Effects of thinning, prescribed burning, and burning season on the physiological performance of ponderosa pine

Gregory D. Peters

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Effects of thinning, prescribed burning, and burning season on the physiological performance of ponderosa pine

by

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B.S. Western Washington University, Bellingham, WA 1998

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for the degree of

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Effects of thinning, prescribed burning, and burning season on the physiological performance of ponderosa pine

Director: Anna Sala

ABSTRACT

Low elevation ponderosa pine (Pinus ponderosa Dougl. ex. Laws.) forests of the northern Rocky Mountains historically experienced frequent, low intensity fires that maintained open, uneven-aged stands. A century of fire suppression has led to denser ponderosa pine forests with higher competition for resources, higher tree stress, and greater risk of insect attack and stand destroying fire. Active management intended to restore historic stand conditions includes selective thinning and prescribed fire application. Little is known about the differential effects of these management practices on the physiological performance of ponderosa pine. We examined the performance of second growth ponderosa pine trees nine years after the application of four treatments: thinning, thinning followed by spring (wet) prescribed fire, thinning followed by fall (dry) prescribed fire, and unthinned control stands. We measured stand structural characteristics, resource availability, and tree performance parameters in three replicates of each treatment at the Lick Creek Experimental Site in the Bitterroot National Forest. Thinning resulted in similar reductions in basal area in each thinned and burned stand relative to control stands. Soil moisture content did not differ between any treatments over the field season. Soil chemical analyses revealed lower late-spring available ammonium in control stands relative to all other treatments and lower time-integrated nitrate availability in burned stands than in thinned only or control stands. Trees of similar size and structure in the thinned treatment and in both of the thinned and burned treatments displayed higher maximum, leaf area-based rates of photosynthesis (A_{area}) and lower levels of water stress (Ψ) over the course of the growing season, as well as higher rates of post-treatment diameter growth than trees in control stands. These results reflect an overall improvement in long-term physiological performance of trees in the actively managed stands relative to trees in unmanaged control stands. None of several leaf level characteristics, including specific leaf area (SLA), mass-based leaf nitrogen content (N_{leaf}), carbon isotope discrimination (Δ), and nitrogen isotope ratio (δ^{15}N) were significantly different between any of the four treatments. We found no evidence that long-term physiological performance of second growth ponderosa pine is affected positively or negatively by the application of either spring or fall prescribed fire to thinned stands.
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Introduction

Pure and mixed stands of ponderosa pine (Pinus ponderosa Dougl. ex. Laws.) cover millions of hectares across the northern Rocky Mountains (Van Hooser and Keegan 1988). Historically, ponderosa pine forests dominated much of this land forming open stands maintained by low intensity surface fires that burned every 5-25 years (Arno 1988, Martin 1982). Euro-American settlement of the west was followed by a decrease in the fire frequency in much of the ponderosa pine forest systems. In the past century indigenous burning has declined (Barrett and Arno 1982), lightning-caused fires have been actively extinguished, grazing has reduced the cover of flammable herbs (Steele et al. 1986), and ecosystem fragmentation through development and road building has created blocks to the spread of wildfire (Arno 1988). As a consequence, many of the ponderosa pine forests have dramatically changed in the past century (Covington and Moore 1994).

Active management via prescribed fire and thinning are increasingly used to restore historic stand structure, reduce the risk of catastrophic fire, and improve forest productivity in ponderosa pine forests (Arno et al. 1995, Powers and Reynolds 2000). Most ponderosa pine forests in the northern Rocky Mountains are second growth stands with high tree density relative to historic conditions (Hartwell et al. 2000, Harrington 2000). In mesic sites, the exclusion of fire from ponderosa pine stands enables increased understory invasion of more shade-tolerant species such as Douglas-fir (Agee, 1993). In drier sites where Douglas-fir is not common, the absence of fire allows continuous recruitment of ponderosa pine. The denser stands resulting from fire exclusion display greater competition for resources and greater risk of pathogen outbreaks, insect attack,
and stand-replacing fires (Feeney et al., 1998). This suggests that partial restoration of historic conditions may be realized by removing competing trees through active management.

Thinning, which is used to restore historic structural conditions, is often followed by prescribed fire, which is used to reduce fuel. Numerous studies have examined the effects of thinning and prescribed fire on tree growth, nutrient cycles, mortality, and recruitment in ponderosa pine systems (Monleon et al. 1997, Arno et al. 1996). Little is known, however, about the relative long-term effects of thinning and prescribed fire on the physiological performance of second-growth ponderosa pine.

In old growth stands, thinning and prescribed fire have positive short-term effects on old growth ponderosa pine physiological performance. Reduction in stand density can cause increases in available water due to reduced stand-level water use and interception of rain and snow by foliage (Feeney et al. 1998). Mechanical thinning also can result in improved tree water status, photosynthetic rate, and resin production in old growth ponderosa pine (Kolb et al. 1997). One year after treatment, thinning and thinning followed by prescribed fire resulted in improved performance and water availability in old growth ponderosa pine. However, there was no difference between thinning only and thinning plus fire (Feeney et al. 1998, Sala et al. unpublished). These results suggest that, in the short term, thinning may benefit the physiological performance of old growth ponderosa pine as effectively as thinning followed by burning. It is unknown if fire may provide longer-term, additional benefits compared to thinning alone for younger, second growth ponderosa pine.
One possible mechanism for long-term benefits to ponderosa pine from fire is through nutrient cycles. Fire exclusion in low elevation ponderosa pine systems may have negative consequences on nitrogen cycles (Covington and Sacket 1984, DeLuca 2000) and several studies have shown increases in mineral soil nitrogen availability immediately after fire (Covington and Sackett 1992; Kaye and Hart 1998). However, the increase in available nitrogen following fire is usually temporary, and it is not clear whether or not fire improves long-term nitrogen availability in ponderosa pine forests (Harrington 1999, DeLuca and Zouhar 2000).

In addition to the direct effects of fire on soil nitrogen status through volatilization and mineralization, nutrient cycling in ponderosa pine forests can be altered by fire-caused changes in understory composition (Newland and DeLuca, 2000) that occur in response to shifts in fire regimes (Harris and Covington, 1983). Fire suppression in ponderosa pine systems has led to a general shift from grass to shrub dominance (Fule et al. 1997). This change in understory affects the soil quality, flammability, and tree growth in ponderosa pine stands (Busse et al. 1996). Furthermore, the density of nitrogen fixing plants may be affected by fire (Newland and DeLuca, 2000). Leaf nitrogen content is directly related to leaf properties and photosynthetic capacity (Reich et al. 1997). Direct and indirect effects of different management practices on soil nitrogen availability may, therefore, have consequences for the physiological performance of ponderosa pine.

Historically, ponderosa pine forests of the northern Rocky Mountains burned during the late summer and early fall (Agee, 1993). However, most prescribed fire is conducted during spring months when conditions are cooler, moister and support better
smoke dispersal. During the spring, increased water and nutrient availability may promote relatively fast fine root production and high physiological activity. Prescribed burning in spring has been shown to reduce fine root productivity of ponderosa pines resulting in lower growth rates and higher mortality relative unburned trees (Grier 1989, Swezy and Agee 1991). Fires applied in different seasons and of different intensities and severities have also been shown to have dramatically different effects on understory species composition (Harrington 1985, Howe 1994). These results suggest that the response of ponderosa pine to prescribed fire may be sensitive to the season, particularly in light of different pine phenology at different times of the year. More detailed data are needed to understand the implications of the seasonal timing and intensity and severity of prescribed fire for the physiological performance of ponderosa pine.

Here we examined potential direct long-term effects of fire, relative to thinning alone, and of burning season on ponderosa pine physiological performance in western Montana. We compared understory species composition, soil resource availability, and physiological performance of ponderosa pine nine years after the implementation of the following four management practices: prescribed fall (dry) burning preceded by thinning, prescribed spring (wet) burning preceded by thinning, thinning alone, and untreated control. Specifically, we addressed the following two questions:

1) How do thinning and prescribed fire treatments affect long-term ponderosa pine physiological performance relative to untreated controls?
2) Are there differences in long-term ponderosa pine performance between stands receiving thinning only, thinning followed by spring fire, and thinning followed by fall fire?

Appropriate restorative ecosystem management in ponderosa pine forests acknowledges the historic role of fire as a natural disturbance that played an important role for not only trees, but in an interacting system of flora, fauna and their environment. The research reported here focuses on a few elements of the overall ecosystem management goal. However, management decisions guided toward restoring second growth ponderosa pine to historic old growth conditions will benefit from an understanding of potential long-term impacts of fire relative to thinning alone on individual trees. Therefore, the research presented here provides a valuable piece of the critical base of knowledge needed to restore ponderosa pine forests.

Methods

Study Site

The study area is located in the Lick Creek Experimental Site in the Bitterroot National Forest, Montana. The stands used in this study occupy a moderately steep, south facing ridge near 1500m of elevation between the Lost Horse and Rock Creek drainages of the Bitterroot Mountains in western Montana. The study site has been managed for decades. The Lick Creek site was selected for this research because it offers multiple unique advantages. First, the site enabled a comparison of the physiological response of ponderosa pines to different treatments applied to similar, adjacent stands.
(i.e. site to site variability is minimized). Second, the treatments were replicated within
the site allowing for solid statistical analyses. Third, the experimental procedures
(prescribed burning and thinning) are carefully documented by scientists at the Fire
Sciences Laboratory (USFS, RMRS), who also collected a large amount of
complementary data (stand structure, soils, etc.) for the different treatments.

The site was dominated by pole-sized ponderosa pines about 70 years of age that
arose after selective cutting. A small portion of the remaining trees were Douglas-fir.
The stand was pre-commercially thinned in the 1960’s and slash was left untreated. Trees
responded rapidly to this treatment with substantial increases in basal area. In 1992, nine
study units of approximately 3-4 hectares each within the site were commercially thinned
to reduce basal area to approximately 15 m²/ha with the objective of maximizing tree
growth (Arno 1999). Only merchantable timber was removed, leaving slash on the site.
For logistical reasons, the nine thinned units were adjacent to each other and located
immediately to the south of three additional study units, which were left unthinned to
serve as controls.

All 12 units are located adjacent to each other on the dry, south-facing slope. In
this paper, we use the term “treated unit” to distinguish the actively managed stands from
the non-managed control units. Within the nine treated units the following active
management practices were randomly assigned to each of three units: thinning only =
thin-only; thinning followed by wet, spring prescribed fire = spring-burn; thinning
followed by dry, fall prescribed fire = fall-burn. Two fall-burn sites were burned in
September and one in October of 1993 and the spring-burn sites were burned in May
1994, both when trees were actively growing.
At the initiation of the study, 0.04 hectare plots were laid out 33m apart within each of the 12 units. Within each unit, twelve of these plots that were most representative of the overall density and basal area of the unit were selected for intensive sampling of stand characteristics, resource availability and tree responses. No single measurement type was duplicated within any one plot. All measurements were taken during the summer, 2001.

Stand characteristics

Leaf area index (LAI), expressed as m² projected needle area/ m² ground, was measured at the end of the growing season with a Licor 2000 Plant Canopy Analyzer (Lincoln, Nebraska) in 10 plot centers selected at random from the 12 in each unit. A consistently cloudy day was selected for sampling to ensure consistency of measurements under scattered light and reduce variability caused by direct light. Open sky reference measurements were taken from a nearby clearcut before and after the 10 measurements from each unit.

The understory vegetation was sampled in early July. Percent understory cover was estimated visually within 1-meter radius circular sub plots centered at a random number of paces (between 1 and 9) along a randomly selected compass line from the center of each of the 12 plots per unit. Such sampling was necessary because plot centers may have received a disproportionate amount of human foot traffic. Vegetation cover estimates were recorded for each of the following functional groups of understory plants: grasses, herbs, shrubs, ericaceous species, leguminous (nitrogen-fixing) species, and spotted knapweed, as well as downed woody material, pine needles, and bare ground.
Tree seedling occurrences were tallied within 2-meter radius circular plots that were centered on the same sampling point as the cover plots.

Soil Resource Availability

Available nitrogen was measured in two ways: 1) Soil cores were collected on June 25 to provide a one-time measurement of soil available nitrogen during spring. 2) Resin capsules (Unibest, Bozeman, Montana) were installed on June 18 and removed on August 8 to provide a time-integrated analysis of the movement of available nitrogen through the soil.

Soil cores were collected from 5 plots per unit for chemical analysis of nitrate and ammonium. Cores were removed using a soil probe to a depth of 10 cm beneath the surface of mineral soil. Five cores from each plot were combined to make a composite sample from each plot. The composite samples were extracted in KCl and analyzed for ammonium (Willis et al. 1993) and nitrate (Yang et al. 1998) concentration. KCl extracts were temporarily stored in a cool, dark environment and were filtered with 1 gram of acid washed, activated charcoal to remove potential organic acid contamination before nitrate analyses. All nitrate and ammonium concentration values were adjusted for soil moisture content, and are reported on a dry weight basis. In addition to these analyses, a portion of soil from each core was incubated in an anaerobic environment for 2 weeks at 25 C to induce microbial conversion of mineralizable nitrogen to ammonium. This sample was then analyzed for ammonium concentration and the initial concentration of ammonium was subtracted from this value to yield an estimate of potentially mineralizable nitrogen (PMN).
Resin capsules were installed in 10 plots per unit at 10 cm beneath the surface of the mineral soil. Resin capsules absorb and retain nitrate and ammonium ions as the nitrate passes through with the movement of water and ammonium diffuses through the soil. Shortly after removal, the resin capsules were analyzed for ammonium and nitrate concentration after three series of KCl extraction.

Soil moisture was measured at 15, 30, and 45 cm depths beneath the surface of mineral soil in 6 plots per unit. We inserted 61 cm long, 5 cm diameter PVC pipes in the soil prior to the first measurements in early June. Soil was removed from the pipe with a soil auger. PVC caps were installed to keep precipitation from entering the pipes. Volumetric percent soil moisture was measured at each depth (15, 30, and 45 cm) using time domain reflectometry with a Sentry 200 Troxler (Research Triangle Park, North Carolina) over several sampling dates throughout the field season. In nine plots the granitic sand and rock were hard enough to prevent inserting the PCV to a depth of 45 cm. Therefore there are no data at 45 cm for these plots, although sample size was never reduced to less than 4 per unit.

Tree response

Six trees within each unit were selected based upon their 1994 post-treatment diameter, crown ratio (the proportion of tree height with live foliage), and degree of fire-induced crown scorch as recorded in a database provided by Mick Harrington (USFS, RMRS Fire Laboratory, Missoula, MT). The purpose of non-random tree selection was to reduce the possibly confounding effects of differing tree size or crown scorch on tree response to treatment. Tree selection criteria were: diameter between 25-31 cm, a crown
ratio between 60-70% and crown scorch levels between 10-20% in burned units. From among these possible trees, six were selected at random for sampling in each unit, with no two trees selected in the same 0.04 ha plot. Tree diameter, crown ratio, and local basal area were measured for all 72 selected trees in 2001 to verify consistency of tree characteristics and explore the possibility of changes over time.

Tree diameter at breast height (DBH), 1.4m above the ground, was measured from all 6 selected trees in each unit at the end of the 2001 field season. Tree height and crown ratio were measured at the end of the summer with a Criterion 400 Survey Laser. Analysis of 2001 tree diameter and crown ratio data showed no significant differences due to treatment; these parameters were consistent and thus not confounding factors for tree response results. Basal area (m² wood/m² ground) was measured at the end of the summer in each of the six plots per unit selected for individual tree measurements. Measurements were centered on the selected trees. A variable radius basal area tool with 10X conversion factor was used to provide an index of local tree competition and quantify treatment differences. An index of the amount of foliage per tree was calculated for each unit by dividing LAI by basal area. This yielded a proportion in each unit of leaf area relative to cross-sectional bole area at breast height.

Net photosynthesis and needle water potential were measured in 3 trees per unit that were selected at random from the six trees used for structural measurements. Three trees were used for these measurements because of time restraints; field trials suggested peak performance of pines only during late morning and early afternoon. Measurements were taken between 8:30 am and 1:00 pm. Because of the time required to collect these data, measurement were taken over the course of three days such that trees from one unit
of all four treatments were measured each of the three days. We used telescoping pruners to harvest sunlit branchlets from mid-canopy on the south side of selected trees. Immediately after harvest, several 1-year old fascicles were removed from the branch and placed in a sealed, Zip-lock bag with a damp paper towel and transported in a portable cooler for water potential measurement. At the same time, the branchlet was placed in an unsealed Zip-lock bag with a damp paper towel and kept in the sun to keep it from rapidly desiccating without dramatically restricting gas exchange. This procedure was repeated for all 36 trees 4 times over the field season, with two 3-day sampling periods in July and two sampling periods in August. Within each three-day sampling period, the weather was consistently clear with minimal day-to-day temperatures variation.

The foliage samples were transported to a work station for gas exchange and water potential measurements. While the water potential needles were kept in a cooler, 3 bundles (nine needles) were removed from the branch and inserted in the cuvette of a LICOR 6400 Photosynthesis System (Lincoln, Nebraska) to record area-based carbon assimilation ($A_{area}$) and stomatal conductance ($g_s$). The humidity was controlled to be near ambient conditions, PAR (Photosynthetically Active Radiation: 400-700nm) was controlled at 1000 $\mu$mol/m$^2$/s with an external light supply and the carbon dioxide concentration was controlled at 400ppm from an external supply cartridge. Such conditions were intended to measure gas exchange at near optimal CO$_2$ and light conditions. Light intensity, however, was not at saturation levels because of the need to maintain battery power. Field trials of light response curves using the LICOR 6400 suggest light saturation above 1500 $\mu$mol/m$^2$/s for the ponderosa pine at the study site. After the gas exchange rates stabilized and were recorded, water potential ($\Psi$) was
measured from one fascicled bundle of three needles from the cooler. Water potential was measured from the fascicular portion of one needle per tree with a PMS pressure bomb (Corvallis, Oregon).

At the end of the growing season we harvested terminal branchlets from all 6 trees per plot for analysis of foliar morphology, longevity, and chemistry. Several leaf-level characteristics were measured as integrated indicators of physiological performance. 1) Leaf nitrogen content ($N_{\text{leaf}}$), which is closely related to photosynthetic capacity (Reich et al. 1997). 2) Nitrogen stable isotopes, as potential indicators of nitrogen sources from the soil (Nadelhoffer and Fry 1994). Relative enrichment in $^{15}$N may indicate use of deeper soil source for resources uptake (Schulze et al. 1994), which may be related to higher tree stress. 3) Specific Leaf Area (SLA), which is tightly correlated with leaf photosynthetic capacity (Reich et al. 1997). 4) Leaf life span, because long leaf lifespan is associated with high relative resource use efficiency and lower net photosynthetic rates (Gower et al. 1993), and therefore may indicate lower productivity. 5) Leaf carbon isotope ratios, which indicate the time-averaged ratio between leaf internal and air CO$_2$ concentration ($C_i/C_a$); high long-term $C_i/C_a$ is indicated by high discrimination against $^{13}$C, which reflects lower water use efficiency and may indicate higher productivity (Ehleringer and Osmond 1989). These leaf level characteristics may vary as linked groups of traits between treatments, and these interacting traits can affect overall tree productivity (Reich et al. 1992, Reich et al. 1998).

SLA was measured as projected leaf area divided by dry weight of 20 needles per tree. After oven drying (60 C) each needle cohort separately, we calculated the percentage of total branch foliage that was represented by the three youngest years of
needles as an index of relative investment in younger needles. One-year old needles were ground to a fine powder (60 mesh) and weighed with precision for analysis of total nitrogen concentration, carbon stable isotope ratio, and nitrogen stable isotope ratio. The samples were sealed in small tin capsules and shipped to the University of Georgia, Atlanta for chemical analysis. Mass-based leaf nitrogen content and nitrogen isotope ratio ($\delta^{15}N$) were provided from these analyses. Carbon isotope ratio ($\delta^{13}C_{\text{plant}}$) was analyzed relative to PeeDee Belemnite and expressed as discrimination ($\Delta$) following Franquhar and Richards (1984):

$$\Delta = (\delta^{13}C_{\text{air}} - \delta^{13}C_{\text{plant}}),$$

where $\delta^{13}C_{\text{air}}$ was assumed to be -8‰.

Tree diameter growth was measured for all six trees per unit. All trees were cored to the pith using an increment borer at breast height from a side-slope position. We recorded the total xylem width and the total width of the 9 tree rings since thinning in 1992 for comparison with the width of the preceding 9 years of growth. These data were used to calculate ratios of the area of wood produced at breast height since treatment to the area produced during the same number of growing seasons before treatment. It is important to note that there was a year of growth between thinning and burning treatments, such that growth after fire application occurred for only 8 of the 9 years measured.

Data Analysis

The treatments of thinning and prescribed fire were applied to the site units, not to the individual sampling plots. To avoid pseudoreplication, all plot-level
measurements were considered sub-samples and the unit means were considered the ultimate sample, such that n=12 (3 per treatment). Most data were analyzed using one-way ANOVA with treatments as a factor (with 4 levels) and using Least Significant Difference (LSD) posteriori test for multiple mean comparisons. Physiological measurements that were repeated through the season (photosynthesis, conductance, water potential) were also analyzed using Repeated Measures ANOVA, with the treatment and sampling date as factors. Treatment x date interactions were explored in the Repeated Measures ANOVAs. Differences were determined significant at the $\alpha = 0.05$ level.

Results should be interpreted conservatively because the high number of response variables in this study renders the study-wide likelihood of a type I error higher than the chosen $\alpha = 0.05$. All response variables measured in this study displayed normal distributions. With few noted exceptions, most variables also displayed homogeneity of variance

**Results**

**Stand characteristics**

Leaf Area Index nine years after treatment was significantly higher in control units than in all other treatment units ($P < 0.05$). There were no significant differences in LAI between thin-only, spring-burn, and fall-burn units (Fig. 1). Basal area displayed the same pattern, with higher basal area in control units relative to treated units ($P < 0.001$), and no differences between the treated units (Fig. 2). These results reflect the lower amount of foliage and tree basal area in treated units due to the removal of trees in 1992. The mean proportion of leaf area to cross sectional bole area was lower (839
m²/m²) in control units than in the thin-only, spring-burn, and fall-burn units (1192, 1336, and 1138 m²/m² respectively) although none of the differences were significant.

Understory vegetation cover differed due to treatment (Fig. 3). There was a trend of lower cover of knapweed in control units than treated units, although the differences were not significant. There was significantly (P < 0.01) higher cover of nitrogen fixing legumes (predominantly *Lupinus* species) in the control units than in all treated units. Ericaceous cover tended to be lower in fall-burn units, although the difference was not significant. Grass cover was significantly higher in control units than in fall-burn units (P < 0.05) and no other differences were significant. Cover of all other herbs did not differ significantly due to treatment, but was generally lowest in control units. Shrub cover was similar between treatments. The percent cover of knapweed, legumes, other herbs, and downed woody material did not satisfy homogeneity of variance tests. However, in light of the small sample size (n = 3 per treatment) all data were analyzed assuming equal variance.

The cover of non-vegetative ground cover types also differed between treatments (Fig. 4). Cover of downed woody material was significantly highest in thin-only treatments (P < 0.05), reflecting the unburned slash due to thinning. Bare ground was significantly higher in units of both burning treatments relative to control and thin-only units due to the consumption of live and dead organic fuels (P < 0.05). Most of the duff was composed of needles, which covered significantly less ground in spring-burn units relative to all other treatments (P < 0.05). Although there were no significant differences, there were generally less tree seedlings of both ponderosa pine and Douglas-
fir in control units, more ponderosa pine seedlings in burned units, and less Douglas-fir seedlings in fall-burn units relative to thin and spring-burn units (Fig. 5).

Resource availability

We found mixed evidence for treatment effects on nitrogen availability. Ammonium availability in June, based on soil core analysis, was significantly lower in control units than in all treated units ($P < 0.05$, Fig. 6). However, this trend was not corroborated by the time-integrated ammonium availability measured with resin capsules (Fig. 7), which showed no significant differences between treatments. Based on June soil core and resin capsule data nitrate availability was lower in burned units (Figs. 8 & 9) relative to thin-only and control units. These differences were statistically significant for resin capsules data only ($P < 0.05$). There were no significant treatment effects for potentially mineralizable nitrogen (Fig. 10), but the tendency for lower PMN values in spring-burn units was consistent with the tendency for lower ammonium availability estimated from resin capsules in spring-burn units.

Soil moisture availability was not significantly different between any treatments throughout the season at any of the three sampling depths (Figs. 11-13). Soil moisture was relatively high at all depths in early June, and declined at all depths through June and July. Intense local thunderstorms dropped heavy rains on the site during the afternoons of July 29 and 30. This is reflected by the relatively high soil moisture values recorded in early August, even as deep as 45 cm. Following these storms, a hot August dried the soils to the lowest moisture levels measured during the field season. Soil moisture increased at all depths with the onset of fall rains.
Tree response

Photosynthetic rates ($A_{area}$) remained relatively constant throughout the season with only weak declines in August ($P_{date} > 0.05$, Figure 14). Overall, $A_{max}$ was lower in the control trees relative to trees in any treatment ($P_{treatment} < 0.05$; 2 way ANOVA, Figure 15). Stomatal conductance ($g_s$) followed similar patterns to photosynthesis (Fig. 16), although there was a significant ($P < 0.05$) date effect in addition to overall significantly ($P < 0.05$) lower values in the control than in any of the treated stands (Fig. 17). When analyses were conducted for the three treated units, there was no effect of treatment for any of the gas exchange variables.

Leaf water potential ($\Psi$) values were not significantly different between treatments for any sampling date through the summer (Fig. 18). However, trees in control units tended to have lower (more negative) $\Psi$ values than in the treated units for both sampling dates in July. Regardless of treatment, $\Psi$ declined to values close to -2.0 MPa daily as the day warmed and the air dried. Because of the strong decrease toward constant values, early morning $\Psi$ was used as a better indicator of whole tree water stress. Therefore, water potential data were reexamined with the removal of data collected after 10:00 AM when trees began reaching constant $\Psi$ values near -2.0 MPa. Such analysis revealed significant water potential declines during the summer ($P_{date} < 0.05$, Figure 19) and overall significantly lower (more stressed) early morning $\Psi$ values in control trees relative to trees from treated strands ($P_{treatment} < 0.05$; 2 way ANOVA, Figure 20). There was also a significant treatment x date interaction (Figure 19).
Specific leaf area was not different between trees of any treatment (Fig 21). Overall, spring-burn trees had slightly lower SLA than other trees, but this difference was not significant.

Total foliage dry weight was significantly higher for spring-burn trees than for control trees (Fig. 22, $P < 0.05$). Although not statistically significant, fall-burn trees exhibited lower mean foliage production than thin-only and spring-burn trees. Control trees displayed significantly lower proportions of young (1-3 year old) foliage than trees in all other treatments (Fig. 23).

Leaf chemical analysis revealed no significant differences in foliar nitrogen content ($N_{\text{leaf}}$), foliar nitrogen isotope ratio ($\delta^{15}N$), or foliar carbon isotope discrimination ($\Delta$) due to treatment (Figs 24-26). Although none of the differences were significant, $\delta^{15}N$ means were higher in foliage from burned units than in foliage from control or thin-only units (Fig. 25). This trend is corroborated by the fact that the pooled $\delta^{15}N$ values from control and thin-only were significantly ($P < 0.05$) lower than the pooled values from both burned units.

The ratio of wood growth 9 years after treatment to wood growth 9 years before treatment was significantly lower in control trees than in all other treatments, except the fall-burn ($P < 0.05$, Fig. 27). This reflects lower relative wood production in control trees after treatment initiation in 1992. Similar to foliage production, fall-burn trees tended to display lower productivity relative to trees from the thin-only and spring-burn treatments, although these differences were not significant.
Discussion

The results of this case study may have important implications for forest management in the northern Rocky Mountains. The two most important findings for ponderosa pine management in this study are: 1) Treatments of thinning and thinning followed by prescribed spring or fall fire improved the long term physiological performance of second growth ponderosa pines relative to untreated controls. 2) The improvement in performance was not different between these three management options. These findings suggest that the similar improvement in tree performance from different active management practices resulted primarily because the removal of trees resulted in similar basal area between treated units. Lower conifer competition in the treated units combined with higher light availability due to decreased total leaf area is the most probable explanation for the improved physiological performance of the pines in actively managed units.

As expected, the thinning prescription in 1992 had long-term effects on the structure of the treated stands. Nine years after treatment, LAI and basal area were higher in the control unit relative to any of the treated units. Because most mature ponderosa pines survived in both the spring-burn and fall-burn units, there were no significant, long-term differences in overall stand structure between managed units. There was an observed tendency towards higher ponderosa pine seedling densities in spring-burn and fall-burn units. Such differences could potentially result in changes in forest age structure in the long-term depending upon whether or not fire is periodically reintroduced.

Understory sampling demonstrated both predictable results and surprising patterns. As expected (Sandberg 1980, Harrington 1987, Fule et al. 1997), burned units
had lower cover of woody material, small trees, pine needles, and shrubs. The tendency of higher cover of spotted knapweed in burned units is consistent with the higher levels of bare ground and corroborates the fact that expansion by exotic weeds can be a risk of active forest management. However, the higher cover of legumes and grasses found in control units conflicts with previous studies in ponderosa pine that show increased cover of nitrogen fixing species and grasses after fire (Andariesse and Covington 1986, Sparks et al. 1998, Newland and Deluca 2000). There is a possibility that these differences were due to the non-random assignment of control units nearer to the ridge top where the slope is less steep than in treated units. Another possibility is that the differences we found were prevalent before the treatments were applied due to the active management history of the site (Arno 1999); for example, tree removal in the 1960's may have provided significant opening of the forest canopy to allow for expansion of legumes.

Unfortunately, we do not have understory vegetation surveys from before treatment application to verify such hypotheses. Regardless of the underlying explanation, the higher cover of nitrogen-fixing species in control units did not result in higher available nitrogen in control soils as measured by any of the techniques used in this study.

Fire is known to cause large, short-term increases in available mineral nitrogen in ponderosa pine systems (Kovacic et al. 1986, Monleon et al. 1997). Deluca and Zouhar (2000) showed that ammonium levels peaked sharply immediately after fire and declined to pre-fire levels within 2-3 years. Interestingly, nine years after treatment, we found significantly higher soil ammonium concentrations in June from treated units relative to control units. Such long-term effects are, therefore, not due to prescribed fire but most likely due to the decay of underground portions of trees killed in the thinning treatments.
This pattern, however, was not corroborated from the time-integrated resin capsule data. The lack of treatment differences in PMN is also consistent with the lack of differences in time-integrated (resin capsule) ammonium availability. While we did not find significant treatment differences in time-integrated ammonium availability, temporary flushes of ammonium (as detected from our June sampling), may be ecologically important if such flushes occur during the most active part of the growing season.

Nitrate levels are also known to increase following fire in ponderosa pine systems, although not as immediately as do ammonium levels, and to decline thereafter to levels at or below those before fire and remain suppressed for as long as 12 years (Kovacic et al. 1986, Covington and Sackett 1992). Consistent with these patterns, our results from resin capsules and one-time sampling in June suggest that nitrate availability nine years after treatment was lower in burned units than in thin units and control units.

The $\delta^{15}$N results suggest relative enrichment of $^{15}$N in leaf tissue from trees in burned units compared to trees in unburned units. The significantly higher foliar $\delta^{15}$N from burned units is consistent with findings of Sala et al. (unpublished) in old growth ponderosa pine in which trees receiving prescribed fire displayed higher relative foliar $^{15}$N than trees in unburned stands. Numerous studies support a positive relationship between soil depth and soil $^{15}$N abundance (Shearer et al. 1978, Mariotti et al. 1980, Tiessen et al. 1984). The relative $^{15}$N enrichment in burned units may reflect acquisition of soil resources from greater depth due to fire damage to surface roots. Alternatively, relative enrichment in response to fire may be due to strong discrimination against the heavier isotope during partial combustion.
We did not find treatment differences in soil water availability; soil moisture content changed nearly identically in all treatments in response to both precipitation and drought. It is possible that higher LAI in the control units relative to the treated units may have been offset by lower individual tree water use in the control units due to stronger daily declines of needle water potential that induced stomatal closure. This is consistent with the lower early morning needle water potential in the control stands.

In general, the resource availability measurements in this study reveal no significant treatment effects on long-term soil moisture content, and only moderate plant-available nitrogen differences. Neither the slightly higher ammonium availability in treated stands nor the slightly lower nitrate availability in burned stands had measurable effects on leaf-level nitrogen status at Lick Creek, as evidenced by the lack of treatment effect on $N_{\text{leaf}}$. However, while there were no between-treatment differences in $N_{\text{leaf}}$, there may be higher tree-level nitrogen in treated units as evidenced by the trend towards higher mean proportion of foliage per tree in treated units. If treated trees have more foliage, then the treatments may have improved tree-level nitrogen status despite of our lack of strong evidence for consistent, treatment-induced differences in available nitrogen.

In spite of the between-treatment similarities in soil resource availability, some of the measured indices of tree growth and physiological status provide evidence that long-term ponderosa pine performance at the study site was improved by the application of both thinning and thinning followed by fire. Overall, $A_{\text{area}}$, $g_s$, early morning $\Psi$, percent of foliage allocated to younger needles and relative wood production were significantly lower in the control units than in all treated units. These findings are not surprising since
tree competition for resources was presumably higher in control units, and basal area reduction frequently improves growth of ponderosa pine because of the release from competition (Fiddler et al. 1989, Arno et al. 1996).

Water availability strongly influences ponderosa pine performance. Ponderosa pines of the northern Rocky Mountains are most physiologically active during the early summer (Marshall et al. 2001). Summer drought reduces water availability and trees close stomata in response, which slows carbon assimilation and growth rates (Zhang et al. 1997, Olivas-Garcia et al. 2000). Ponderosa pine is very susceptible to xylem cavitation and prevents destructive embolisms by closing stomata at the onset of water stress (Piñol and Sala 2000, Maherali and DeLucia 2000). This is consistent with the fact that the absolute minimum leaf water potential during the 2001 growing season at the Lick Creek site was -2.2 MPa. The onset of summer drought explains the general decrease in photosynthesis, conductance, and water potential through August (Law et al. 2001). The heavy precipitation of July 29th and 30th may have maintained high gas exchange later in the summer than is common in ponderosa pine, as soil moisture can influence photosynthesis and conductance in ponderosa pine (Panek and Goldstein 2001). Higher soil moisture from these precipitation events apparently did not entirely compensate for the heat and dry air of late summer because photosynthesis in ponderosa pine is also highly sensitive to vapor pressure deficit (Kolb and Stone 2000). Morning water potential values were relatively low in all treatments during the August 1-3 sampling period, and declined dramatically by August 22 when photosynthesis and conductance values were lowest. The lack of differences in carbon isotope discrimination between treatments suggests that none of the treatments induced
important differences in time-averaged \( C_i/C_a \). It is possible that time-averaged \( C_i/C_a \) was similar between control trees and treated trees for different reasons; earlier stomatal closure in control trees and higher rates of photosynthesis in treated trees may have led to similar long-term \( C_i/C_a \) values.

While one-year old needles from control trees exhibited overall lower photosynthetic rates relative to trees from managed stands, there were no significant differences in SLA or leaf nitrogen content due to treatment. Cregg (1993) also reported minimal SLA differences in ponderosa pine in response to environmental conditions.

The lack of correlation between \( N_{\text{leaf}} \) and \( A_{\text{area}} \) is surprising in light of previous results that support a tight correlation between maximum photosynthetic rate \( (A_{\text{max}}) \) and \( N_{\text{leaf}} \) (Reich et al. 1997; Carey et al. 1998; Nagel and O’Hara 2001). It is important to note that we measured mass-based leaf nitrogen content and area-based photosynthesis. It is highly unlikely that this methodology obscured a nitrogen-photosynthesis relationship; Nagel and O’Hara (2001) suggest that relationships between \( A_{\text{max}} \) and \( N_{\text{leaf}} \) are consistent in ponderosa pine regardless of how these parameters are expressed. More likely is that treatment induced differences in \( \Psi \) controlled differences in \( A_{\text{area}} \) at Lick Creek. Although temperature, PAR, humidity, time since foliage excision, and CO\(_2\) concentration were all tightly controlled in our \( A_{\text{area}} \) measurements, foliar \( \Psi \), and thus the degree of stomatal opening, were determined by the individual tree measured. While \( A_{\text{max}} \) may be correlated to \( N_{\text{leaf}} \) at Lick Creek, differences in \( A_{\text{area}} \) as measured in this study are, consistent with previous studies, ultimately determined to a large degree by tree water status (Zhang et al. 1997, Dang et al. 1997, Panek and Goldstein 2001).
The tendency for higher total foliage production in treated stands (significantly different only between control and spring-burn units) is consistent with the improved performance of trees in managed units, because increased photosynthesis and water status support improved growth (Powers and Reynolds 1999). The longevity of foliage also may have important implications for tree performance. The lower proportion of foliage mass in younger leaves represents a greater relative investment in older leaves in control trees; trees in control units retained foliage longer than trees in managed units. Older pine needles tend to have lower rates of photosynthesis (Clark et al. 1995). Furthermore, trees with relatively longer lived foliage tend to have lower relative growth rates and lower production efficiency (Reich et al. 1992). The trees in the control units may retain foliage longer on their branches to compensate for lower needle level photosynthetic capacity or to serve as storage tissue for nutrients (Gower et al. 1993).

The improved physiological performance of pines in managed stands correlates with higher rates of relative wood production since treatment implementation compared to control trees. Based on our tree ring analysis, trees in managed units exhibited a release from competition that was not evident in control trees. However, these treatment differences were statistically significant between control and thin-only and control and spring-burn but not between control and fall-burn. Many trees from fall-burn units exhibited a delayed competition release response 2-3 years after treatment (rather than an immediate response as observed in the thin-only and spring-burn treatments). One likely explanation is that greater fire-induced damage in fall-burn trees triggered a stress response that temporarily reduced growth. The tree core data suggest that although the
Fall prescribed fire may have induced more damage to trees in the short-term, long-term tree performance was not severely hindered by the application of fire in the fall.

Inferences drawn from $A_{\text{area}}$ data at Lick Creek should be tempered by the consideration of several caveats. Despite keeping PAR below saturation levels, our reported rates of photosynthesis probably overestimated actual photosynthesis because of the relatively high carbon dioxide concentration (400 ppm) maintained in the LICOR 6400 chamber. Furthermore, $A_{\text{area}}$ was measured for one-year old foliage and sampling only one-year old foliage may not have thoroughly quantified tree-level performance. Further studies of ponderosa pine physiological performance at Lick Creek would benefit from exploring the possibility of foliar age-related differences in photosynthesis, particularly in light of the treatment-induced differences in leaf longevity revealed in this study. Finally, our research was a case study at a site with a unique combination of site history and treatment application. The Lick Creek site has an active management history including fire exclusion and timber harvest. The treatments applied in this study in the 1990’s represent a sample of the many management options used in ponderosa pine forests. Thinning in this study reflects only the specific thinning applied: the removal of merchantable trees with a target remaining basal area of approximately 15 m²/ha, without slash removal.

While active management by either thinning or thinning followed by prescribed fire ameliorated tree performance, our results suggest that the specific treatments did not have major influences on the long-term tree performance. In general, indicators of tree performance (gas exchange, growth, and foliage production) were similar for trees in thin-only, spring-burn, and fall-burn units throughout the season. The only exception was
a tendency for fall-burn trees to exhibit slightly lower wood and foliage production even nine years after treatment implementation. Again, such lower response relative to thin-only and spring-burn may relate to a stronger initial stress response to more intense fire in the fall. Apparently the lower time-integrated soil nitrate concentration we found in burned units relative to thin units did not have any long-term effect on foliage performance or wood growth. While more studies are necessary to make generalizations, there is no evidence from this case study that the application of prescribed fire after thinning improves long-term second-growth ponderosa pine performance to a greater extent than thinning alone. On the contrary, our results suggest that dry, fall fires may cause an initial differential carbohydrate allocation that delays the benefits of reducing competition by thinning alone. However, there is no evidence that the season of fire application or severity of fire after thinning affects long-term pine performance. These results are not consistent with some previous studies that have found a reduction in ponderosa pine performance induced by spring fire (Grier 1989, Busse et al. 2000), but do emphasize that ultimately, ponderosa pine response to management is very sensitive to the specific conditions (physiological activity of the trees, fire characteristics, etc.) under which management is implemented.

There are two important philosophically and practically different perspectives from which to interpret the findings from this case study. The first is that if the primary goals of land owners or land managers are to improve the health and productivity of ponderosa pines while reducing the immediate risk of stand-destroying wildfire, thinning alone may serve as a sufficient surrogate for the role historically played by fire (Scott and Fletcher 1998). Indeed, no additional physiological benefits for pines due to the addition
of fire can be inferred from this study. An important caveat to this conclusion is that fire may retard the future invasion of competing conifers in ponderosa pine stands. Fire readily kills seedlings and saplings. Therefore, the benefits for pine health and the reduction of fire risk may be shorter lived when fire does not follow thinning.

The second perspective through which to interpret this research takes into account the goal of ecological restoration. This perspective acknowledges that fire can benefit elements of ponderosa pine forests other than tree performance per se and reduced fire risk. Fire may help restore historic understory vegetation composition (Sparks et al. 1998, White and Loftin 2000), which can improve the quantity and quality of forage for wildlife (Merrill et al. 1982, Carlson et al. 1993). Although still controversial, fire reduces the organic soil and duff layers, which may improve nutrient cycling (White 1986). The temporary peak in available nitrogen following fire supplies an important burst of resources, stimulates understory growth and flowering, and may restore more labile nutrient cycling on a stand-level scale (DeLuca and Zouhar 2000). Fire often kills some trees, which can create forest heterogeneity and gaps for seedling recruitment and establishes standing dead trees, which provide numerous benefits to many wildlife species. Fire is a natural, historically recurrent disturbance to which ponderosa pine communities are well adapted; there may be profound, complicated ecological benefits from fire that are as yet unknown. Furthermore, ecological benefits of fire may depend upon the season of fire application. From an ecological restoration perspective, this case study provides evidence that the addition of prescribed fire to thinned ponderosa pine does not necessarily induce a reduction in pine performance relative to thinning alone. Therefore, in light of other benefits of fire to ponderosa pine systems, this study suggests
that fire may be applied in the fall or spring after stand thinning, as applied in this study, without degrading long-term ponderosa pine health or productivity.
Literature Cited


Figure 1. Leaf Area Index (LAI) for each treatment. Error bars represent 1 standard error. Different letters denote significant differences at $\alpha=.05$. 
Figure 2. Basal area around studied trees in each treatment. Error bars represent 1 standard error. Different letters denote significant differences at α=.05.
Figure 3. Understory vegetation composition of different functional groups for each treatment. K=knapweed, L=legume, E=ericaceous species, G=grass, H=other herbaceous, S=non-ericaceous shrub. Error bars represent 95% Confidence Intervals of the mean. Within each cover type, different letters denote significant differences at $\alpha=0.05$. 
Figure 4  Percent cover of non-vegetative ground cover types in each treatment. Error bars represent 95% Confidence Intervals of the mean. Within each cover type, different letters denote significant differences at $\alpha = .05$. 
Figure 5. Tree seedling density within each treatment. Error bars represent 95% Confidence Intervals of the mean.
Figure 6. Soil ammonium concentration in each treatment measured on June 25. Error bars represent 1 standard error. Different letters denote significant at $\alpha=.05$. 
Figure 7. Ammonium concentration of resin capsules from each treatment. Error bars represent 1 standard error.
Figure 8. Soil nitrate concentration in each treatment measured on June 25. Error bars represent 1 standard error.
Figure 9. Nitrate concentration of resin capsules from each treatment. Error bars represent 1 standard error. Different letters denote significant differences at $\alpha=.05$. 
Figure 10. Potentially mineralizable nitrogen (PMN) in each treatment from soils collected June 25. Error bars represent 1 standard error.
Figure 11. Percent volumetric soil moisture content at 15 cm depth for each treatment throughout the field season. Error bars represent 1 standard error.
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Figure 15. Net photosynthesis of one year old needles from selected trees in each treatment from all sampling dates. Error bars represent 1 standard error. Different letters denote significant differences at $\alpha=.05$. 
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Figure 18. Leaf water potential values of one-year old needles from each treatment throughout the sampling season. Error bars represent 1 standard error.
Figure 19. Early morning leaf water potential values of one year old needles from each treatment. Error bars represent 1 standard error. Within each date, different letters denote significant differences at $\alpha=.05$. 
Figure 20. Early morning leaf water potential values of one year old needles from each treatment from all sampling dates. Error bars represent 1 standard error. Different letters denote significant differences at $\alpha=0.05$.
Figure 21. Specific leaf Area (SLA) of one-year old needles from each treatment. Error bars represent 1 standard error.
Figure 22. Total dry weight of foliage from harvested terminal branchlets from each treatment. Error bars represent 1 standard error. Different letters denote significant differences at $\alpha=.05$. 

- Control
- Thin
- S-burn
- Fallburn
Figure 23. The percent of total branchlet foliar dry weight represented by 1-3 year old foliage in each treatment. Error bars represent 1 standard error. Different letters denote significant differences at $\alpha=.05$. 
Figure 24. Nitrogen content of one-year old foliage from each treatment. Error bars represent 1 standard error.
Figure 25. Nitrogen isotope ratio of one-year old needles from each treatment. Error bars represent 1 standard error.
Figure 26. Carbon isotope discrimination in tissue of one-year old foliage from each treatment. Error bars represent 1 standard error.
Figure 27. The ratio of diameter adjusted wood production 9 years after treatment to 9 years before treatment. Error bars represent 1 standard error. Different letters denote significant differences at $\alpha=0.05$. 