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DECADAL SCALE RESPONSES OF SOIL AND ECOSYSTEM PROCESSES TO FOREST RESTORATION IN ROCKY MOUNTAIN CONIFER FORESTS

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DECADAL SCALE RESPONSES OF SOIL AND ECOSYSTEM PROCESSES TO
FOREST RESTORATION IN ROCKY MOUNTAIN CONIFER FORESTS

By

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Decadal Scale impacts of soil and ecosystem processes to forest restoration treatments in Rocky Mountain Conifer forests

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Decades of fire suppression have left much of the forest in the intermountain western United States exceedingly dense, and forest restoration techniques – including thinning and prescribed fire – are increasingly being used in an attempt to mitigate the potentially disastrous effects of severe wildfire, to enhance tree growth and regeneration, and to stimulate soil nutrient cycling. While many of the short-term effects of forest restoration have been established, the long-term effects on soil biogeochemical and ecosystem processes are largely unknown. In this thesis I present two manuscripts documenting and synthesizing these long-term impacts. The first chapter focuses on the decadal scale impacts of various restoration techniques on soil carbon (C) and nitrogen (N) dynamics. We conducted this study eleven years after the restoration treatments were implemented in a ponderosa pine (Pinus ponderosa var. scopulorum)/Douglas fir (Pseudotsuga menziesii var. glauca) forest at the Lubrecht Fire and Fire Surrogates Study (FFS) site in western Montana. Despite short-term (< 3 y) increases in soil N pools and N cycling rates following prescribed fire, long-term soil N pools and N mineralization rates were not significantly different from values in the experimental controls and have declined significantly over time. Integrated measures such as foliar nutrient concentrations and litter decomposition rates in the experimental plots were not different from control plots, suggesting that nutrient cycles in temperate coniferous forests are resilient to disturbance following long periods of fire suppression. In the second chapter I examined decadal scale impacts of restoration treatments on patterns of tree regeneration density and composition, and examined the factors that drove these patterns. We found all active treatments increased ponderosa pine density and decreased Douglas fir density relative to the control. The thin-and-burn was the only treatment that has created a favorable balance of ponderosa pine to Douglas fir regeneration. Finally, we found that heat load index, overstory basal area, canopy cover and surface fuels were important predictors of regeneration density and composition. Overall, these manuscripts provide scientists, forest managers and policymakers valuable information on long-term ecological effects, efficacy and longevity of various restoration prescriptions.
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Chapter 1: Long-term patterns in soil carbon and nitrogen dynamics show resilience following forest restoration treatments in Rocky Mountain conifer forests.

Introduction

Decades of fire suppression have increased forest stand density, promoted the build up of surface and canopy fuels, and encouraged fire intolerant and shade tolerant species throughout many U.S. forests (Keane et al. 2002, Mackenzie et al. 2004, Hessburg et al. 2005). In the extensive, fire-adapted ponderosa pine (*Pinus ponderosa*) forests of the intermountain west (Van Hooser and Kegan 1988), fire suppression and regional climatic changes have contributed to a substantial increase in the occurrence of severe stand replacing wildfires in the past two decades (Flannigan et al. 2006, Westerling et al. 2006, Flannigan et al. 2009). In response to this change, forest managers are increasingly using forest restoration prescriptions to reduce fire-prone fuels, reestablish historical stand structure, limit the risk of insect outbreaks, and enhance forest productivity. Restoration techniques often include silvicultural thinning, prescribed fire or combinations of these treatments, and all have been shown, generally, to reduce the risk of uncharacteristically severe wildfires in the short term (Stephens et al. 2009, Fiedler et al. 2010, Prichard et al. 2010, Hudak et al. 2011). However, the long-term effects of forest restoration on soil nutrient cycling and other ecological processes in ponderosa pine forests is largely unknown.

Prior to significant fire suppression, low elevation ecosystems dominated by ponderosa pine were characterized by low severity, lightning caused fires with a return interval of 10-50 years (Arno et al. 1995; 1997, Barrett et al. 1997). This cycle promoted relatively low-density, savanna-like forests dominated by vigorous, large-diameter ponderosa pines (Arno 1995, Hessburg et al. 2005). In contrast to many contemporary western forests, the forest landscape preceding recent settlement was also characterized by a heterogeneous mosaic of varying stand
ages, densities and fire histories (Swanson et al. 1994, Li et al. 2001). Frequent fire also released
plant available nutrients to forest soils, supporting relatively high rates of productivity and
decomposition, and limiting the accumulation of soil organic matter and woody materials
(Boerner 1982, Hungerford 1991, Keane et al. 2002). Thus, in addition to reducing fuels, some
have argued that reintroducing fire into these landscapes is critical for restoring healthy nutrient
cycles and enhancing tree growth (Neary et al. 1999, DeLuca and Sala 2006).

Plant growth in temperate forests is most commonly limited by N availability (Mandzak
and Moore 1994, Elser et al. 2007, LeBauer and Treseder 2008), and in semiarid forests like
those prevalent throughout the intermountain west, low mean annual temperature, dry climate,
the production of high C:N conifer litter, and the production of plant secondary metabolites all
contribute to relatively low soil N concentrations and low N cycling rates, perpetuating
ecosystem N limitation (Mandzak and Moore 1994). Further, understory plant community
composition has changed considerably as a result of fire suppression (Mackenzie et al. 2004,
Hessburg et al. 2005), and the fire-suppressed community is often characterized by slow growing
late-successional species with high nutrient use efficiency and low litter quality that contributes
to low rates of N mineralization (Aerts 1997, Keane et al. 2002). Similarly, previous studies of
ponderosa pine forests in western Montana found that with increasing time since fire, inorganic
N pools, rates of decomposition and nitrification decline (DeLuca and Sala 2006, Mackenzie et
al. 2004, 2006). Thus, while fire suppression can lead to overall increases in ecosystem N capital
as woody materials and plant litter accumulate, the majority of this N is bound up in organic
forms of N that are effectively unavailable to plants.

Forest restoration treatments have been shown to emulate resource pulses created by
natural disturbances such as wildfire (e.g., Covington and Sackett 1992; Monleon et al. 1997;
In general, short term effects of prescribed fire typically include a pulse of fire liberated inorganic N to soils. Decreased plant uptake and improved microclimatic conditions created by thinning and/or burning have also been shown to stimulate N mineralization and nitrification rates post-treatment, often creating a delayed pulse in NO$_3^-$ availability (e.g. White 1986, Kaye and Hart 1998, Gundale et al. 2005). Thinning alone has been shown to increase growth via thinning-driven increases in soil water availability in ponderosa pine forests (Feeney et al. 1998, Kaye et al. 2005, Sala et al. 2005, Skov et al. 2005, Fajardo et al. 2007) and may suppress nutrient cycling by its addition of high C:N ratio woody substrates (logging residues). Such effects may, in turn cause substantial microbial immobilization of available N (DeLuca and Zouhar 2000), but generally have only subtle (if any) effects on soil nutrient dynamics (DeLuca and Zouhar 2000, Gundale et al. 2005, but see Kaye and Hart 1998). However, while the short-term effects of forest restoration on C and N pools, nutrient cycling and some other ecosystem processes have been examined in considerable detail, we lack a similar understanding of the effects of treatments over the long-term.

To help bridge this critical gap, the Fire and Fire Surrogates (FFS) Study was established by the Joint Fire Sciences Program in 2000. The FFS is unique in that it was among the first to comprehensively manipulate and assess the effects of different forest restoration treatments on a host of forest and ecological parameters throughout an extensive network of sites. Considering the enormous costs and challenges of forest restoration, reliable long-term data assessing the benefits (e.g., treatment longevity and ecological impacts) are critical. While providing some valuable insights, other studies that have attempted to assess the long-term impacts of forest restoration on soil and ecosystem processes have relied on either chronosequence approaches where consistent measurements did not exist at a single site (e.g. Monleon et al. 1997, DeLuca
and Zouhar 2000), a retrospective approach (e.g. Grady and Hart 2006), or long-term measurements at a site which had no early or mid-term data for purposes of comparison (e.g. Sala et al. 2005). By contrast, this study provides a unique dataset combining early, mid and long-term (12 year) measurements highlighting the impacts of different restoration treatments on soil and ecosystem processes. By standardizing methodology at a single controlled site, it will allow for comparison between other FFS study sites across a number of forest ecosystems.

Previous work by Gundale and others (2005) at the Lubrecht FFS study site showed that in the short-term (<3 y), prescribed fire enhanced inorganic N concentrations in organic and mineral soil horizons and stimulated short-term organic matter decomposition rates. Further, when used in combination, thinning + burning enhanced net N mineralization and net nitrification relative to other treatments (Gundale et al. 2005). Analysis also showed a strong correlation between net mineralization and nitrification and the quantities of fine fuels consumed in prescribed burns (Gundale et al. 2005). Finally, treatments utilizing prescribed fire were shown have significantly greater heterogeneity in TIN pools, a significant predictor of understory species diversity (Gundale et al. 2006).

Here, we addressed two fundamental questions, with the overall goal of assessing the long-term efficacy and longevity of the FFS treatments from a nutrient cycling perspective: first, what are the long-term (decadal-scale) patterns in C and N dynamics following different forest restoration treatments and have documented short-term impacts of treatments on these processes persisted?; and second, how have initial pulses of inorganic N availability and rates of N cycling impacted ecosystem processes that govern forest productivity in the long-term? Based on short-term data from our site and other pertinent literature, we hypothesized that initial pulses of N availability and N mineralization have led to long-term increases in foliar N concentrations and
litter decomposition rates that have likely increased stand productivity in the burned treatments relative to controls and those that have received thinning alone.

**Methods**

*Study Site and Restoration Treatments*

The study was conducted at the FFS Northern Rocky Mountains site located at the Lubrecht Experimental Forest, ~ 50 km northeast of Missoula, MT, USA (Youngblood et al. 2005). Experimental plots (within three blocks) were established in second growth forest of the Douglas fir habitat type, consisting of mixed age ponderosa pine and Douglas fir with variable amounts of co-occurring lodgepole pine (*Pinus contorta*), Rocky Mountain Juniper (*Juniperus scopulorum*) and western larch (*Larix occidentalis*). Mean annual temperature at Lubrecht is 7°C and annual precipitation averages 550 mm, with approximately half falling as snow. Elevations of the experimental units range from 1230 to 1388 m (Nimlos 1986). Soils in Block 1 were formed from tertiary sediment and classified as clayey-skeletal, mixed, Typic Eutroboralfs. Soils in Block 2 were formed over Belt colluvium and are classified as loamy-skeletal, mixed, frigid, Udic Ustochrepts. Soils in Block 3 were also formed from tertiary sediment and are classified as fine, mixed, Typic Eutroboralfs (Nimlos 1986).

The Lubrecht FFS study included a randomized block experimental design where three 36 ha blocks were each divided into four 9 ha experimental units containing one of four randomly assigned treatments: untreated control; burn-only; thin-only; and thin-and-burn (See Fig. 2). Each nine ha experimental unit was further subdivided using into a 6 × 6 grid creating 36 equally spaced grid points as a permanent references. Ten grid points were randomly selected to mark the center of 20 m × 50 m (0.1ha) plots that were used for sampling (See Fig. 2). Thinning treatments were completed on snowpack during winter of 2001 utilizing a cut-to-length harvest
system, and were designed with a reserve basal area of 11.5 m$^2$ ha$^{-1}$ and specified prioritizing ponderosa pine as leave trees while reducing the density of shade-tolerant Douglas fir. Prescribed burn plots were established by broadcast burning as conditions allowed during the spring and early summer of 2002. The experimental control plots (one per block) remained untreated (Weatherspoon 2000). For the purposes of this study, "fine fuels" consist of surface fuels including 100-hour fuels, 10-hour fuels, 1-hour fuels (2.5–7.6, 0.6–2.5, 0–2.5 cm diameters, respectively) and soil O horizon materials consumed by prescribed burns as previously measured in 2002 using Brown’s transects and duff spikes and described in Gundale et al. (2005). For a more detailed description the study site, design and restoration treatments, see Weatherspoon (2000), Gundale et al. (2005) or Fiedler et al. (2010).

**Sampling Design**

Previous sampling at the site included an immediate post-treatment sampling event in the summer of 2002 and a mid-term sampling event in July 2004. New data for the current study were collected in the summer of 2013 and spring of 2014. Mineral soil and forest floor material (hereafter denoted as O horizon) were sampled from each block inside the ten randomly selected and previously sampled plots (Weatherspoon 2000). Subsamples of mineral soil were collected in opposing corners of each plot and combined to create one composite soil sample per plot. Subsamples of O horizon were also collected in opposing corners of each plot but were analyzed independently to compute a mean bulk density value for each plot. In the laboratory, after O horizon bulk density measurements were made, individual O horizon samples were combined and homogenized for further analyses. To allow comparison with previous results, methods and timing of sampling events were consistent with those used by Gundale et al. (2005).
Soil biogeochemical analyses

We sampled mineral soils to a depth of 10 cm using a 7 cm diameter bulb corer. The forest floor was sampled by collecting the entire organic (O) horizon (Oi, Oe and Oa horizons including undecomposed and partially decomposed litter, other fine organic matter and roots) inside a 10 cm diameter polyvinyl chloride (PVC) ring. We calculated O horizon depths by measuring the O horizon from the mineral soil to the top of the litter layer and averaging three adjacent measurements before inserting the PVC ring into the O horizon. Samples were transported to the laboratory in a cooler on ice and stored in a refrigerator at 4°C until they were extracted. Mineral soils were homogenized and sorted using a 2 mm sieve to remove stones and roots. Inorganic N concentrations were measured on field moist soil extractions performed on the day of collection.

We extracted inorganic N from mineral soil by shaking ~10 g fresh soil in 40 ml 2M KCl for one hour. For the O horizon samples, ~5 g of homogenized sample was extracted in 25 ml of 2M KCl. Samples were then centrifuged, decanted and filtered through Whatman #1 filter paper using a vacuum manifold. Inorganic N (NH₄⁺ and NO₃⁻) concentrations were analyzed colorimetrically on a microplate reader (BioTek Instruments, Winooski, VT) using the Salicylate-Hypochlorite method (Weatherburn 1967) and Vanadium Reduction method (Doane and Horwath 2003), respectively. Total inorganic N (hereafter TIN) was calculated as the sum of NH₄⁺ and NO₃⁻ concentrations.

We measured available P using the Bray-1 method (Bray and Kurtz 1945). Briefly, ~8 g of air dried soil was extracted in 40 ml NH₄F (Bray) solution by vigorously shaking for one minute and then filtering the extracts through Whatman #1 filter paper using a vacuum manifold.
Samples were subsequently analyzed colorimetrically on a microplate reader (BioTek Instruments, Winooski, VT) using a method modified from Oberson et al. (1997).

We assessed net ammonification, net nitrification and net N mineralization rates (the sum of net ammonification and net nitrification values) in mineral soils using the buried bag method (Eno, 1960). Briefly, one sample was returned to the laboratory for immediate processing and analyzed as described above, while an adjacent intact core was buried in a polyethylene bag, analyzed for inorganic N concentrations after a 28 d in situ incubation. Net N transformation rates for each treatment are reported as the mean difference between inorganic N concentrations before and after the in situ incubation. Mineral soil gravimetric water content was determined by oven drying a subsample at 105° C for 48 hours. O horizon samples returned to the laboratory were oven dried (48 hours at 65° C) to compute bulk density. Gravimetric water content values were further used to report all available nutrient pools on a soil dry weight basis.

In order to measure soil total C and N stocks, we oven-dried O horizon material and finely ground the material using a coffee mill. Mineral soils were air-dried and ground to pass a 0.106 mm mesh sieve. Total C and N in mineral soil and O horizon samples were measured by dry combustion analysis on an elemental analyzer (Carlo Erba Instruments, Milano, Italy). A randomly selected subset of the total mineral soil and O horizon samples was used for this analysis. Mineral soil pH was measured on air dry soil using a 2:1 (solution:soil) suspension of 0.01M CaCl₂.

Foliar and Litter N

We collected ponderosa pine foliage from sunlit branches in the mid canopy of ten trees of similar size in three random plots from each treatment unit in July 2013. One-year-old foliage was harvested from branches using an extendable pole saw. Second years’ growth foliage is
commonly sampled in tree physiology studies to assess nutrient concentrations (e.g., Feeney et al. 1998, Kolb et al. 1998, Sala et al. 2005) and tends to have low seasonal variability in N content relative to current years’ foliage (Hatcher et al. 1990). Fresh ponderosa pine litter was collected on a tarp by shaking or swatting the trees. Pine litter and foliage were dried (48 hours at 65° C) and finely ground using a coffee mill. Total C and N concentrations of ponderosa pine foliage and litter were measured by dry combustion analysis on an elemental analyzer (Carlo Erba Instruments, Milano, Italy).

Non-symbiotic N fixation

We assessed free-living N fixation rates in surface soil samples collected in July 2013 in five random plots from each treatment unit. Five samples were collected per plot for a total of 75 samples per treatment. Samples consisted of ~ 3 cm of forest floor material collected in 2.5 cm diameter (23 ml) clear plastic tubes, which were then sealed with caps containing septa and transported back to the laboratory in a cooler for immediate processing and analysis. Rates of free-living N fixation in the forest floor were evaluated using the acetylene reduction (ARA) method (Schöllhorn and Burris 1967, Belnap 1996) and adapted from Reed et al. (2007).

Briefly, following collection, ~10% of the headspace in each tube was removed and evacuated to the atmosphere. Tubes were then subsequently injected with an equal volume of acetylene gas. Samples were then allowed to incubate for 24 hours at room temperature (21° C) under fluorescent light to allow for ethylene production. After the incubation period, 14 ml of headspace was removed, transferred to a 10 ml Vacutainer (Becton-Dickinson, New Jersey, USA) and injected into a gas chromatograph equipped with a flame ionization detector (Shimadzu Scientific Instruments, Kyoto, Japan) to assess total ethylene production. One sample from each plot was incubated without acetylene to account for natural ethylene production, and
five control tubes were injected with acetylene but incubated without soil. A conversion ratio of 3:1 (moles ethylene: moles N) was used to compute rates of N fixation as previously established by DeLuca et al. (2002) and Matzek and Vitousek (2003). The area of the core was used to convert N fixation rates to an area basis, and 200 days was used to establish an average growing season length for N fixation activity.

**Decomposition**

We assessed litter decomposition rates using an in-situ incubation in the study plots utilizing Whatman 540 cellulose filter paper as a common substrate (Fox and Cleave 1983, McClellan et al. 1990, Vitousek et al. 1994). A common substrate was used rather than litter for logistical reasons as was with short-term data from Gundale et al. (2005). Filter paper was placed in 2 mm opening mesh fiberglass bags and placed horizontally between the surface of the mineral soil and organic horizon at each plot. Filter paper was oven dried (80°C) for 24 hours, weighed and placed in the field in September 2013. The decomposition bags were removed from the field in May 2014. Upon collection, the filter paper was oven dried (80°C) for 24 hours, brushed clean and weighed.

**Statistical Analyses**

We performed all statistical analyses using R (Version 3.0.1, R Core Development Team 2013). All plot-level data was averaged, and each nine ha treatment unit was considered the unit of replication ($n = 3$ per treatment). All data were tested for normality using a Shapiro-Wilkes test. We used a blocked one-way analysis of variance (ANOVA) to test for differences in response variables among treatments. We performed ANOVAs using a nonlinear mixed effects model to account for heterogeneity of variances in many of our variables (Pinheiro et al. 2013).
In this model, we entered treatment as a fixed factor and block as a random factor. We used an $\alpha$ level of 0.05 as a threshold to determine significant differences among treatments.

To assess differences in soil metrics between sampling dates, we used a repeated measures ANOVA under the aforementioned nonlinear mixed effects model where treatment, year and a treatment $\times$ year interaction term were used as fixed model effects. When a significant result was observed, we used Dunnett-Tukey-Kramer post-hoc tests that accommodated heterogeneity of variances and unequal sample sizes to determine which treatments differed (Lau 2009). When variables did not meet the normality assumptions of parametric statistics, or could not be transformed to normality, we performed nonparametric Kruskal-Wallis tests to test for significant differences between treatments. We used Pearson’s correlation coefficients to test for significant linear correlations between variables. Heterogeneity in TIN pools was calculated for each treatment by averaging the mean standard deviations from each nine ha treatment unit.

**Results and Discussion**

*Soil C, N and P Pools*

In contrast to early and mid-term findings presented by Gundale et al. (2005), our data generally show only subtle long-term effects of treatments on soil C and N dynamics. Despite significant increases in available N pools and N cycling rates in several treatments one and three years after the treatments were implemented, we found no significant differences in inorganic N pools among treatments in summer 2013 (i.e., 12 years after the experiment began) (Table 1). Eleven years post-treatment, soil inorganic N concentrations in all treatments were uniformly low and were dominated by NH$_4^+$, as is common in temperate forest ecosystems (e.g., Schimel and Bennett 2004). Lack of available NH$_4^+$, low mean annual temperature and low moisture conditions tend to limit the accumulation of NO$_3^-$ (Booth et al. 2005, Shrawat 2008). Similarly,
over the long term, NO$_3^-$ concentrations in most plots were very low or undetectable, and did not exceed 8% of the TIN pool on any sampling date (Table 1). Available N pools in the O horizon were 2-5 fold higher than those in mineral soils on a mass basis, though no significant differences were observed among treatments in this pool (Table 1).

Short-term pulses in nutrient availability and nutrient cycling following restoration treatments have been observed in a multiple short-term studies in the inland northwest (e.g., Monleon and Cromack 1996, DeLuca and Zouhar 2000, Kaye et al. 2005). These pulses emulate those created by low-intensity wildfire that characterized low-elevation ponderosa pine ecosystems prior to active fire suppression (Arno 1995; 1997) and are important in driving patterns of species composition, successional trajectories, maintaining nutrient fluxes and enhancing productivity (Johnson et al. 1998, Sala et al. 2005, DeLuca and Sala 2006). However, in the eleven years since the Lubrecth FFS treatments were initiated, TIN pools in the burn-only and thin-and-burn treatments have decreased significantly. For example, since the first year after treatment (2002), TIN concentrations in the thin-and-burn treatment have declined by ~ 80% and by > 50% since 2004 (Fig. 3). In the burn-only treatment, the TIN pool has decreased by nearly 45% since 2002 and by more than 30% since 2004. In conjunction with these long-term decreases in inorganic N pools, spatial heterogeneity in the TIN pool (expressed as standard deviation of mean) has also declined significantly over time in the thin-and-burn and burn-only treatments (Fig. 4), though we observed no significant temporal changes in TIN pool heterogeneity in the thin-only and control treatments. Current levels of variation did not differ significantly by treatment in summer 2013 or spring 2014, indicating greater resource homogeneity between treatments that may have implications for species diversity in the long-
term, as variability in available N has been shown to drive patterns in understory plant diversity (Gundale et al. 2006).

Several possible mechanisms could contribute to the relatively rapid attenuation of nutrient pulses that we observed in the long-term. For example, plant and microbial N uptake, leaching, erosion, denitrification and N adsorption by phenolic compounds could all help explain declines in soil N since the treatments were implemented (Grier 1975, Hungerford et al. 1991, Monleon et al. 1997, Hättenschwiler and Vitousek 2000). Next, DeLuca and Sala (2006) posited that many western US forests may exhibit a legacy or “memory effect” following initial restoration treatments that reflects significant accumulation of organic materials, woody surface fuels and shade intolerant species in the understory with prolonged fire suppression. De Luca et al argue that a single application of a restoration treatment may be insufficient to "reset" forest nutrient cycles, thus prolonging relatively low rates of N cycling processes. Finally, soil is known to have qualities that may confer resilience to disturbance and long-term perturbations; above and belowground biotic communities, in particular, are responsible for much of the resilience of soil N cycling and vegetation following disturbance (DeAngelis 1980, Seybold et al. 1999). Together, our results add to the growing body of evidence suggesting that frequent prescribed fires are needed to maintain the previously observed, short-term increases in N cycling and availability.

Over the long-term, treatment effects on total soil C and N pools appear to be largely limited to the O horizon. Pools of total C and N in the upper mineral soil layer (0-10cm) did not differ by treatment when expressed on a mass basis (Table 2). Early and mid-term data at the site yielded similar results. The low severity of the prescribed fires observed at the site may explain why the effects on C and N pools were largely limited to the forest floor (Gundale et al. 2005).
The absence of significant changes in total C and N pools in mineral soil has been noted in other restoration studies (Kaye et al. 2005, Boerner et al. 2008, Giai and Boerner 2008), and suggests low intensity, prescribed fire restoration treatments, in general, do not impact C and N pools in mineral soils to the extent of natural disturbances such as wildfire (e.g. Baird et al. 1999).

Depth of the O horizon differed significantly among treatments ($P < 0.01$), with depths significantly lower in the thin-and-burn treatment compared to other treatments (Table 3). Total dry mass of the O horizon on an area basis was also significantly lower in the thin-and-burn treatment (data not shown). Thus, C content on an area basis was significantly lower in this treatment ($P < 0.001$). This result was also observed immediately following restoration in both burn-only and thin-and-burn treatments but became marginally insignificant by year three (Gundale et al. 2005). Given the low stand density observed post-treatment in the thin-and-burn treatment, it is likely the forest floor, and hence C pools, may take a significant amount of time to recover compared to other treatments (Metlen and Fiedler 2006). Neither total C nor N differed significantly by treatment when expressed on a mass basis (Tables 2 and 3).

Finally, there were no significant treatment differences in available (Bray) P or mineral soil pH among treatments (Table 3). The relatively low severity prescribed burns experienced at the site likely limited volatilization of most mineral nutrients and resulted in minimal production of ash rich in base cations (Gundale et al. 2005). This effect is also confirmed in low intensity lightning fires as reported by Hatten et al. (2005) and in other forest restoration studies such as DeLuca and Zouhar (2000).

*Treatment effects on non-symbiotic N fixation*

Given that N availability commonly limits productivity in most temperate conifer forests (Mandzak and Moore 1994) and that the potential for overall ecosystem N losses following
prescribed burning is high (Boerner 1982, Hungerford et al. 1991), N fixation may provide an important N input to these systems, especially after fire (Ahlgren and Ahlgren 1975, Newland and DeLuca 2000, Johnson et al. 2005). Moreover, changes in microclimate such as increased soil moisture and light availability following forest restoration may provide favorable conditions for free-living N fixing organisms (Jurgenson et al. 1979; 1990). Nonetheless, we found consistently low rates of free-living N fixation in sampling of O horizon materials across all treatments (Table 3). In general, rates of N fixation (average 0.36 kg N ha\(^{-1}\) 200 day growing season\(^{-1}\), when averaged across all treatments) were low relative to N mineralization rates, but may still be an important source of plant-available N in these N limited forests. However, atmospheric wet N deposition rates in the northern Rockies were measured to be 3.89 kg N ha\(^{-1}\) yr\(^{-1}\) in 2013 (National Atmospheric Deposition Program, Glacier National Park – Fire Weather Station MT-05), suggesting free-living N fixation is a relatively minor component of new N inputs to this system.

When expressed on an area basis, rates of free-living N fixation differed significantly by treatment (\(P < 0.01\)), with rates lowest in the thin-only treatment and highest in the control treatment (Table 3). Variability in N fixation rates was high, however, likely reflecting the notable heterogeneity in distribution of non-symbiotic N fixing organisms and microsites that favor high N fixation rates. Burgoyne and DeLuca (2009) found no significant differences in rates of non-symbiotic N fixation in mineral soil or woody roots at our site four years post-treatment. The recovery of forest floor observed in our treatments and the cut-to-length system employed in harvesting thinned treatments left slash and other woody material on-site and likely avoided many impacts on free-living N fixing organisms.

*Soil N Transformations*
Short-term measurements at our site showed a significant increase in net N mineralization in the thin-and-burn treatment, though this effect was ephemeral and became non-significant by three years post-treatment (Gundale et al. 2005). Some previous studies have also shown significantly lower rates of N mineralization in burn treatments relative to controls in the short-term following forest restoration (Monleon et al. 1997, DeLuca and Zouhar 2000, Grady and Hart 2006). Here, however, we found that N mineralization rates did not differ significantly among restoration treatments in 2013, eleven years post-treatment (Table 1). Rates of net N mineralization have also decreased significantly over time in several of the treatments. Values of net N mineralization in the thin-and-burn treatment from sampling in summer 2013 show a decrease of nearly 75% compared to those from 2002, and the burn-only treatment shows a nearly 70% decrease over the same time period (Fig. 3). As net ammonification has not differed significantly by treatment at any summer sampling date (Gundale et al. 2005) (see Table 1), these declines are likely due to a decrease in net nitrification over time.

Rates of net nitrification from the thin-and-burn treatment have declined by nearly 95% since treatment initiation in 2002. Similarly, rates of net nitrification in the burn-only treatment have declined by nearly 90% over the same time interval (Fig. 3). Rates of nitrification are strongly limited by available NH$_4^+$ substrate (Booth et al. 2005). Therefore, it is likely that the observed decline in this form of inorganic N over time due to plant and microbial immobilization has paralleled a decline in nitrification rates. Yet, despite these declines, nitrification rates remain significantly higher in the thin-and-burn treatment compared to other treatments ($P=0.02$) (Table 1). Despite the persistence of this significant treatment effect, overall rates of nitrification were very low and therefore unlikely to be of considerable biological significance. However, while observed NO$_3^-$ concentrations were low relative to other forms of N at our site, their role in plant
growth and nutrient dynamics may be underappreciated. Stark and Hart (1997) showed that gross mineralization rates are often high despite often low or undetectable concentrations in soil and that NO$_3^-$ was a dynamic N pool. NO$_3^-$ has also been shown to be an important form of plant N uptake in ponderosa pine forests (Norton and Firestone 1996).

Next, we found significant positive linear relationships between the average quantity of fine fuels consumed in each unit of the thin-and-burn and burn-only treatments and average rates of net N mineralization and nitrification ($R^2=0.77$, $P=0.022$ and $R^2=0.78$, $P=0.019$, respectively) (Fig. 5a & b). These relationships have persisted since 2002, though their strength has weakened slightly over time. The persistence of this relationship over time suggests there is some long-term impact of prescribed fire on N dynamics that is influenced by fire severity - either directly or indirectly. One mechanism that may help to explain the persistence of this relationship is produced directly by fuel consumption during wildfire or prescribed fire: charcoal. Charcoal can have pronounced effects on nutrient cycling by adsorbing polyphenolic compounds known to inhibit nitrification and increase the cation exchange capacity of soils (DeLuca et al. 2006, Ball et al. 2010, Clough et al. 2010). Several studies in unmanaged ponderosa pine forests of western Montana have also highlighted the importance of charcoal in promoting nitrification (DeLuca et al. 2006, DeLuca and Sala 2006, Mackenzie and DeLuca 2006). It is possible that these benefits of charcoal could be responsible for the long-term response of increased nitrification rates in the thin-burn treatment relative to other treatments at our site. Prescribed burns in the thin-and-burn treatment consumed greater quantities of fine fuels compared to the burn-only treatment, likely creating more charcoal in this treatment overall (Gundale et al. 2005). Gundale et al. (2005) found no significant differences in total polyphenols in mineral soils one and three years post treatment. However, a comprehensive survey of charcoal content and polyphenol content in
forest floor and mineral soil would be needed to further assess this effect in the long-term as charcoal is incorporated into the mineral soil.

Finally, though soil moisture is positively correlated with rates of N mineralization (Booth et al. 2005) and we observed significantly higher soil moisture during spring sampling (data not shown), we detected few significant seasonal trends in N dynamics. Inorganic N pools appear to have greater seasonal variation than rates of N mineralization or nitrification, as net N mineralization rates did not differ significantly by sampling date, but did differ significantly by treatment in spring 2014 ($P = 0.045$) (Table 1). Soil inorganic N pools and rates of N mineralization are inherently variable in time and space (Monleon et al. 1997) and sampling from one point in time may not be sufficient to capture overall N dynamics. Despite this, our results showing a long-term temporal trend in N dynamics are robust across sampling dates.

*Long-term impacts of forest restoration on ecosystem properties and processes*

Short-term responses of prescribed burns in burn-only and thin-and-burn treatments at the Lubrecht FFS site showed immediate increases in inorganic N pools and rates of N mineralization that persisted until at least three years post-treatment in 2004. By 11 years post-treatment, none of these soil metrics were significantly different from the control treatment, reflecting a pronounced decline over the past eight years. But to what extent did the short term increases drive changes in other ecosystem properties? Restoration treatments including thinning and prescribed fire have potential to impact plant productivity, microclimate, and ecosystem properties, both indirectly and directly. For example, increases in temperature and soil moisture often observed following thinning treatments (Aussenac 2000, Meyer 2001) may increase rates of decomposition, promoting more rapid nutrient cycling and increases in plant productivity (Bissett and Parkinson 1980, Kaye and Hart 1998, Gundale et al. 2005, Hart et al. 2006).
Similarly, N pulses following restoration may influence foliar nutrients and litter chemistry, which may alter forest nutrient cycling after initial N pulses have subsided (Kolb et al. 1998, Feeney et al. 1998).

In temperate regions, initial leaf N concentration correlates with decomposition rates (Aerts 1997), and leaf N concentrations directly influence photosynthetic capacity and other leaf properties (Reich 1997, Bond et al. 1999). Multiple studies from the inland Northwest show foliar N concentrations inadequate to afford optimum tree growth (e.g. Shafii et al. 1989, Brockley et al. 1991, and Mandzak and Moore 1994) and studies show that foliar nutrient concentrations in N limited conifer ecosystems often increase following N fertilization (e.g. Trofymow et al. 1991, Mandzak and Moore 1994, Brockley and Sheran 1994, Weetman et al. 1997). However, the short-term pulses of available N and increased N cycling rates were at this site (Gundale et al. 2005) have not translated to differences in foliar nutrient concentrations over the longer-term. We found no significant differences in ponderosa pine foliar or litter N concentrations or C:N ratios among treatments (Table 3), and values of foliar N were similar to those from observed by Moore et al. (2004) across a range of undisturbed sites from the inland northwest. While we lack pretreatment data illustrating initial variation in foliar chemistry, our results suggest there were not long-term treatment impacts of an initial N pulse on this important metric that directly influences plant productivity and decomposition rates. Though other studies have linked soil nutrient status to foliar nutrient concentrations (e.g. Van Den Dreissche 1974, Van Den Dreissche and Dangerfield 1975), foliar nutrient concentrations within a plant functional types are strongly physiologically constrained (McGroddy et al. 2004) and variation within species is also driven by environmental and site factors such as latitude (Grunke 2010), bedrock lithology (Moore et al. 2004), light availability (Kranabetter 2010) and foliage age.
(Hatcher et al. 1990). It should also be noted that while treatments such as thinning and prescribed burning may not alter foliar N content on a mass basis, many studies show that they frequently increase leaf area index (LAI) and hence foliar N on an area basis, potentially increasing rates of photosynthesis and productivity (Gholz 1986, Raison et al. 1992, Vose 1994).

The process of decomposition regulates soil nutrient supply and is a significant part of nutrient cycles in forest ecosystems (Aerts 1997). While Gundale et al. (2005) showed higher decomposition rates in burn-only and thin-and-burn treatments following treatments, these differences have not persisted in the long-term; decomposition rates did not differ significantly among treatments (Table 3). Overall, these results illustrate that despite initial pulses in N cycling and availability following burn treatments, this short-term response has not led to long-term increases in foliar N concentrations or decomposition rates that would support enhanced productivity. This suggests that either the N pulses released by treatments were ephemeral and not strong enough to elicit this long-term ecosystem scale response or that their impact is difficult to detect, having been diluted in the long-term across vegetation, soil and microbial pools. Either way, it appears unlikely that a single treatment application following a long period of fire suppression is sufficient to enhance soil and ecosystem processes to the extent that an increase in ecosystem N fertility and forest productivity are realized in the long term.

Importance of frequent fire in restoring ponderosa pine ecosystems

The FFS study sought to assess the effectiveness of structural (such as thinning) and process (such as prescribed fire) treatments in accomplishing restoration goals. Thinning alone can reduce risk of extreme fire behavior by reducing canopy bulk density, increasing height to the live crown and reducing ladder fuels when small diameter trees are removed (Agee and Skinner 2005). In a summary of short-term findings from the FFS network, the thin-only
treatment was very similar to control treatments in most variables and had minimal impact on the reduction in quantities of surface fuels, often an important restoration goal. In this sense, thinning without prescribed fire does not appear to be an effective fire surrogate (McIver et al. 2012).

By contrast, fire is a dominant disturbance in many temperate coniferous forests, has a profound impact on forest structure and fuel accumulation, and creates a diverse mosaic of forest successional states (Arno et al. 1997, Swanson et al. 2010). Low elevation ponderosa pine forests are fire-adapted ecosystems that experienced frequent, low-severity fires in the cultural and natural environment that preceded active fire suppression throughout the previous century (Arno 1995). Consequently (and not surprisingly), it appears that the use of fire is critical to meet the goals of forest restoration in these ecosystems. Further, it appears repeated treatments (e.g., frequent fire that simulates the historical natural fire return intervals) will be necessary to ensure successful restoration and encourage rapid rates of nutrient cycling, forest composition and productivity that likely historically characterized these ecosystems (Reinhardt et al. 2008).

Larson et al. (2013) argued that the reestablishment of a frequent fire regime in ponderosa pine systems crucial for restoration success. They found that if fire was not followed by a second in between 5 and 20 years the potential for the system to revert to an undesirable secondary state could ensue.

Several studies have also assessed the impact of frequent, recurring fire and interval burning on C and N dynamics in western forests. In a survey of wilderness sites in western Montana, DeLuca and Sala (2006) found soils in sites that had experienced several wildfires per century had significantly higher NO$_3^-$ pools and rates of nitrification compared to those that had gone unburned over this time period. In ponderosa pine forests of northern Arizona, Covington
and Sackett (1986) found frequent interval burning maintained increased concentrations of inorganic N in soils. Wright and Hart (1997), however, found 20 years of prescribed fire at two year intervals reduced total N, potentially mineralizable N and available N pools relative to controls. This highlights the importance of designing prescriptions to meet restoration goals and take into account local or regional fire histories. For example, establishing an interval burning regimen at least every 20 years for low elevation ponderosa pine forests would be in agreement with historic fire return intervals (Arno et al. 1995; 1997) and could serve to increase rates of nutrient cycling and ameliorate stagnated rates of forest productivity. Burning at this moderate frequency would minimize excessive losses of soil C and N capital, allow for some natural ponderosa pine regeneration and minimize establishment of fire-intolerant Douglas fir. However, despite the ecological benefits of such a strategy, the high costs of implementing restoration frequently may preclude frequent fire treatments.

Finally, seasonality of prescribed burns is an important determinant of the magnitude of fire effects on soil properties (Sala et al. 2005, Hamman et al. 2008), and should be carefully considered by forest managers. Unlike others in the FFS network, our site utilized spring prescribed burns. Thus, some of our results may be unique to the timing of this restoration treatment. Spring prescribed burns are outside of the season of when historic fires generally burned and are generally lower in severity than late summer or fall burns, thereby minimizing the impacts on forest soils (Hamman et al. 2008).

Conclusions and management implications

From a nutrient cycling perspective, our results provide a robust and consistent long-term dataset that highlights the resilience of low elevation ponderosa pine forests to a single disturbance following a long period of fire suppression. While our study strongly suggests that
the direct and indirect effects of thinning and prescribed fire on nutrient cycling and N pools are largely ephemeral, other research indicates long-term benefits of treatments, including reducing risk and severity of future wildfires (Stephens et al. 2009, Fiedler et al. 2010, Prichard et al. 2010, Hudak et al. 2011), improved soil water status (Skov et al. 2004, Sala et al. 2005), increased tree growth and photosynthetic rates (Sala et al. 2005) and increased understory biodiversity (Gundale et al. 2006). Therefore, the goals of any restoration prescription should be clearly established and the effects on multiple ecosystem properties assessed when evaluating their efficacy (Ruiz-Jaen and Aide 2005, Reinhardt et al. 2008). Any long-term reduction in soil fertility and site productivity as a result of forest restoration would be an unintended consequence with implications for forest productivity and treatment longevity. This does not appear to be the case, as pools of N and rates of N mineralization in the long-term appear very similar between treatments. These data suggest there is long-term equivalence among these contrasting treatments in terms of soil and ecosystem processes. In other words, our results suggest that some of the other objectives of restoration (e.g., reducing fuels and recreating some aspects of historic stand structure and composition) can be realized without significant long-term impacts on soil C and nutrient cycling, but that these fire-adapted ecosystems require frequent fire to assure restoration success.

Despite significant differences in stand density and composition observed in the thin-only treatment relative to untreated controls at our site (Metlen and Fiedler 2006, Fiedler et al. 2010), we observed no significant treatment effects in terms of TIN pools or TIN heterogeneity nor have there been any significant temporal changes in these metrics. Differences in N transformation rates between the thin-only and untreated control over time have also been minimal. While thinning has been shown to increase winter snowpack relative to dense stands
(Stottlemyer et al. 2001, Woods et al. 2006, Heffelfinger 2012) and may alter forest microclimate
(Aussenac 2000, Meyer et al. 2001) these potential factors do not seem to have significantly
impacted C or N dynamics in the long-term. Thinning alone may reduce the extreme fire
behavior during wildfires, but is unlikely to meet other restoration goals such as limiting the
accumulation of surface fuels and stimulating nutrient cycling and appears best suited to areas
where prescribed burning is not practical or feasible.

Finally, our data suggest that, in terms of stimulation of decomposition and other soil
processes, treatment longevity is quite short - especially where low severity prescribed burns and
thinning follow long periods of fire suppression. Restoration treatments are costly and often
difficult to implement (Reinhardt et al. 2008). Therefore, forest restoration treatments should be
prescribed to meet a host of management and ecological objectives in areas with a high risk of
severe wildfire and/or where forest health can be improved feasibly on a large scale.

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Arno, Stephen F. et al. Restoring Fire-Dependent Ponderosa Pine Forests in Western Montana.


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Yelenik, Stephanie, Steven Perakis, and David Hibbs. Regional Constraints to Biological Nitrogen Fixation in Post-Fire Forest Communities. 2013. Ecology 94:739–750.

Table 1. Extractable NH$_4^+$, NO$_3^-$ from mineral soil (0-10cm), net nitrogen ammonification and net nitrification (28 day in-situ incubation) from mineral soil (0-10cm) from sampling dates in summer 2013 and spring 2014 and extractable NH$_4^+$ and NO$_3^-$ from the organic (O) horizon in summer 2013.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Control</th>
<th>Thin-only</th>
<th>Burn-only</th>
<th>Thin-and-Burn</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mineral soil</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NH$_4^+$ (mg kg$^{-1}$)$^a$</td>
<td>1.11 (0.13)</td>
<td>1.18 (0.09)</td>
<td>1.05 (0.07)</td>
<td>1.12 (0.68)</td>
</tr>
<tr>
<td>2013***</td>
<td>0.80 (0.11)$^a$</td>
<td>0.92 (0.12)$^a$</td>
<td>1.08 (0.13)$^a$</td>
<td>1.59 (0.13)$^b$</td>
</tr>
<tr>
<td>NO$_3^-$ (mg kg$^{-1}$)$^a$</td>
<td>0.00 (0.00)</td>
<td>0.03 (0.02)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
</tr>
<tr>
<td>2014$^*$</td>
<td>0.04 (0.02)$^b$</td>
<td>0.02 (0.01)$^a$</td>
<td>0.09 (0.03)$^b$</td>
<td>0.09 (0.03)$^b$</td>
</tr>
<tr>
<td>Net Ammonification$^b$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(mg NH$_4^+$ kg$^{-1}$ 28 days$^{-1}$)</td>
<td>2.18 (0.42)</td>
<td>1.58 (0.32)</td>
<td>0.99 (0.18)</td>
<td>1.65 (0.27)</td>
</tr>
<tr>
<td>2013$^*$</td>
<td>2.33 (0.42)$^b$</td>
<td>1.72 (0.26)$^b$</td>
<td>1.83 (0.26)$^b$</td>
<td>1.05 (0.28)$^a$</td>
</tr>
<tr>
<td>Net Nitrification$^b$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(mg NO$_3^-$ kg$^{-1}$ 28 days$^{-1}$)</td>
<td>0.04 (0.02)$^a$</td>
<td>0.03 (0.03)$^a$</td>
<td>0.05 (0.02)$^a$</td>
<td>0.22 (0.08)$^b$</td>
</tr>
<tr>
<td>2014</td>
<td>0.10 (0.05)</td>
<td>0.10 (0.04)</td>
<td>-0.01 (0.03)</td>
<td>0.11 (0.05)</td>
</tr>
<tr>
<td>Net N Mineralization$^a$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(mg N kg$^{-1}$ 28 days$^{-1}$)</td>
<td>2.21 (0.41)</td>
<td>1.61 (0.35)</td>
<td>1.05 (0.20)</td>
<td>1.86 (0.31)</td>
</tr>
<tr>
<td>2014$^*$</td>
<td>2.43 (0.42)$^b$</td>
<td>1.83 (0.27)$^b$</td>
<td>1.82 (0.25)$^b$</td>
<td>1.16 (0.28)$^a$</td>
</tr>
<tr>
<td><strong>O Horizon</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NH$_4^+$ (mg kg$^{-1}$)$^b$</td>
<td>3.29 (0.22)</td>
<td>3.63 (0.48)</td>
<td>4.26 (0.83)</td>
<td>5.00 (1.10)</td>
</tr>
<tr>
<td>NO$_3^-$ (mg kg$^{-1}$)$^b$</td>
<td>0.10 (0.06)</td>
<td>0.01 (0.01)</td>
<td>0.12 (0.06)</td>
<td>0.11 (0.08)</td>
</tr>
</tbody>
</table>

Data presented as mean ± (S.E.), n=3. Asterisks denote a significant difference between treatments from a one-way ANOVA or non-parametric Kruskal-Wallis test at $P<0.05$. Letters following each variable indicate the statistical test used: ANOVA$^a$, Kruskal-Wallis$^b$. Means followed by the same letter are not significantly different at $P<0.05$ (Dunnett-Tukey-Kramer post-hoc test). $P$-values: *$<0.05$, **$<0.01$, ***$<0.001$. 

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Table 2. Total carbon (C), nitrogen (N) and C:N ratio from mineral soil (0-10cm) and organic (O) horizons and O horizon bulk density (B_d).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Control</th>
<th>Thin-only</th>
<th>Burn-only</th>
<th>Thin-and-Burn</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mineral soil</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total C (g kg(^{-1}))</td>
<td>17.59 (3.77)</td>
<td>12.59 (2.36)</td>
<td>12.36 (2.18)</td>
<td>21.62 (4.13)</td>
</tr>
<tr>
<td>Total N (g kg(^{-1}))</td>
<td>0.95 (0.19)</td>
<td>0.72 (0.15)</td>
<td>0.77 (0.12)</td>
<td>1.17 (0.14)</td>
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<tr>
<td>C:N Ratio(^a)</td>
<td>18.61 (2.49)</td>
<td>17.44 (1.33)</td>
<td>16.15 (0.87)</td>
<td>18.90 (0.85)</td>
</tr>
</tbody>
</table>

| **O Horizon**            |          |           |           |               |
| Total C (g kg\(^{-1}\)) | 401.36 (16.23) | 383.98 (21.41) | 414.17 (14.09) | 361.90 (17.73) |
| Total N (g kg\(^{-1}\)) | 11.88 (0.85)  | 10.51 (1.17)  | 12.15 (0.87)  | 13.90 (1.69)  |
| Total C (Mg ha\(^{-1}\)) | 12.36 (0.50)\(^b\) | 12.16 (0.68)\(^b\) | 12.69 (0.43)\(^b\) | 8.21 (0.40)\(^a\) |
| Total N (Mg ha\(^{-1}\)) | 0.37 (0.03)   | 0.33 (0.04)   | 0.37 (0.03)   | 0.32 (0.04)   |
| C:N Ratio\(^a\)         | 34.66 (2.76)  | 38.91 (4.54)  | 35.05 (2.80)  | 27.16 (2.12)  |

Data presented as mean ± (S.E.), n=3 from sampling in summer 2013. Asterisks denote a significant difference between treatments from a one-way ANOVA or non-parametric Kruskal-Wallis test at P<0.05. Letters following each variable indicate the statistical test used: ANOVA\(^a\), Kruskal-Wallis\(^b\). Means followed by the same letter are not significantly different at P<0.05 (Dunnett-Tukey-Kramer post-hoc test). P-values: *<0.05, **<0.01, ***<0.001.
Table 3. Organic horizon depth, soil pH, available (Bray) phosphorus (P) in mineral soil (0-10 cm), free living nitrogen (N) fixation (per 200 day growing season), ponderosa pine foliar N, foliar C:N ratio, litter N and litter C:N ratio and decomposition (as % mass loss).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Control</th>
<th>Thin-only</th>
<th>Burn-only</th>
<th>Thin-and-Burn</th>
</tr>
</thead>
<tbody>
<tr>
<td>O Horizon Depth (cm)</td>
<td>3.27 (0.26)b</td>
<td>3.73 (0.36)b</td>
<td>3.37 (0.29)b</td>
<td>2.37 (0.18)a</td>
</tr>
<tr>
<td>Soil pH</td>
<td>5.30 (0.05)</td>
<td>5.40 (0.05)</td>
<td>5.38 (0.06)</td>
<td>5.39 (0.04)</td>
</tr>
<tr>
<td>Bray P (mg kg$^{-1}$)</td>
<td>40.69 (3.41)</td>
<td>49.64 (5.21)</td>
<td>44.47 (4.91)</td>
<td>46.14 (5.00)</td>
</tr>
<tr>
<td>N Fixation (kg ha$^{-1}$)</td>
<td>0.49 (0.55)b**</td>
<td>0.25 (0.28)a</td>
<td>0.32 (0.54)b</td>
<td>0.41 (0.51)b</td>
</tr>
<tr>
<td>Foliar N (% dry mass)</td>
<td>0.99 (0.08)</td>
<td>0.89 (0.06)</td>
<td>0.93 (0.02)</td>
<td>0.96 (0.03)</td>
</tr>
<tr>
<td>Foliar C:N Ratio</td>
<td>49.87 (3.78)</td>
<td>55.79 (3.77)</td>
<td>52.68 (1.00)</td>
<td>51.61 (1.21)</td>
</tr>
<tr>
<td>Litter N (% dry mass)</td>
<td>0.67 (0.12)</td>
<td>0.59 (0.05)</td>
<td>0.61 (0.08)</td>
<td>0.52 (0.05)</td>
</tr>
<tr>
<td>Litter C:N Ratio</td>
<td>79.29 (12.81)</td>
<td>85.15 (7.27)</td>
<td>85.50 (10.30)</td>
<td>98.94 (11.54)</td>
</tr>
<tr>
<td>% Mass Loss</td>
<td>31.84 (2.87)</td>
<td>35.74 (4.05)</td>
<td>29.96 (4.63)</td>
<td>35.32 (11.54)</td>
</tr>
</tbody>
</table>

Data presented as mean ± (S.E.) n=3. Asterisks denote a significant difference between treatments from a one-way ANOVA or non-parametric Kruskal-Wallis test at P<0.05. Letters following each variable indicate the statistical test used: ANOVAa, Kruskal-Wallisb. Means followed by the same letter are not significantly different at P<0.05 (Dunnett-Tukey-Kramer post-hoc test). P-values: *<0.05, **<0.01, ***<0.001.
Figure Captions

**Figure 1.** Simplified conceptual model showing hypothesized impacts of a) active fire suppression and b) forest restoration practices involving fire on the N cycle of a semiarid forest ecosystem. The model illustrates how forest restoration can minimize pools and fluxes of soil organic N while enhancing nutrient mineralization and improving availability of inorganic forms of N. Sizes of arrows and boxes represent the relative contribution of the N fluxes and pools, respectively.

**Figure 2.** Diagram of a) layout of a single experimental block (n=3) showing the different restoration treatments in each experimental unit (four per block) and b) layout of a single sampling plot (n=10 per experimental unit) where soil samples were taken in quadrants 4 and 7.

**Figure 3.** A) Total inorganic N (TIN) concentrations, B) net N mineralization rates and C) net nitrification rates in 2002, 2004 and 2013. Treatments include: control (closed circles), thin-only (closed squares), burn-only (open circles) and thin-and-burn (open triangles). Data presented as mean ± S.E. Asterisks indicate a significant treatment effect, $P$-values: *$<0.05$, **$<0.01$, ***$<0.001$. Data from 2002 and 2004 from Gundale et al. (2005).

**Figure 4.** Standard deviations (SD) of total inorganic N concentrations (TIN) in soils sampled in 2002, 2004 and 2013. Treatments include: control (closed circles), thin-only (closed squares), burn-only (open circles) and thin-and-burn (open triangles). Data presented as mean ± S.E. Asterisks indicate a significant treatment effect, $P$-values: *$<0.05$, **$<0.01$, ***$<0.001$. 

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**Figure 5.** Fine fuels consumed versus rates of a) net N mineralization and b) net nitrification ($R^2=0.77$, $p=0.022$ and $R^2=0.78$, $p=0.019$, respectively). Data presented as means from each 9 ha unit of the burn-only and thin-and-burn treatments from sampling in summer 2013.

**Figure 1.**
Figure 2.
Figure 3 a-c.
Figure 4.
Figure 5a.
Figure 5b.
Chapter 2: Patterns and controls of tree regeneration and composition following forest restoration treatments in low elevation ponderosa pine (*Pinus ponderosa*) forests of western Montana.

**Introduction**

Decades of active fire suppression in the U.S. have significantly altered forest stand structure, density and composition relative to historic conditions (Keane 2002). These changes have also been linked to unprecedented increases in wildfire incidence and extreme fire behavior in many western forests (Westerling et al. 2006). Land managers are increasingly utilizing forest restoration techniques such as silvicultural thinning and prescribed fire to address these concerns. In addition to reducing excessive fuel accumulation and reducing the risk of uncharacteristic wildfire activity, a common goal of forest restoration activities is the ability of treatments to encourage sustainable natural tree regeneration and the reestablishment of historic stand composition prior to recent settlement (Ruiz-Jaen and Aide 2005, Clewell and McDonald 2009). Though post-treatment canopy tree composition and density can be used as an indicator of a treatment’s effectiveness in restoring a desirable stand composition and structure, it is through the process of seedling regeneration and recruitment that the following generations of the forest community will be characterized.

Low elevation interior ponderosa pine (*Pinus ponderosa var. scopulorum*) forests are fire dependent ecosystems which cover ~16 million hectares in the continental U.S. (Van Hooser and Kegan 1988). Prior to recent settlement, these forests were characterized by low severity, lightning caused fires with a return interval of 10-50 years (Arno et al. 1995; 1997, Barrett et al. 1997). This cycle promoted relatively low-density, savanna-like forests dominated by vigorous, large-diameter ponderosa pines (Arno 1995, Hessburg et al. 2005). Over the past century, however, fire suppression has encouraged the development of dense, low productivity
homogenous forests (Keane 2002). As a result, basal area of fire intolerant species such as Douglas fir (*Pseudotsuga menziesii var. glauca*) has increased significantly in forests of the interior western U.S., and that of ponderosa pine has declined significantly (Hartwell et al. 2000).

Conifer regeneration is typically governed by supply side (seed source, reproductive output) and environmental factors that promote favorable microsites for seedling establishment and survival (Donato et al. 2009). In addition to controlling regeneration directly by providing seed source, overstory trees may provide facilitative effects that influence seedling establishment and survival by mitigating environmental extremes which may be even more critical in dry forests (Bertness and Callaway 1994, Callaway and Walker 1997). Further, overstory tree density and composition has been shown to have variable effects on overall regeneration patterns, but is generally the dominant driver in patterns of both regeneration density and composition (Catovsky and Bazzaz 2002). Ponderosa pine has been shown to regenerate episodically during favorable environmental conditions, but disturbances such as fire and others that create canopy openings have been shown to be important drivers of regeneration events (Brown and Wu 2005). Fire has long been recognized as an important factor in promoting ponderosa pine regeneration by enhancing the seedbed and providing increased nutrient and moisture availability (Sackett 1984). Forest restoration treatments involving thinning can significantly reduce stand density and alter composition of the remaining trees, creating favorable conditions for regeneration and growth of shade intolerant species such as ponderosa pine (Fiedler et al. 2010). Given the high costs of forest restoration and the logistical challenges in establishing large-scale treatments (Reinhardt et al. 2008), it is critical we understand the
impacts of different types of treatments (thinning and burning alone or in combination) on this crucial ecosystem process that defines several restoration goals.

As environmental and reproductive conditions for significant regeneration may occur only once per decade in ponderosa pine forests (Bailey and Covington 2002) and seedling mortality in the short-term is typically high (Harrington and Sackett 1990), these impacts may be difficult to assess in short-term studies. While numerous studies of natural regeneration have been conducted in undisturbed forests, following wildfire and large-scale timber harvests, we lack a similar understanding of regeneration patterns following restoration treatments, especially at longer time scales. The Joint Fire Science Program’s Fire and Fire Surrogates Study (FFS), established in 2000 (Weatherspoon 2000), provides an ideal framework to assess these long-term impacts of commonly used restoration treatments with implications for treatment longevity and success.

In this study we addressed two fundamental questions: first, what are the decadal scale patterns in regeneration density and distribution following forest restoration and what factors influence these patterns?: and second, how do the different restoration treatments influence species composition of natural regeneration and does this differ by seedling size class? We hypothesize that active restoration treatments will favor ponderosa pine and decrease Douglas fir regeneration relative to the control treatment, but that treatments which include both structural and process based restoration (i.e. thinning in addition to prescribed burning) will best help to achieve this goal.
Methods

Study Site, Sampling Design and Restoration Treatments

The study was conducted at the FFS Northern Rocky Mountains site located at the Lubrecht Experimental Forest, ~ 50 km northeast of Missoula, MT, USA (Youngblood et al. 2005). Experimental plots (within three blocks) were established in second growth forest of the Douglas fir habitat type, consisting of mixed age ponderosa pine and Douglas fir with variable amounts of co-occurring lodgepole pine (*Pinus contorta*), Rocky Mountain Juniper (*Juniperus scopulorum*) western larch (*Larix occidentalis*) and trembling aspen (*Populus tremuloides*). Mean annual temperature at Lubrecht is 7°C and annual precipitation averages 550 mm, with approximately half falling as snow. Elevations of the experimental units range from 1230 to 1388 m (Nimlos 1986).

The Lubrecht FFS study included a randomized block experimental design where three 36 ha blocks were each divided into four 9 ha experimental units containing one of four randomly assigned treatments: untreated control; burn-only; thin-only; and thin-and-burn. Each nine ha experimental unit was further subdivided using into a 6 × 6 grid creating 36 equally spaced grid points as a permanent references. Ten grid points were randomly selected to mark the center of 20 m × 50 m (0.1ha) plots that were used for sampling soils and other overstory variables. Thinning treatments were completed on snowpack during winter of 2001 utilizing a cut-to-length harvest system, and were designed with a reserve basal area of 11.5 m² ha⁻¹ and specified prioritizing ponderosa pine as leave trees while reducing the density of shade-tolerant Douglas fir. Prescribed burn plots were established by broadcast burning as conditions allowed during the spring and early summer of 2002. The experimental control plots (one per block) remained untreated (Weatherspoon 2000). For the purposes of this study, "fine fuels" consist of
surface fuels including 100-hour fuels, 10-hour fuels, 1-hour fuels (2.5–7.6 cm, 0.6–2.5 cm, 0–2.5 cm diameters, respectively) and soil O horizon materials consumed by prescribed burns. “Total surface fuels” include 1000-hour (both sound and rotten), 100-hour, 10-hour and 1-hour fuels plus O horizon materials. Fuels used in this analysis were previously quantified post-treatment in 2002 using Brown’s transects and duff spikes and described in Gundale et al. (2005). For a more detailed description the study site, design and restoration treatments, see Weatherspoon (2000), Gundale et al. (2005) or Fiedler et al. (2010).

**Field Sampling**

To assess tree regeneration in the different restoration treatments, we established four 60m² microplots around the perimeter of each rectangular plot, one in each cardinal direction (see Figure 1). Sampling was conducted outside of the experimental plot boundaries to eliminate disturbance from destructive sampling within the plot boundary. Seedlings of ponderosa pine (*Pinus ponderosa* var. *scopulorum*), Lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii* var. *glauca*), trembling aspen (*Populus tremuloides*), rocky mountain juniper (*Juniperus scopulorum*) and western larch (*Larix occidentalis*) were counted in each microplot. Seedling species and size class were also recorded. Seedlings were considered trees with a height ≥5cm and <1.37m (breast height). This reduced the highly variable pool of current year seedlings with limited long-term viability and excluded trees typically included in the ‘sapling’ category. Seedlings were further divided into three size classes: those between 5cm and 10cm (hereafter small seedlings), those between 10cm and 50cm (hereafter medium seedlings), and those between 50cm and 137cm (hereafter large seedlings).

Treatment units at the Lubrecht FFS site were harvested in the winter of 2001 and spring of 2002; therefore by the summer of 2014 thirteen growing seasons have elapsed since treatment
establishment. To assess which seedlings have regenerated since treatment units were established, we first sampled a random subset of each ponderosa pine and Douglas fir seedlings from each size class and treatment. The seedlings sampled were either harvested completely or a cross-section of the stem at the root collar was sampled. We found all seedlings sampled from the small (5-10cm) size class were <13 years of age. For the other size classes, we measured basal diameter at the root collar and determined thresholds for basal diameter where seedlings were ≤13 years of age. Seedling counts for each regeneration microplot were averaged to create a composite mean for each sampling plot (n=120). Seedling counts were subsequently averaged for each treatment to yield a total count per hectare for each species and size class.

Laboratory Aging of Seedlings

All seedling samples were oven dried at 80°C for 24 hours prior to aging. Stem cross sections were sanded and growth rings counted using a dissecting microscope. For seedlings where growth rings were absent or difficult to count distinguish, terminal bud scars were counted to assess when seedlings were established, which has been shown to be an accurate predictor of age for these species in the Rocky Mountain region (Urza and Sibold 2013).

Data Analysis

As a measure of direct solar radiation and heat load, we calculated heat load index (HLI) for each plot (McCune and Keon 2002), a metric that combines the influences of latitude, slope and aspect. Stand and site variables utilized in this analysis such as basal area, slope and aspect were previously measured by other investigators in initial work at the Lubrecht FFS site. For most analyses, we only considered regeneration of ponderosa pine (PIPO) and Douglas fir (PSME), as other species were of minor consequence and contributed less than 3.5% of basal area of the overstory trees across the experimental units. We performed all statistical analyses
using R (Version 3.0.1, R Core Development Team 2013). All plot-level data was averaged, and each nine ha treatment unit was considered the unit of replication (n = 3 per treatment). As regeneration densities were typically positively skewed, we used a log(x+1) transformation to better meet parametric assumptions. We used a blocked one-way analysis of variance (ANOVA) to test for differences in response variables among treatments. We performed ANOVAs using a nonlinear mixed effects model to account for heterogeneity of variances in many of our variables (Pinheiro et al. 2013). In this model, we entered treatment as a fixed factor and block as a random factor. We used an \( \alpha \) level of 0.05 as a threshold to determine significant differences among treatments.

When a significant result was observed, we used Dunnett-Tukey-Kramer post-hoc tests that accommodated heterogeneity of variances to determine which treatments differed (Lau 2009). When variables did not meet the normality assumptions of parametric statistics, or could not be transformed to normality, we performed nonparametric Kruskal-Wallis tests to test for significant differences between treatments. We used Spearman’s rank order correlation coefficients to test for significant statistical dependence between variables and an ecological response ratio as an effect index of regeneration densities in response to restoration treatments (Hedges et al. 1999). In this method, we calculated the response ratio by dividing the natural logarithm of the experimental value (regeneration density in the active treatment) by the natural logarithm of the control value (mean regeneration density in the control treatment).

**Results**

*Overall Density, Distribution and Composition*
When all species and size classes were considered together, there was no significant difference in seedling densities by treatment \((P=0.98)\). Across all treatments, Douglas fir dominated the regeneration composition, averaging 65.5% of the total regeneration density (Table 1). A ratio of ponderosa pine to Douglas fir regeneration densities showed a significantly higher ratio in the thin-and-burn treatment relative to all other treatments \((P<0.001)\) (Figure 4). Ponderosa pine regeneration densities did differ by treatment when all size classes were included, with all active treatments showing a significantly greater density of this species relative to the control \((P=0.005)\). In contrast, Douglas fir regeneration densities did not differ significantly by treatment at any age class \((P=0.36)\) (Figure 2). When regeneration densities were normalized and expressed as the number of seedlings per unit of conspecific basal area, there remained no significant treatment effect on Douglas fir regeneration and ponderosa pine regeneration was only significantly increased in the thin-and-burn treatment relative to the other treatments (Figure 3).

The density of small ponderosa pine seedlings was significantly greater in the thin-and-burn treatment compared to the control \((P=0.03)\). Similarly, the density of medium sized ponderosa pine seedlings was significantly greater in the thin-and-burn treatment relative to the control \((P=0.03)\) (Table 1). Finally, the density of large ponderosa pine seedlings in the thin-only treatment was significantly greater than those in the control or burn-only treatments \((P<0.01)\). Canopy cover differed significantly by treatment, where values from the thin-and-burn treatment were significantly lower than the control and burn-only treatments \((P<0.0001)\) (Table 1). Finally, ecological response ratios showed that all active treatments decreased Douglas fir density relative to the control treatment, with no significant treatment differences in effect size \((P=0.20)\). In contrast, all active treatments increased ponderosa pine seedling density relative to
the control treatment, with only a marginal difference by treatment suggesting a greater effect in
the thin-and-burn relative to the burn-only treatment ($P=0.052$) (Figure 4).

*Relationships between regeneration patterns and site variables*

We found significant statistical correlations between regeneration densities and a number
of site and environmental factors. For both ponderosa pine and Douglas fir, conspecific basal
area and the percent of total basal area contributed by the particular species were significantly
positively correlated with regeneration densities (Table 2). For a given plot, however, the percent
of total basal area occupied by the particular species was correlated more strongly with
regeneration densities. We found no significant relationship between densities of ponderosa pine
and Douglas fir at the microplot scale in the thin-only and thin-and-burn treatment ($P=0.15$ and
0.07, respectively), while there was a significant positive correlation between ponderosa pine and
Douglas fir densities in the control and burn-only treatments ($P=0.01$ and 0.006, respectively).
Ponderosa pine regeneration densities were significantly positively correlated with HLI, while
Douglas fir was significantly negatively correlated with HLI (Table 2). Ponderosa pine
regeneration densities were significantly negatively correlated with both total basal area and
percent canopy cover (Table 2), while densities of Douglas fir was not. Only large seedlings of
ponderosa pine were significantly positively correlated with fine fuel consumption (a proxy for
fire severity). Finally, Douglas fir regeneration densities were significantly positively correlated
with total surface fuel loads (Table 2).

**Discussion**

*Patterns in Regeneration Density and Composition*

Our results show that in all active forest restoration treatments, Douglas fir continues to
regenerate at levels equal or greater than control treatments and dominates total regeneration.
This may be due to a combination of Douglas fir’s greater dispersal relative to ponderosa pine (Ryker and Losensky 1993), its broader preferences for seedbed characteristics (Burns 1990) and shade tolerance (Burns 1990). The seedling densities we report in active restoration treatments are significantly greater than those reported in short-term studies following restoration in northern Arizona (Bailey and Covington 2002) and eastern Oregon (Youngblood et al. 2006) and a decade following restoration in Montana (Fajardo et al. 2007). While we lack site-specific information regarding reproductive output of overstory trees, both thinning and prescribed burning were shown to increase reproductive output of ponderosa pine relative to an untreated control at another site in western Montana (Peters and Sala 2008), which may help to explain some of the increases in ponderosa pine regeneration in all active treatments relative to the control. Neither Douglas fir nor ponderosa pine are seedbanking species and their seeds are rarely viable longer than 1-2 years (Jones 1974, Burns 1990), thus we expect current canopy composition and availability of seed source to be driving supply side controls of regeneration densities.

*Site factors associations*

Given Douglas fir’s shade tolerance and preference for shady, cool and north facing slopes for establishment (Burns 1990), it is not surprising that its densities were not correlated with canopy cover and negatively correlated with HLI. Similarly, in ponderosa pine, as a shade intolerant species (Barton 1992), we would expect its seedlings to show a negative relationship to canopy cover and total basal area while preferring warmer, open sites as evidenced by a positive correlation with HLI. The persistence of these relationships across all treatments suggest these fundamental controls are still important in driving regeneration following forest restoration.
Further, the weaker relationship between Douglas fir seedling densities and its overstory abundance compared to ponderosa pine (Figure 7), suggests a possible seed source effect. Douglas fir has lighter seeds than ponderosa pine and has been shown to disperse twice as far (Ryker and Losensky 1993). This may help to explain the high density of Douglas fir seedlings across all treatments relative to its basal area contribution (Figure 3), and suggests that restoration prescriptions wishing to reduce subsequent regeneration of Douglas fir should adequately reduce the species from the overstory composition. Finally, given Douglas fir densities were positively correlated with surface fuel loads (Table 2), we would expect treatments that retain high amounts of surface fuels may serve to favor this species. Microsites buffered from temperature and moisture extremes by woody debris have been shown to encourage regeneration and survival of conifers (Gray and Spies 1997). In support, Fajardo et al. (2007) also found that percent cover of woody debris was significantly positively correlated with Douglas fir regeneration at another restoration site in western Montana.

*Relationships between ponderosa pine and Douglas fir*

The statistical relationship between ponderosa pine and Douglas fir densities varied by treatment, but both ‘closed canopy’ treatments (control and burn-only) showed a significant positive relationship while the ‘open canopy’ treatments (thin-only and thin-and-burn) showed no significant correlation. This suggests that where canopy cover and stand density are high (as in the control and burn-only treatments), both Douglas fir and ponderosa pine regenerate together and may utilize similar microsites favorable to regeneration. Similarly, across a single managed forest site in western Montana, Fajardo et al. (2006) found no spatial differences in establishment between the two species, suggesting they occupy similar microsites.
Influence of fire on long-term regeneration patterns

The amount of fine fuels consumed was only significantly correlated with ponderosa pine regeneration densities in the largest size class, suggesting the influence of fire severity has not continued to structure regeneration densities in younger recruits. Although fire is known to prepare a more favorable mineral soil seedbed for ponderosa pine (Sackett 1984), it is likely that the re-accumulation of forest floor materials and recovery of understory vegetation has homogenized microsite availability. Despite this, the density of small and medium ponderosa pine seedlings is significantly greater in the thin-and-burn relative to the other active treatments, suggesting the combination of fire and thinning may be key to encouraging ponderosa pine regeneration. We observed significantly higher ponderosa pine seedlings in the thin-and-burn treatment relative to its basal area when compared to the other active treatments (Fig. 3), suggesting factors other than overstory tree composition may be driving these increases. Both the thin-only and the thin-and-burn treatment significantly decreased total stand basal area relative to the burn-only and control treatments (Fiedler et al. 2010), suggesting factors other than light availability (canopy opening) are driving differences between the thin-only and thin-and-burn treatment.

Management Implications

While there are no concrete targets for tree regeneration or composition following restoration, largely due to a lack of historical data and a debate over ‘reference conditions’ for forest restoration (Laughlin et al. 2004), it is clear that none of the restoration treatments has impaired the ability of either Douglas fir or ponderosa pine to regenerate in sustainable numbers. In terms of the ability of restoration treatments to reestablish a historic stand composition, our study offers some limited evidence: while there were no significant differences in Douglas fir
densities by treatment (Figure 2), the thin-and-burn treatment has significantly increased the amount of ponderosa pine relative to Douglas fir (Figures 4 and 5). This suggests that this treatment, which incorporates both structural and process restoration techniques, best alleviates ponderosa pine regeneration constraints of light availability and lack of adequate seedbed, and appears to be the only treatment we assessed that can accomplish this restoration goal.

In terms of treatment longevity, our study shows that ~12 years post-treatment, there are several hundred well established large seedlings per hectare (Table 1). Ponderosa pine can begin to survive surface fire at ~6 years of age, and while Douglas fir seedlings typically exhibit high mortality due to fire, they develop fire resistant stems at ~40 years of age (Bradley 1992). In a South Dakota ponderosa pine forest, Battaglia et al. (2008) found 15 years following forest restoration prescribed fire could not maintain a low-density forest due to size and density of regeneration. In light of our data, this suggests that repeated treatments (i.e. frequent fire) will be necessary to maintain the effectiveness of forest restoration in the long-term.

References


**Table 1.** Regeneration densities for all species (*Pinus ponderosa, Pseudotsuga menziesii, Larix occidentalis, Pinus contorta, Juniperus communis*) and individually for each size class of ponderosa pine and Douglas fir.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Control</th>
<th>Thin</th>
<th>Burn</th>
<th>Thin/Burn</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>All species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density (seedlings ha⁻¹)</td>
<td>1990 (428)</td>
<td>3169 (409)</td>
<td>3490 (740)</td>
<td>3126 (455)</td>
</tr>
<tr>
<td><strong>Ponderosa pine</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density (seedlings ha⁻¹)**</td>
<td>277 (64)a</td>
<td>1085 (236)ab</td>
<td>871 (285)ab</td>
<td>1715 (313)b</td>
</tr>
<tr>
<td>5-10cm (small)*</td>
<td>92 (44)a</td>
<td>372 (125)ab</td>
<td>536 (202)ab</td>
<td>945 (357)b</td>
</tr>
<tr>
<td>10-50cm (medium)***</td>
<td>149 (27)a</td>
<td>581 (123)bc</td>
<td>303 (89)ab</td>
<td>725 (128)c</td>
</tr>
<tr>
<td>50-137cm (large)**</td>
<td>26 (10)a</td>
<td>131 (38)b</td>
<td>32 (14)a</td>
<td>85 (27)ab</td>
</tr>
<tr>
<td><strong>Douglas fir</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density (seedlings ha⁻¹)</td>
<td>1826 (434)</td>
<td>2236 (466)</td>
<td>2558 (697)</td>
<td>1089 (261)</td>
</tr>
<tr>
<td>5-10cm (small)</td>
<td>166 (319)</td>
<td>97 (28)</td>
<td>222 (49)</td>
<td>56 (13)</td>
</tr>
<tr>
<td>10-50cm (medium)</td>
<td>1526 (378)</td>
<td>1725 (354)</td>
<td>2107 (602)</td>
<td>1003 (263)</td>
</tr>
<tr>
<td>50-137cm (large)</td>
<td>37 (21)</td>
<td>217 (79)</td>
<td>217 (110)</td>
<td>68 (28)</td>
</tr>
<tr>
<td><strong>Canopy Cover (%)</strong></td>
<td>49.2 (2.2)a</td>
<td>40.9 (1.9)ab</td>
<td>45.4 (2.3)a</td>
<td>31.1 (2.1)b</td>
</tr>
</tbody>
</table>

Data presented as mean ± (S.E.), n=3. Asterisks denote a significant difference between treatments from a one-way ANOVA. Means followed by the same letter are not significantly different at P<0.05 (Dunnett-Tukey-Kramer post-hoc test). P-values: *<0.05, **<0.01, ***<0.001.
Table 2. Non-parametric Spearman’s rank order correlations between regeneration densities and site variables.

<table>
<thead>
<tr>
<th>Variable One</th>
<th>Variable Two</th>
<th>Correlation Coefficient (Rho)</th>
<th>n</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ponderosa pine regeneration density (seedlings ha(^{-1}))</td>
<td>Ponderosa pine basal area (m(^2) ha(^{-1}))</td>
<td>0.18</td>
<td>120</td>
<td>0.05</td>
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<td></td>
<td>Ponderosa pine basal area (% of total)</td>
<td>0.62</td>
<td>120</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Canopy Cover (%)</td>
<td>-0.34</td>
<td>480</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Total Basal Area (m(^2) ha(^{-1}))</td>
<td>-0.30</td>
<td>120</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Heat Load Index (HLI)</td>
<td>0.24</td>
<td>120</td>
<td>0.008</td>
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<tr>
<td></td>
<td>Douglas fir regeneration density (across all treatments, seedlings ha(^{-1}))</td>
<td>-0.003</td>
<td>480</td>
<td>0.95</td>
</tr>
<tr>
<td>Douglas fir regeneration density (seedlings ha(^{-1}))</td>
<td>Douglas fir basal area (m(^2) ha(^{-1}))</td>
<td>0.57</td>
<td>120</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Douglas fir basal area (% of total)</td>
<td>0.62</td>
<td>120</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Heat Load Index (HLI)</td>
<td>-0.46</td>
<td>120</td>
<td>&lt;0.0001</td>
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<tr>
<td></td>
<td>Total Surface Fuels (Mg ha(^{-1}))</td>
<td>0.22</td>
<td>120</td>
<td>0.015</td>
</tr>
<tr>
<td>Large ponderosa pine (50-137cm) regeneration density (seedlings ha(^{-1}))</td>
<td>Fine fuel consumption (Mg ha(^{-1}))</td>
<td>0.30</td>
<td>60</td>
<td>0.02</td>
</tr>
</tbody>
</table>
Figure Captions

Figure 1. Diagram of regeneration microplot (n=120 per treatment) layout around a sampling plot (n=30 per treatment)

Figure 2. Seedling densities of Douglas fir (PSME) and ponderosa pine (PIPO) across all size classes in each treatment. Data presented as mean ± S.E., n=3. Means within a species followed by the same letter are not significantly different at P<0.05.

Figure 3. Seedling densities of Douglas fir and ponderosa pine across all size classes in each treatment, expressed as number of seedlings per unit of conspecific basal area. Data presented as mean ± S.E., n=3. Means within a species followed by the same letter are not significantly different at P<0.05.

Figure 4. Ratio of seedling composition between Ponderosa pine and Douglas fir at the plot scale. Ratios greater than one indicate a seedling composition dominated by ponderosa pine. Data presented as mean ± S.E., n=3. Means within a species followed by the same letter are not significantly different at P<0.05.

Figure 5. Ecological response ratio showing the impact of active treatments on ponderosa pine and Douglas fir seedling densities relative to the control treatment. Positive values indicate an increase in density relative to the control treatment and negative values represent a decrease. Means within a species followed by the same letter are not significantly different at P<0.05.
Figure 6. Ponderosa pine regeneration density (all treatments) versus percent basal area occupied by this species. Shown with exponential regression fit, $R^2=0.31$.

Figure 7. Douglas fir regeneration density (all treatments) versus percent basal area occupied by this species. Shown with linear regression fit, $R^2=0.1$

Figure 8. Ponderosa pine regeneration density (microplot scale, all treatments) as a function of canopy cover.
Figure 2.
Figure 3.
Figure 4.
Figure 5.
Figure 6.
Figure 7.

\[ y = 807.98 + 52.995x \quad R^2 = 0.097541 \]
Figure 8.