
Effects of Restoration Thinning on Presettlement *Pinus ponderosa* in Northern Arizona

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Abstract

In the 100 years following the arrival of Euro-American settlers in northern Arizona, *Pinus ponderosa* (ponderosa pine) forests changed from open, low-density stands to closed, high-density stands. The increase in tree density has been detrimental to the vigor of old-growth trees that established before settlement (presettlement trees). In this study, we examined whether the vigor of presettlement trees could be improved by restoring the original stand structure by thinning the ponderosa pines that established after settlement (postsettlement trees). The restoration treatment caused the following changes in the presettlement trees and their environment in the first year following thinning: an increase in volumetric soil water content between May and August, an increase in predawn xylem water potential in July and August, a decrease in midday xylem water potential in June and August, an increase in net photosynthetic rate in August, an increase in foliar nitrogen concentration in July and August, and an increase in bud and needle size. The results show that the thinning restoration treatment improved the condition of presettlement ponderosa pines by increasing canopy growth and the uptake of water, nitrogen, and carbon.

Introduction

Before Euro-American settlement in the southwestern United States, *Pinus ponderosa* (ponderosa pine) forests were characterized by a dense grass understory and highly flammable leaf litter that carried low-intensity ground fires every 2–20 years (Cooper 1960; Weaver 1974; Dieterich 1980; Arno 1988; Swetnam & Baisan 1996). These fires maintained relatively open forests and savannas (Pearson 1950; Cooper 1960; Covington & Moore 1994; Swetnam & Baisan 1996). Following settlement by non-indigenous peoples, however, pines invaded meadows and increased in density in forested areas because of fire suppression, a reduction of grass cover caused by livestock overgrazing, and a good seed-production year in 1918 followed by a favorable, warm, wet climate for seedling establishment (Cooper 1960; Dieterich 1980; Madany & West 1983; Covington & Moore 1994; Savage et al. 1996; Swetnam & Baisan 1996). This increase in tree density in southwestern ponderosa pine forests has caused unhealthy characteristics such as a decrease in the growth rate and an increase in the mortality of old-growth trees (Sutherland 1983; Biondi 1996), an increase in ponderosa pine water stress (Kolb et al. 1998), a decrease in key resistance mechanisms of ponderosa pine against insects (Kolb et al. 1998), a stagnation of nutrient cycling rates (Covington & Sackett 1992; Kaye & Hart 1998), a decrease in the growth and diversity of herbaceous plants (Covington & Moore 1994; Covington et al. 1997; Dahms & Geils 1997), ecosystem simplification because of the dominance of ponderosa pine (Covington & Moore 1994; Covington et al. 1997), and an increase in fire severity and size (Covington & Moore 1994).

There is presently much interest in improving forest health by restoring the stand structure and disturbance regime that was present before Euro-American settlement in southwestern ponderosa pine forests. We have initiated such a restoration project at the G. A. Pearson Natural Area in northern Arizona, which contains a relict old-growth stand of ponderosa pine in which the effects of restoration treatments on a suite of ecosystem characteristics are being examined (Covington et al. 1997; Kaye & Hart 1998; Feeney et al. 1998). Understanding the response of presettlement trees to restoration treatments is an important component of this project because of their great scarcity and value. The term "presettlement" is used to refer to the old-growth ponderosa pines that established in northern Arizona before 1876 (the approximate date of settlement by Euro-Americans), and "postsettlement" is used to refer to ponderosa pines that established in northern Arizona after 1876. Because the presettlement trees are old (>121 years) and have been suppressed by competition from the postsettlement trees for decades (Sutherland

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1983), it is unknown whether they are responsive to restoration treatments.

This paper addresses whether restoration of pre-Euro-American stand structure by thinning can reverse the decline in vigor of the presettlement ponderosa pines. Tree vigor was measured by canopy growth and the uptake of essential resources (carbon, nitrogen, phosphorus, and water).

Methods

Study Area

The study area is in a 4.7-ha portion of the G. A. Pearson Natural Area in the Fort Valley Experimental Forest, Coconino National Forest. The site is located 14.5 km northwest of Flagstaff, Arizona, U.S.A. (111°44'30'' W, 35°16'11'' N). At an elevation of 2195–2255 m, the topography of the site is level or very gently rolling, having slopes of 0–5% with a south-southwest aspect (Avery et al. 1976; White 1985; Covington et al. 1997). The site has a relatively homogeneous climate, topography, geology, soil parent material, soil type, biota, and disturbance history (Avery et al. 1976; White 1985).

The study site has a cold and subhumid temperature with a pronounced drought in May and June (Schubert 1974). Scattered late-summer afternoon thundershowers starting in late June or July result in highly variable annual precipitation. Precipitation in August, the wettest month, averages 82 mm. From 1909 to 1990, the average annual precipitation was 564 mm, the summer maximum air temperature was 36.1°C, the winter minimum air temperature was –38.3°C, and the mean annual temperature was 6.0°C (National Oceanic and Atmospheric Administration 1990). Snow can accumulate from November through March and accounts for about half of the annual precipitation (Schubert 1974). The frost-free growing season has averaged 94 days (Avery et al. 1976).

The soil parent material at the study site is derived from late-Tertiary basalt lava flows and volcanic cinders. The soil is classified as a Brolliar stony clay-loam, a fine, smectitic, Typic Argiboroll (Miller et al. 1995).

Trees at the study site are a naturally seeded, virgin (i.e., never logged) stand of the southwestern variety of ponderosa pine (var. *scopulorum*), also recognized as type 237 by the Society of American Foresters (Eyre 1980). Typical of the Southwest, the stand structure at the study site is currently uneven-aged with even-aged postsettlement groups, varying in size from a few trees to several hectares (Pearson 1950; Cooper 1960; Schubert 1974), and uneven-aged presettlement groups (White 1985). The site index of the study area is 24.2–25.9 m per 100 years (Avery et al. 1976). The oldest pine in the Natural Area is greater than 600 years (Biondi et al. 1994).

Covington et al. (1997) described the ponderosa pine stand at the study site as being dominated by pole-sized trees (10–37 cm diameter at breast height [dbh], 74–116 years old) with scattered groups of presettlement trees (37–105 cm dbh, 121–600 years old), dense thickets of sapling-sized trees (<10 cm dbh, 57–73 years old), a few scattered tree seedlings, and a few bunchgrass openings. Understory vegetation is comprised mainly of *Festuca arizonica* (Arizona fescue), *Muhlenbergia montana* (mountain muhly), *Sitanion hystrix* (squirreltail), several forbs, and *Ceanothus fendleri* (Fendler buckbrush). A reconstruction of stand composition using dendrochronological techniques showed that tree density at the study site has increased from about 59 trees/ha in 1876 to about 3095 trees/ha in 1992 (Covington et al. 1997).

Livestock grazing occurred on the site from 1876 to about 1920 (U.S. Forest Service, unpublished data). Fires have not occurred in the area since 1876; before that, low-intensity ground fires in the general area of the study site occurred at an average interval of about 2 years (Dieterich 1980).

Restoration Treatment

In the fall of 1993, 2.76 ha of the study area was thinned and 1.52 ha was left unthinned to serve as a control (Fig. 1). The thinning treatment removed most postsettlement trees to emulate the more open stand conditions typical before Euro-American settlement (Figs. 2 & 3). Presettlement forest reference conditions were established by stand reconstruction (Covington & Moore 1994; Covington et al. 1997). Tree ages were determined by counting and cross-dating increment cores (Stokes & Smiley 1968) from all presettlement trees and a 5% subsample of all postsettlement trees. In the thinned block, all presettlement trees were retained, as were postsettlement trees 40.6 cm dbh or larger. Smaller-diameter postsettlement trees that were near stumps, snags, and downed presettlement logs were also retained to emulate the clumped pattern characteristic of presettlement forests. Tree density in the thinned block was reduced from an average of 2647 trees/ha to 151 trees/ha; tree density in the unthinned control block remained at 4585 trees/ha.

Pretreatment Comparisons

Because average tree density differed between the control and thinned blocks prior to treatment, several pretreatment conditions were compared between blocks to assess their degree of similarity prior to thinning (Table 1). Three sets of variables were used for the pretreatment comparisons. First, mineral soil sampled before thinning in 1993 was analyzed for organic matter content (OM), total nitrogen concentration [N_T], and total

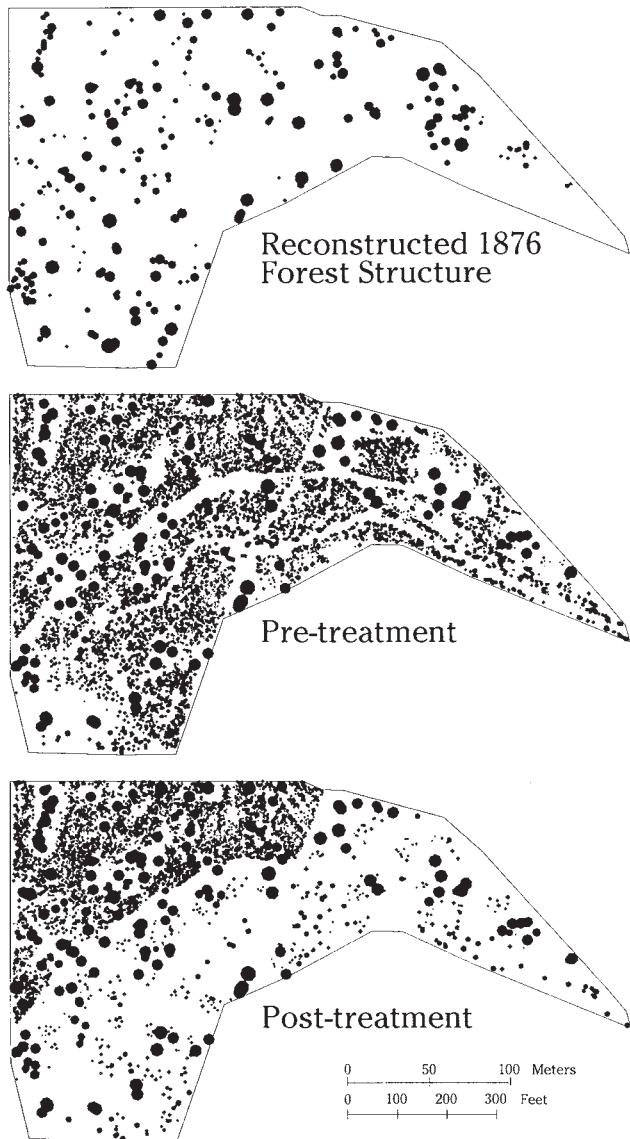


Figure 1. Canopy maps of the study area within the G. A. Pearson Natural Area, Arizona, based on stand reconstruction (Covington et al. 1997): the reconstructed 1876 forest structure, pretreatment structure (1992, prior to the thinning treatment), and posttreatment structure (1993, after the thinning treatment). Black areas represent the canopies of ponderosa pine trees.

phosphorus concentration ($[P_T]$). Second, xylem water potential (Ψ_L) of 1-year-old needles from the lower crown was compared among nine randomly selected presettlement trees in the control block and 15 randomly selected presettlement trees in the thinned block in the summer of 1993. Third, dbh, 1989–1993 stem basal area increment at breast height (BAI), age, and three measures of competition were compared among 10 randomly selected presettlement trees in each of the control and thinned blocks; these same 20 trees were



Figure 2. Increases in tree density have occurred in southwestern ponderosa pine forests since Euro-American settlement, as shown by this view of G. A. Pearson National Area, Arizona, in 1992 (photography by the Ecological Restoration Program, Northern Arizona University).

used for the posttreatment growth and physiological measurements in 1994. Random selections of trees were limited to presettlement trees with little crown dieback, similar dbh, and a similar amount of pretreatment competition.

Pretreatment competition on each presettlement tree was measured by a diameter-distance competition index (CI) based on the sum of the ratios of the dbh of



Figure 3. This view in 1997 from the same location as in Figure 2 shows the effects of a thinning treatment that restored the stand to a tree density and structure similar to that documented for presettlement forests (photography by the Ecological Restoration Program, Northern Arizona University).

each subject presettlement tree and its neighboring trees, weighted by the distances between the subject and neighboring trees (formula 1 in Lorimer 1983). Neighboring trees were used in the CI if they occurred within a circle with a radius of 40 times the dbh of the subject tree (Sutherland et al. 1991). The three CIs calculated for each presettlement tree were CIPRE, which measures competition from other presettlement trees only; CIPOST, which measures competition from post-settlement trees only; and CITOTAL, which measures competition from both presettlement and postsettlement trees.

Predawn Ψ_L for the pretreatment comparisons was measured weekly during the 1993 growing season on 1-year-old needles from one lower canopy twig for each tree. The needles were collected with a pole pruner within about 2 hours before dawn. A plastic bag containing a slightly moist paper towel was used to store about 12 needles for each study tree. The bags of needles were kept in the dark in an insulated box at about 4°C for less than 4 hours before measurement. Ψ_L was measured with a pressure chamber (Model 1000, Plant Moisture Systems, PMS Instrument Co., Corvallis, Oregon, U.S.A.) by conventional techniques (Ritchie & Hinckley 1975). An earlier experiment showed no significant difference ($p > 0.05$) in Ψ_L between needles

measured immediately after collection from the tree and those stored as described for up to 4 hours (data not shown), which is similar to results for other conifers (Kaufmann & Thor 1982). Also, the first three needles having Ψ_L measurements within 0.1 MPa were averaged and used as the Ψ_L for each tree (Schmid et al. 1991).

Pretreatment mineral soils were collected in the summer of 1993 to a depth of 15 cm from one location in each of 52 plots randomly located in patches dominated by presettlement trees, postsettlement trees, and bunchgrass openings. The soil was air-dried and sieved to <2 mm, and rock-free samples were ground with mortar and pestle to a flour-like consistency. Soil OM was determined by mass loss following ignition after heating crucibles containing about 1 g of the soil at 550°C for 5 hours to consume the organic matter by oxidation (Chapman 1976). Soil $[N_T]$ and $[P_T]$ were determined colorimetrically on a LACHAT flow-injection analyzer (Quik-Chem AE Automated Ion Analyzer System, LACHAT ZELLWEGER Analytic Instruments Inc., Milwaukee, Wisconsin, U.S.A.) following modified micro-Kjeldahl digestion procedures (Parkinson & Allen 1975; Jones & Bradshaw 1989; LACHAT Instruments, Inc. 1992a, 1992b).

There was no significant difference ($p > 0.05$) in any pretreatment characteristic between the control and

Table 1. Average pretreatment characteristics for the thinned and control treatment blocks.¹

Characteristic	Control	Thinned	F Ratio	p Value
Living tree density, 1992				
Density (trees/ha)	4585	2647	n.a. ²	n.a.
Mineral soil characteristics, 0–15 cm depth, sampled in 1993				
<i>n</i>	15	37		
OM (%)	8.05	7.29	1.80	0.186
$[N_T]$ (g/kg)	1.34	1.18	1.77	0.189
$[P_T]$ (g/kg)	1.23	1.28	1.36	0.249
Presettlement ponderosa pines sampled in 1993				
<i>n</i>	9	15		
Early season Ψ_L (MPa)	−0.66	−0.68	0.06	0.817
Late season Ψ_L (MPa)	−0.42	−0.47	1.38	0.252
Presettlement ponderosa pines sampled in 1994				
<i>n</i>	10	10		
dbh (cm)	68.84	65.00	1.05	0.320
BAI5YR (cm ²)	14.70	14.83	0.00	0.962
Age (year)	233.4	162.4	5.87	0.026*
CIPRE (m/m)	0.677	0.776	0.57	0.459
CIPOST (m/m)	7.008	6.735	0.32	0.580
CITOTAL (m/m)	7.685	7.511	0.20	0.660

¹The *F* ratios and *p* values test the null hypothesis of no significant difference between thinned and control blocks prior to treatment. * Indicates significant differences ($p \leq 0.05$) between thinned and control block. *n*, sample size; OM, organic-matter content times 100%; $[N_i]$, soil total nitrogen concentration; $[P_i]$, soil total phosphorus concentration; early-season Ψ_L , average foliage predawn water potential for May and June of 1993; late-season Ψ_L , average foliage predawn water potential for July and August of 1993; BAI5YR, stem basal area increment over 5 years prior to thinning (1989–1993); CIPRE, diameter-distance competition index for presettlement tree neighbors; CIPOST, diameter-distance competition index for postsettlement tree neighbors; CITOTAL, diameter-distance competition index for all tree neighbors.

²n.a., not applicable (no statistical comparison could be made).

thinned blocks, except for the age of the trees that were used in the 1994 post-treatment comparisons (Table 1). The 10 presettlement trees in the thinned block were significantly younger than the 10 presettlement trees in the control block. Because leaf physiological characteristics of ponderosa pine can vary with tree age (Yoder et al. 1994), tree age was used as a covariate to adjust means to the same average age in all post-treatment analyses that compared trees between thinned and control blocks. Overall, the results of the pretreatment comparisons show similar levels of soil resource availability and tree-to-tree competition for the control and thinned blocks prior to thinning.

Posttreatment Comparisons

Soil volumetric moisture content (θ), Ψ_L , needle gas exchange, and foliar $[N_T]$ and $[P_T]$ were compared between the 10 presettlement trees in the control block and the 10 presettlement trees in the thinned block in the first growing season following thinning (May–August, 1994). In September 1994, needle, stem, and bud length, bud mass, and foliar $[N_T]$ and $[P_T]$ were compared across canopy crown positions and between treatments.

Soil θ was measured weekly, and Ψ_L and leaf physiological characteristics were measured at 2-week intervals. Measurements of θ (Topp et al. 1982a, 1982b; Rundel & Jarrell 1989) were at the canopy drip-line and southeast of each tree over 0–15 and 15–30 cm of mineral soil depth using a time domain reflectometry system (Model 6050X1 Trase System I, Soilmoisture Equipment Corp., Santa Barbara, California, U.S.A.). Midday Ψ_L was measured for a randomly selected half of the trees from each treatment block during the 90 minutes before noon and, for the remainder of the trees, during the 90 minutes after noon. Both predawn and midday Ψ_L of all 20 trees were measured on the same day, except for 28 July and 11 August, when midday Ψ_L was measured on the following day. Time of measurement—before noon or after noon—was not a significant ($p > 0.05$) source of variation in midday Ψ_L (data not shown).

Trees were sampled for Ψ_L by cutting one twig from the lower canopy of each tree with a pole pruner. Only twigs that were in full sun were sampled at midday. Immediately after each twig was detached from the tree, the previous year's needles were cut from three fascicles just distal to the fascicle sheath. A preliminary experiment showed that the Ψ_L of needles cut within 20 seconds of twig detachment was not significantly different ($p > 0.05$) from the Ψ_L of needles cut directly from the tree (data not shown). Measurements of Ψ_L were restricted to needles that elongated in 1993 at all sampling dates, except in August, when needles that

elongated in 1994 were also measured. Techniques for measuring Ψ_L were similar to those described for the pretreatment comparisons.

We measured needle gas exchange at midday at a photosynthetic photon flux density (PPFD) greater than 1000 $\mu\text{mol}/\text{m}^2/\text{second}$ using the same detached twigs sampled for the midday Ψ_L measurements. Light saturation of net photosynthetic rate (P_n) and stomatal conductance to water vapor (G_w) for ponderosa pine occurs at a PPFD of about 600 $\mu\text{mol}/\text{m}^2/\text{second}$ (Bassman 1987; Kolb & Robberecht 1996). On cloudy days, a lamp (75W halogen 12VDC) was used to maintain a minimum of 1000 $\mu\text{mol}/\text{m}^2/\text{second}$ PPFD. Each needle gas exchange measurement was made in less than 205 seconds after twig detachment with six fully expanded needles (i.e., two three-needle fascicles) from the most distal needles of the age class. Another preliminary experiment showed similar P_n and G_w for up to about 250 seconds for needles on detached twigs as for those on twigs attached to the tree (data not shown). Gas exchange was also measured on needles that elongated in the current year (1994) in August, when they were long enough to fit into the measurement cuvette.

P_n and G_w were measured with a computer-controlled, closed-system, portable infrared gas analyzer system (LI-6200, LI-COR, Inc., Lincoln, Nebraska, U.S.A.). The needle gas exchange measurements were made between 10:30 to 13:30 hours using the same schedule described for the midday Ψ_L measurements. Time of measurement (before noon or after noon) was not a significant ($p > 0.05$) source of variation in P_n or G_w (data not shown).

P_n was calculated on the basis of total needle surface area by using the length and the average diameter of the needles placed in the measurement chamber based on an approximation of a cylinder consisting of three isometric needle components (Svenson & Davies 1992). Because there was a strong positive correlation between treatment-by-date means of G_w and P_n ($r = 0.90$, $n = 16$, $p < 0.0001$), only the P_n data are presented.

Foliage $[N_T]$ and $[P_T]$ were measured on needle samples of the same age class from the same twigs used for other physiological measurements. Needles were ground to pass through a 20-mesh screen with a Thomas-Wiley intermediate mill (3383-L10 series, Thomas Scientific, Swedesboro, New Jersey, U.S.A.). The $[N_T]$ and $[P_T]$ were determined colorimetrically in a similar manner to that used with the pretreatment soil samples. $[N_T]$ and $[P_T]$ were calculated on the basis of needle surface area to facilitate comparisons with P_n , and on the basis of needle dry mass to facilitate comparisons with most other studies.

In September 1994, sunlit twigs from upper-, middle-, and lower-canopy positions of all 20 study trees were sampled for an analysis of twig growth and needle $[N_T]$

and $[P_T]$. Twigs from the lower canopy and from some of the middle canopy were sampled with a pole pruner. The upper-canopy twigs and the balance of the middle-canopy twigs were sampled by means of 12-gauge buck shot and a shotgun. Two twigs from each canopy location were collected, and the length, diameter, and oven-dry mass of their terminal buds were measured. Stem elongation and the length of the longest needles were measured on both the 1993 and 1994 year's growth on these twigs.

Data Analyses

All statistical tests were conducted with a significance level threshold of $p \leq 0.05$ by means of SAS software (SAS Institute, Inc. 1989). A one-way analysis of variance (ANOVA) was used to compare control and thinned treatment blocks for each of the eight dates. Tree age was used as a covariate to adjust all means to a common tree age for all variables except θ . For the August sample dates, a two-way ANOVA was used with needle age class (1993, 1994), treatment, and their interaction as factors. For the September sampling over canopy positions, a three-way ANOVA was used to compare treatments, crown positions, year of needle elongation (1993, 1994), and their interactions for needle $[N_T]$ and $[P_T]$ and with tree age as a covariate. The other twig, needle, and bud characteristics from September were analyzed with a two-way ANOVA, with treatment, canopy position, and their interaction as factors and tree age as a covariate. To adjust for any pretreatment differences in twig and needle growth, maximum 1993 needle length was used as an additional covariate for the analysis of maximum 1994 needle length, and 1993 stem length as an additional covariate for the analysis of 1994 stem length.

Results

The θ_{0-15} decreased from May to mid-July, and then increased during monsoonal rains in late July and August (Figs. 4A and 4C). A similar temporal trend occurred for θ_{15-30} , but with less soil water recharge from the monsoonal rains (Fig. 4B). The θ_{0-15} was higher in the thinned treatment versus the control treatment on every date and was significantly higher on six of the 15 dates (Fig. 4A). The θ_{15-30} also tended to be higher in the thinned treatment versus the control treatment, but the differences were not significant (Fig. 4B).

Predawn Ψ_L varied between about -0.5 and -1.0 MPa, with the lowest values occurring in mid-July and late August (Fig. 5A). Predawn Ψ_L was significantly higher in the thinned treatment than in the control treatment on 16 July for 1-year-old needles and on 26 August for both 1-year-old and current-year needles (Fig. 5A), with no significant differences between treat-

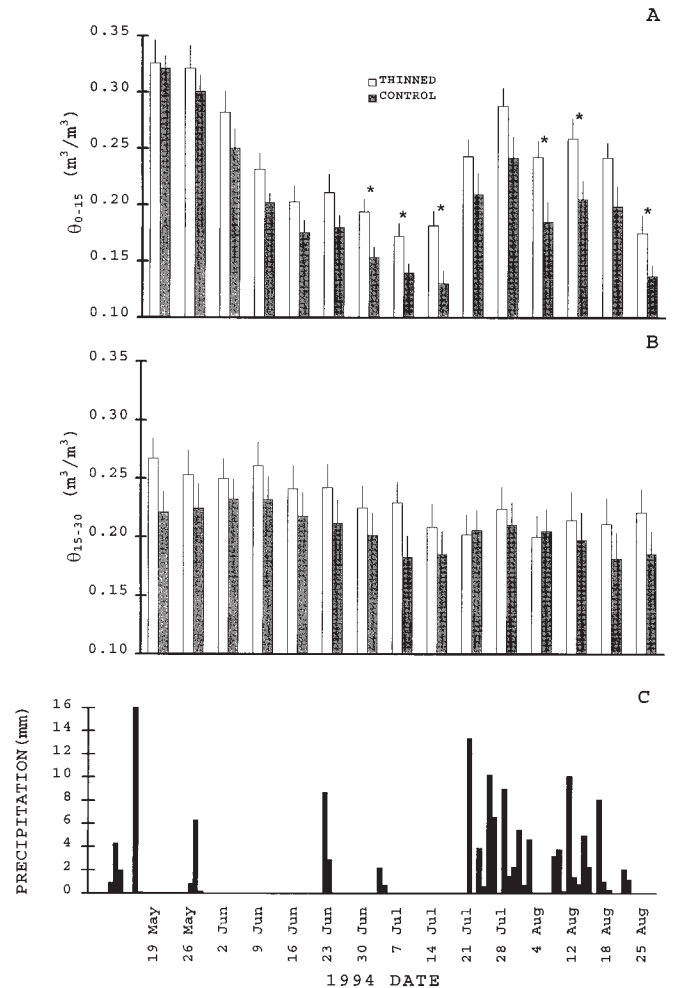


Figure 4. Average volumetric water content (θ) of the mineral soil over 0–15 cm (A) and 15–30 cm (B) for thinned and control treatments on 15 dates. Error bars show one standard error of the mean. Treatment means differed significantly ($p \leq 0.05$) on the dates marked with an asterisk. Daily precipitation for May through August of 1994 at the study site (C).

ments on other dates. Although predawn Ψ_L differed significantly between 1-year-old and current-year needles in August, the treatment-by-needle-age interaction was not significant, indicating similar differences in predawn Ψ_L between the thinned and control blocks for both needle ages.

Midday Ψ_L varied between about -1.3 and -1.7 MPa and generally decreased throughout the season (Fig. 5B). Midday Ψ_L was significantly higher in the control treatment than in the thinned treatment on 16 June and 26 August (Fig. 5B), with no significant differences between treatments on other dates. On 26 August, treatment differences in midday Ψ_L depended on needle age, as indicated by a significant treatment-by-needle-age interaction. Specifically, midday Ψ_L for both needle-age classes was higher in the control than in the

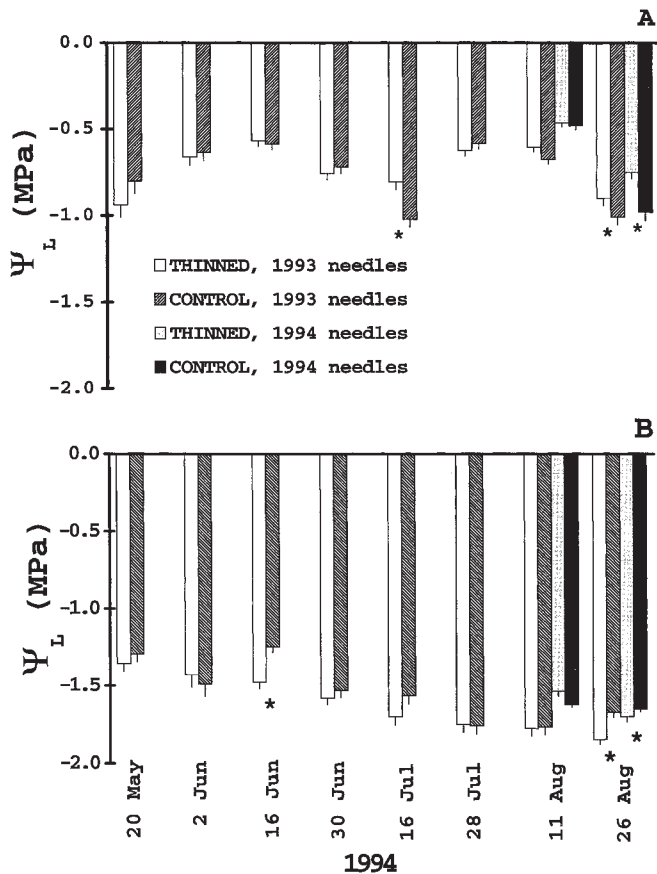


Figure 5. Average predawn (A) and midday (B) xylem water potential (Ψ_L) of 1-year-old (1993) and current-year (1994) needles for thinned and control treatments on eight dates. Error bars show one standard error of the mean. Treatment means differed significantly ($p \leq 0.05$) on the dates marked with an asterisk.

thinned treatment, but the difference was greater for 1993 needles (Fig. 5B).

P_n did not differ significantly between treatments except on 26 August, when the P_n of both 1-year-old and current-year needles was higher in the thinned than in the control treatment (Fig. 6). Also, treatment differences in P_n approached statistical significance on 16 July ($p = 0.07$), when P_n was again higher in the thinned than in the control treatment (Fig. 6).

The $[N_T]$ of 1-year-old needles tended to be greater in the thinned than in the control treatment in July and August, but treatments differed significantly only on 16 July on the basis of needle area (Fig. 7). The $[N_T]$ of current-year needles in August also tended to be higher in the thinned treatment than in the control treatment, but the differences were not significant. In August and September, current-year needles had significantly greater $[N_T]$ than 1-year-old needles on the basis of needle mass (Fig. 7B).

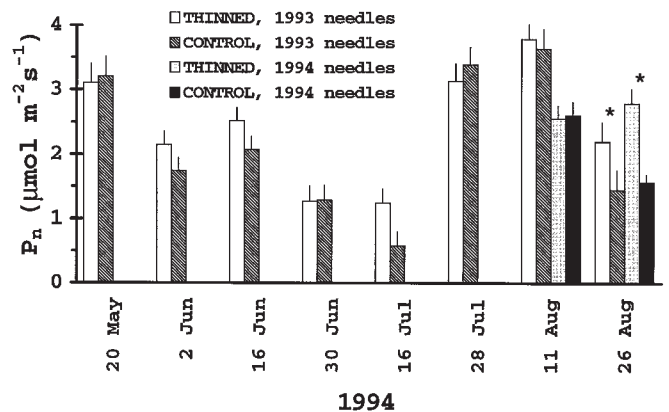


Figure 6. Average net photosynthetic rate based on needle surface area (P_n) of 1-year-old (1993) and current-year (1994) needles for thinned and control treatments on eight dates. Error bars show one standard error of the mean. Treatment means differed significantly ($p \leq 0.05$) on the dates marked with an asterisk.

The $[P_T]$ of 1-year-old needles did not differ significantly between thinned and control treatments except on 16 June, when $[P_T]$ was higher in the control on the basis of mass (Fig. 8). In August and September, current-year needles had significantly greater $[P_T]$ than 1-year-old needles on the basis of needle area and mass (Fig. 8).

In September, the length of the longest current-year needles was significantly greater in the thinned than in the control treatment (Table 2). There was also a significant difference between thinned and control treatments for bud growth. Buds were significantly longer, wider, and heavier in the thinned than in the control treatment (Table 2). Bud diameter also differed significantly across canopy positions: the widest buds occurred in the upper canopy and the narrowest buds the lower canopy (Table 2). The treatment-by-canopy-position interaction was significant only for bud mass, for which the difference between the thinned and control treatments increased from the lower canopy to the upper canopy (Table 2). There were no statistically significant differences between treatments or canopy positions for stem elongation. The $[P_T]$ and $[N_T]$ of needles also did not differ significantly among canopy positions (data not shown).

Discussion

Our leaf physiological data should be interpreted with the caveat that all measurements were made in the lower portion of the canopy of large trees. Of the physiological variables that we measured, differences among the lower-, middle-, and upper-canopy positions were likely greatest for Ψ_L because of the decrease in Ψ_L that

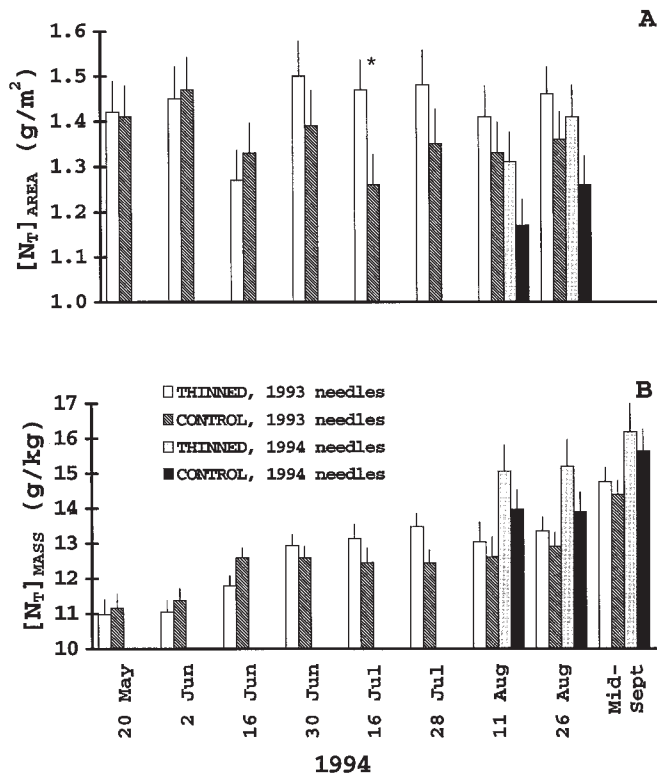


Figure 7. Average total needle nitrogen concentration based on needle surface area ($[N_T]_{AREA}$ (A) and needle mass ($[N_T]_{MASS}$ (B) of 1-year-old (1993) and current-year (1994) needles for thinned and control treatments on eight dates. Error bars show one standard error of the mean. Treatment means differed significantly ($p \leq 0.05$) on the dates marked with an asterisk.

often occurs with increasing tree height (Fredericksen et al. 1996; Ryan & Yoder 1997). Exposure to sunlight for much of the day was similar for these canopy positions of the presettlement trees because there was little shading of the canopy by other trees, even in the control treatment. Foliage $[N_T]$, a good predictor of leaf gas-exchange characteristics (Kozlowski & Pallardy 1997; Reich et al. 1997), also did not differ among lower-, middle-, and upper-canopy positions. Thus, our use of the lower canopy for the leaf physiological measurements likely resulted in values of Ψ_L that were greater (less negative) than would have been found higher in the canopy. Our P_n values for the lower canopy may be greater than would have been found higher in the canopy because of the greater Ψ_L in the lower canopy.

Thinning of the postsettlement trees increased the needle length and bud size of the presettlement trees, indicating a negative influence of postsettlement trees on the growth of presettlement trees. This conclusion agrees with the results of two correlative studies at our study site (Sutherland 1983; Biondi 1996), where growth

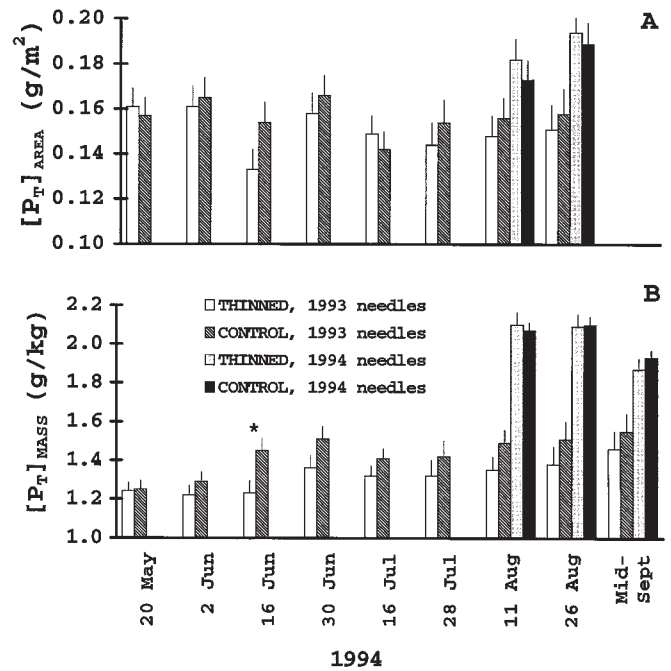


Figure 8. Average total needle phosphorus concentration based on needle surface area ($[P_T]_{AREA}$ (A) and needle mass ($[P_T]_{MASS}$ (B) of 1-year-old (1993) and current-year (1994) needles for thinned and control treatments on eight dates. Error bars show one standard error of the mean. Treatment means differed significantly ($p \leq 0.05$) on the dates marked with an asterisk.

rates of the presettlement trees have declined since the establishment of the postsettlement trees.

Because the postsettlement trees generally did not shade the crowns of the presettlement trees, the negative influence of the postsettlement trees on the presettlement trees likely resulted from competition for soil resources. Of the characteristics that we measured, competition for soil water between postsettlement and presettlement trees best explains the positive growth response of the presettlement trees to thinning of the postsettlement trees. The θ_{0-15} was consistently higher in the thinned than in the control treatment, with significant differences on several dates. Because the majority of conifer roots occur near the soil surface (Curtis 1964; Vogt et al. 1987; Grier 1989; Jackson et al. 1996), thinning of the postsettlement trees should have reduced active tree-root density near the soil surface, making more soil water available to the remaining presettlement trees. Indeed, the larger difference in θ between treatments at the 0–15 cm depth compared with the 15–30 cm depth likely resulted from the presence of most of the fine roots of the competing postsettlement trees near the soil surface. Our results on the short-term effects of thinning on soil water content agree with most previous similar studies of conifers (Della-Bianca

Table 2. Average September 1994 canopy growth characteristics for three canopy positions (lower, middle, and upper) and thinned and control treatments.¹

Canopy Position	Treatment	Maximum Needle Length (mm)	Stem Growth (mm)	Bud Length (mm)	Bud Width (mm)	Bud Mass (g)
Lower	Control	159.4	25.7	17.6	5.9	0.18
	Thinned	179.4	27.3	19.1	6.3	0.19
Middle	Control	154.7	27.5	15.6	5.8	0.15
	Thinned	172.0	24.5	20.0	6.9	0.23
Upper	Control	157.5	26.7	14.8	6.5	0.14
	Thinned	175.8	26.1	20.7	7.6	0.30
Significant Effects (<i>p</i> value)		trt ² (<i>p</i> = 0.001)		trt (<i>p</i> = 0.001)	trt (<i>p</i> = 0.010), position (<i>p</i> = 0.026)	trt (<i>p</i> = 0.002), trt* position ² (<i>p</i> = 0.033)

¹Significant (*p* ≤ 0.05) sources of variation from a two-way analysis of variance with treatment, crown position, and their interaction as factors are shown with probability values.

²trt = treatment; trt* position = treatment by canopy position interaction.

& Dils 1960; Bay & Boelter 1963; Sucoff & Hong 1974; Helvey 1975; Donner & Running 1986; Aussenac & Granier 1988; Cregg et al. 1990; Stogsdill et al. 1991). Finally, significantly greater predawn Ψ_L in the thinned than in the control treatment provides further evidence that the thinning increased water availability to the presettlement trees.

While the thinning treatment increased θ_{0-15} and predawn Ψ_L on some dates, midday Ψ_L was significantly lower in the thinned than in the control treatment on two dates. This difference may have resulted from a higher transpiration rate by the presettlement trees in the thinned versus the control treatment as a consequence of greater G_w .

Nitrogen is generally recognized as limiting ponderosa pine growth in northern Arizona (Potter 1964; Klemmedson et al. 1990). At our study site, Kaye & Hart (1998) reported an increase in gross organic nitrogen mineralization and a decrease in gross nitrate immobilization in the thinned treatment versus the control. Consistent with this increase in soil nitrogen mineralization, presettlement trees in the thinned treatment showed greater nitrogen uptake that resulted from a small increase in needle $[N_T]$ combined with an increase in needle length. Consequently, we conclude that the postsettlement and presettlement trees were competing for nitrogen, and that increased nitrogen uptake was partially responsible for the stimulation of presettlement canopy growth by the restoration treatment.

In contrast, there is no evidence that the postsettlement and presettlement trees were competing for phosphorus. Needle $[P_T]$ did not differ significantly between treatments except for one date, when $[P_T]$ was lower in

the thinned than in the control treatment, perhaps because of a growth dilution effect (Kozłowski & Pallardy 1997). Also, there is evidence suggesting that phosphorus may not be limiting to ponderosa pine at our study site. In a greenhouse fertilizer trial using ponderosa pine seedlings in soil from a ponderosa pine stand with basalt-derived soil similar to that of our study, Potter (1964) found no growth response to the addition of phosphorus and concluded that it was not deficient. Klemmedson (1994) and Wright (1996) studied soils near our study site at the Chimney Springs Prescribed Burning Interval Study, Fort Valley Experimental Forest, and concluded that the soil was rich in phosphorus due to the basal parent material.

The restoration treatment also increased carbon uptake by the presettlement trees. On 16 July, P_n was about 100% greater in the thinned treatment than in the control treatment, and the difference approached statistical significance (*p* = 0.07). On 26 August, P_n differed significantly between treatments and was about 40% greater in the thinned treatment than in the control treatment for 1-year-old needles and about 80% greater for current-year needles. For current-year needles, greater P_n (Fig. 6) combined with longer needle length in the thinned versus the control treatment (Table 2) resulted in a substantial increase in photosynthetic capacity, which also contributed to the greater canopy growth in the thinned treatment.

In summary, our results support our initial hypothesis that restoration of the pre-Euro-American stand structure by thinning would improve the vigor of ancient, presettlement ponderosa pines. Increased canopy growth and increased uptake of water, nitrogen, and

carbon indicated improved tree vigor. These results suggest that appropriate forest management can be used to maintain scarce, presettlement trees in the ponderosa pine forests of the Southwest.

Acknowledgments

We thank S. C. Hart (School of Forestry, Northern Arizona University) for comments on an earlier version of the manuscript and for assistance with the soil and foliar nutrient analyses. We also thank E. Tercilla and K. Holmberg for their help in the field and laboratory. This research was supported by grants from the National Science Foundation (DEB-9322706), the Mission Research Program of the School of Forestry of Northern Arizona University, and the McIntire-Stennis Program.

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