as surrogates for restoration treatments) and wildfire could be quantified. Retrospective studies, while commonly used, are not as robust as true experimental designs in terms of generalizing conclusions because treatments are not applied randomly to experimental units and also because of the potential for uneven initial conditions (Powers, 1989). To minimize these limitations, we randomly selected stands from well-defined treatment groups across a large landscape area. United States Forest Service records were used initially to identify potential stands. Ten stands of 20 ha or greater in area were then chosen at random from each stand condition that met the following criteria (Bailey et al., 2001):

- **Unmanaged stands (UN):** stands dominated by dense patches of even-aged, small diameter ponderosa pine trees [ $<40$  cm diameter at breast height (1.37 m)] and not having received a density altering treatment within the last 20 years, such that the stands have  $>90\%$  crown closure. Mean basal area in UN stands was  $35\text{ m}^2$  per hectare and tree density averaged 815 trees per hectare.
- **Thinned stands (TH):** stands of even-aged ponderosa pine trees as above, with greater than 30% basal area removed between 1988 and 1995, of which 50% or more came from diameter classes  $<30$  cm. The percent of basal area removed in TH stands ranged from 32 to 59% with a mean of 40%.
- **Thinned plus burned stands (TB):** stands like those from TH above that also received a broadcast burn treatment within 3–4 years following thinning (1989–1997). The percent of basal area removed in TB stands ranged from 33 to 70% and averaged 57%.
- **Wildfire stands (WF):** stands like the unmanaged stands that were consumed by the Hochderffer stand-replacing wildfire in 1996 in which a total of approximately 6520 ha burned. Ponderosa pine tree mortality was greater than 90% in these stands.

For our study, four stands out of the ten selected stands were randomly chosen from each treatment. Soil types did not vary dramatically among stands, being composed primarily of Typic Argiborolls and Mollic Eutroboralfs with flow basalt and basaltic cinders as the parent materials (Miller et al., 1995). The only exception occurred in the TB stand at the Cinder Pit site where soils derived from limestone parent materials were also found; however, these soils comprised less than 30% of the total stand area and were still classified as Mollic Eutroboralfs. Total C, total N, and inorganic C concentrations in the mineral soil from these limestone derived soils were similar to values found from basalt-derived soils within the TB treatment (data not shown).

The study areas within each stand were either 20 or 33 ha in area and were separated from other study areas by distances ranging from 500 m to 40 km. Within each stand, we created ten  $20 \times 20$ -m plots equidistant from each other. Plots within a stand were either all 150 or 200 m apart from each other

depending on the stand size (20 ha stands had plots 150 m apart and 33 ha stands had plots 200 m apart). Sampling points within plots were established by taking a random compass bearing from either the northwestern (net N mineralization, microbial biomass) or northeastern (net soil CO<sub>2</sub> efflux) plot corner and then following this bearing for a distance of 3 m. These bearings and distances were used across all plots from all stand treatments. The sampling point for net soil CO<sub>2</sub> efflux was separated from sampling points of net N mineralization and microbial biomass to minimize disturbance effects from soil coring (i.e., severing roots) on gas flux. Soil cores taken for subsequent measurements were constrained to within a 1-m radius from these initial sampling locations.

We measured rates of net N transformations *in situ* in two of the four replicates (selected at random), at each of the 10 plots over 2 periods: summer–fall period (19 May 2003 to 19 November 2003) and winter–spring period (19 November 2003 to 1 June 2004). Soil samples for determination of microbial biomass, soil properties, and measurements of soil net CO<sub>2</sub> efflux were taken monthly during the middle of each month between June and August 2003, at each of the 10 plots within each stand (4 treatments × 4 replicates × 10 plots = 160 measurements).

### 2.2. Soil sampling and soil chemical and physical properties

Mineral soil cores (4.8 cm diameter × 15 cm depth) taken for determination of soil pools and processes were all handled similarly. Mineral soil cores were sieved field-moist (<4-mm fraction retained), weighed, and subsamples were taken for gravimetric water content (GWC; 105 °C for 48 h). Soils collected for analysis of microbial C and N (see below) were also used for determination of mineral soil total C and N, laboratory incubations, and soil pH following air-drying. For total C and N determinations, monthly soil samples (June, July, and August) were composited by plot by taking equal air-dry masses from each monthly sample. Air-dried soils were ground with a mortar and pestle and then analyzed for total C and N concentrations following combustion using a FLASH EA 1112 Elemental Analyzer (CE Elantech Inc., Lakewood, NJ, USA). Similarly, plot composites were further composited by stand for determination of soil pH (1:2, w/v, 0.01 M CaCl<sub>2</sub>; McLean, 1982) and for laboratory incubations (see below).

Soil cores taken from each plot for microbial biomass and net N transformation methods were used to calculate bulk density (<4-mm oven-dry mass per unit volume;  $n = 7$  per plot). Soil cores taken for *in situ* net N transformation measurements were used to calculate forest floor areal density ( $n = 4$  per plot) by determining oven-dry mass (70 °C for 48 h) of the O horizon matter and discarding materials >5 mm diameter.

### 2.3. *In situ* net nitrogen transformation rates

We measured net N transformation rates *in situ* using the resin-core method (DiStefano and Gholz, 1986) as modified by

Kaye and Hart (1998a). This modification allows the estimation of both forest floor (O horizon) and mineral soil (0–15 cm depth) net N transformation rates within the same incubation system. Mineral soil net ammonification was calculated as the difference in soil NH<sub>4</sub>-N pool size between the incubated and the initial soil core plus NH<sub>4</sub>-N adsorbed on a mixed-bed, ion exchange resin (IER) bag placed below the mineral soil. Similarly, net nitrification was calculated as the difference in soil NO<sub>3</sub>-N pool size between the incubated and the initial soil core plus NO<sub>3</sub>-N adsorbed on the IER bag placed below the mineral soil. Forest floor net N transformation rates were calculated in a similar manner except changes in NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> pool sizes of forest floor material contained within the core were used along with an IER bag placed below the forest floor horizon (immediately above the underlying mineral soil core). Forest floor net N transformation rates include through-fall inputs. A forest floor was frequently absent in the TB and WF stands, but a resin bag was still placed on top of the mineral soil to capture inorganic N from throughfall alone.

Inorganic N pool sizes before and after 6 months of incubation were determined by extracting 30 g mineral soil with 50 mL of 2 M KCl, 5 g forest floor samples with 25 mL of 2 M KCl, and IER bags with 100 mL of 2 M KCl. All extracts were mechanically shaken for 1 h, filtered with Whatman #1 filters (pre-leached with deionized water), and frozen until analyzed for inorganic N. Mineral soil, forest floor, and IER bag extracts were analyzed for NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> on a Lachat AE Flow-Injection Analyzer (Lachat Instruments, Inc., Milwaukee, WI, USA), using the indophenol-blue (Lachat Instruments Inc., 1990) and cadmium reduction-diazotization (Lachat Instruments Inc., 1992) methods, respectively. Mass-based values were converted to an area basis using the bulk density of the mineral soil and the mean areal density of forest floor.

### 2.4. Laboratory incubations

Laboratory incubations, in which soils were exposed to constant moisture and temperature, were used to elucidate the factors controlling rates of net N transformations and soil net CO<sub>2</sub> efflux observed in the field. Laboratory incubations were performed according to the method of Hart et al. (1994a). Three soil replicates were incubated from each stand composite. Ten grams of air-dry soil were added to a 120 mL specimen cup and placed inside of a 0.98 L Mason jar. The soil was brought approximately to field capacity by adding deionized water. Field capacity was estimated as the highest measurement of GWC observed in the field across treatments (~30%). To maintain soil moisture during the incubation, 30 mL of deionized water were added to the Mason jar prior to placement of the specimen cup. The jars were sealed and placed in a dark growth chamber for 28 days at laboratory temperature (20–22 °C). Headspace gas was sampled after 6, 14, and 28 days using a needle and syringe through a butyl rubber septum inserted through the jar top. Following each sampling, Mason jars were opened, purged with ambient air, and re-sealed. Carbon dioxide concentration of the headspace gas was analyzed on a gas chromatograph using a thermal conductivity

detector (Shimadzu GC-8A, Shimadzu Scientific Instruments, Columbia, MD, USA).

Inorganic N pool sizes before and after 28 days of incubation were determined by extracting the subsamples with 50 mL of 2 M KCl, and analyzing the filtered extracts for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  as described previously. Net N transformation rates were determined by the net changes in inorganic N pools over the 28-day incubation period. Specific rates of net C mineralization were calculated by dividing the rates of  $\text{CO}_2\text{-C}$  efflux over the 28-day period by the soil total C concentrations. Similarly, the specific rates of net N mineralization were calculated by dividing the rates of net N mineralized by soil total N concentrations. The ratio of  $\text{CO}_2\text{-C}$  to net N mineralized was also determined to provide an index of potential gross N immobilization during the incubation (Schimel, 1986).

### 2.5. Soil microbial biomass and inorganic nitrogen pool sizes

Soil microbial C and N in the mineral soil (0–15 cm) were determined using the chloroform ( $\text{CHCl}_3$ ) fumigation–extraction method (Brookes et al., 1985; Vance et al., 1987; Haubensak et al., 2002). Approximately 30 g of sieved, field-moist mineral soil were extracted with 100 mL of 0.5 M  $\text{K}_2\text{SO}_4$ . A 30-g subsample of mineral soil was also placed inside a dessicator with a beaker containing 30 mL of  $\text{CHCl}_3$ . The dessicator was repeatedly evacuated to boil the  $\text{CHCl}_3$  and then left under vacuum for 5 days (Haubensak et al., 2002). After 5 days, the  $\text{CHCl}_3$  was removed from the soil by repeated evacuations and then the soil subsamples were immediately extracted with 100 mL of 0.5 M  $\text{K}_2\text{SO}_4$ . Extracts were mechanically shaken for 1 h, filtered with Whatman #1 filters (pre-leached with deionized water), and frozen until analyzed for C and N.

Organic C concentrations in unfumigated and fumigated extracts were determined by ultraviolet-enhanced persulfate oxidation using a Dohrmann DC-80 Carbon Analyzer with infrared detection (Tekmar-Dohrmann, Cincinnati, OH, USA). Microbial C was calculated by subtracting organic C in the unfumigated extracts from organic C in the fumigated extracts and dividing by a  $k_{\text{EC}}$  of 0.39 (Sparling et al., 1990). Total N ( $\text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^- +$  dissolved organic N) in the extracts were determined using an in-line ultraviolet-enhanced persulfate digestion method (Lachat Instruments Inc., 2001) followed by colorimetric analysis (Lachat Instruments Inc., 1992) on a Lachat AE Flow-Injection Analyzer. Microbial N was calculated by subtracting the N in the unfumigated extract from the N in the fumigated extract and then dividing by a  $k_{\text{EN}}$  of 0.45 (Jenkinson, 1988). Mineral soil pool sizes of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were determined by analyzing the  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in the unfumigated  $\text{K}_2\text{SO}_4$  extracts using the same method as for the KCl extracts.

### 2.6. In situ soil net $\text{CO}_2$ efflux

We measured the net  $\text{CO}_2$  efflux from the soil (O horizon and mineral soil) using the soda-lime static chamber technique (Edwards, 1982). This method is correlated with the IRGA static-chamber method across a range of respiration rates found

in ponderosa pine forests and other environments (Kaye and Hart, 1998b; Knoepp and Vose, 2002). We followed the procedure for determination of soil net  $\text{CO}_2$  efflux as described by Kaye and Hart (1998b). The net  $\text{CO}_2$  efflux over a 24-h period was calculated as the net weight gain of the soda lime over the incubation period multiplied by a correction factor of 1.69 (Grogan, 1998). The correction factor accounts for the water released in the reaction of soda lime with  $\text{CO}_2$ .

### 2.7. Statistical design

Gravimetric water content, *in situ* net N transformations, microbial C and N, pool sizes of  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , and *in situ* soil net  $\text{CO}_2$  efflux were statistically analyzed using a repeated measures analysis of variance (RM ANOVA) with sample date as the repeated factor. Treatment effects were assessed with four replicates from each treatment (stand means), except for *in situ* net N transformation rates that had only two replicates. When a treatment by sample date interaction occurred, treatment effects were analyzed separately for each sampling date using one-way ANOVA. Similarly, sampling date effects were analyzed with one-way ANOVA for each treatment separately. All sample date effects were assessed with three replicate sampling dates (June, July, and August), except for *in situ* net N transformation rates that consisted of two replicate periods (summer–fall and winter–spring). When ANOVA tests were significant, Student–Neuman–Keuls post hoc procedures were used to separate means.

All other response variables (soil total C and N, soil bulk density, forest floor density, soil pH, and laboratory soil net C and N transformation rates) were analyzed using one-way ANOVA. Treatment effects were assessed with four stand replicates from each treatment. When ANOVA tests were significant, Student–Neuman–Keuls post hoc procedures were used to separate means.

Correlation analyses were conducted in order to determine the relationships between ecosystem processes and properties. Pearson correlation coefficients were calculated to test the relationships between *in situ* and laboratory rates of net N transformations at the stand level ( $n = 8$ ). Annual litterfall, used as a measure of C availability, was correlated to the mean of the three monthly measurements (June, July, and August) of microbial C and N across all treatments at the stand level ( $n = 16$ ); annual litterfall was also correlated to microbial respiration measured in the laboratory across all treatments at the stand level ( $n = 16$ ). All statistical analyses were performed with JMP 5.0 (SAS Institute Inc., Cary, NC, USA). Due to the high variability inherent in measurements of ecosystem processes and properties across a large and heterogeneous landscape, we used an alpha level of 0.10 to test for statistical significance to decrease the possibility of committing a type II error.

## 3. Results

### 3.1. Soil physical and chemical properties

Soil total C did not differ significantly among treatments (Table 1). The quality of organic C for heterotrophic utilization,

Table 1  
Selected mean (and one standard error) mineral soil and aboveground ecosystem characteristics in southwestern ponderosa pine stands subjected to unmanaged, thinned, thinned plus burned, and wildfire treatments

Ecosystem characteristic	Treatment			
	Unmanaged	Thinned	Thinned plus burned	Wildfire
<b>Mineral soil</b>				
Total C ( $\text{g kg}^{-1}$ ) <sup>a</sup>	25.0 (0.40) a	26.8 (1.0) a	25.4 (2.6) a	24.6 (2.2) a
Total N ( $\text{g kg}^{-1}$ ) <sup>a</sup>	1.4 (0.03) ab	1.6 (0.03) a	1.5 (0.06) ab	1.2 (0.15) b
C:N <sup>a</sup>	18.1 (0.8) b	17.2 (0.5) b	16.8 (1.2) b	21.7 (1.4) a
GWC June ( $\text{kg kg}^{-1}$ )	0.12 (0.01) a	0.11 (0.00) a	0.10 (0.00) a	0.09 (0.01) a
GWC July ( $\text{kg kg}^{-1}$ )	0.12 (0.02) a	0.09 (0.01) a	0.12 (0.00) a	0.11 (0.01) a
GWC August ( $\text{kg kg}^{-1}$ )	0.26 (0.01) a	0.29 (0.01) a	0.22 (0.02) a	0.21 (0.01) a
pH <sub>0.01 M CaCl<sub>2</sub></sub> <sup>a</sup>	5.27 (0.03) b	5.29 (0.06) b	5.49 (0.09) ab	5.79 (0.15) a
Bulk density ( $\text{mg/m}^3$ ) <sup>a,b</sup>	0.80 (0.04) a	0.87 (0.02) a	0.93(0.03) a	0.86 (0.05) a
<b>Aboveground</b>				
Forest floor ( $\text{kg m}^{-2}$ ) <sup>c,d</sup>	6.13 (0.14) a	3.58 (0.72) b	2.89 (0.17) b	0.00 (0.00) c
Litterfall ( $\text{g m}^{-2} \text{ year}^{-1}$ ) <sup>c,d,e</sup>	311 (41) a	213 (25) b	148 (27) b	0.00 (0.00) c
Herbaceous cover (%) <sup>e</sup>	20.4 (2.8) b	33.2 (4.7) b	35.8 (4.0) b	64.9 (1.9) a

Mineral soil characteristics are for the upper 15 cm of soil. Gravimetric water content is denoted as GWC. Different letters in the same row denote significant differences ( $p < 0.10$ ) in characteristics among treatments.

<sup>a</sup> Mineral soils used were composites from all three sampling dates (June, July and August).

<sup>b</sup> <4 mm oven-dry mass unit volume.

<sup>c</sup> Materials <5 mm diameter only.

<sup>d</sup> No forest floor or litterfall was present at wildfire stands.

<sup>e</sup> Data borrowed with permission from Sabo (2006).

as measured by specific rates of net C mineralization, differed significantly by treatment (Fig. 3A). The WF stands had the lowest specific rates of net C mineralization, while the other treatments had higher rates and were statistically similar. Despite differences among treatments in soil total N (Table 1), specific rates of net N mineralization were similar (Fig. 3B). The C:N ratio of the mineral soil was significantly higher in the WF stands, while the other three treatments had similar C:N ratios (Table 1).

Repeated measures ANOVA indicated that GWC differed significantly by sampling date ( $p < 0.001$ ) but not by treatment ( $p < 0.148$ ); an interaction did not occur ( $p = 0.166$ ). One-way ANOVA of sampling date showed that GWC was significantly higher ( $p < 0.001$ ) in August than in either June or July (Table 1). Mineral soil pH was higher in WF stands than either UN or TH stands, while the TB stands were statistically similar

to all other stand conditions (Table 1). The bulk density of the soil did not differ significantly by treatment (Table 1). Forest floor areal density was highest in the UN stands, while the TH and TB stands had less forest floor (Table 1). The high fire severity of the Hochderffer wildfire resulted in complete consumption of the forest floor; no forest floor was present 7 years after the fire during our 2003 measurements.

### 3.2. *In situ* and laboratory net nitrogen transformation rates

Forest floor, mineral soil, and forest floor plus mineral soil *in situ* rates of net ammonification, nitrification, and N mineralization varied significantly by treatment (Fig. 4), with forest floor rates of net ammonification and N mineralization highest in the WF stands (forest floor rates include N derived

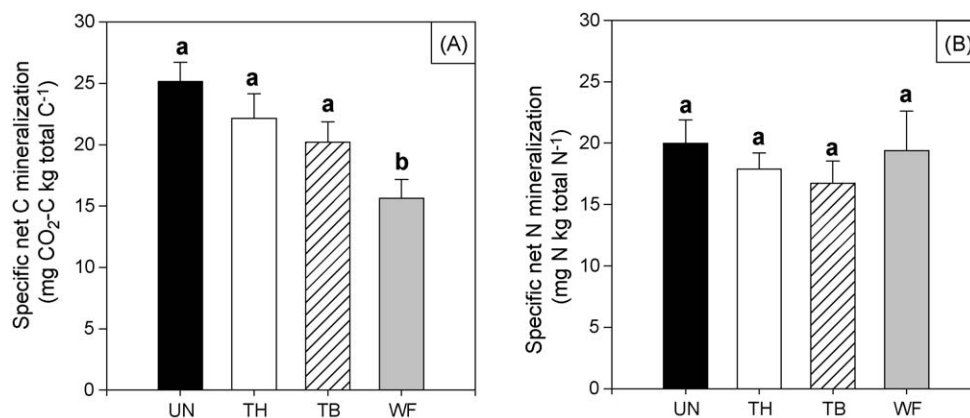


Fig. 3. Specific net C mineralization rates (A) and specific net N mineralization rates (B) during a 28-day laboratory incubation of mineral soils (0–15 cm) from southwestern ponderosa pine stands subjected to unmanaged (UN), thinned (TH), thinned plus burned (TB), and wildfire (WF) treatments. Vertical lines denote one standard error of the mean. For each rate, bars with different lowercase letters are statistically different ( $p < 0.10$ ).

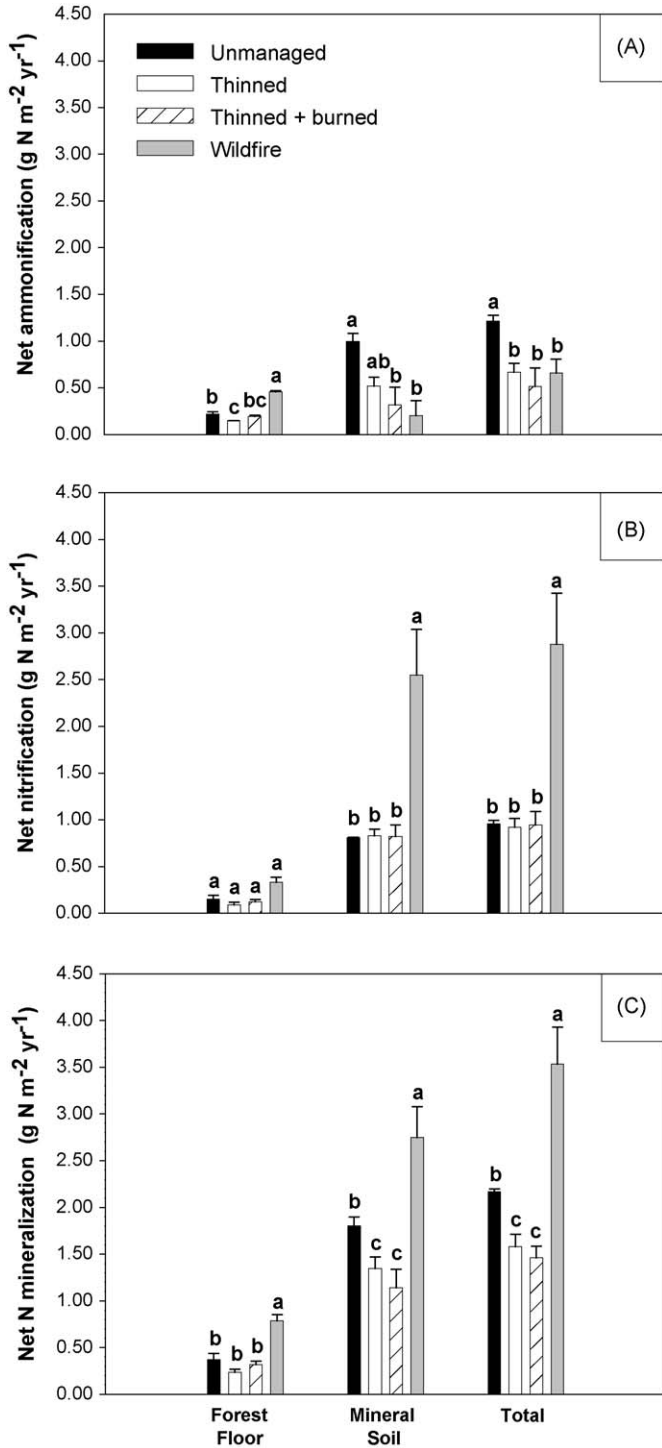


Fig. 4. Annual rates of net ammonification (A), net nitrification (B), and net N mineralization (C) measured *in situ* (0–15 cm mineral soil) in southwestern ponderosa pine forests subjected to unmanaged, thinned, thinned plus burned, and wildfire treatments. Forest floor rates include throughfall. No forest floor was present at the wildfire stands. Vertical lines denote one standard error of the mean. For each component (forest floor, mineral soil, and total) and net N transformation, bars with different lowercase letters are statistically different ( $p < 0.10$ ).

from throughfall). Forest floor rates of net nitrification were similar. Mineral soil rates of net ammonification were highest in the UN stands and lowest in the TB and WF stands, with the TH stands being intermediate. Rates of net nitrification in the

mineral soil were about 2.5 times higher in the WF stands than the other treatments. Mineral soil and total (forest floor plus mineral soil) rates of net N mineralization were highest in WF stands, lowest in TH and TB stands, and intermediate in UN stands. Patterns of statistical significance were consistent between the two incubation periods for all rates of N transformations in the forest floor, mineral soil, and forest floor plus mineral soil (treatment by incubation period interaction was not significant; data not shown). Summer–fall rates of total (forest floor plus mineral soil) net ammonification were not significantly different from winter–spring rates ( $p = 0.329$ ), while net nitrification ( $p < 0.015$ ) and net N mineralization ( $p < 0.008$ ) were significantly higher over the summer–fall period.

Patterns of laboratory rates of net N transformations among treatments were not consistent with *in situ* rates. During a 28-day laboratory incubation, rates of net ammonification differed by treatment (Table 2), with the highest rates in the TH stands, lowest rates in the TB and WF stands, and intermediate rates in UN stands. Rates of net nitrification also differed by treatment with the WF and TB stands having the highest rates, TH the lowest, while the UN was intermediate. However, net N mineralization did not differ by treatment. Potential gross N immobilization index was similar among treatments ( $p = 0.130$ ; Table 2).

Stand-level correlations ( $n = 8$ ) revealed that annual rates of *in situ* net ammonification and nitrification in the mineral soil were correlated to laboratory rates ( $r = 0.82$ ,  $p < 0.002$  and  $r = 0.49$ ,  $p < 0.050$ , respectively). However, there was no significant correlation between *in situ* and laboratory rates of net N mineralization ( $r = 0.09$ ,  $p = 0.476$ ). When wildfire treatments were excluded from the correlation analysis ( $n = 6$ ), a significant relationship between *in situ* and laboratory rates of net N mineralization was found ( $r = 0.75$ ,  $p < 0.030$ ).

### 3.3. Soil microbial biomass and inorganic nitrogen pool sizes

Repeated measures ANOVA showed that microbial C and N differed significantly by treatment ( $p < 0.001$  for both C and N), sampling date ( $p < 0.001$  for both C and N), and a significant interaction between treatment and sampling date also occurred ( $p < 0.010$  for C,  $p < 0.030$  for N). Although interactions occurred, the rankings of the means were consistent for both microbial C and N (UN > TH > TB > WF) for each sampling date, suggesting that the interaction was driven by the magnitude of the response to treatment across sampling dates (Fig. 5). Microbial C and N were found to be well correlated to annual litterfall across all treatments ( $r = 0.87$ ,  $p < 0.001$ ,  $n = 16$  for C,  $r = 0.83$ ,  $p < 0.001$ ,  $n = 16$  for N).

Pool sizes of  $\text{NH}_4^+$  differed significantly by sampling date but not among treatments (Fig. 6A), and pool sizes of  $\text{NO}_3^-$  varied significantly by treatment but not by sampling date (Fig. 6B). The WF stands had consistently higher pool sizes of  $\text{NO}_3^-$  across sampling dates. Increasing microbial biomass and  $\text{NH}_4^+$  pool sizes from June and July to August followed precipitation patterns (Fig. 2).

Table 2  
Selected mean (and one standard error) laboratory rates of net N transformations ( $\text{mg N kg}^{-1} 28 \text{ day}^{-1}$ ) and potential gross immobilization ( $\text{kg CO}_2\text{-C kg N}^{-1} 28 \text{ day}^{-1}$ ) in soils from southwestern ponderosa pine stands subjected to unmanaged, thinned, thinned plus burned, and wildfire treatments

N transformation rate	Treatment			
	Unmanaged	Thinned	Thinned plus burned	Wildfire
Net ammonification	6.3 (5.3) ab	13.9 (4.1) a	-3.2 (1.4) b	-5.0 (0.8) b
Net nitrification	20.1 (4.4) ab	13.6 (2.4) b	28.3 (1.7) a	26.1 (2.1) a
Net mineralization	26.4 (2.7) a	27.5 (2.5) a	25.1 (1.9) a	21.1 (2.4) a
Gross N immobilization index	24.5 (2.9) a	21.7 (1.3) a	20.2 (0.9) a	18.2 (1.3) a

Different letters in the same row denote significant differences ( $p < 0.10$ ) in characteristics among treatments.

3.4. *In situ* soil net  $\text{CO}_2$  efflux and laboratory microbial respiration

For rates of *in situ* soil net  $\text{CO}_2$  efflux, treatment and sampling date were both statistically significant (RM ANOVA:  $p < 0.020$  and  $0.001$ , respectively), while an interaction between treatment and sampling date also occurred ( $p < 0.001$ ). In June, rates of soil net  $\text{CO}_2$  efflux were highest in the

UN and WF stands, lowest in TH stands, while rates in TB stands were intermediate (Fig. 7A). There were no treatment differences in July and rates were similar to June except in TH and TB stands where rates increased. In August, rates of soil net  $\text{CO}_2$  efflux increased in all treatments, following patterns of precipitation and increased water availability (Fig. 2 and Table 1). The UN stands had higher rates of soil net  $\text{CO}_2$  efflux in August than the other treatments.

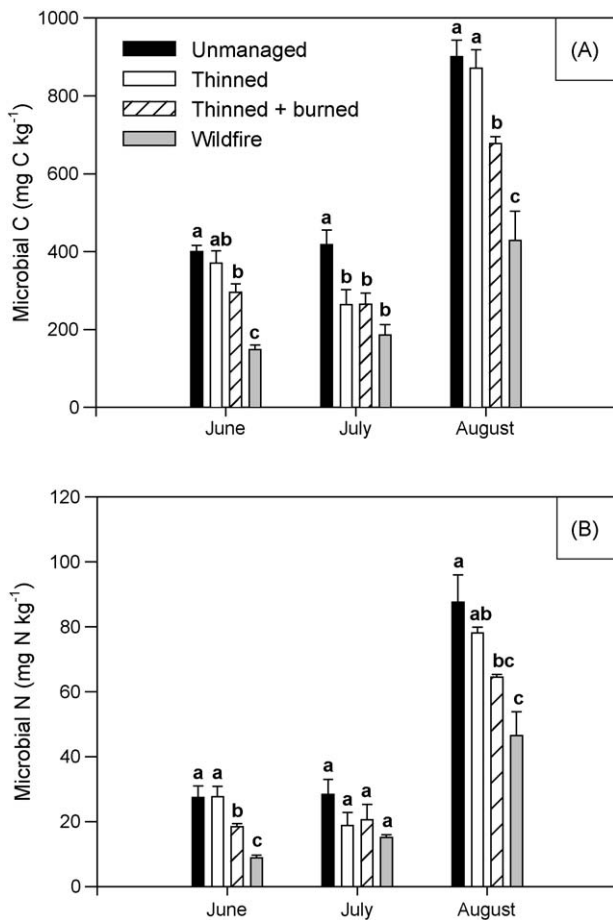


Fig. 5. Microbial carbon (A) and nitrogen (B) in mineral soil (0–15 cm) of southwestern ponderosa pine forests during the growing season subjected to unmanaged, thinned, thinned plus burned, and wildfire treatments. Vertical lines denote one standard error of the mean. For each monthly measurement and microbial characteristic, bars with different lowercase letters are statistically different ( $p < 0.10$ ).

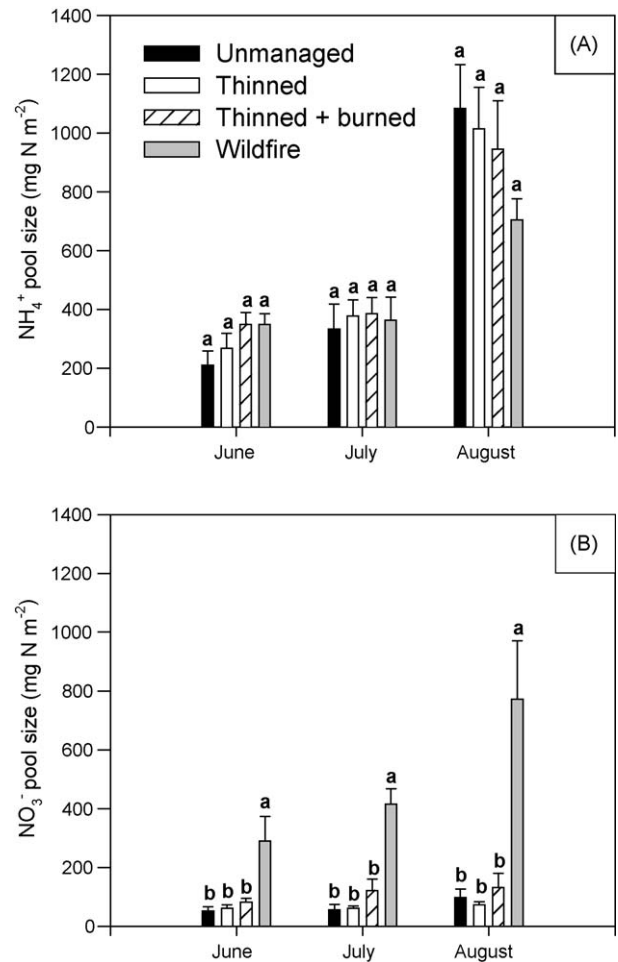


Fig. 6. Ammonium ( $\text{NH}_4^+$ ; A), and nitrate ( $\text{NO}_3^-$ ; B) pool sizes measured over the growing season in mineral soil (0–15 cm) of ponderosa pine forests subjected to unmanaged, thinned, thinned plus burned, and wildfire treatments. Vertical lines denote one standard error of the mean. For each sample date and inorganic N pool, bars with different lowercase letters are statistically different ( $p < 0.10$ ).



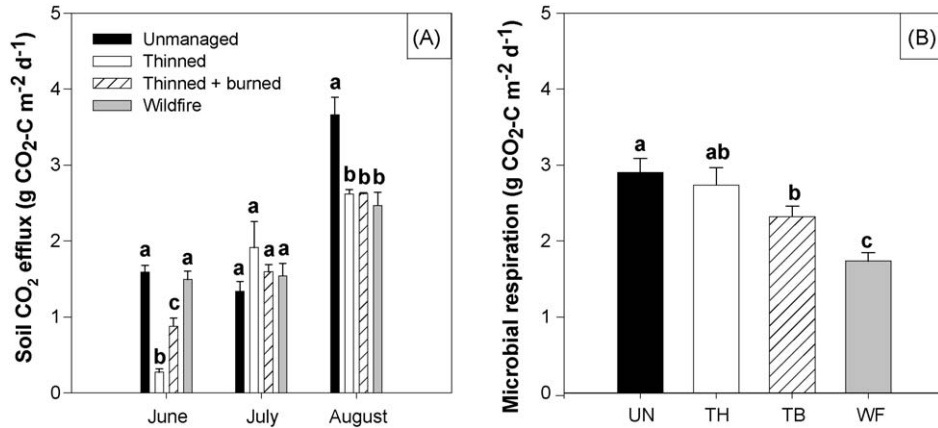


Fig. 7. *In situ* soil net CO<sub>2</sub> efflux (A) measured over the growing season of 2003 and microbial respiration (B) from mineral soil (0–15 cm) measured in the laboratory over a 28-day incubation period from southwestern ponderosa pine forests subjected to unmanaged, thinned, thinned plus burned, and wildfire treatments. Vertical lines denote one standard error of the mean. For each process and within sampling date (for A), bars with different lowercase letters are statistically different ( $p < 0.10$ ).

Treatment significantly affected microbial respiration (net CO<sub>2</sub> efflux from sieved soil) over a 28-day incubation period under standard conditions of temperature and moisture (Fig. 7B). Microbial respiration during laboratory incubations was correlated to annual litterfall across all stand treatments ( $r = 0.70$ ,  $p < 0.001$ ,  $n = 16$ ). However, *in situ* soil net CO<sub>2</sub> efflux was not significantly correlated to annual litterfall ( $p = 0.789$ ,  $n = 16$ ).

#### 4. Discussion

Our research has several advantages over past studies on the effects of forest management on ecosystem pools and processes in southwestern ponderosa pine forests of the US. The retrospective design allows assessment of longer-term treatment effects today, as a true experimental design in which we initiated the treatments would require waiting several years to decades before longer-term results were obtained (Powers, 1989). By designing our study using large stand areas on a landscape scale of approximately 750 km<sup>2</sup>, the forests stands used in our study have minimal edge effects and are representative of many southwestern ponderosa pine forests that have had large trees selectively removed in the past. This design allows us to extrapolate our results to other ponderosa pine forests across the southwestern US to a degree not possible with the few, relatively recent experimental studies that have been conducted to date in this region. Additionally, the inclusion of a wildfire treatment allows evaluation of the potential impacts on ecosystem function if silvicultural management that reduces the fire hazard of these forests is not implemented.

##### 4.1. Ecosystem responses to forest management and wildfire

Net primary production (NPP) controls the amount of C inputs to the soil, while these C inputs, in turn, drive soil microbial metabolism (Zak et al., 1990; Shen et al., 1997; Ekblad and Nordgren, 2002; Wardle, 2002). A positive

correlation has been found between aboveground NPP and microbial C across a diverse and wide range of ecosystems in the US (Zak et al., 1994). As predicted, we found a gradient of decreasing C availability from unmanaged to thinned to thinned plus burned to wildfire stands; evidenced from patterns of annual litterfall and forest floor biomass (Table 1). This gradient of decreasing C availability conformed to patterns of microbial C and N (Fig. 5) and laboratory rates of microbial respiration (Fig. 7B), all of which were well correlated to annual litterfall. Laboratory measures of specific C mineralization (Fig. 3A) also closely followed the gradient of decreasing C availability; however, *in situ* rates of net soil CO<sub>2</sub> efflux generally followed this pattern when soils were wet and warm (Fig. 7A, August), but not when soils were dry and warm (Fig. 7A, June). Taken together, these results suggest that microbial activity is closely coupled to aboveground C inputs in southwestern ponderosa pine forests. Hence, reductions in C inputs via silvicultural treatments or wildfire will likely reduce the size and activity of the soil microflora.

We hypothesized that higher rates of microbial activity should lead to higher rates of net N transformations (Hart et al., 1994b). Consistent with this hypothesis, we found higher *in situ* rates of net N mineralization in unmanaged stands compared to thinned and thinned plus burned stands (Fig. 4). However, the wildfire stands had the highest net N mineralization rates despite having the lowest C inputs (Fig. 4). Wildfire stands also had the highest pool sizes of NO<sub>3</sub><sup>-</sup> (Fig. 6). Furthermore, wildfire stands had a greater relative amount of net mineralized N being nitrified than the other stands. These results suggest greater N availability to plants in the wildfire stands (Hart et al., 1994a,b).

Several factors may account for the higher rates of net N mineralization and nitrification in the wildfire stands compared to the other stands, including: differences in substrate quality, reduced gross N immobilization, and changes in soil microclimate. The quality of substrate available for microbial metabolism influences rates of net N mineralization (Powers, 1990; Nadelhoffer et al., 1991; Scott and Binkley, 1997;

Schweitzer et al., 2004). Substrate quality may have increased in wildfire stands compared to other stands due to either increased herbaceous inputs relative to pine inputs (Table 1), or due to charcoal inputs in wildfire stands (DeLuca et al., 2002; Hart et al., 2005). Charcoal has been found to sorb soil phenolic compounds that bind proteins (DeLuca et al., 2002). Thus, removal of phenols from the soil solution may lead to increased rates of N mineralization by soil microorganisms and subsequent nitrification by autotrophic bacteria (Wardle et al., 1998; DeLuca et al., 2002). However, if substrate quality improved in wildfire stands, we would have also expected to find higher rates of net N mineralization and nitrification in soils from wildfire stands during laboratory incubations under standard and constant temperature and moisture conditions. Instead, laboratory incubations showed similar rates of net N mineralization and nitrification in wildfire stands compared to the other stands (Table 2). In addition, soil C:N, specific C mineralization, and specific N mineralization have been widely cited as indicators of substrate quality for microorganisms (Schimel, 1986; Powers, 1990; Zak et al., 1994). We found higher soil C:N ratios (Table 1) and lower specific C mineralization (Fig. 3) in wildfire stands than the other stands, suggesting poorer substrate quality in soils from wildfire stands. In contrast, specific N mineralization rates were similar among stands (Fig. 3). Taken together, these results suggest that higher substrate quality was likely not responsible for the higher *in situ* rates of net N mineralization and nitrification in wildfire stands.

Reduced C inputs and lower microbial biomass in wildfire stands could result in increased rates of net N mineralization and nitrification by reducing gross N immobilization (Schimel, 1986; Burke et al., 1989; Hart et al., 1994b). However, rates of potential gross immobilization, as measured in laboratory incubations under constant and standard conditions of temperature and moisture, were statistically similar among treatments (Table 2). Hence, a reduction in gross N immobilization in soils from wildfire stands is likely not the reason for higher rates of net N mineralization or nitrification observed in the field.

The soil microclimate affects microbial activity and rates of N transformations, with increases in soil temperature and moisture generally leading to increased rates of net N transformations (Paul and Clark, 1996). Fluctuations in moisture (drying–rewetting events) may also increase rates of net N transformations (Fierer and Schimel, 2002). Previous studies have found that soil temperatures generally increase following wildfire because of increases in absorption of solar radiation by the soil (O'Neill et al., 2002; Treseder et al., 2004; Hart et al., 2005; Wolfson et al., 2005). Reductions in transpiration and canopy interception due to overstory removal by fire would be expected to lead to increased soil moisture. However, increased surface evaporation due to higher soil temperatures, reduced water infiltration because of the formation of water repellent soils, and loss of the porous O horizons may result in lower soil moisture following wildfire (Hart et al., 2005). These counteracting hydrological processes make predictions of wildfire impacts on soil moisture more

uncertain. During our study, we did not detect higher soil GWC in wildfire stands compared to other stands and did not measure soil temperature. However, measurements of soil temperature taken every 2 weeks from May to October in 2004 (Grady and Hart, 2006) showed that soil temperature was often higher in wildfire stands compared to other stands. In addition, in 2004, we found dramatic fluctuations in soil moisture in the wildfire stands over the growing season, with wildfire stands having either the highest or lowest soil moisture compared to the other stands. Hence, we speculate that the higher *in situ* rates of net N transformations in the wildfire stands were most likely the result of soil microclimatic differences in wildfire stands compared to the other stands.

#### 4.2. Comparison with southwestern ponderosa pine forest restoration

Much of the previous research evaluating the effects of thinning and thinning plus burning on ecosystem processes in southwestern ponderosa pine forests has been conducted at the Gus Pearson Natural Area (GPNA), near Flagstaff, AZ (Kaye and Hart, 1998a,b; Boyle et al., 2005; Kaye et al., 2005). Two treatments were applied at GPNA: a thinning restoration treatment where most of the trees that had established prior to Euro-American settlement (circa 1876) were thinned and the aboveground biomass of these trees removed from the site; a composite restoration treatment where a similar thinning treatment was followed by a forest floor manipulation and a prescribed burn (which is being repeated on a 4-year cycle). The forest floor manipulation in the composite restoration treatment includes raking aside the Oi layer, removing the Oa and Oe layers from the site, and then returning the Oi layer along with the addition of ~670 kg/ha of native grass and forb clippings from a nearby area. This forest floor manipulation was designed to emulate the fuel loadings that were likely present prior to fire exclusion (Covington et al., 1997). These treatments resulted in a decrease in tree density from over 4100 to ~150 trees/ha, but a decline in tree basal area only from 36 to ~17 m<sup>2</sup>/ha. Herbaceous production increased dramatically following these treatments; aboveground herbaceous production was from 3 to 12 times higher in treated plots compared to control plots from 2 to 11 years following treatment (Kaye et al., 2005; Moore et al., 2006).

Researchers at GPNA have found that thinning and composite restoration treatments have led to increased gross and net N transformations (Kaye and Hart, 1998a), and increased short (1–2 years) and longer-term (8 years) net soil CO<sub>2</sub> efflux (Kaye and Hart, 1998b; Boyle et al., 2005, respectively), but no change in the size of the microbial biomass (Boyle et al., 2005). Apparently, these increases in microbially mediated processes are due to increases in substrate quality and soil temperature following restoration treatments (Hart et al., 2005; Kaye et al., 2005). Increased substrate quality in restored plots has occurred due to dramatic increases in high quality herbaceous litter inputs with a concomitant reduction in low quality pine litter (Hart et al., 2005).

In contrast to the results at GPNA, we found that net N transformation rates and net soil CO<sub>2</sub> efflux were reduced following thinning and thinning plus burning, and microbial C and N pools tended to be smaller following these treatments. Reasons for these contrasting results could be due to different starting points prior to treatment. For instance, at GPNA, control stands had exceptionally high tree densities and only a 7% herbaceous cover (Kaye et al., 2005), while unmanaged stands in our study averaged 815 trees/ha and about 20% herbaceous cover (Sabo, 2006). Furthermore, thinning alone and thinning plus burning both did not result in statistically significant increases in herbaceous cover (Table 1). Hence, these treatments likely had only a modest effect on the quality of litter inputs to the soil, but significantly reduced the quantity of C inputs (Table 1). Apparently, presumed increases in soil temperature following thinning and thinning plus burning treatments in our study were not great enough to offset the effects of reductions in C inputs, resulting in lower soil process rates in these managed stands compared to unmanaged stands. Under field conditions, Hart et al. (2006) found similar annual rates of net N mineralization and microbial N following a restoration treatment in a ponderosa pine forest near GPNA. They also speculated that the lack of response in net N mineralization was due to relatively small changes in understory production following the restoration treatment. Taken together, these studies suggest that both the magnitude and direction of the impact of restoration treatments on soil processes are dependent on the initial stand conditions prior to these treatments.

## 5. Conclusions

Contemporary southwestern ponderosa pine forests have abnormally high fuel loads and are at high risk for catastrophic wildfire. Active forest management, either by thinning or thinning plus burning, has been advocated to restore the structure of forests to within their historic range of variability (Covington et al., 1994) and to reduce fire hazard. Our results suggest that restoration treatments with modest reductions in stand density will decrease belowground biological activity and soil N availability to plants in many of these forests where the understory vegetation is still relatively abundant. Furthermore, our results suggest that catastrophic wildfires in these forests lead to long-term sustained increases in N availability, and these increases in N supply may assist in vegetative recovery. However, because this increase in available N coincides with relatively low plant biomass (essentially devoid of trees) and soil microbial biomass, there is increased potential for continued N loss from the ecosystem via leaching and gaseous N emissions; large losses of ecosystem N could ultimately result in decreased site productivity if not offset by N fixation and deposition. We recommend that restoration and fire-hazard reduction efforts be focused on areas with currently low herbaceous production. Restoration treatments applied to these stand conditions will likely lead to increased C substrate quality, microbial biomass, net soil CO<sub>2</sub> efflux, rates of net N mineralization, and recovery of bunchgrass communities.

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## References

- Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol. Appl.* 12, 1418–1433.
- Bailey, J.D., Wagner, M.R., Smith, J.J., 2001. Stand treatment impacts on forest health (STIFH): structural responses associated with silvicultural treatments. In: Van Riper III, C., Thomas, K.A., Stuart, M.A. (Eds.), *Proceedings of the Fifth Biennial Conference of Research on the Colorado Plateau*. U.S. Geological Survey/FRESC Report Series USGSFRES/COPL/2001/24.
- Boyle, S.I., Hart, S.C., Kaye, J.P., Waldrop, M.P., 2005. Restoration and canopy type influence soil microflora in a ponderosa pine forest. *Soil Sci. Soc. Am. J.* 69, 1627–1638.
- Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biol. Biochem.* 17, 837–842.
- Burke, I.C., Reiners, W.A., Schimel, D.S., 1989. Organic matter turnover in a sagebrush steppe landscape. *Biogeochem.* 7, 11–31.
- Choromanska, U., DeLuca, T.H., 2002. Microbial activity and nitrogen mineralization in forest mineral soils following heating: evaluation of post-fire effects. *Soil Biol. Biochem.* 34, 263–271.
- Cooper, C.F., 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecol. Monogr.* 30, 129–164.
- Covington, W.W., Moore, M.M., 1994a. Southwestern ponderosa pine forest structure and resource conditions: changes since Euro-American settlement. *J. For.* 92, 39–47.
- Covington, W.W., Moore, M.M., 1994b. Post-settlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. *J. Sust. For.* 2, 153–181.
- Covington, W.W., Sackett, S.S., 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *For. Sci.* 30, 183–192.
- Covington, W.W., Sackett, S.S., 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *For. Ecol. Manage.* 54, 175–191.
- Covington, W.W., Everett, R.L., Steele, R.W., Irwin, L.I., Daer, T.A., Auclair, A.N.D., 1994. Historical and anticipated changes in forest ecosystems of the Inland West of the United States. *J. Sust. For.* 2, 13–63.
- Covington, W.W., Fule, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. *J. For.* 95, 23–29.
- Covington, W.W., Fulé, P.Z., Hart, S.C., Weaver, R.P., 2001. Modeling ecological restoration effects on ponderosa pine forest structure. *Rest. Ecol.* 9, 421–431.
- DeLuca, T.H., Nilsson, M.C., Zackrisson, O., 2002. Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. *Oecologia* 133, 206–214.
- DeLuca, T.H., Zouhar, K.L., 2000. Effects of selection harvest and prescribed fire on the soil nitrogen status of ponderosa pine forests. *For. Ecol. Manage.* 138, 263–271.

- DiStefano, J., Gholz, H.L., 1986. A proposed use of ion exchange resin to measure nitrogen mineralization and nitrification in intact soil cores. *Commun. Soil Sci. Plant Anal.* 17, 989–998.
- Edwards, N.T., 1982. The use of soda-lime for measuring respiration rates in terrestrial ecosystems. *Pedobiologia* 28, 321–330.
- Ekblad, A., Nordgren, A., 2002. Is growth of soil microorganisms in boreal forests limited by carbon or nitrogen availability. *Plant Soil* 242, 115–122.
- Fierer, N., Schimel, J., 2002. Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. *Soil Biol. Biochem.* 34, 777–787.
- Fort Valley Arizona Meteorological Data, 2005. Data set. Available online [[http://www.rmrs.nau.edu/weather/stations/ftv\\_coop/](http://www.rmrs.nau.edu/weather/stations/ftv_coop/)]. USDA For. Serv. Rocky Mountain For. Range Exp. Stn.
- Fulé, P.F.W.W., Covington, Moore, M.M., 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecol. Appl.* 7, 895–908.
- Grady, K.C., Hart, S.C., 2006. Carbon sequestration potential in southwestern ponderosa pine forests: Impacts of management and wildfire. *Global Change Biol.*, submitted for publication
- Grogan, P., 1998. CO<sub>2</sub> flux measurement using soda lime: correction for water formed during CO<sub>2</sub> adsorption. *Ecology* 79, 1467–1468.
- Hart, S.C., Stark, J.M., Davidson, E.A., Firestone, M.K., 1994a. Nitrogen mineralization, immobilization and nitrification. *Methods of Soil Analysis. Part 2. Microbiological and Biochemical Properties.* SSSA Book Series, no. 5. American Society of Agronomy, Madison, WI, USA, pp. 985–1018.
- Hart, S.C., Nason, G.E., Myrold, D.D., Perry, D.A., 1994b. Dynamics of gross nitrogen transformations in an old-growth forest: the carbon connection. *Ecology* 75, 880–891.
- Hart, S.C., DeLuca, T.H., Newman, G.S., MacKenzie, D.M., Boyle, S.I., 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *For. Ecol. Manage.* 220, 166–184.
- Hart, S.C., Selmants, P.C., Boyle, S.I., Overby, S.T., 2006. Carbon and nitrogen cycling in southwestern ponderosa pine forests. *For. Sci.*, submitted for publication
- Haubensak, K.A., Hart, S.C., Stark, J.M., 2002. Influences of chloroform exposure time and soil water content on C and N release in forest soils. *Soil Biol. Biochem.* 34, 1549–1562.
- Jenkinson, D.S., 1988. Determination of microbial biomass carbon and nitrogen in soils. In: Wilson, J.R. (Ed.), *Advances in Nitrogen Cycling in Agricultural Ecosystems.* CAB, Wallingford, pp. 368–386.
- Kaye, J.P., Hart, S.C., 1998a. Ecological restoration alters nitrogen transformations in a ponderosa pine-bunchgrass ecosystem. *Ecol. Appl.* 8, 1052–1060.
- Kaye, J.P., Hart, S.C., 1998b. Restoration and canopy type effects on soil respiration in a ponderosa pine-bunchgrass ecosystem. *Soil Sci. Soc. Am. J.* 62, 1062–1072.
- Kaye, J.P., Hart, S.C., Cobb, R.C., Stone, J.E., 1999. Water and nutrient outflow following the ecological restoration of a ponderosa pine-bunchgrass ecosystem. *Restor. Ecol.* 7, 252–261.
- Kaye, J.P., Hart, S.C., Fulé, P.C., Covington, W.W., Moore, M.M., Kaye, M.W., 2005. Initial carbon, nitrogen, and phosphorus fluxes following ponderosa pine restoration treatments. *Ecol. Appl.* 15, 1581–1593.
- Knoepp, J.D., Vose, J.M., 2002. Quantitative comparison of *in situ* soil CO<sub>2</sub> flux measurement methods. Research Paper SRS-28. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, 11 pp.
- Lachat Instruments, Inc. 1990. QuikChem Method No. 12-107-06-1-B. Milwaukee, WI, USA.
- Lachat Instruments, Inc. 1992. QuikChem Method No. 12-107-04-1-B. Milwaukee, WI, USA.
- Lachat Instruments, Inc. 2001. QuikChem Method No. 10-107-04-3-B. Milwaukee, WI, USA.
- Litton, C.M., Ryan, M.G., Knight, D.H., Stahl, P.D., 2003. Soil-surface carbon dioxide efflux and microbial biomass in relation to tree density 13 years after a stand replacing fire in a lodgepole pine ecosystem. *Global Change Biol.* 9, 680–696.
- McLean, E.O., 1982. Soil pH and lime requirement. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), *Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties.* 2nd ed. American Society of Agronomy, Inc., Soil Science Society of America, Inc., Madison, WI, USA, pp. 199–223.
- Miller, G., Ambos, N., Boness, P., Reyer, D., Robertson, G., Scalzone, K., Steinke, R., Subirge, T., 1995. *Terrestrial Ecosystem Survey of the Cocino National Forest.* USDA Forest Service, Southwestern Region, 405 pp.
- Monleon, V.J., Choromack, K., Landsberg, J.D., 1997. Short and long term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Can. J. For. Res.* 27, 369–378.
- Moore, M.M., Casey, C.A., Bakker, J.D., Springer, J.D., Fule, P.Z., Covington, W.W., Laughlin, D.C., 2006. Herbaceous vegetation responses (1992–2004) to restoration treatments in a ponderosa pine forest. *Range Ecol. Manage.* 2, 135–144.
- Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R., Laundre, J.A., 1991. Effects of temperature and substrate quality on element mineralization in six arctic soils. *Ecology* 72, 242–253.
- O'Neill, K.P., Kasischke, E.S., Richter, D.D., 2002. Environmental controls on soil CO<sub>2</sub> flux following fire in black spruce, white spruce, and aspen stands of interior Alaska. *Can. J. For. Res.* 32, 1525–1541.
- Paul, E.A., Clark, F.E., 1996. *Soil Microbiology and Biochemistry.* 2nd ed. Academic Press, Inc., San Diego, CA, USA.
- Powers, R.F., 1989. Retrospective studies in perspective: strengths and weaknesses. In: Dyck, W.J., Mees, C.A. (Eds.), *Research Strategies for Long-term Site Productivity.* Proceedings of the IEA/BE A3 Workshop, Seattle, WA, August 1988. IEA/BE A3 Report No. 8. Forest Research Institute, New Zealand, *Bulletin* 152, pp. 47–62.
- Powers, R.F., 1990. Nitrogen mineralization along an altitudinal gradient: interactions of soil temperature, moisture, and substrate quality. *For. Ecol. Manage.* 30, 19–29.
- Prieto-Fernandez, A., Villar, M.C., Carballas, M., Carballas, T., 1993. Short-term effects of a wildfire on the nitrogen status and its mineralization kinetics in an Atlantic forest soil. *Soil Biol. Biochem.* 25, 1657–1664.
- Prieto-Fernandez, A., Acea, M.J., Carballas, T., 1998. Soil microbial and extractable C and N after wildfire. *Biol. Fertil. Soils* 27, 132–142.
- Sala, A., Peters, G.D., McIntyre, L.R., Harrington, M.G., 2005. Physiological responses of ponderosa pine in western Montana to thinning, prescribed fire and burning season. *Tree Phys.* 25, 339–348.
- Sabo, K.E., 2006. Overstory and understory production in varying stand structural types in northern Arizona ponderosa pine forests. MS Thesis. Northern Arizona University, Flagstaff, AZ, USA.
- Schimel, D.S., 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. *Biogeochemistry* 2, 345–357.
- Schweitzer, J.A., Bailey, J.K., Rehill, B.J., Martinsen, G.D., Hart, S.C., Lindroth, R.L., Keim, P., Whitham, T.G., 2004. Genetically based trait in a dominant tree affects ecosystem processes. *Ecol. Lett.* 7, 127–134.
- Scott, N.A., Binkley, D., 1997. Foliage litter quality and annual net N mineralization: comparisons across North American forest sites. *Oecologia* 111, 151–159.
- Shen, R.F., Brookes, P.C., Powlson, D.S., 1997. Effect of long-term straw incorporation on soil microbial biomass and C and N dynamics. *Pedosphere* 7, 297–302.
- Sparling, G.P., Feltham, C.W., Reynolds, J., West, A.W., Singleton, P., 1990. Estimation of soil microbial C by a fumigation-extraction method: use on soils of high organic matter content, and a reassessment of the  $k_{EC}$  factor. *Soil Biol. Biochem.* 22, 301–307.
- Swetnam, T.W., Betancourt, J.L., 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J. Climate* 11, 3128–3147.
- Treseder, K.K., Mack, M.C., Cross, A., 2004. Relationships among fire, fungi, and soil dynamics in Alaskan boreal forests. *Ecol. Appl.* 14, 1826–1838.
- Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass. *Soil Biol. Biochem.* 19, 703–707.
- Wardle, D.A., Zackrisson, O., Nilsson, M.-C., 1998. The charcoal effect in boreal forests: mechanisms and ecological consequences. *Oecologia* 115, 419–426.
- Wardle, D.A., 2002. *Communities and Ecosystems: Linking the Aboveground and Belowground Components.* Princeton University Press, Princeton, NJ, USA.
- Welch, T.G., Klemmedson, J.O., 1973. Influence of the biotic factor and parent material on distribution of nitrogen and carbon in ponderosa

- pine ecosystems. In: Bernier, B., Winget, C.H. (Eds.), *Proceedings of the Fourth North American Forest Soils Conference*, Les Presses de l'université Laval, Laval University, Quebec, Canada, pp. 159–178.
- Wolfson, B.A.C., Kolb, T.E., Sieg, T.H., Clancy, K.M., 2005. Effects of post-fire conditions on germination and seedling success of diffuse knapweed in northern Arizona. *For. Ecol. Manage.* 216, 342–358.
- Zak, D.R., Grigal, D.F., Gleeson, S., Tilman, D., 1990. Carbon and nitrogen cycling during old-field succession: constraints on plant and microbial biomass. *Biogeochemistry* 11, 111–129.
- Zak, D.R., Tilman, D., Parmenter, R.R., Rice, C.W., Fisher, F.M., Vose, J., Milchunas, D., Martin, C.W., 1994. Plant production and soil microorganisms in late-successional ecosystems: a continental-scale study. *Ecology* 2333–2347.