

Physiological responses of ponderosa pine in western Montana to thinning, prescribed fire and burning season

ANNA SALA,^{1,2} GREGORY D. PETERS,¹ LORNA R. MCINTYRE¹ and MICHAEL G. HARRINGTON³

¹ Division of Biological Sciences, The University of Montana, Missoula, MT 59812, USA

² Corresponding author (sala@mso.umt.edu)

³ Fire Sciences Laboratory, USFS Rocky Mountain Research Station, P.O. Box 8089, 5775 Highway 10, Missoula, MT 59807, USA

Received May 9, 2003; accepted August 28, 2004; published online January 4, 2005

Summary 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 exclusion has contributed to denser ponderosa pine forests with greater competition for resources, higher tree stress and greater risk of insect attack and stand-destroying fire. Active management intended to restore a semblance of the more sustainable historic stand structure and composition includes selective thinning and prescribed fire. However, little is known about the relative effects of these management practices on the physiological performance of ponderosa pine. We measured soil water and nitrogen availability, physiological performance and wood radial increment of second growth ponderosa pine trees at the Lick Creek Experimental Site in the Bitterroot National Forest, Montana, 8 and 9 years after the application of four treatments: thinning only; thinning followed by prescribed fire in the spring; thinning followed by prescribed fire in the fall; and untreated controls. Volumetric soil water content and resin capsule ammonium did not differ among treatments. Resin capsule nitrate in the control treatment was similar to that in all other treatments, although burned treatments had lower nitrate relative to the thinned-only treatment. Trees of similar size and canopy condition in the three thinned treatments (with and without fire) displayed higher leaf-area-based photosynthetic rate, stomatal conductance and mid-morning leaf water potential in June and July, and higher wood radial increment relative to trees in control units. Specific leaf area, mass-based leaf nitrogen content and carbon isotope discrimination did not vary among treatments. Our results suggest that, despite minimal differences in soil resource availability, trees in managed units where basal area was reduced had improved gas exchange and growth compared with trees in unmanaged units. Prescribed fire (either in the spring or in the fall) in addition to thinning, had no measurable effect on the mid-term physiological performance and wood growth of second growth ponderosa pine.

Keywords: forest management, photosynthesis, *Pinus ponderosa*, prescribed burning, soil nitrogen, water potential.

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 region where frequent (typically 5–25 year intervals), low-intensity surface fires maintained open, sustainable and biologically diverse stands (Martin 1982, Arno 1988). Euro-American settlement in western North America was followed by a decrease in fire frequency in most ponderosa pine forests. In the past century, in particular, reduced indigenous burning (Barrett and Arno 1982), active suppression of lightning and human-caused fires, reduction of flammable fine fuel cover by grazing (Savage and Swetnam 1990) and new barriers to wildfire spread due to human-induced ecosystem fragmentation (Arno 1988) have contributed to dramatic changes in ponderosa pine forests (Covington and Moore 1994). In the northern Rocky Mountains, these changes have resulted in the dominance of second growth stands with higher tree density, greater living and dead biomass and altered species composition relative to historic conditions (Hartwell et al. 2000). These stands experience greater competition for resources and greater risk of pathogen outbreaks, insect attack and stand-replacing fires (Feeney et al. 1998, Keane et al. 2002). Because of these negative effects, there is increasing use of prescribed fire and thinning to partially restore historic conditions (Arno et al. 1995, Powers and Reynolds 2000).

Numerous studies have examined the effects of thinning and prescribed fire on tree growth, mortality and recruitment, as well as on changes in nutrient cycles and understory vegetation structure and function in ponderosa pine ecosystems (e.g., Arno et al. 1996, Monleon et al. 1997, Kaye and Hart 1998, Busse et al. 2000). Little is known, however, about the mid- (8–20 years) and longer-term effects of thinning and prescribed fire on the physiological performance of second growth ponderosa pine.

Ponderosa pine physiology is sensitive to stand structure (Nagel and O'Hara 2002) and has been shown to respond positively to reductions of basal area (Kolb et al. 1998, McDowell

et al. 2003) and the use of low-severity prescribed fire. In the short term (1–3 years), thinning alone or thinning followed by burning has resulted in increased soil water availability and improved physiological performance of second growth (Skov et al. 2004) and old growth (Feeney et al. 1998) ponderosa pine. However, longer-term (> 5 years) effects on ponderosa pine of thinning followed by prescribed fire relative to thinning alone are unknown.

A possible mechanism for mid- to long-term effects of fire on ponderosa pine is through nutrient cycling. Fire exclusion in low-elevation ponderosa pine systems may have negative consequences on nitrogen cycles, with the accumulation of large stores of organic nitrogen (Covington and Sackett 1984, Wright and Hart 1997, DeLuca 2000). Several studies have shown temporary increases in mineral soil nitrogen concentration after fire (Kovacic et al. 1986, White 1986, Covington and Sackett 1984, 1992, Monleon et al. 1997, DeLuca and Zouhar 2000). However, this effect does not appear to persist, and it has been shown that, within 1 to 2 years after the fire, several indices of nitrogen availability and transformation rates begin to decline with time (Monleon et al. 1997, DeLuca and Zouhar 2000). Because leaf nitrogen content directly impacts leaf properties and photosynthetic capacity (Reich et al. 1997), direct and indirect effects of different management practices on soil nitrogen availability may have lasting consequences for the physiological performance of ponderosa pine.

Historically, ponderosa pine forests of the northern Rocky Mountains typically burned during the late summer and early fall (Agee 1993). However, much prescribed burning in the northern Rocky Mountains is conducted during the spring, when conditions are cooler and wetter, to reduce burn severity and improve smoke dispersal. Prescribed burning in spring, a period of high physiological activity, has been shown to reduce fine root biomass of ponderosa pines when large amounts of biomass were consumed (Grier 1989), and to reduce growth rates and increase mortality relative to unburned trees (Swezy and Agee 1991, Landsberg 1994, Busse et al. 2000). In contrast, Wyant et al. (1983) reported positive growth responses to prescribed burning in the fall and Feeney et al. (1998) found no negative effects of fall burning in previously thinned stands. However, no studies to date have directly compared responses to spring and fall burning.

Here, we examined mid-term (8 and 9 years post-treatment) effects of three treatments on physiological performance and growth in a western Montana ponderosa pine forest. We compared soil resource availability, tree physiological performance and wood radial increment after the implementation of four management practices: stand thinning followed by prescribed burning in the spring, prescribed burning in the fall, or no burning; and untreated control. Specifically, we addressed the following questions: (1) How do thinning and prescribed fire treatments affect mid-term ponderosa pine physiological performance relative to untreated controls? (2) Are there differences in mid-term ponderosa pine performance among stands receiving thinning only, thinning followed by spring fire and thinning followed by fall fire?

Materials and methods

Study site and treatments

The study area is located in the Lick Creek Experimental Site in the Bitterroot National Forest of western Montana (46°5' N, 114°15' W). The site is semi-arid, with approximately 500 mm mean annual precipitation, about half of which falls as snow (Gruell et al. 1982). The study was conducted on a stand occupying a moderately steep (15°), south-facing slope (elevation approximately 1500 m) that has been actively managed for about 90 years. The site is dominated by ponderosa pines about 70 years of age, which arose after selective cutting. A small portion of the remaining trees were Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco). The original stand of old ponderosa pine was selectively harvested around 1909 and again in the 1950s. The stand was pre-commercially thinned in the 1960s and slash was left untreated. Trees responded rapidly to the thinning treatment, with substantial increases in diameter growth (Arno 1999).

In 1991, twelve study units, approximately 3–4 ha each, were established adjacent to each other in a research design of four treatments with three replicates. Nine units received a stand density reduction treatment and three units located immediately upslope were left unthinned to serve as controls. Such non-random assignment of control units was necessary to minimize fire hazard. Three of the nine thinned units received one of the three prescribed fire treatments, assigned randomly: spring burn, fall burn or no burn. In this paper, we use the term “treated unit” to distinguish the thinned units from the untreated control units. The following terminology is used to designate the three types of treated unit: thinning only = “thin-only”; thinning followed by prescribed fire in the spring, under wet conditions = “spring-burn”; thinning followed by prescribed fire in the fall, under dry conditions = “fall-burn.” Within each of the twelve units, twelve 0.04-ha circular plots were laid out systematically (33 m apart) for sampling of stand characteristics, soil resource availability and tree response.

Treatments were initiated in 1992, when all thinning units were commercially thinned to reduce Douglas-fir of all sizes and remove smaller ponderosa pine, with the objectives of reducing competition and the potential for crown fire for the remaining pines (Harrington 1999a). Only merchantable trees (20–30 cm in diameter 1.4 m above ground) were removed and some of the slash was left on the site. Basal area (m^2 wood ha^{-1}) was reduced from a preharvest mean of approximately $21 \text{ m}^2 \text{ ha}^{-1}$, 93% of which was ponderosa pine, to approximately $14 \text{ m}^2 \text{ ha}^{-1}$, 98% of which was ponderosa pine. Stand density was reduced from 420 trees ha^{-1} to 280 trees ha^{-1} , leaving a fairly uniform distribution of trees. The fall-burn units were burned in either September or October of 1993, when buds were set and radial growth was complete. The spring-burn sites were burned on two consecutive days in May 1994, when buds were expanding. To avoid high midday temperatures, fires were applied during the early morning when temperatures were between 10 and 23 °C, humidity was between 35 and 75% and wind speed was less than 8 km h^{-1} , using strip head fires. Fuel loads were generally light, and a

significant fraction of litter and much of the woody debris (including slash) were consumed in both the spring and fall burns, with greater woody and forest floor reduction in fall burn units (mean pre-fire forest floor consumption of 41 and 70%, respectively). Fuel moisture contents were generally higher in the spring, with the exception of litter, which had higher moisture content in the fall due to cool mornings with high relative humidity (Harrington 1999b). About 60% of standing trees between 2 and 18 cm DBH were killed in both the fall and the spring burn, mostly as a result of crown scorch (Harrington 1999a). Only 3% of trees greater than 18 cm DBH (the majority smaller than 25 cm DBH) were dead 4 years after either the spring or fall burn.

Stand characteristics

Leaf area index (LAI), calculated as projected needle area divided by ground area, was measured at the end of the 2001 growing season with a Li-Cor 2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE) at ten plot centers selected at random from the twelve in each unit. Basal area was measured at the end of summer 2001 in six plots per unit using a variable-radius basal area prism with 10 \times conversion factor (Shiver and Borders 1996). For each unit, leaf area: cross-section bole area at breast height was calculated as LAI divided by basal area to assess whether treatments influenced the relative proportion of foliage to wood.

Soil resources

On June 25, 2001, mineral soil was sampled in six plots selected at random from the twelve units, and analyzed for nitrate and ammonium. Five soil cores per plot (distributed at 1-m intervals along the slope, starting 1 m south of the plot center) were removed with a soil probe to a depth of 10 cm beneath the surface of mineral soil. The five samples from each plot were combined. A 30-g subsample was oven-dried at 105 °C for 72 h to calculate soil water content. Ammonium and nitrate were extracted by placing 30 g of fresh mineral soil in 50 ml of 2 M KCl, shaking for 30 min, and filtering the extracts through Whatman 42 ash-free filter paper on a vacuum extraction manifold. Extracts were analyzed for ammonium following the Berthelot reaction method (Willis et al. 1993) and for nitrate by nitration of salicylate as described by Yang et al. (1998). All nitrate and ammonium concentration values were corrected for water content and reported on a dry mass basis.

Anaerobically mineralizable nitrogen (AMN; Binkley and Hart 1989) was measured from each composite sample per plot as an estimate of potentially available nitrogen. Ten ml of deionized water was added to 5.0 g of moist field soil in a 50-ml centrifuge tube. Dinitrogen gas was added to the headspace, the tubes sealed and incubated at 25 °C for 14 days to allow for microbial conversion of mineralizable nitrogen to ammonium without subsequent formation of nitrate. After the incubation period, 10 ml of 4 M KCl was added to each tube, the contents shaken for 30 min and the extracts then filtered through Whatman 42 ash-free filter paper on a vacuum extraction manifold. Ammonium was analyzed as described above and expressed on a soil dry mass basis. The initial concentration of ammonium was subtracted from this value to yield an

estimate of AMN.

Time-integrated nitrate and ammonium availability was assessed by the resin capsule method, whereby ionic resin capsules buried in the mineral soil absorb nitrate and ammonium moving through by mass flow (Binkley 1984). On June 18, 2001, ionic resin capsules (Unibest, Bozeman, MT) were installed in 10 plots per unit at 10 cm beneath the surface of the mineral soil. Resin capsules were inserted into the soil by creating a 2.5-cm-diameter hole at a 45° angle to the soil surface with a stainless steel soil probe. Capsules were removed on August 6, returned to the laboratory and brushed clean of mineral soil. Nitrate and ammonium were extracted from the resin capsules with three successive, 30-min, agitated rinses of 10 ml of 2 M KCl (Kjønaas 1999, Morse et al. 2000). The collected total of 30 ml of KCl extract was centrifuged at 1000 g for 10 min, and the supernatant analyzed for nitrate and ammonium, as described above.

Volumetric percent soil water was measured periodically with a frequency domain reflectometry probe (Sentry 200 Troxler, Research Triangle Park, NC) throughout the summers of 2001 and 2002. The probe (approximately 40 cm long and 5 cm in diameter) has an active band that measures the surrounding soil water in a cylinder approximately 10 cm long and 25 cm in diameter. This is placed at each required soil depth by inserting the probe into a pre-installed and emptied PVC pipe (60 cm long \times 5 cm in diameter), which was capped between measurements. Soil water measurements were taken in six plots per unit at 5–15, 20–30 and 35–45 cm depths beneath the surface of the mineral soil.

Tree response

Trees for sampling were selected based on the following 1994 post-treatment measurements: DBH between 25–31 cm; a crown ratio (the proportion of tree height with live foliage) between 60 and 70%; and crown scorch (the percentage of crown length with foliage killed by fire) between 10 and 20% in burned units. These criteria represented the dominant size class, mean crown ratio and mean fire damage in burned units. From among these trees, six were selected at random for sampling in each unit, with no two trees selected in the same 0.04-ha plot. All six trees per unit were assessed for foliar morphology and chemistry, and three trees were randomly selected for the measurements of gas exchange and needle xylem water potential (Ψ).

Projected leaf area-based photosynthesis (A_{area}) and Ψ of 1-year-old needles were measured over four periods throughout the 2001 season (two in July and two in August), as follows. During each period, measurements were taken over the course of three consecutive days such that trees from one unit per treatment were measured each day. On each day, measurements were taken between 0830 h and 1300 h in three consecutive sets, each including one tree per unit. Although such stratified sampling (1 tree per treatment per set \times 4 treatments \times 3 sets per day \times 3 days = 36 trees) unavoidably encompassed large variability, it prevented treatment bias due to variation in environmental conditions on a given day and during a given time period.

We used telescoping pruners to harvest sunlit branchlets

from the mid-canopy on the south side of each tree. Immediately after harvest, several 1-year-old fascicles were removed from the branch and placed in a sealed plastic bag with a damp paper towel and transported in a portable cooler to a central work station for measurement of Ψ within 15 min. Xylem water potential was measured from the fascicular portion of one needle per tree with a pressure chamber (PMS Instruments, Corvallis, OR). The branchlet was also transported to the work station for concurrent gas exchange measurements. Projected leaf area-based photosynthesis (A_{area}) and stomatal conductance (g_s) were measured with a Li-Cor 6400 Photosynthesis System for three fascicles (nine needles) from each tree at each sampling time. For all gas exchange measurements, humidity was held near ambient; photosynthetically active radiation (PAR: 400–700 nm) was above saturation (Kolb and Robberecht 1996) at $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ from an external light source; and carbon dioxide concentration was controlled at $400 \mu\text{mol mol}^{-1}$.

Additional gas exchange measurements were conducted on July 8–10, 2002, to explore the relationship between needle age and A_{area} . We measured A_{area} for 1-, 3-, 5- and 6–7-year-old foliage from the same trees that were sampled with the same protocol in 2001. To corroborate findings from 2001, we also measured predawn water potential (Ψ_{predawn}) of the same trees during two sampling periods in 2002 (June 17–19 and July 29–31).

At the end of the growing season, we harvested terminal, mid-canopy branchlets from all six selected trees per unit for analysis of foliar morphology, longevity and chemistry. Specific leaf area (SLA) was measured as projected leaf area (measured with an image analysis system; Moccha, Jandel Scientific, San Rafael, CA) divided by dry mass of 20 1-year-old needles per tree. After oven-drying (60°C) each needle cohort separately, we calculated the total foliage mass as well as the percentage of total branch foliage 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 ($<0.2 \text{ mm}$ mesh), weighed to the nearest μg , sealed in small tin capsules and shipped to the University of Georgia (Atlanta, GA) for chemical analysis. Whole-leaf tissue chemistry measurements included leaf mass-based

nitrogen concentration (N_{mass}) and stable carbon isotope ratio ($\delta^{13}\text{C}_{\text{plant}}$) (Ehleringer and Osmond 1989). Carbon isotope ratio ($\delta^{13}\text{C}_{\text{plant}}$) was analyzed relative to the Vienna PeeDee-Belmonte standard and expressed as discrimination (Δ) following Farquhar and Richards (1984), where $\Delta = (\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}})$, and $\delta^{13}\text{C}_{\text{air}}$ was assumed to be -8‰ .

All six selected trees per unit were cored with an increment borer at 1.4 m above ground on the west side. We recorded total xylem width (to the nearest 0.01 mm), total width of the nine tree rings since thinning in 1992 and total width of the preceding nine growth rings. We calculated the ratio of the wood area at breast height produced since treatment to the area produced during the same number of growing seasons before treatment (radial wood increment ratio). Because there was a year of growth between thinning and burning treatments, ratios for burning treatments include an initial growing season when only thinning had been applied.

Data analysis

All plot-level measurements were considered subsamples and the unit means were considered true replicates ($n = 3$ per treatment). Most data were analyzed by one-way analysis of variance (ANOVA) with treatment as a factor (4 levels). Multiple mean comparisons were made by Least Significant Difference (LSD) posteriori tests. One-way (treatment) repeated measured ANOVA was used for physiological measurements conducted throughout the season. Photosynthesis measurements in 2002 were analyzed with a two-way (treatment and needle age) ANOVA ($\alpha = 0.05$). With the exception of radial wood increments, all data met assumptions of normality (Kolmogorov-Smirnov tests) and homogeneity of variance (Levene's test). Unit means of radial wood increment ratio were inversed to meet assumptions of normality and homogeneity of variance.

Results

Stand characteristics

Leaf area index 9 years after treatment was significantly higher in control units than in all treated units ($F = 6.86$, $P < 0.05$; Table 1). There were no significant differences in LAI

Table 1. Leaf area index (LAI), basal area (BA), total foliage mass per terminal branchlet, % young foliage per branchlet (by mass), specific leaf area (SLA), leaf nitrogen concentration and carbon isotope discrimination (Δ), 8 and 9 years after treatment: control = untreated; thin-only = thinned only; spring-burn = prescribed fire in the spring, after thinning; and fall-burn = prescribed fire in the fall, after thinning. Data are means \pm SE ($n = 3$); within a row, data followed by different letters differ at $P < 0.05$.

	Treatment			
	Control	Thin-only	Spring-burn	Fall-burn
LAI ($\text{m}^2 \text{m}^{-2}$)	2.5 (0.2) a	1.9 (0.1) b	1.8 (0.1) b	1.9 (0.1) b
BA ($\text{m}^2 \text{ha}^{-1}$)	29.4 (1.9) a	16.3 (0.6) b	13.5 (1.2) b	16.8 (0.9) b
Foliage mass (g)	29.9 (2.9) a	38.1 (3.6) a	44.8 (4.1) a	33.8 (2.8) a
% Young foliage	41.2 (2.2) a	54.6 (3.3) b	52.1 (3.3) b	59.0 (3.1) b
SLA ($\text{m}^2 \text{kg}^{-1}$)	3.9 (0.1) a	4.0 (0.1) a	3.7 (0.1) a	3.8 (0.0) a
Leaf nitrogen (g N kg^{-1})	11.6 (0.2) a	12.1 (0.4) a	11.5 (0.2) a	11.9 (0.3) a
Δ (‰)	17.3 (0.1) a	17.7 (0.1) a	17.4 (0.2) a	17.4 (0.3) a

Table 2. Mean NH₄⁺ and NO₃⁻ content in resin capsules installed for 48 days during early summer 2001 in each treatment. Anaerobically mineralizable nitrogen (AMN), and NH₄⁺ and NO₃⁻ pool sizes per treatment were determined on June 25, 2001. Control = untreated; thin-only = thinned only; spring-burn = prescribed fire in the spring, after thinning; and fall-burn = prescribed fire in the fall, after thinning. Data are means ± SE (*n* = 3); within a row, data followed by different letters differ at *P* < 0.05.

	Treatment			
	Control	Thin-only	Spring-burn	Fall-burn
NH ₄ ⁺ (µg N capsule ⁻¹)	0.46 (0.04) a	0.54 (0.05) a	0.37 (0.07) a	0.50 (0.10) a
NO ₃ ⁻ (µg N capsule ⁻¹)	116.2 (8.0) ab	131.5 (12.8) a	89.2 (5.5) b	86.5 (3.6) b
AMN (mg N kg ⁻¹)	6.0 (0.7) a	4.7 (0.6) a	4.0 (1.0) a	5.4 (0.6) a
NH ₄ ⁺ (mg N kg ⁻¹)	0.07 (0.01) a	0.11 (0.01) b	0.11 (0.01) b	0.11 (0.01) b
NO ₃ ⁻ (mg N kg ⁻¹)	9.6 (2.0) a	7.2 (2.9) a	5.4 (1.4) a	6.3 (1.0) a

among thin-only, spring-burn and fall-burn units (Table 1). Basal area was higher in control units relative to treated units (*F* = 10.89, *P* < 0.001), with no differences among treated units (Table 1). The mean proportion of leaf area to cross-sectional bole area did not differ significantly among treatments (839, 1192, 1336 and 1138 m² m⁻² in control, thin-only, spring-burn and fall-burn units, respectively; *P* > 0.05).

Resource availability

Ammonium pool sizes in June 2001 were significantly lower in control units than in all treated units (*F* = 4.33, *P* < 0.05; Table 2). June 2001 nitrate pool sizes and AMN did not differ among treatments (Table 2). In contrast to pool sizes, time-integrated ammonium availability measured with resin capsules did not differ among treatments (Table 2). Mean nitrate availability (resin capsule data) was similar in control units relative to other treatments, but lower in burned units relative to thin-only units (*F* = 6.98, *P* < 0.05; Table 2).

Soil water content (% soil volume) was not significantly different among treatments throughout either the 2001 or 2002

growing season at any of the three sampling depths (Figure 1). Soil water at all depths declined throughout the 2001 and 2002 summer seasons with the exception of a temporary increase in early August 2001 following localized, short intense rains. Values increased at all depths in 2001 with the onset of fall rains.

Tree response

Photosynthetic rates and *g*_s declined significantly (*F* = 19.2, *P*_{date} < 0.01, and *F* = 8.50, *P*_{date} < 0.05, respectively) throughout the 2001 growing season (Figure 2). When all dates were considered, *A*_{area} and *g*_s tended to be lower in the control trees relative to trees in other treatments but differences were not significant at α = 0.05 (*F* = 3.39, *P*_{treatment} < 0.1, and *F* = 3.26, *P*_{treatment} < 0.1, respectively; Figure 2). When only June and July dates were considered, both *A*_{area} and *g*_s were significantly lower in control trees relative to trees in other treatments (*F* = 3.91; *P*_{treatment} = 0.05, and *F* = 5.5; *P*_{treatment} = 0.02, respectively). The treatment × date interaction was not significant for *A*_{area} but was significant for *g*_s (*F* = 4.81, *P* < 0.05). In July 2002, we

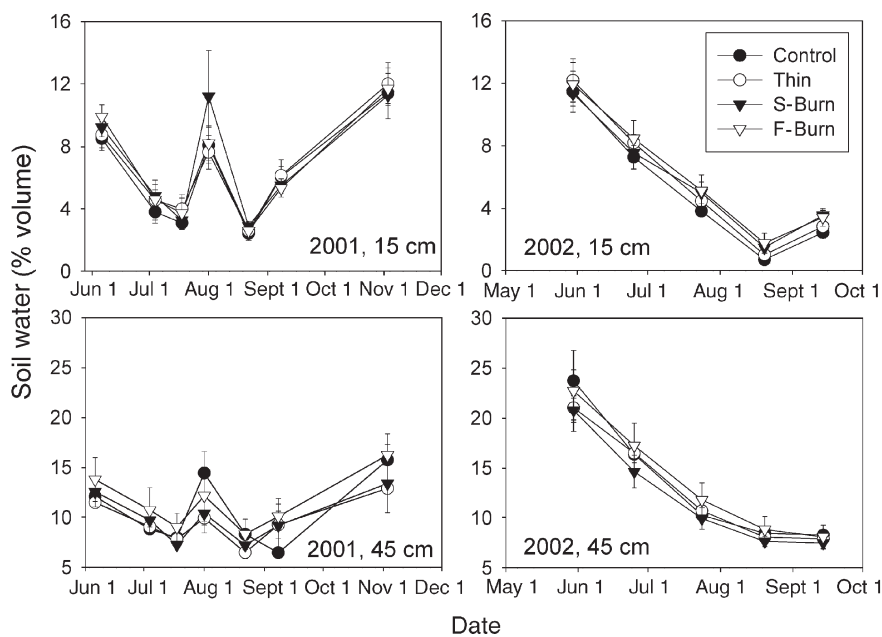


Figure 1. Volumetric soil water content at 15- and 45-cm depths through the 2001 and 2002 field seasons in all treatments. (Thin = after thinning; S-Burn = spring-burn after thinning; and F-Burn = fall-burn after thinning.) The same patterns were found at 30-cm depth (not shown). Error bars represent one standard error (*n* = 3 per treatment). There were no treatment differences on any date or at any soil depth.

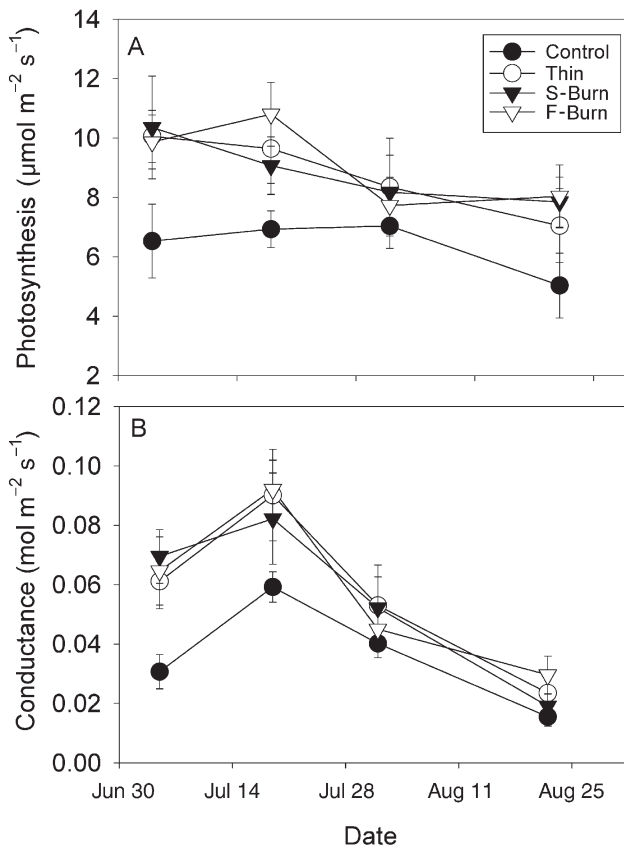


Figure 2. Net photosynthetic rate (A) and stomatal conductance (B) of 1-year-old needles from selected trees in each treatment throughout the 2001 sampling season. (Thin = after thinning; S-Burn = spring-burn after thinning; and F-Burn = fall-burn after thinning.) Error bars represent one standard error ($n = 3$ per treatment).

found no evidence for a treatment effect on needle-age-related differences in A_{area} (Figure 3). Although older needles showed significantly lower A_{area} than younger needles ($F = 16.45$, $P_{\text{age}} < 0.001$), neither treatment nor the treatment \times age interaction were significant.

Needle xylem water potential values were not significantly different among treatments for any sampling date through the 2001 summer (data not shown). Regardless of treatment, Ψ declined to values close to -2.0 MPa as the air warmed and dried during the day. Because of the strong decrease toward constant values, early morning Ψ (2001) and Ψ_{predawn} (2002) were used as indicators of whole-tree water stress. Therefore, 2001 Ψ data were reexamined after removing data collected after 1000 h, when trees began reaching constant Ψ values near -2.0 MPa. Early morning water potential declined significantly during the summer ($F = 19.07$, $P_{\text{date}} < 0.01$). Overall, control trees had significantly lower early morning Ψ values than trees in treated stands ($F = 5.14$, $P_{\text{treatment}} < 0.05$; Figure 4). The treatment \times date interaction was not significant ($F = 3.40$, $P > 0.05$). Predawn Ψ also declined significantly during summer 2002 ($F = 303.83$, $P_{\text{date}} < 0.001$). The treatment ($F = 15.83$, $P < 0.01$) and treatment \times date interaction ($F = 13.64$, $P < 0.05$) effects were significant, because of similar values in

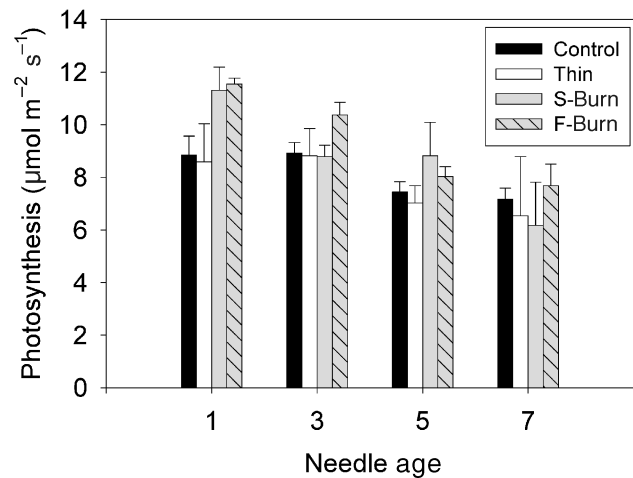


Figure 3. Net photosynthetic rate in needles of different ages in each treatment during July 8–10, 2002. (Thin = after thinning; S-Burn = spring-burn after thinning; F-Burn = fall-burn after thinning.) Error bars represent one standard error ($n = 3$ per treatment). There were no significant treatment and treatment \times age effects.

June but large differences in July, when Ψ was lower in control units.

Total terminal branch foliage dry mass did not differ significantly among treatments (Table 1). Control trees had a significantly lower ($F = 7.217$, $P < 0.05$) proportion of young (1- to 3-year-old) foliage than trees in all other treatments (Table 1). Foliar nitrogen concentration (N_{mass}), foliar carbon isotope discrimination (Δ) and specific leaf area (SLA) did not differ among treatments (Table 1).

The radial wood increment ratio was close to 1 in the control treatment, but increased significantly ($F = 10.64$; $P < 0.01$) in all other treatments, with no differences among them (Figure 5).

Discussion

Results from this study in western Montana show improved gas exchange, water status and growth of second growth ponderosa pine 9 years after thinning and 8 years after thinning followed by prescribed burning, relative to untreated controls, notwithstanding that most indices of soil resource availability were similar among treatments. Our results also show that, in the mid-term, thinning and thinning followed by prescribed burning in either spring or fall had similar effects on tree physiological responses and radial wood growth.

Fire and thinning have been shown to cause substantial, short-term increases (up to 1 year) in inorganic nitrogen pools (Kovacic et al. 1986, White 1986, Covington and Sackett 1992, Monleon et al. 1997, DeLuca and Zouhar 2000) and transformation rates in the mineral soil of ponderosa pine systems (Kaye and Hart 1998—but see Monleon et al. 1997). However, such pulses are usually temporary, and within 1 to 2 years ammonium or nitrate pool sizes (Covington and Sackett 1992, Monleon et al. 1997, DeLuca and Zouhar 2000), net mineral-

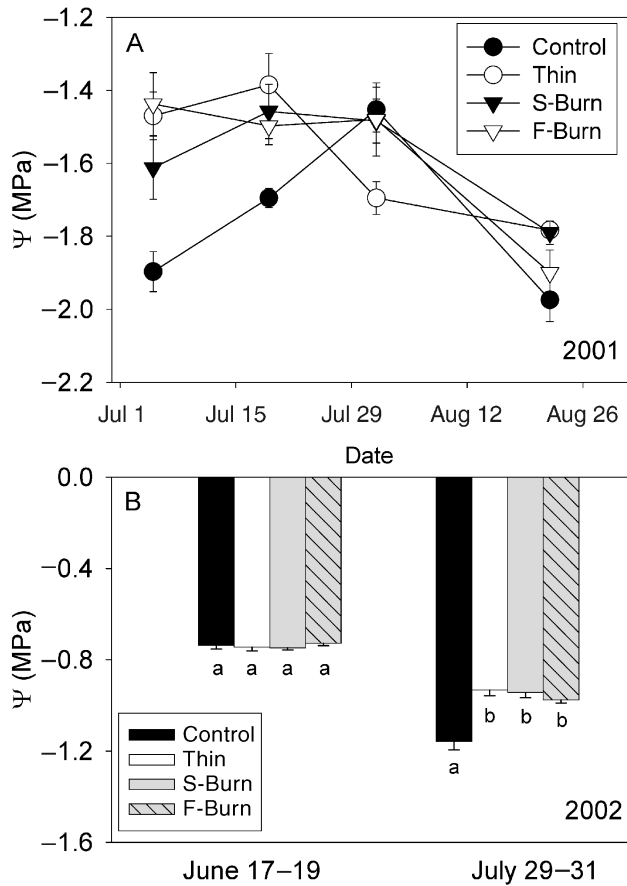


Figure 4. (A) Xylem water potential (between 0830 and 1000 h) of 1-year-old needles from each treatment throughout the 2001 sampling season. There was a significant ($P < 0.01$) treatment and treatment \times date effect. (B) Predawn xylem water potential of 1-year-old needles from each treatment during two sampling periods in 2002. Within a date, different letters denote statistically significant differences ($P < 0.05$). (Thin = after thinning; S-Burn = spring-burn after thinning; F-Burn = fall-burn after thinning.) Error bars represent one standard error ($n = 3$ per treatment).

ization rates (Monleon et al. 1997), microbial activity and potentially mineralizable nitrogen (DeLuca and Zouhar 2000) return to or fall below pretreatment values. Our results show that, although an initial pulse of available nitrogen may have occurred immediately after treatment at our site, it was undetectable 8 or 9 years after treatment. This was supported by the similar resin capsule nitrate and ammonium values among each of the treatments and the control. Similar AMN among treatments also suggests that the amount of stored nitrogen in the soil available for mineralization was similar among the treatments. Consistent with soil data, leaf-level nitrogen concentration (N_{area}) was similar among treatments. Similar proportion of foliage area relative to bole cross section among treatments suggests that similar N_{area} did not result from dilution in treated units relative to control. While soil nitrate pool sizes were similar in all treatments, we found higher soil ammonium pool sizes in all treated units relative to controls based on a single sampling in June. However, pool sizes are ex-

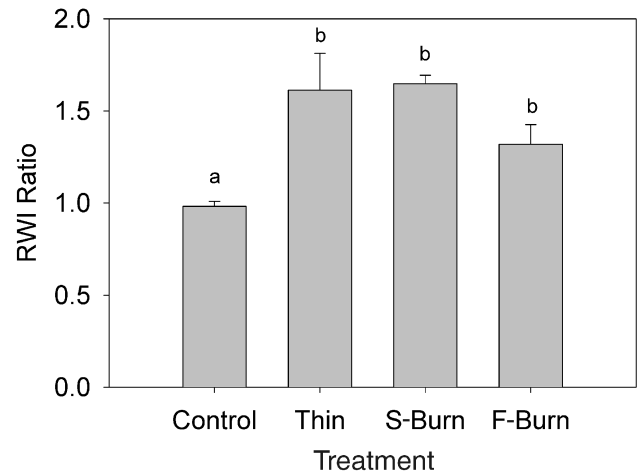


Figure 5. Radial wood increment (RWI) ratio (the ratio of wood produced 9 years after treatment relative to the increment 9 years before) for the different treatments. Statistics were calculated with inverse-transformed data, but plotted data are re-transformed. (Thin = after thinning; S-Burn = spring-burn after thinning; F-Burn = fall-burn after thinning.) Error bars represent one standard error ($n = 3$ per treatment). Different letters denote statistically significant differences ($P < 0.05$).

tremely variable over time (Monleon et al. 1997, Wright and Hart 1997) and may be smaller than the fluxes themselves (Stark and Hart 1997). Therefore, it is not surprising that pool size differences at one time do not correspond with time-integrated results. We also found lower nitrate availability in burned units (based on resin capsules) relative to thin-only units, but not to controls. Similar values in burned and controls suggest that differences between burned and thin-only units are not due to fire alone. Apparently, such differences were not related to understory cover and composition either, because preliminary surveys revealed no differences between thinned-only and burned units (Peters 2002). Additional measurements of nitrogen cycling components and turnover rates would be necessary to corroborate these differences and explain potential mechanisms.

The lack of treatment differences in soil water content during the summers of 2001 and 2002 and the nearly identical response in all treatments to both precipitation and drought suggests that treatment did not affect soil water content. However, lower early morning water potential and stomatal conductance in July 2001 (prior to late July rains) and lower predawn water potential in July 2002 in control units indicate that trees in these units were more water-limited than trees in treated units. Several explanations for these results are possible. First, volumetric soil water measurements may not accurately reflect soil water potential throughout the rooting zone in each treatment. Second, lower basal area and tree density in treated units may result in greater water availability per tree and lower water stress. Higher overall conductance from roots to leaves in trees from treated units (i.e., due to an increase of fine roots or conductance of wood produced after treatment) could also result in lower water stress despite similar soil water

content (Tyree and Zimmermann 2002).

Although differences among treatments in soil resource availability and leaf nitrogen content were minimal, A_{area} and g_s in June and July, early morning Ψ , Ψ_{predawn} and proportion of foliage allocated to younger needles were higher in all treated units relative to the control units. These findings indicate that, 8 and 9 years after treatment, physiological activity of ponderosa pine at the study site was improved to a similar degree by either thinning or thinning followed by fire. Comparable results have been obtained in second growth (Skov et al. 2004) and old growth ponderosa pine in western Montana (A. Sala, unpublished data) and in northern Arizona (Feeney et al. 1998, Skov et al. 2004). Decreases in net photosynthetic rates with increasing needle age measured in 2002 (see also Clark et al. 1995) suggest that control trees did not compensate for lower relative A_{area} in young needles with increased A_{area} in older needles. Taken together, our gas exchange and leaf biomass results suggest higher branch-level carbon assimilation in trees from treated units relative to controls. This is consistent with significantly higher radial wood increment measured in treated units.

Lower A_{area} in June and July for trees in control units compared with treated units was unrelated to decreases in SLA, N_{mass} or N_{area} (not shown). This is in contrast to well-documented correlations between SLA or N_{area} and leaf area-based photosynthetic capacity across and within species (Reich et al. 1997, Carey et al. 1998). The lack of such correlation in our study may indicate that lower photosynthesis in control units was not due to reduced photosynthetic capacity, but rather to increased stomatal limitations to gas exchange. Consistent with this, McDowell et al. (2003) found that photosynthetic capacity of ponderosa pine did not change in response to thinning treatments. Furthermore, ponderosa pine is among the temperate conifers most vulnerable to water-stress-induced xylem cavitation (Piñol and Sala 2000, Martínez-Vilalta et al. 2004) and strong stomatal closure in response to environmental and soil drought (Zhang et al. 1997, Kolb and Stone 2000, Olivas-Garcia et al. 2000, Law et al. 2001, Marshall et al. 2001, Panek and Goldstein 2001, Stout and Sala 2003) prevents xylem water potential from reaching critical values that induce xylem cavitation. This strong stomatal control is consistent with the high sensitivity of photosynthesis to leaf water status (Zhang et al. 1997, Dang et al. 1997, Kolb and Stone 2000, Panek and Goldstein 2001). In our study, rapid decreases of needle water potential during the day to similar values in all treatments and relatively high absolute minimum leaf water potential values (-2.2 MPa) measured at the site are consistent with high drought sensitivity in ponderosa pine. Lower predawn and early morning water potentials in control units relative to all other treatments were likely responsible for greater stomatal closure and lower photosynthetic rates in control trees. Most likely, the CO_2 concentration we maintained in the chamber during measurements ($400 \mu\text{l l}^{-1}$) was too low to prevent water-stress-induced stomatal limitations to CO_2 diffusion in control trees.

We found no differences in leaf carbon isotope discrimination among treatments. Similar results were reported by Skov

et al. (2004) and Wallin et al. (2004) for ponderosa pine in northern Arizona. Time-integrated ratio of leaf internal (C_i) to external (C_a) carbon dioxide concentration may have remained unchanged in treated units relative to controls if increases of C_i due to greater stomatal conductance were offset by similar photosynthesis-induced decreases in C_i . Greater light in treated units relative to denser controls (foliage for isotope analyses was sampled in the mid-canopy) may have further contributed to lower C_i in trees from treated units and to offsetting the effect of treatment-induced increases in stomatal conductance.

Overall, our results suggest that the reduced June and July leaf-level photosynthetic rate of trees in untreated control units compared with trees in treated units is primarily a response to limiting water rather than nitrogen. However, we cannot discount the possibility of a positive treatment-induced effect on leaf nitrogen concentration and photosynthesis shortly after treatment applications. For instance, Feeney et al. (1998) reported increases in N_{mass} (N on a mass basis) in response to thinning + first-entry prescribed burning relative to thinning alone in old growth ponderosa pine in northern Arizona 1 and 2 years after treatment.

While active management improved tree performance (see also Powers and Reynolds 1999), our results show that physiological activity and growth did not vary in response to the specific type of treatment applied (thinning or thinning followed by prescribed fire). Similar results were found by Feeney et al. (1998), suggesting that the application of low-severity prescribed fire after thinning does not necessarily affect ponderosa pine performance relative to thinning alone. Furthermore, we found that the season in which fire was applied after thinning (spring or fall) did not affect physiological activity or growth in the mid-term. However, ponderosa pine physiology and growth in response to prescribed fire appears to be sensitive to the specific conditions (including tree health, weather and fire and fuel characteristics) under which management is implemented. Prescribed fire has been shown both to reduce (Grier 1989, Sutherland et al. 1991, Landsberg 1994, Busse et al. 2000) and increase (Wyant et al. 1983, Feeney et al. 1998) ponderosa pine growth indicators. Spring burns, particularly when associated with significant forest floor consumption, tend to produce negative growth responses (Grier 1989, Landsberg 1994, Busse et al. 2000) and greater mortality (Swezy and Agee 1991), and low-intensity fall burns, positive responses (Wyant et al. 1983, Feeney et al. 1998). The lack of response to prescribed fire and season of fire that we report may result from the relatively light fuel loads and the lower forest floor consumption in the spring burn relative to the fall burn.

Our study has some limitations. First, the site was repeatedly managed until the 1960s. Second, for logistical reasons, control units were not randomized among actively treated units. Third, we do not have pretreatment measurements and therefore we cannot exclude the possibility that the differences we found existed prior to treatment. However, this is unlikely because previous management was similar in all units and the overall site was uniform (Arno 1999). Further, our results are

consistent with those of other studies (Feeney et al. 1998, Kolb et al. 1998, McDowell et al. 2003, Skov et al. 2004, Wallin et al. 2004). If the primary goals of land owners or managers are to improve the health and productivity of ponderosa pine trees and to reduce the immediate risk of severe wildfire, results from this study suggest that thinning alone with subsequent fuel management may serve that purpose.

However, restorative ecosystem management in ponderosa pine forests acknowledges the historic role of fire as a natural ecosystem-level disturbance (see Allen et al. 2002). In the long-term, periodic fire may have many ecological effects beyond those examined here (Carlson et al. 1993). If such fire effects are desired, this study suggests that they can be achieved by fall or spring fire applications under the conditions described here after stand thinning without reducing ponderosa pine physiological activity and growth relative to a thinning-only treatment.

Acknowledgments

Funding for this study and access to the Lick Creek Experimental Area was provided by the USFS RMRS Fire Sciences Laboratory through the Bitterroot Ecosystem Management Project (BEMRP; JVA 01-JV-11222048-149). The Bitterroot National Forest team, particularly Sharon Ritter, assisted us with site access and permits. Dr. Brian Steele helped in the design and data analysis. Thanks to Dr. Tom DeLuca for his help with soil methods, laboratory assistance and manuscript preparation. For help in the field, we thank Sarah Weldon, Nathan Blackburn, Judy Perkins and Joslin Heyn. The government of Catalonia (Spain) provided funding to A. Sala during her sabbatical (PIV 192002). Thanks to the Institut de Ciència i Tecnologia Ambiental, University Autonomous of Barcelona for their hospitality.

References

- Agee, J.K. 1993. Fire ecology of pacific northwest forests. Island Press, Washington, DC, 493 p.
- Allen, C.D., M. Savage, D.A. Falk et al. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol. Appl.* 12:1418–1433.
- Arno, S.F. 1988. Fire ecology and its management implications in ponderosa pine forests. *In* Ponderosa Pine: The Species and its Management. Eds. D.M. Baumgartner and J.E. Lotan. Symp. Proc. Washington State University, Pullman, WA, pp 133–140.
- Arno, S. F. 1999. Ecosystem based management treatments. *In* Eighty-Eight Years of Change in a Managed Ponderosa Pine Forest. Eds. H.Y. Smith and S.F. Arno. USDA Forest Service, Rocky Mt. Res. Stn. Gen. Tech. Rep. GTR-23, pp 22–26.
- Arno, S.F., M.G. Harrington, C.E. Fiedler and C.E. Carlson. 1995. Restoring fire-dependent ponderosa pine forests in western Montana. *Restoration and Management Notes* 13:32–36.
- Arno, S.F., M.G. Harrington, C.E. Fiedler and C.E. Carlson. 1996. Using silviculture and prescribed fires to reduce fire hazard and improve health in ponderosa pine forests. Proc. 17th Annual Forest Vegetation Management Conference 17:114–118.
- Barrett, S.W. and S.F. Arno. 1982. Indian fires as an ecological influence in the northern Rockies. *J. For.* 80:647–651.
- Binkley, D. 1984. Ion exchange resin bags factors affecting estimates of nitrogen availability. *Soil Sci. Soc. Am. J.* 48:1181–1184.
- Binkley, D. and S.C. Hart. 1989. The components of nitrogen availability assessments in forest soils. *Adv. Soil Sci.* 10:57–112.
- Busse, M.D., S.A. Simon and G.M. Riegel. 2000. Tree growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of central Oregon. *For. Sci.* 46:258–268.
- Carey, E.V., R.M. Callaway and E.H. DeLucia. 1998. Increased photosynthesis offsets costs of allocation to sapwood in an arid environment. *Ecology* 79:2281–2291.
- Carlson, P.C., G.W. Tanner, J.M. Wood and R.R. Humphrey. 1993. Fire in key deer habitat improves browse, prevents succession, and preserves endemic herbs. *J. Wildl. Manage.* 57:914–928.
- Clark, C.S., J.A. Weber, E.H. Lee and W.E. Hogsett. 1995. Accentuation of gas exchange gradients in flushes of ponderosa pine exposed to ozone. *Tree Physiol.* 15:181–189.
- Covington, W.W. and M.M. Moore. 1994. Post-settlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. *J. Sustain. For.* 2:153–181.
- Covington, W.W. and S.S. Sackett. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *For. Sci.* 30:183–192.
- Covington, W.W. and S.S. Sackett. 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *For. Ecol. Manage.* 54:175–191.
- Dang, Q.L., H.A. Margolis, M.R. Coyea, M. Sy and G.J. Collatz. 1997. Regulation of branch-level gas exchange of boreal trees: roles of shoot water potential and vapor pressure difference. *Tree Physiol.* 17:521–535.
- DeLuca, T.H. 2000. Soils and nutrient considerations. *In* The Bitterroot Ecosystem Management Research Project: What We Have Learned. Symp. Proc. USDA Forest Service, Rocky Mt. Res. Stn. P-17, pp 23–25.
- DeLuca, T.H. and K.L. Zouhar. 2000. Effects of selection harvest and prescribed fire on the soil nitrogen status of ponderosa pine forests. *For. Ecol. Manage.* 138:263–271.
- Ehleringer, J.H. and C.B. Osmond. 1989. Stable isotopes. *In* Plant Physiological Ecology: Field Methods and Instrumentation. Eds. R.W. Pearcy, J. Ehleringer, H.A. Mooney and P.W. Rundel. Chapman and Hall, London, pp 281–300.
- Farquhar, G.D. and R.A. Richards. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Aust. J. Plant Physiol.* 11:539–552.
- Feeney, S.R., T.E. Kolb, W.W. Covington and M.R. Wagner. 1998. Influence of thinning and burning restoration treatments on pre-settlement ponderosa pines at the Gus Pearson Natural Area. *Can. J. For. Res.* 28:1295–1306.
- Fiddler, G.O., D.R. Hart, T.A. Fiddler and P.M. McDonald. 1989. Thinning decreases mortality and increases growth of ponderosa pine in northeastern California. USDA Forest Service, Pacific Southwest For. Range Exp. Stn. Res. Pap. PSW-194, 11 p.
- Grier, C.C. 1989. Effects of prescribed springtime underburning on production and nutrient status of a young ponderosa pine stand. *In* Multisource Management of Ponderosa Pine Forests. Eds. A. Teale, W.W. Covington, and R.H. Hamre. USDA Forest Service, Rocky Mt. For. Range Exp. Stn. Gen. Tech. Rep. RM-185, pp 71–76.
- Gruell, G.E., W.C. Schmidt, S.F. Arno and W.J. Reich. 1982. Seventy years of vegetative change in a managed ponderosa pine forest in western Montana—implications for resource management. USDA Forest Service, Intermountain For. Range Exp. Stn. Gen. Tech. Rep. INT-130, 42 p.
- Harrington, M.G. 1999a. Stand structure response to harvesting and prescribed burning on shelterwood cutting and commercial thinning units. *In* Eighty-Eight Years of Change in a Managed Ponderosa Pine Forest. Eds. H.Y. Smith and S.F. Arno. USDA Forest Service, Rocky Mt. Res. Stn. Gen. Tech. Rep. GTR-23, pp 28–31.
- Harrington, M.G. 1999b. Prescribed burn weather, fuel moistures, and fuel reduction on all cutting units. *In* Eighty-Eight Years of Change in a Managed Ponderosa Pine Forest. Eds. H.Y. Smith and S.F. Arno. USDA Forest Service, Rocky Mt. Res. Stn. Gen. Tech. Rep. GTR-23, pp 27–28.

- Hartwell, M.G., P. Alaback and S.F. Arno. 2000. Comparing historic and modern forests on the Bitterroot Front. *In* The Bitterroot Ecosystem Management Research Project: What We Have Learned. Symp. Proc. USDA Forest Service, Rocky Mt. Res. Stn. P-17, pp 11–16.
- Kaye, J.P. and S.C. Hart. 1998. Ecological restoration alters nitrogen transformations in a ponderosa pine–bunchgrass ecosystem. *Ecol. Appl.* 8:1052–1060.
- Keane, R.E., K.C. Ryan, T.T. Veblen, C.D. Allen, J. Logan and B. Hawkes. 2002. Cascading effects of fire exclusion in Rocky Mountain ecosystems: a literature review. USDA Forest Service, Rocky Mt. Res. Stn. Gen. Tech. Rep. GTR-91, 24 p.
- Kjønaas, O.J. 1999. In situ efficiency of ion exchange resins in studies of nitrogen transformation. *Soil Sci. Soc. Am. J.* 63:399–409.
- Kolb, P.E. and R. Robberecht. 1996. *Pinus ponderosa* seedling establishment and the influence of competition with the bunchgrass *Agropyron spicatum*. *Int. J. Plant Sci.* 157:509–515.
- Kolb, T.E. and J.E. Stone. 2000. Differences in leaf gas exchange and water relations among species and tree sizes in an Arizona pine oak forest. *Tree Physiol.* 20:1–12.
- Kolb, T.E., K.M. Holmberg, M.R. Wagner and J.E. Stone. 1998. Regulation of ponderosa pine foliar physiology and insect resistance mechanisms by basal area treatments. *Tree Physiol.* 18:375–381.
- Kovacic, D.A., D.M. Swift, J.E. Ellis and T.E. Hakonson. 1986. Immediate effects of prescribed burning on mineral soil nitrogen in ponderosa pine of New Mexico. *Soil Sci.* 141:71–76.
- Landsberg, J.D. 1994. A review of prescribed fire and tree growth response in the genus *Pinus*. *In* Proc. 12th Conf. on Fire and Forest Meteorology. Soc. Am. For., Bethesda, MD, pp 326–346.
- Law, B.E., A.H. Goldstein, P.M. Anthoni, M.H. Unsworth and J.A. Panek. 2001. Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. *Tree Physiol.* 21:299–308.
- Marshall, J.D., G.E. Rehfeldt and R.A. Monserud. 2001. Family differences in height growth and photosynthetic traits in three conifers. *Tree Physiol.* 21:727–734.
- Martin, R.E. 1982. Fire history and its role in succession. *In* Proceedings of Forest Succession and Stand Development Research in the Pacific Northwest. Ed. J.E. Means. Oregon State University, Corvallis, OR, pp 92–99.
- Martínez-Vilalta, J., A. Sala and J. Piñol. 2004. The hydraulic architecture of Pinaceae – a review. *Plant Ecol.* 171:3–13.
- McDowell, N., J.R. Brooks, S.A. Fitzgerald and B.J. Bond. 2003. Carbon isotope discrimination and growth response of old ponderosa pine trees to stand density reductions. *Plant Cell Environ.* 26: 631–644.
- Monleon, V.J., K. Chromack and J.D. Landsberg. 1997. Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Can. J. For. Res.* 27:369–378.
- Morse, C.C., I.V. Yevdokimov and T.H. DeLuca. 2000. In situ extraction and analysis of rhizosphere carbon of native and invasive plant species. *Comm. Soil Sci. Plant Anal.* 31:725–742.
- Nagel, L.M. and K.L. O'Hara. 2001. The influence of stand structure on ecophysiological leaf characteristics of *Pinus ponderosa* in western Montana. *Can. J. For. Res.* 31:2173–2182.
- Nagel, L.M. and K.L. O'Hara. 2002. Diurnal fluctuations of gas exchange and water potential in different stand structures of *Pinus ponderosa*. *Trees* 16:281–290.
- Olivas-Garcia, J.M., B.M. Cregg and T.C. Hennessey. 2000. Genotypic variation in carbon isotope discrimination and gas exchange of ponderosa pine seedlings under two levels of water stress. *Can. J. For. Res.* 30:1581–1590.
- Panek, J.A. and A.H. Goldstein. 2001. Response of stomatal conductance to drought in ponderosa pine: implications for carbon and ozone uptake. *Tree Physiol.* 21:337–344.
- Peters, G.D. 2002. Effects of thinning, prescribed burning, and burning season on the physiological performance of ponderosa pine. MS Thesis, University of Montana, Missoula, 61 p.
- Piñol, J. and A. Sala. 2000. Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northwest USA. *Funct. Ecol.* 14:1–8.
- Powers, R.F. and P.E. Reynolds. 1999. Ten year responses of ponderosa pine plantations to repeated vegetation and nutrient control along an environmental gradient. *Can. J. For. Res.* 29:1027–1038.
- Powers, R.F. and P.E. Reynolds. 2000. Intensive management of ponderosa pine plantations: sustainable productivity for the 21st century. *J. Sustain. For.* 10:249–255.
- Reich, P.B., M.B. Walters and D.S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. *Proc. Nat. Acad. Sci. USA* 94:13,730–13,734.
- Savage, M. and T.W. Swetnam. 1990. Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. *Ecology* 71:2374–2378.
- Shiver, B.D. and B.E. Borders. 1996. Sampling techniques for forest resource inventory. John Wiley and Sons, New York, 356 p.
- Skov, K.R., T.E. Kolb, and K.F. Wallin. 2004. Tree size and drought affect ponderosa pine physiological response to thinning and burning treatments. *For. Sci.* 50:81–91.
- Stark, J. M. and S.C. Hart. 1997. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. *Nature* 385:61–64.
- Stout D.L. and A. Sala. 2003. Xylem vulnerability to cavitation in *Pseudotsuga menziesii* and *Pinus ponderosa* from contrasting habitats. *Tree Physiol.* 23:43–50.
- Sutherland E.K., W.W. Covington and S. Andariese. 1991. A model of ponderosa pine growth response to prescribed burning. *For. Ecol. Manage.* 44:161–173.
- Swezy, D.M. and J.K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old growth ponderosa pine. *Can. J. For. Res.* 21:626–634.
- Tyree, M.T. and M.H. Zimmermann. 2002. Xylem structure and the ascent of sap. 2nd Edn. Springer, Berlin, 283 p.
- Van Hooser, D.D. and C.C. Keegan III. 1988. Distribution and volumes of ponderosa pine forests. *In* Ponderosa Pine: the Species and its Management. Eds. D.M. Baumgartner and J.E. Lotan. Symp. Proc. Washington State University, Pullman, WA, pp 1–6.
- Wallin, K.F., T.E. Kolb, K.R. Skov and M.R. Wagner. 2004. Seven-year results of thinning and burning restoration treatments on old growth ponderosa pines at the Gus Pearson Natural Area. *Restor. Ecol.* 12:239–247.
- White, C.S. 1986. Effects of prescribed fire on rates of decomposition and nitrogen mineralization in a ponderosa pine ecosystem. *Biol. Fertil. Soils* 2:87–95.
- White, C.S. and S.R. Loftin. 2000. Response of two semiarid grasslands to cool-season prescribed fire. *J. Range Manage.* 53:52–61.
- Willis, R.B., G.J. Schwab and C.E. Gentry. 1993. Elimination of interferences in the colorimetric analysis of ammonium in water and soil extracts. *Com. Soil Sci. Plant Anal.* 24:1009–1019.
- Wright, R.J. and S.C. Hart. 1997. Nitrogen and phosphorous status in a ponderosa pine forest after 20 years of interval burning. *Ecoscience* 4:526–533.
- Wyant, J.G., R.D. Laven and P.N. Omi. 1983. Fire effects on shoot growth characteristics of ponderosa pine in Colorado. *Can. J. For. Res.* 13:620–625.
- Yang, J.E., E.O. Skogley, B.E. Schaff and J.J. Kim. 1998. A simple spectrophotometric determination of nitrate in water, resin, and soil extracts. *Soil Sci. Soc. Am. J.* 62:1108–1115.
- Zhang, J.W., Z. Feng, B.M. Cregg and C.M. Schumann. 1997. Carbon isotopic composition, gas exchange and growth of three populations of ponderosa pine differing in drought tolerance. *Tree Physiol.* 17:461–466.