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# Tree Size and Drought Affect Ponderosa Pine Physiological Response to Thinning and Burning Treatments

Kjerstin R. Skov, Thomas E. Kolb, and Kimberly F. Wallin

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**ABSTRACT.** Thinning and burning treatments based on presettlement (prior to Euro-American settlement) stand conditions have been proposed for improving the vigor and growth of *Pinus ponderosa*. No study has examined effects of different levels of such thinning treatments on tree water, carbon, and nitrogen relations, or compared effects between postsettlement (trees established after Euro-American settlement) and presettlement (established before Euro-American settlement) trees. We investigated responses of presettlement and postsettlement trees to three levels of thinning and burning (unthinned/unburned control, light thinning/burning, heavy thinning/burning) over 2 yr that differed in precipitation in northern Arizona. Both thinning treatments consistently increased predawn water potential of both tree sizes compared with the control. Effects of thinning on leaf gas exchange varied between tree sizes and measurement times. Thinning increased net photosynthetic rate and stomatal conductance only when soil water availability was lowest, and increases were greater for postsettlement than presettlement trees. In contrast, thinning had no effect on foliar nitrogen concentration.

Our results suggest greater positive effects of restoration thinning on tree water and carbon relations for postsettlement versus presettlement trees, and under drought versus nondrought conditions. Photosynthetic response to thinning in old trees may be constrained by physiological factors associated with large size such as low soil-to-leaf hydraulic conductance. *For. Sci.* 50(1):81–91.

**Key Words:** Water relations, photosynthesis, nitrogen, stomatal conductance, carbon isotope, *Pinus ponderosa*, Arizona.

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**P**AST AND CURRENT land management practices have altered forests of the Southwestern United States and associated forest management issues (Cooper 1960, Covington and Moore 1994, Covington et al. 1997, Fulé et al.

1997). Fire suppression, overgrazing, and other factors produced today's dense ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws) forests, which contain thickets of slow-growing young trees, declining old-growth trees, and high fuel load-

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**Acknowledgments:** Funding for this study was provided by the Northern Arizona University, School of Forestry Mission Research Program, the McIntire Stennis Program, and the USDA Forest Service (RMRS-99168-RJVA). We also thank M. Wagner and J. Bailey (Northern Arizona University School of Forestry) for their critical review of the manuscript, M. Gaylord, B. Paul, D. Fischer, K. Simonin, J. Jerman, S. Stephens, J. Perrone, and K. Maplesweet (Northern Arizona University) for their invaluable assistance, and B. Burch (Northern Arizona University, Department of Mathematics and Statistics) for statistical advice.

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Manuscript received July 9, 2002, accepted May 14, 2003.

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ing (Covington and Moore 1994, Covington et al. 1997, Dahms and Geils 1997). Land managers, researchers, and concerned citizens' groups are experimenting with possible solutions to these undesirable conditions that would reduce forest floor fuel loading, reduce "ladder fuels" in the understory, increase growth and insect resistance of trees, and stimulate productivity of declining old trees, which are scarce due to past harvests.

Possible solutions range from no action to complete restoration of forest structure to the open conditions that were common prior to Euro-American settlement (presettlement) because of frequent surface fires (Weaver 1951, Swetnam and Baisan 1996, Fulé et al. 1997, Mast et al. 1999, Moore et al. 1999). Proactive treatments being considered include thinning, prescribed burning, or a combination thereof. No action would likely result in extreme forest changes that are difficult to predict or control, such as stand-replacing fire and insect outbreaks (Covington et al. 1997, Fulé et al. 1997). The use of the presettlement forest as a model for today's forest management is another possible solution (Covington et al. 1997, Moore et al. 1999). Such a model uses evidence of local presettlement stand structure and natural disturbance regime as a reference condition to define desired future conditions. Presettlement stand structure and disturbance regime are considered to best approximate the environment under which native species evolved (Moore et al. 1999). Limitations of this strategy include the difficulty of knowing presettlement conditions, possible changes in climate since presettlement times, and lack of information about effectiveness of treatments based on presettlement conditions (Wagner et al. 2000, Baker and Ehle 2001).

Previous restoration or thinning studies in southwestern ponderosa pine forests either focused on postsettlement trees in stands that were evenly thinned using traditional silvicultural prescriptions (Ronco et al. 1985, Cochran and Barrett 1993, Kolb et al. 1998), or focused on presettlement trees in stands fully restored to presettlement structure and tree density (Covington et al. 1997, Feeney et al. 1998, Stone et al. 1999). No previous research has compared response to restoration treatments between presettlement and postsettlement ponderosa pine trees that have grown for 80 or more years under intense competition caused by high tree density. Both presettlement and postsettlement ponderosa pine trees grow slowly when stressed by severe tree-to-tree competition and can be released from competition by appropriate thinning (Ronco et al. 1985, Cochran and Barret 1993, Kolb et al. 1998, Feeney et al. 1998, Stone et al. 1999, Latham and Tappeiner 2002). However, presettlement, or large old trees, differ physiologically from younger trees and may respond differently to thinning. For example, they may have higher maintenance respiration demands because they may have more living, nonphotosynthetic tissue than younger trees (Waring and Schlesinger 1985, Ryan and Waring 1992, Ryan et al. 1995). More branch junctions and a longer root-leaf hydraulic path length may decrease hydraulic conductance in old trees, which may limit photosynthetic rate (Ryan and Yoder 1997). Slow growth of old ponderosa pine trees has

been attributed to these factors (Yoder et al. 1994, Hubbard et al. 1999, Williams et al. 2001).

This study compares the influences of restoration thinning and burning treatments on water, carbon, and nutrient relations of presettlement and postsettlement ponderosa pines. The treatments include an untreated control and two levels of thinning (light, heavy) combined with an understory burn. Trees left on site were selected based on site-specific evidence of presettlement stand structure (Covington et al. 1997, Moore et al. 1999). We expected heavier thinning to decrease competition for water and nutrients and increase carbon gain for both presettlement and postsettlement trees. We anticipated higher leaf gas exchange and photosynthetic rates in postsettlement trees than in presettlement trees, and a greater response in these rates to thinning for postsettlement than presettlement trees.

## Methods

### Study Site

The study site is within the Fort Valley Experimental Forest (USDA Forest Service, Rocky Mountain Research Station) located 10 km northwest of Flagstaff, Arizona (N35°15'58", W111°42'1", elevation 2200 m). Mean annual precipitation is 57 cm divided between winter snow and late summer rain. The soils are classified as a basaltic, fine montmorillonitic complex of frigid Typic Argiborolls and Mollic Eutroboralfs (Mast et al. 1999). The average growing season is 94 days (Schubert 1974). Ponderosa pine dominates the Fort Valley Forest (99.8% of trees in plots), and untreated average stand density was 1345 trees ha<sup>-1</sup> with an average basal area of 36.7 m<sup>2</sup> ha<sup>-1</sup> (Fulé et al. 1999). Trees less than 30 cm diameter at breast height (1.4 m above the base of each tree, hereafter referred to as dbh) dominate this forest and trees with dbh above 40 cm occur occasionally.

### Thinning and Burning Treatments

The experiment included three levels of thinning: none (control), light, and heavy. Each level was randomly assigned to a single 17 ha plot. All plots have similar elevation, slope, and aspect, and are located within 1 km of each other. The unthinned control had a dense stand of pole-sized postsettlement trees with some larger, interspersed presettlement trees. All presettlement trees were retained in thinned treatments. Selection of postsettlement leave trees on thinned sites was based on evidence of presettlement trees. Evidence of presettlement trees included snags, downed trees, stumps, and stumpholes. Leave trees were located within a 60 m radius of each presettlement tree evidence. The heavy thinning treatment retained an average of 1.5 replacement trees ≥40 cm dbh or three smaller trees for every evidence of a presettlement tree. The light thinning treatment retained three replacement trees ≥40 cm dbh or six smaller trees for every evidence of a presettlement tree. If possible, larger trees were chosen over smaller trees for retention. All thinning treatments included understory broadcast burns and unthinned controls were not burned.

Thinnings occurred between December 1998 and September 1999. Trees were felled by chainsaws, and boles were hauled to landings and removed from the site. The heavy

thinning treatment was completed in April 1999, and the light thinning was finished September 1999. In the summer of 2000, branches were piled by hand and machine. These piles were burned in February 2001. After slash piles were burned, low-intensity, understory broadcast burns consumed remaining fuels (including duff, litter, and any remaining branches). These broadcast burns were conducted in May 2001 using spot/strip-firing techniques with drip-torches. Before burning, duff and needle litter were raked away from the base of every presettlement tree to minimize heat girdling. This was not necessary for postsettlement trees due to relatively low amounts of litter at their base. Fires were low intensity to minimize damage to tree roots, boles, or crown. Flame lengths were 15–30 cm in needle litter and 60–120 cm in woody slash. Rate of spread was between 0 and 40 m h<sup>-1</sup>. Grassy areas did not carry fire. All trees used in our study had less than 10% bole or crown scorch. Crown and bole scorch below 50% have little effect on water potential or photosynthetic rate of most conifers (Ducrey et al. 1996, Ryan 2000, Wallin et al. 2003).

### Pretreatment Condition and Comparisons

The three treatment areas were similar but not identical prior to implementation of thinning and burning treatments. Basal area (BA), trees per hectare (TPH), and stand density index (SDI, Reineke 1933) prior to treatment in 1998 show a dense forest crowded with small trees (Table 1). Because the maximum SDI for ponderosa pine in northern Arizona is thought to be 450–600 (Martinez 1999), this forest was 45–80% of maximum stocking before treatment. The light thinning reduced stand basal area by 43% from 38 m<sup>2</sup>ha<sup>-1</sup> to 22 m<sup>2</sup>ha<sup>-1</sup>, and the heavy thinning reduced BA by 46% from 33 m<sup>2</sup>ha<sup>-1</sup> to 18 m<sup>2</sup>ha<sup>-1</sup>. The unthinned control was 40 m<sup>2</sup> ha<sup>-1</sup> (Table 1).

We compared pretreatment values of leaf carbon isotope ratio and bole radial growth rate of trees among treatment areas to investigate pretreatment differences in tree physiological characteristics and growth. The ratio of two carbon isotopes—carbon 12 (<sup>12</sup>C) and carbon 13 (<sup>13</sup>C)—in leaf structural tissue ( $\delta^{13}\text{C}$ ) is a time-integrated measure of leaf internal CO<sub>2</sub> concentration, which depends on the balance between photosynthesis and stomatal conductance (Farquhar and Lloyd 1993). Water deficits or other factors that reduce stomatal conductance often increase assimilation of <sup>13</sup>C relative to <sup>12</sup>C, and increase  $\delta^{13}\text{C}$  (Farquhar et al. 1989, Kozlowski and Pallardy 1997). Foliar  $\delta^{13}\text{C}$  of leaves (bulk tissue) formed in 1998 (before treatments) was not significantly different among treatment areas ( $P = 0.110$ ,  $df = 2$ ), tree sizes ( $P = 0.340$ ,  $df = 1$ ), and their interaction was not significant ( $P = 0.39$ ,  $df = 2$ ). This finding suggests a similar balance between photosynthesis and stomatal conductance, and similar leaf internal CO<sub>2</sub> concentration, for trees in the three treatments areas prior to treatment.

Tree size ( $P = 0.022$ ,  $df = 1$ ) and the thinning treatment  $\times$  tree size interaction ( $P = 0.025$ ,  $df = 2$ ) were significant sources of variation in average radial growth rate 10 yr prior to treatment (1988–1998), but treatment did not significantly influence growth ( $P = 0.710$ ,  $df = 2$ ). Presettlement tree growth did not differ among treatments areas before treatment ( $P > 0.15$ ). Average growth of postsettlement trees did not differ between the control and lightly thinned plots ( $P = 0.784$ ), but was significantly higher in the heavily thinned plot ( $P = 0.013$ ), which also had the lowest pretreatment BA (Table 1). Overall, these pretreatment comparisons suggest similar stand stocking and tree growth rates for the control and lightly thinned plots. Resource availability to postsettlement trees prior to thinning appeared to be greatest in the heavily thinned plot, whereas resource availability to presettlement trees prior to thinning was similar in all plots.

### Tree Sampling

In May 2000, we haphazardly selected 12 trees in each treatment plot for a total of 36 trees. Three trees were selected from each of four size classes: small postsettlement (13–19 cm dbh, 14.8 m average height), medium postsettlement (23–29 cm dbh, 17.8 m average height), large postsettlement (33–39 cm dbh, 20.5 m average height), and presettlement (more than 60 cm dbh, 27.4 m average height). Most postsettlement trees in this area established in the 1919 regeneration event (Savage et al. 1996) and therefore were approximately 80 yr old at the time of our study. Presettlement trees in this area are 150–450 yr old (Mast et al. 1999). Selected trees had no visible insect or physical damage and appeared disease-free. Presettlement trees were an exception; most of them were lightly infested with dwarf mistletoe (*Arceuthobium spp.*) in the lower crown (Dwarf Mistletoe Rating of 1 or 2, Hawksworth 1977). Sampled trees in each treatment area were located within 200 m of one another with similar slope and aspect.

In 2001, we altered our sampling population in response to the first year's results because almost no characteristics of tree water, carbon, or nutrient relations differed among the three tree size classes of postsettlement trees in 2000 (see results). In 2001 we measured ten presettlement trees and ten postsettlement trees in each of the three treatment areas ( $n = 60$  in total). Diameter at breast height of sampled postsettlement trees in 2001 ranged between 10 and 40 cm dbh (average height 17.7 m), and presettlement trees were similar to those described for 2000.

### Water Relations

We measured predawn ( $\Psi_{PD}$ ) and midday (1100–1300 hrs;  $\Psi_{MD}$ ) xylem water potential on needles of each tree in June and August of 2000, and June and September of 2001.  $\Psi_{PD}$  approximates soil water potential and soil water available at the root/soil interface (Kozlowski and Pallardy 1997).

**Table 1. Pretreatment (1998) basal area (BA), trees per hectare (TPH), stand density index (SDI, Reineke 1933), posttreatment BA, and postthinning percent reduction in BA for each treatment area (from Fulé et al. 1999).**

Treatment	Pretreatment			Posttreatment BA	
	BA (m <sup>2</sup> ha <sup>-1</sup> )	TPH	SDI	BA (m <sup>2</sup> ha <sup>-1</sup> )	% BA Reduction
Control	40	1106	335	40	0
Light thin and burn	38	1948	362	22	43
Heavy thin and burn	33	1186	293	18	46

June is typically the driest part of the growing season in northern Arizona, whereas late August and early September are at the end of the summer rainy season. For each sample month, trees in all treatment areas were measured during 3 consecutive days, and trees in the same treatment area were measured on 1 day. The order of measurement of treatment areas and trees within treatment areas was determined randomly for each month.

We measured water potential in the field using a pressure chamber (Model 1000, PMS Instruments, Corvallis, OR, USA). We clipped twigs from sunlit branches (except at predawn) from the middle of the canopy, excised 1 yr old needles and stored them immediately in a sealed plastic bag with a damp paper towel. The plastic bag was immediately placed into a dark, cool container until measurement. All needles were measured within 1 hr of excision. This procedure of sampling, storing, and measuring water potential results in values similar to those acquired from immediate measurements (Kaufmann and Thor 1982, T.E. Kolb, unpublished data). For each tree, we measured water potential on several needles until we obtained three values within 0.1 MPa, and we used the mean of these three values for each tree.

### Leaf Gas Exchange

We measured net photosynthetic rate ( $A_{net}$ ) and stomatal conductance ( $g_s$ ) on 1 yr old needles from the same twigs cut for water potential measurements at midmorning (0800–1000 hr) and midday (1100–1300 hr). Measurements were made within 1 min. of excision (Yoder et al. 1994, Feeney et al. 1998, Stone et al. 1999) using a LI-6200 portable photosynthesis system (Li-Cor Inc., Lincoln, NE) with a 250 ml cuvette. We measured two fascicles per tree for 30 s at high light intensity ( $PAR > 800 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). These fascicles were then used to calculate total leaf surface area. Radii for each needle were measured, and the average for each fascicle was used to calculate the total surface area contained in the cuvette (Svenson and Davis 1992).

Because  $A_{net}$  and  $g_s$  were measured over 3 consecutive days within a month for the three treatment areas, and trees in each treatment area were measured on different days, apparent differences in leaf gas exchange among treatments could be confounded with differences among measurement days in environmental factors that influence leaf gas exchange, such as vapor pressure deficit (VPD). However, there was little evidence of such confounding factors in our study. The order of measurement of treatment areas within each month was random to prevent systematic bias. Midday vapor pressure deficit (VPD) differed among treatment areas by a maximum of 0.48 kPa in June 2000 (overall mean = 4.18 kPa), 0.48 kPa in August 2000 (overall mean = 3.69 kPa), 0.26 kPa in June 2001 (overall mean = 3.97 kPa), and 0.91 kPa in September 2001 (overall mean = 3.51 kPa), and no treatment area had consistently high or low VPD. Plots of  $A_{net}$  and  $g_s$  versus VPD pooled over measurement times and months within each year (e.g., Hubbard et al. 1999) revealed differences among treatment areas (data not shown) identical to the results of our ANOVA comparisons.

We calculated leaf-level soil-to-leaf hydraulic conductance ( $K_1$ ) for each tree at midday.  $K_1$  was calculated as:

$$K_1 (\text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}) = \frac{\text{Transpiration rate } (\text{mol m}^{-2} \text{s}^{-1})}{(\Psi_{\text{soil}} - \Psi_{\text{leaf}}) (\text{MPa})}$$

Leaf-level transpiration rate was recorded by the LI-6200 concurrently with  $A_{net}$ .  $\Psi_{\text{soil}}$  was assumed to be equivalent to  $\Psi_{PD}$ , and  $\Psi_{MD}$  was measured at the time of the transpiration measurement (midday). We only present  $K_1$  results for 2001. In 2000, extreme drought conditions resulted in little or no difference between  $\Psi_{PD}$  and  $\Psi_{MD}$  and transpiration rate was near zero in many cases; therefore many values of  $K_1$  in 2000 were close to zero.

### Foliar Nitrogen and Carbon Isotope Ratio ( $\delta^{13}\text{C}$ )

We measured foliar nitrogen concentration in current-year leaves collected in late September of 2000 and 2001 after leaf growth was complete. In late September 2000 and 2001, we sampled leaves formed in those years and measured  $\delta^{13}\text{C}$  of whole leaf tissue. Between 0900 and 1300 hr, we excised twigs from sunlit branches in the mid-canopy of trees with a pole-pruner or shotgun. Needles were oven dried at 70°C for 48 hr. We ground dried needles in a Thomas-Wiley mill (3383-L10 series, Thomas Scientific, Swedesboro, NJ) to 20 mesh. Ground samples were analyzed for total nitrogen concentration and  $\delta^{13}\text{C}$  with a continuous-flow mass spectrometer (Ceinstrument NC2100 and Delta Plus XL Finnigan, MAT, San Jose, CA) at the Colorado Plateau Stable Isotope Analysis Facility, Northern Arizona University. Nitrogen concentration was based on leaf area ( $\text{g m}^{-2}$ ) and leaf mass ( $\text{mg g}^{-1}$ ). Hydraulic resistance to water flow from soil to leaf may vary with path length and affect  $\delta^{13}\text{C}$  (Walcroft et al. 1995, Warren and Adams 1999); thus we estimated path length by measuring branch height and length of each sampled tree with a clinometer and logger's tape to use as a covariate in analysis of  $\delta^{13}\text{C}$ . However, path length was not a significant covariate with  $\delta^{13}\text{C}$  and will not be considered henceforth.

Measurements of  $\delta^{13}\text{C}$  were made on whole leaf tissue without pretreatment to remove cellulose because: (1) such pretreatment typically does not change the pattern of isotopic differences, only the absolute amount (Tans and Mook 1980, Schleser 1992); (2) whole-tissue  $\delta^{13}\text{C}$  has been shown to be sensitive to variations in water availability in many studies (e.g., McNulty and Swank 1995, MacFarlane and Adams 1989, Pate 2001); (3) differences in chemical concentration of tissues, which can bias  $\delta^{13}\text{C}$  comparisons (Ehleringer 1989, Pate 2001), among leaves from the different treatments and years of leaf expansion in our study are assumed to be small because all sampled leaves grew in a high light environment and were not senescent; (4) leaf whole-tissue  $\delta^{13}\text{C}$  is largely determined by the  $\delta^{13}\text{C}$  of carbon used for leaf synthesis because structural nonlabile carbon constitutes the most mass of leaf tissues (Pate 2001).

### Data Analysis

We used SAS JMP software (SAS Institute Inc. Cary, NC USA) to perform repeated measures analysis of variance (ANOVA) for tree physiological data in each year with sample month as the repeated measure and treatment, tree size, and their interactions as factors. Years were analyzed

**Table 2. Probability values for repeated measures analysis of variance of physiological data for years 2000 and 2001. Sources of variation are month (June and August 2000; June and September 2001), treatment (control, light thin and burn, heavy thin and burn), tree size (small, medium, large and presettlement in Year 2000; presettlement and postsettlement in Year 2001) and their interactions.**

	Month	Treatment	Size	Month × treatment	Treatment × size	Month × size	Month × size × treatment
Year 2000							
Degrees of freedom	1	2	3	2	6	3	6
Predawn $\Psi_{PD}$	<0.001	<0.001	0.410	<0.001	0.656	0.116	0.006
Midday $\Psi_{MD}$	0.001	0.005	0.272	<0.001	0.828	0.072	0.526
Midmorning $A_{net}$	<0.001	0.118	0.716	0.415	0.999	0.527	0.923
Midmorning $g_s$	<0.001	0.133	0.416	<0.001	0.655	0.201	0.866
Midday $A_{net}$	<0.001	0.014	0.829	0.003	0.935	0.558	0.023
Midday $g_s$	<0.001	0.419	0.881	<0.001	0.915	0.484	0.014
Year 2001							
Degrees of freedom	1	2	1	2	2	1	2
Predawn $\Psi_{PD}$	<0.001	<0.001	0.683	<0.001	0.259	0.361	0.853
Midday $\Psi_{MD}$	<0.001	0.0159	0.101	0.084	0.047	0.660	0.010
Midmorning $A_{net}$	0.003	0.005	0.002	0.009	0.345	0.078	0.597
Midmorning $g_s$	<0.001	0.007	0.001	0.212	0.708	0.006	0.625
Midday $A_{net}$	0.861	<0.001	<0.001	<0.001	0.023	0.674	0.221
Midday $g_s$	<0.001	<0.001	0.010	0.002	0.203	0.645	0.017
Midday $K_j$	<0.001	0.496	0.010	0.015	0.319	0.336	0.001

separately because sampled trees changed between years. We used *t*-tests to compare means when factors in the ANOVA were significant. We considered *P*-values less than 0.05 to be significant and values between 0.05 and 0.1 to be marginally significant. Cost and technical constraints prevented measurements on trees in true spatial replicates of all thinning treatments. Our use of individual trees within a 17 ha treatment plot as replicates represents pseudoreplication similar to individual plants within a greenhouse or growth chamber, and may result in incorrect conclusions (Hurlbert 1984). Whereas the scope of our study was constrained by the design, the impact of the treatments on tree density and stand basal area was large compared with pretreatment differences (Table 1), and apparent effects of thinning on tree physiological characteristics were qualitatively similar to other studies on ponderosa pine in northern Arizona (Kolb et al. 1998, Feeney et al. 1998, Stone et al. 1999), ensuring that the results show treatment rather than random effects.

## Results

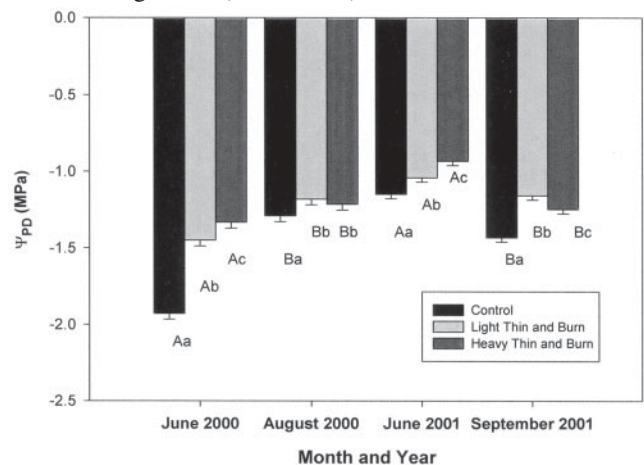
### Water Relations

Year 2001 was wetter than 2000, which was an extremely dry year for northern Arizona. The Palmer Drought Severity Index (PDSI; Palmer 1965) is a measure of meteorological drought based on temperature and precipitation, with -2 indicating moderate drought, -4 indicating extreme drought, and positive numbers indicating wet conditions. Average yearly PDSI was -1.14 in 2001 versus -3.34 in 2000. In the dry season (May-June), PDSI was -0.9 in 2001 versus -4.33 in 2000. In the summer rainy season (July-September), PDSI was -0.01 in 2001 versus -5.24 in 2000 (National Climatic Data Center).

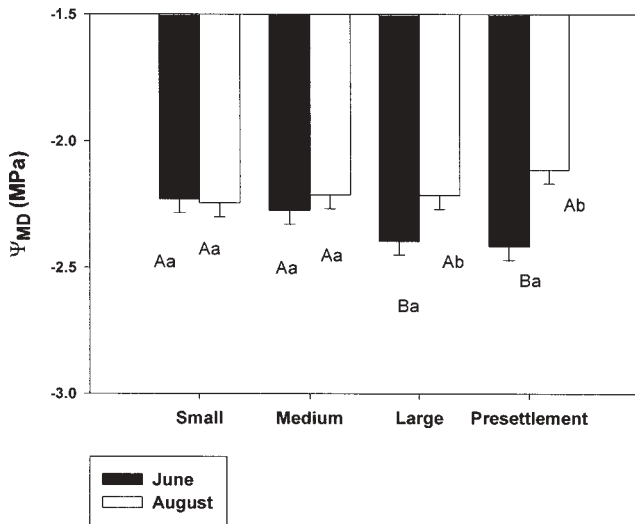
2000  $\Psi_{PD}$  was significantly affected by sample month, treatment, the month × treatment interaction, and the month × treatment × tree size interaction (Table 2).  $\Psi_{PD}$  was higher in August than June, and higher in thinned than control treatments (Figure 1). Year 2000  $\Psi_{MD}$  had similar significant sources of variation as  $\Psi_{PD}$  (Table 2). In addition, the month

× tree size interaction was marginally significant for  $\Psi_{MD}$  (Table 2), and was due to lower  $\Psi_{MD}$  for large postsettlement and presettlement trees than small and medium postsettlement trees in June, whereas  $\Psi_{MD}$  did not differ among tree sizes in August (Figure 2).

In 2001,  $\Psi_{PD}$  was again significantly affected by month, treatment, and the month × treatment interaction (Table 2).  $\Psi_{PD}$  in the control was lower than  $\Psi_{PD}$  in both thinned treatments in both months sampled in 2001 (Figure 1). In June 2001, the heavy thinning treatment had higher  $\Psi_{PD}$  than the light thinning treatment, but in September, their ranking was reversed (Figure 1).  $\Psi_{MD}$  in 2001 varied significantly with month, treatment, the treatment × tree size interaction, and the month × treatment × tree size interaction. While statistically significant, these differences in 2001  $\Psi_{MD}$  were small in magnitude (<0.02 MPa).



**Figure 1. Predawn leaf water potential ( $\Psi_{PD}$ ) for each month (June and August 2000, June and September 2001) and treatment (control, light thin and burn, heavy thin and burn) averaged over presettlement and postsettlement trees. Bars indicate one standard error of the mean. Different capital letters below bars indicate significant differences between months within treatments for each year, and different lowercase letters indicate significant differences among treatments within months for each year ( $\alpha = 0.05$ ).**



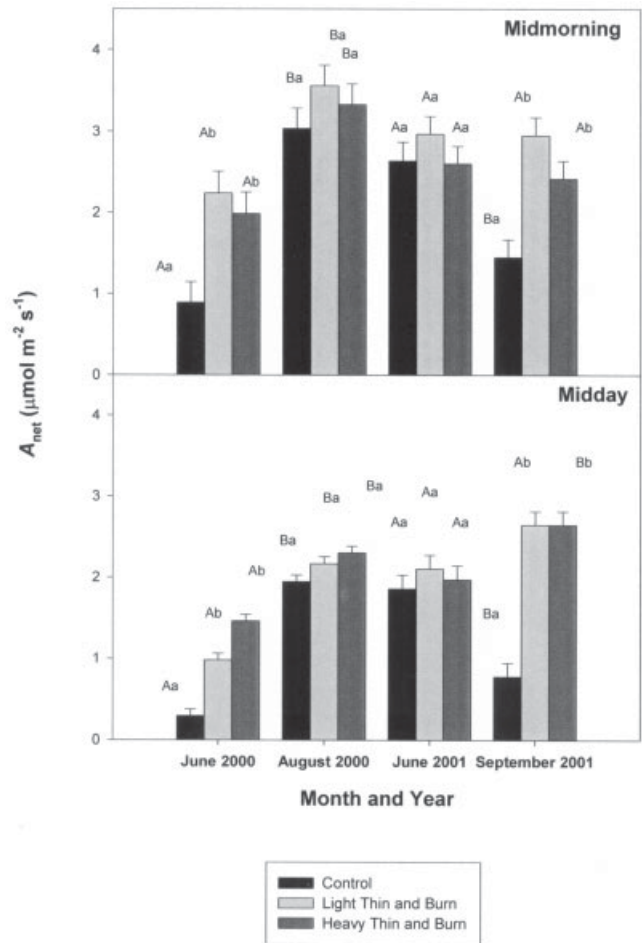
**Figure 2.** Midday leaf water potential ( $\Psi_{MD}$ ) for each month sampled in 2000 (June, August) and tree size (small, medium, large, and presettlement) averaged over treatments. Different capital letters indicate significant differences among tree sizes within months, and different lowercase letters indicate significant differences between months within tree sizes ( $\alpha = 0.05$ ).

### Leaf Gas Exchange

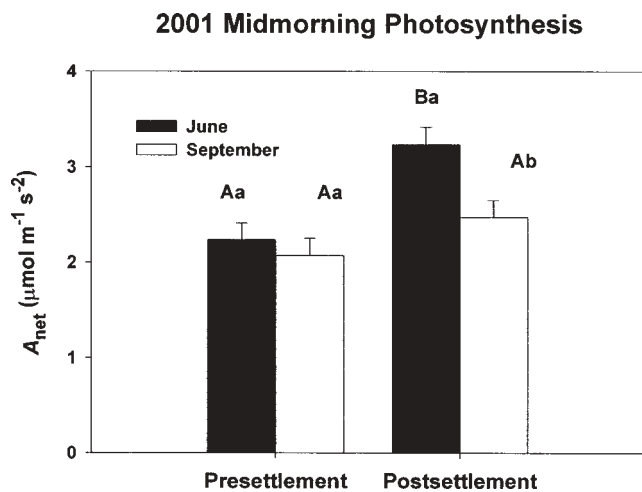
In 2000, both midmorning and midday  $A_{net}$  were significantly higher in August than June (Figure 3). Midday  $A_{net}$  also varied significantly among treatments, and the month  $\times$  treatment and month  $\times$  treatment  $\times$  tree size interactions were significant (Table 2). Midmorning and midday  $A_{net}$  were significantly higher in both thinned treatments than the control in June 2000, with no difference in August (Figure 3).

In year 2001, midmorning  $A_{net}$  was affected by month, treatment, tree size, and the month  $\times$  treatment and month  $\times$  tree size interactions were significant (Table 2). Midmorning  $A_{net}$  did not differ significantly among treatments in June 2001, but was significantly lower for the control than both thinned treatments in September (Figure 3). Midmorning  $A_{net}$  was lower in presettlement than postsettlement trees in June, but not September 2001 (Figure 4). Midday  $A_{net}$  in 2001 was significantly affected by treatment, tree size, and the month  $\times$  treatment and treatment  $\times$  tree size interactions (Table 2). Midday  $A_{net}$  did not differ among treatments in June 2001, but was higher in both thinned treatments than the control in September 2001 (Figure 3). Thinning increased midday  $A_{net}$  of postsettlement trees more than  $A_{net}$  of presettlement trees (Figure 5).

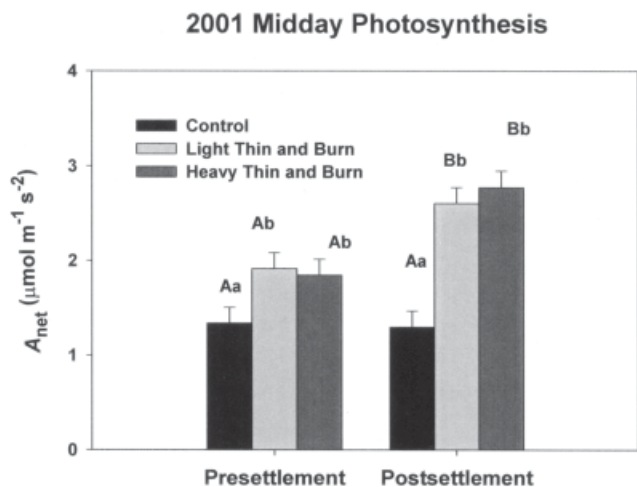
Leaf stomatal conductance ( $g_s$ ) was strongly and positively correlated with  $A_{net}$  in 2000 (midmorning  $P < 0.0001$ ,  $R^2 = 0.7204$ ; midday  $P < 0.0001$ ,  $R^2 = 0.8216$ ) and the pattern of treatment effects was similar for  $A_{net}$  and  $g_s$ . In year 2001,  $g_s$  did not correlate as strongly with  $A_{net}$  as in 2000 (midmorning  $P < 0.0001$ ,  $R^2 = 0.5250$ ; midday  $P < 0.0001$ ,  $R^2 = 0.3245$ ). Midmorning  $g_s$  and  $A_{net}$  in 2001 had similar significant sources of variation (Table 2). Midday  $g_s$  in 2001 was significantly affected by month, treatment, tree size, and the month  $\times$  treatment and month  $\times$  tree size  $\times$  treatment interactions (Table 2). Midday  $g_s$  was significantly higher in June than September (Figure 6). Thinning increased midday  $g_s$



**Figure 3.** Net photosynthetic rate ( $A_{net}$ ) at midmorning and midday for each month (June and August 2000, June and September 2001) and treatment (control, light thin and burn, heavy thin and burn) averaged over presettlement and postsettlement trees. Different capital letters indicate significant differences between months within treatments for each year, and different lowercase letters indicate significant differences among treatments within months for each year ( $\alpha = 0.05$ ).



**Figure 4.** Midmorning net photosynthetic rate ( $A_{net}$ ) in 2001 for each month (June, August) and tree size (presettlement, postsettlement) averaged for all treatments. Different capital letters indicate significant ( $\alpha = 0.05$ ) differences between tree sizes within months, and different lower case letters indicate significant differences between months within tree sizes. Bars indicate one standard error of the mean.



**Figure 5.** Midday net photosynthetic rate ( $A_{net}$ ) in 2001 for each treatment (control, light thin and burn, heavy thin and burn) and tree size (presettlement, postsettlement) averaged over all months. Different capital letters indicate significant differences between tree sizes within treatments, and different lower case letters indicate significant differences among treatments within tree sizes. Bars indicate one standard error of the mean.

of postsettlement trees more than presettlement trees in September 2001 (Figure 6).

In 2001, midday  $K_1$  was significantly affected by month, tree size, and the month  $\times$  treatment and month  $\times$  tree size  $\times$  treatment interactions (Table 2). For presettlement trees,  $K_1$  did not differ among treatments in either June or September. For postsettlement trees,  $K_1$  was higher in the control than both thinned treatments in June, with the opposite result in September (Figure 7).  $K_1$  of postsettlement trees was significantly higher than  $K_1$  of presettlement trees in the control in June and in the light thinning treatment in September (Figure 7).

### Foliar Nitrogen and Carbon Isotope Ratio

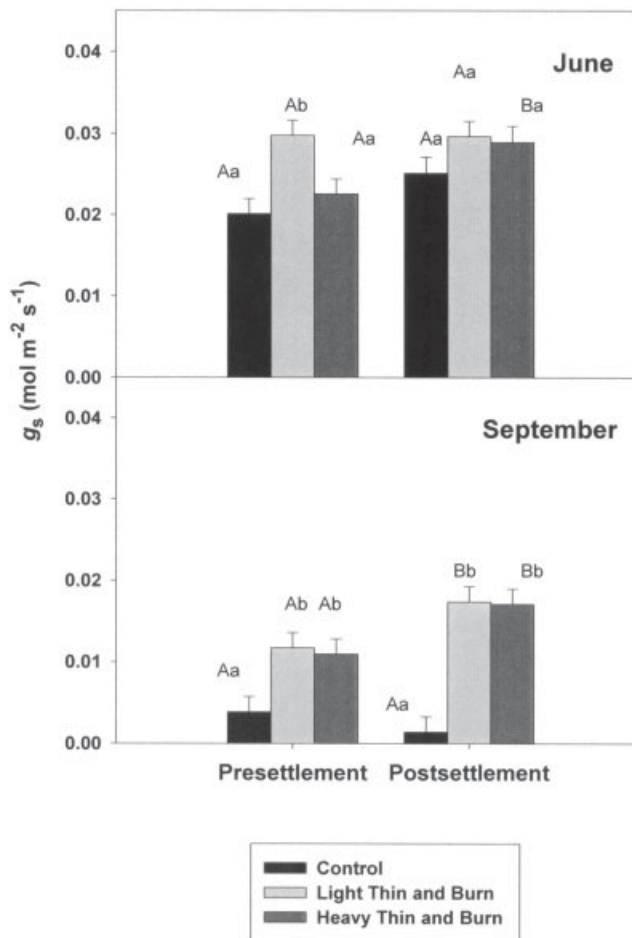
There was no significant difference in nitrogen concentration of current-year leaves among treatments or tree size classes in year 2000 (Table 3). Interaction between treatment and tree size was also nonsignificant.

In year 2001, treatment was not a significant source of variation in foliar nitrogen concentration, but tree size was (Table 3). Presettlement trees had higher nitrogen concentration expressed on both a mass (mean = 15.1 mg g<sup>-1</sup>, SE = 0.604) and an area basis (mean = 1.44 g m<sup>-2</sup>, SE = 0.082) than postsettlement trees (mean = 13.07 mg g<sup>-1</sup>, SE = 0.615; mean = 1.13 g m<sup>-2</sup>, SE = 0.084).

Foliar  $\delta^{13}\text{C}$  did not differ significantly among treatments for leaves formed in 2000 and 2001 (Table 3). Tree size was a significant source of variation for foliar  $\delta^{13}\text{C}$  in 2001, when only two size classes were evaluated (Table 3). In 2001, presettlement trees (mean = -25.84, SE = 0.138) had higher foliar  $\delta^{13}\text{C}$  than postsettlement trees (mean = -26.50, SE = 0.143). Interaction between tree size and treatment effects was not significant for either year.

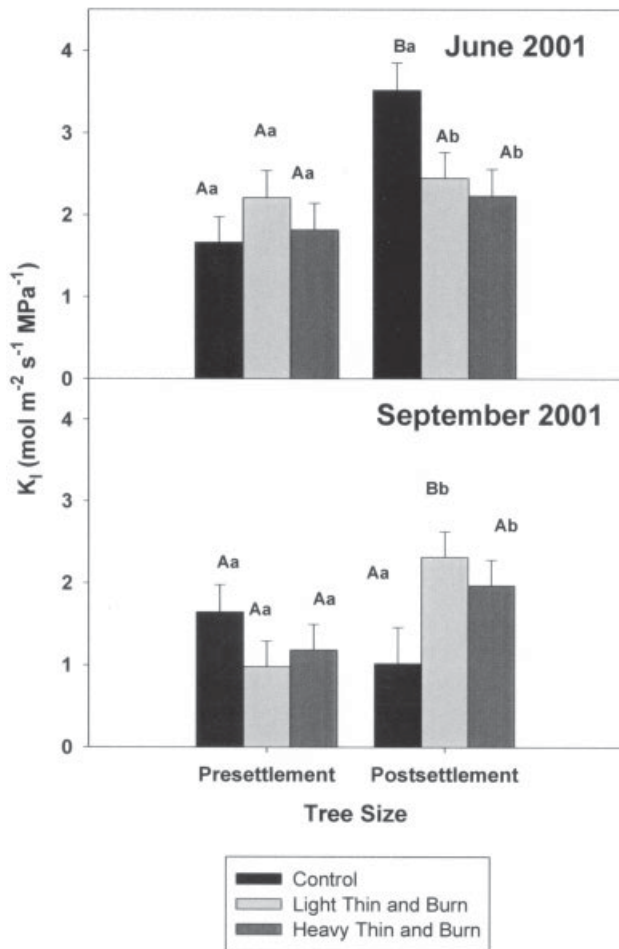
### Discussion

The thin and burn treatments in our study, which retained all presettlement trees and larger postsettlement trees located



**Figure 6.** Midday leaf stomatal conductance ( $g_s$ ) in 2001 for each month (June, September), treatment (control, light thin and burn, heavy thin and burn) and tree size (presettlement, postsettlement). For each month, different capital letters indicate significant differences between tree sizes within treatments, and different lowercase letters indicated significant differences among treatments within tree sizes ( $\alpha = 0.05$ ). Bars indicate one standard error of the mean.

near evidence of dead presettlement trees, improved water availability to both postsettlement and presettlement trees by decreasing tree-to-tree competition. Tree  $\Psi_{PD}$  was higher in the thinned and burned treatments than in the control in both years and seasons. The greatest difference in  $\Psi_{PD}$  between the thinned and burned treatments and the control occurred during the period of extreme drought (June 2000). Feeney et al. (1998) reported similar results for presettlement trees in thinned and burned treatments versus an unthinned/unburned control in a restoration treatment thinned in 1993 located 5 km from our study site. Kolb et al. (1998) observed this same trend for postsettlement trees in treatments thinned to various basal areas at another study site in close proximity to the present study. The lowest seasonal  $\Psi_{PD}$  in these studies (-1.5 MPa, Feeney et al. 1998, -1.3 MPa, Kolb et al. 1998) was higher than the lowest seasonal  $\Psi_{PD}$  in our study in year 2000 (-1.9 MPa). McCullough and Wagner (1987) reported  $\Psi_{PD}$  similar to our lowest measurements (-1.8 MPa) only in ponderosa pines that were trenched (i.e., root pruned) to induce extreme water stress. These comparisons further indicate that tree water stress was unusually severe in our study in year 2000.



**Figure 7.** Midday leaf-level soil-to-leaf hydraulic conductance ( $K_l$ ) in 2001 for each month (June, September), treatment (control, light thin and burn, heavy thin and burn) and tree size (presettlement, postsettlement). Different capital letters indicate significant differences between tree sizes within treatments, and different lowercase letters indicate significant differences among treatments within tree sizes ( $\alpha = 0.05$ ). Bars indicate one standard error of the mean.

Our  $\Psi_{PD}$  results suggest that thinning and burning treatments based on presettlement forest condition ameliorated effects of severe drought on water uptake of both presettlement and postsettlement trees. Such treatments might be effective in maintaining soil water availability in ponderosa pine forests during severe droughts predicted in the future by some

climate change models (Le Houérou 1996, Frederick and Major 1997).

Trees in thinned and burned treatments had higher midmorning and midday  $A_{net}$  than trees in the control, but only during the driest times when  $\Psi_{PD}$  was lowest (June 2000 and September 2001).  $A_{net}$  did not differ among treatments when soil water was more abundant (August 2000, June 2001). Thus, these treatments increased tree carbon acquisition in the middle of the day, especially during droughts when low water availability and low atmospheric humidity can result in low stomatal conductance or stomatal closure. Higher carbon gain of trees in thinned and burned stands may improve growth and carbon-based defenses against insects and pathogens (Larsson et al. 1983, Kolb et al. 1998, Feeney et al. 1998).

The light and heavy thinning had similar effects on tree  $\Psi_{PD}$  and leaf gas exchange. For example,  $\Psi_{PD}$  did not differ consistently between these levels of thinning, and the statistically significant differences did not exceed 0.12 MPa. Moreover,  $A_{net}$  did not differ significantly between the light and heavy thinning treatments at any time. The heavy thinning treatment reduced stand BA slightly more (46%) than the light thinning (43%), and produced a lower posttreatment BA (18 versus 22 m<sup>2</sup> ha<sup>-1</sup>). However, these differences were apparently too small to influence  $\Psi_{PD}$  and  $A_{net}$ . Kolb et al. (1998), at a site 1 km from our study site, reported no differences in  $\Psi_{PD}$  or  $A_{net}$  of ponderosa pines between treatments thinned to 18.4 and 27.6 m<sup>2</sup> ha<sup>-1</sup> except on one measurement date, when  $\Psi_{PD}$  was higher in the treatment with the lowest BA. Treatments studied by Kolb et al. (1998) differed in stand BA by 9.2 m<sup>2</sup> ha<sup>-1</sup>, whereas our light and heavy thinning treatments differed in BA only by 5 m<sup>2</sup> ha<sup>-1</sup>. Thus, in many respects the “light” and “heavy” thinning treatments in our study can be viewed as replicates of a similar treatment, rather than distinctly different treatments.

Higher  $A_{net}$  of trees in the thinned and burned treatments versus the control may have been caused by higher supply of carbon dioxide through stomata (i.e., higher  $g_s$ ), as foliar N concentration, which can influence  $A_{net}$  by altering levels of photosynthetic enzymes (Reich et al. 1994, Kozlowski and Pallardy 1997), did not differ among treatments. Low-intensity prescribed fire may mineralize nitrogen stored in forest floor litter and woody debris and increase nitrogen availabil-

**Table 3.** Results of analysis of variance (df = degrees of freedom,  $P$  =  $F$ -test probability value) for foliar nitrogen concentration and  $\delta^{13}C$ . Sources of variation were thinning treatment (control, light, and heavy), tree size (small, medium, large, and presettlement in Year 2000; presettlement and postsettlement in Year 2001) and their interaction. Foliar  $\delta^{13}C$  and nitrogen results are presented for leaves formed in years 2000 and 2001, and nitrogen results are expressed on a leaf total surface area (g m<sup>-2</sup>) and mass (mg g<sup>-1</sup>) basis.

	Treatment		Size		Treatment × size	
	df	$P$	df	$P$	df	$P$
2000						
$\delta^{13}C$	2	0.3094	3	0.3935	6	0.6337
N (g m <sup>-2</sup> )	2	0.7995	3	0.9286	6	0.0977
N (mg g <sup>-1</sup> )	2	0.1393	3	0.4294	6	0.0956
2001						
$\delta^{13}C$	2	0.5194	1	0.0010	2	0.9892
N (g m <sup>-2</sup> )	2	0.3923	1	0.0108	2	0.7743
N (mg g <sup>-1</sup> )	2	0.3294	1	0.0217	2	0.6323



ity to plants (Ryan and Covington 1986, Monleon and Cromack 1996, Grogan et al. 2000). Feeney et al. (1998) reported an increase in nitrogen concentration in the thinned and the thinned and burned treatments compared with an unthinned, unburned control, for presettlement ponderosa pines at the Gus Pearson Natural Area located near our study site. In contrast, nitrogen concentration in leaves developed in 2000 following thinning treatments, or in 2001 following the spring prescribed burn, did not differ among treatments in our study.

Interestingly, foliar  $\delta^{13}\text{C}$  was not affected by thinning treatments in 2000 or 2001. Since  $\delta^{13}\text{C}$  is often higher in trees with lower  $g_s$  (Farquhar and Lloyd 1993), the lack of treatment effects on  $\delta^{13}\text{C}$  might suggest that thinning did not affect leaf  $g_s$ . However, instantaneous measurements revealed that  $g_s$  in 2001 was lower in the control than in the thinned treatments in September. Foliar  $\delta^{13}\text{C}$  estimates the relative concentration of  $^{12}\text{C}$  and  $^{13}\text{C}$  isotopes in leaf tissue, which is influenced by leaf internal  $\text{CO}_2$  concentration and the ratio between uptake of carbon dioxide by photosynthesis and supply through stomata during assimilation of the carbon used for leaf synthesis (Francey and Farquhar 1982, Farquhar and Lloyd 1993, Pate 2001). This period of assimilation occurs near the time of leaf growth. Consequently,  $\delta^{13}\text{C}$  in our study provided an estimate of leaf gas exchange characteristics only near the time of leaf growth, which occurred between late June and late July in our study. Thus, results for  $\delta^{13}\text{C}$  and  $g_s$  could differ because the physiological process that influenced each characteristic differed in not only temporal scale (i.e., time-integrated versus instantaneous), but also season timing. Moreover, the lack of variation in  $\delta^{13}\text{C}$  among treatments may have occurred because both  $A_{\text{net}}$  and  $g_s$  increased in the thinned and burned treatments, leaving the ratio of  $A_{\text{net}}/g_s$  and leaf internal  $\text{CO}_2$  concentration unchanged.

Presettlement and postsettlement trees differed in  $A_{\text{net}}$  and responded differently to thinning and burning treatments. In 2000, our sample size ( $n = 3$  per tree size class per treatment) likely hindered our ability to detect tree size effects. However, in 2001 when we reduced the number of size classes of postsettlement trees and increased sample size ( $n = 10$  per tree size class),  $A_{\text{net}}$  was consistently higher in postsettlement than presettlement trees in the thinned treatments where  $A_{\text{net}}$  and  $g_s$  were not constrained by intense tree-to-tree competition. Also, stimulation of  $A_{\text{net}}$  and  $g_s$  by the thinning and burning treatments was greater for postsettlement than presettlement trees.

Foliar nitrogen concentration differed between tree sizes, but could not explain higher  $A_{\text{net}}$  in the smaller postsettlement trees. Despite higher foliar nitrogen concentration in presettlement compared to postsettlement trees in 2001,  $A_{\text{net}}$  was generally lower in presettlement trees. Higher foliar nitrogen concentration in presettlement trees may be attributable to fire effects. Presettlement trees had deep layers of duff and litter around their boles, whereas postsettlement trees lacked these deep layers, and were surrounded by more green grass, which did not burn. Ryan and Covington (1986) found that increased soil nitrogen following prescribed fire was

positively correlated with litter depth before burning. Perhaps burning of higher amounts of litter around presettlement trees in our study increased nitrogen available to those trees compared to postsettlement trees.

Our results suggest that lower  $A_{\text{net}}$  of presettlement versus postsettlement trees resulted from a tree-size related difference in water relations, such as stomatal sensitivity to VPD, or root-to-leaf hydraulic conductance (Hubbard et al. 1999, Kolb and Stone 2000, Williams et al. 2001). Consistent with this suggestion, midday leaf-level soil-to-leaf hydraulic conductance ( $K_1$ ) in September 2001 was higher for postsettlement than presettlement trees in the thinned treatments, and thinning stimulated  $K_1$  of postsettlement trees more than presettlement trees at this time. This finding adds to a growing body of information suggesting that productivity of large, old ponderosa pine trees is constrained by low  $K_1$  (Yoder et al. 1994, Hubbard et al. 1999, Williams et al. 2001). Variation in midday  $K_1$  between years and seasons was partly due to variation in  $\Psi_{PD}$ , since  $\Psi_{MD}$  varied little. Low  $K_1$  in year 2000 and September 2001 was associated with low  $\Psi_{PD}$ , which reduced the gradient in water potential between soil and leaf that drives water flow through the tree, and low  $g_s$ , which reduced transpiration rate.

Our results support earlier research by Feeney et al. (1998) and Stone et al. (1999), which showed that thinning prescriptions in northern Arizona ponderosa pine forests based on the stand structure present before Euro-American settlement can reduce tree-to-tree competition for water and increase physiological processes sensitive to water availability, such as  $A_{\text{net}}$  and  $g_s$ . Such beneficial effects of thinning on presettlement trees occur over a range of thinning intensities, ranging from a 62% reduction in stand BA to  $13 \text{ m}^2 \text{ ha}^{-1}$  at the Gus Pearson Natural Area (Feeney et al. 1998, Stone et al. 1999) to a 43% reduction in stand BA to  $22 \text{ m}^2 \text{ ha}^{-1}$  in the light thinning in our study. Moreover, such thinning treatments in our study had larger beneficial effects on  $A_{\text{net}}$  and  $g_s$  of younger, postsettlement trees than old-growth presettlement trees 1 and 2 yr after treatment, and were most pronounced during drought.

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