Seven-Year Results of Thinning and Burning Restoration Treatments on Old Ponderosa Pines at the Gus Pearson Natural Area

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Abstract

We examined the 7-year effects of three restoration treatments on leaf physiology and insect-resistance characteristics of pre-settlement age ponderosa pines (*Pinus ponderosa* Dougl. ex Laws.) at the Gus Pearson Natural Area (GPNA) in northern Arizona. Restoration treatments were: (1) thinned in 1993 to approximate pre-Euro-American settlement stand structure, (2) thinned plus prescribed burned in 1994 and 1998, and (3) untreated control. Tree physiological and insect-resistance characteristics were measured in year 2000, 7 years after thinning, using the same procedures as an earlier study performed in 1996. Consistent with the 1996 results, pre-dawn water potential in 2000 was consistently lower in the control than both thinned treatments. Both thinned treatments continued to have increased foliar nitrogen concentration in leaves 7 years after treatment. However lower leaf nitrogen concentration in the thinned and burned compared with the thinned treatment suggests lower nitrogen availability to trees in repeatedly burned plots. Analysis of leaf gas exchange characteristics and carbon isotope content ($\delta^{13}C$) suggests continued stimulation of photosynthesis by both thinning treatments. Differences among treatments in resin volume, a measure of bark beetle resistance, depended on season of measurement. Trees in both thinning treatments continued to have increased leaf toughness, a measure of resistance to insect folivores. Our results show that many beneficial effects of restoration treatments on carbon, water, and nitrogen relations and insect-resistance characteristics of pre-settlement ponderosa pines continue to be expressed 7 years after treatment at the GPNA.

Key words: bark beetle, carbon isotope discrimination, leaf toughness, nitrogen, photosynthesis, *Pinus ponderosa*, resin, water relations.

Introduction

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests in northern Arizona have changed because of fire suppression and grazing over the last century (Madany & West 1983; Savage & Swetnam 1990; Covington & Moore 1994; Fulé et al. 1997). Stand structure of many of these forests before fire suppression was characterized by groups of old-growth trees interspersed among openings dominated by herbaceous plants (Fulé et al. 1997; Mast et al. 1999). Frequent, low-intensity surface fires maintained this stand structure (Weaver 1951; Dieterich & Swetnam 1984; Covington & Moore 1994; Swetnam & Baisan 1996). Many current stands are comprised of dense thickets of pole-sized trees that have excluded most understory grasses, forbs, and shrubs (Covington & Moore 1994; Dahms & Geils 1997). The over-stocked condition of current stands has generated interest in restoring forest structure to the more open conditions found before Euro-American settlement.

Thinning and prescribed burning can be used to restore open-stand conditions (Covington et al. 1997; Covington 2000). Thinning also stimulates growth and resource uptake of post-settlement (i.e., young trees established after Euro-American settlement in the late 1800s) ponderosa pines (Schubert 1974; Wyant et al. 1983, 1986; Ronco et al. 1985; Kolb et al. 1998). However studies of the response of pre-settlement (i.e., old-growth trees established before Euro-American settlement) ponderosa pines to thinning and burning restoration treatments are limited. For example such studies in the southwestern United States have been limited to the Gus Pearson Natural Area (GPNA) located near Flagstaff, Arizona, and these studies were conducted only 2 and 3 years after thinning (Feeney et al. 1998; Stone et al. 1999).

The restoration experiment at the GPNA consists of two restoration treatments established in 1993–1994, designed to restore stand structure and tree age distribution to conditions similar to those present before Euro-American settlement, and an untreated control. Treatments were based on site-specific information about stand condition in the year 1876 from dendroecological analyses (Covington et al. 1997; Mast et al. 1999). One treatment consisted of thinning most post-settlement trees, and the other treatment combined thinning and prescribed burning. Thinning increased water

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and nitrogen uptake and net photosynthetic rate and radial stem growth of pre-settlement trees in the first 3 years after treatment (Feeney et al. 1998; Stone et al. 1999). Moreover prescribed burning in 1994 (1 year after thinning) had little effect on tree physiology and growth of pre-settlement trees. However resin volume in response to wounding of the phloem, a key tree defense against bark beetles, was greater in the thinned and burned treatment than in the thinned treatment or untreated control (Feeney et al. 1998). In addition foliage toughness, a mechanism of ponderosa pine resistance to insect folivores such as sawflies (McMillin & Wagner 1993; Wagner & Zhang 1993), of pre-settlement trees at the GPNA increased 2 and 3 years after thinning (Feeney et al. 1998). Ponderosa pines resist bark beetle colonization through an integrative process of constitutive and inducible defenses (Wood 1962; Brown et al. 1987). Wounding of resin ducts results in an accumulation of resin, which is a physical barrier against colonizing insects. Increased resin volume provides increased resistance against western (*Dendroctonus brevicomis* LeConte) and mountain pine (*Dendroctonus ponderosae* Hopkins) beetles (Smith 1975; Raffa & Berryman 1982, 1983). Thinning may decrease colonization attempts of mountain pine beetle by increasing distribution of pheromone plumes (McCambridge & Stevens 1982; Larsson et al. 1983; Olsen et al. 1996). Therefore there may be a relationship between restoration treatments, host defenses, and colonization success by bark beetles. However long-term changes in resin defenses of pre-settlement trees and interactions with local beetle populations due to restoration treatments in the southwestern United States are generally unknown.

The objectives of our study were to assess the 7-year effects of restoration treatments at the GPNA on leaf carbon, nitrogen, and water relations and insect-resistance characteristics of pre-settlement-age ponderosa pines. We present data from the year 2000, which was 7, 6, and 2 years after the thinning, first and second prescribed burns, respectively. We also present leaf carbon isotope ratio data from the years 1998–2000 to provide insight into treatment effects on leaf carbon and water relations in years 5, 6, and 7 after thinning. Our hypothesis is that the positive effects of restoration treatments on the physiological condition of pre-settlement trees would continue for 7 years after initial treatment. However we also expected a dampened response of pre-settlement trees to these treatments 7 years after treatment compared to the first 3 years after treatment because of increased occupancy and soil resource use by herbaceous vegetation in thinned plots (Covington et al. 1997; M. M. Moore, School of Forestry, Northern Arizona University, unpublished data).

Methods

Study Site

This study was conducted at the GPNA, within the Coconino National Forest approximately 10 km northwest of

Flagstaff, Arizona The study site is 3 ha in area at an elevation of 2,195–2,255 m with a southwest aspect and 0–5% slope. Soils, derived from basalt and volcanic cinders, are classified as a Brolliar clay loam, fine, smectitic, Typic Argiboroll. Mean annual precipitation is 56.7 cm, with approximately half of it as snow and the other half as rain during the late-summer monsoon season (August–September). Mean annual air temperature in Flagstaff, Arizona is 7.5°C. The climate is subhumid, with early-summer droughts common. The average frost-free growing season is 94 days (Schubert 1974).

The plant community at the GPNA was a previously unharvested ponderosa pine stand containing even-aged groups of pole-sized trees and uneven-aged groups of pre-settlement trees (Schubert 1974). Pole-sized trees (10.0–37.4 cm dbh) are the predominant size class. The greatest Euro-American influences at the GPNA have been livestock grazing, which occurred from 1876 to 1910, and fire suppression. Before our study, the last fire in the vicinity of the GPNA occurred in 1876 (Dieterich 1980).

Experimental Design

The experiment includes two treatments (thinned and thinned-and-burned) and an untreated control. The control was about 1 ha and located nonrandomly on one side of the GPNA (Covington et al. 1997). Each treatment was randomly assigned to five 0.20-ha plots, and the two treatments were interspersed. The control was divided into five 0.20-ha plots for sampling. This experimental design does not have true spatial replication of the control; therefore precautions were taken to strengthen our inferences of treatment effects. Pre-treatment (1992–1993) levels of soil total nitrogen concentration ($p = 0.19$), phosphorus concentration ($p = 0.25$), organic matter mass ($p = 0.19$), and predawn water potential (PWP) ($p = 0.82$ for May to June, $p = 0.25$ for July to August), tree basal area growth rate ($p = 0.96$), stem diameter ($p = 0.32$), and tree-to-tree competition index ($p = 0.66$) of pre-settlement trees did not differ among the areas that were treated (Feeney et al. 1998; Kay & Hart 1998b; Stone et al. 1999). Thus resource availability, tree growth, and tree physiological condition were similar among treatment areas before thinning and burning.

Thinning was conducted to simulate the pre-settlement stand structure (Edminster & Olson 1996; Covington et al. 1997). The average pre-treatment basal area was 34.5 m²/ha, which was retained in the control area. In November 1993 thinned plots were thinned to a basal area of 13.0 m²/ha, with all pre-settlement trees and all trees >40 cm dbh retained (Covington et al. 1997). In addition smaller diameter post-settlement trees were retained near stumps, snags, and down pre-settlement logs to recreate the clumped pattern of the pre-settlement forest. Following the thinning treatment, both thinned areas had an average dbh of 40.9 cm and the control area had an average dbh of

16.6 cm (Covington et al. 1997). Thinned and burned plots were burned under prescribed conditions in 1994 (October) and again in 1998 (October). Before the first burn the organic layers of the forest floor and woody debris were removed by hand raking to simulate pre-settlement forest floor conditions, which would have had little litter and debris due to frequent fire. To simulate grassy forest floor conditions of the pre-settlement forest, dried native grass foliage from a nearby prairie was added (672 kg/ha dry biomass) to the burned plots before the first burn. Fire characteristics of the 1994 burn were described in Covington et al. (1997): flame length averaged 15 cm with maximum lengths of 60 cm. For the second fire in 1998 flame length averaged 11 cm with maximum lengths of 180–240 cm that occurred in fallen limbs and needles of wind-thrown trees.

We sampled 30 pre-settlement trees (two per 0.2-ha plot) for water relations, leaf gas exchange, nitrogen and carbon relations, and insect-resistance characteristics. An additional 38 pre-settlement trees were included in the measurements of bark beetle-resistance characteristics ($n = 68$; four or five trees per plot). All measured trees were the same trees measured by Feeney et al. (1998), except for four trees that died between 1997 and 2000 (Kolb et al. 2001). In year 2000 the measurement trees ranged in age from 123 to 431 years, with an average age of 234 years (1 se = 15.3 years).

Leaf Water Relations

We measured PWP, mid-morning (MMWP), and mid-day (MWP) leaf water potential in June and August 2000 with a pressure chamber (Plant Moisture Stress Instrument Co., Corvallis, OR, U.S.A.) on lower crown, 1-year-old needles. Needles were excised, sealed in a plastic bag with slightly moistened paper towel, and placed in the dark in a cooler. We made all measurements within 2 hr of needles being removed from the tree (Kaufmann & Thor 1982). Measurements were made until three readings were obtained within 0.1 MPa of each other for each sample tree. We used the average value for these three measurements for each tree.

Leaf Gas Exchange

Instantaneous net photosynthetic rate (P_n), stomatal conductance to water vapor (g_s), and internal leaf CO_2 concentration (C_i) were measured over a 30-s period with a portable, closed-system LI-6200 infrared gas analyzer (LI-COR Inc., Lincoln, NE, U.S.A.) on needles of each study tree on 10 June and 21 August 2000. The measurements were conducted on sunlit, 1-year-old needles on excised branches from the lower to mid-crown at 0800 and 1100 hours. Two two- or three-needle fascicles were used for each measurement. Net photosynthetic rate and g_s were expressed on a total leaf area basis (all sides). Electronic digital calipers (Model CD-6″ BS, Mitutoya Corp.,

Tokyo, Japan) were used to measure average leaf radius, and total leaf area was estimated by a geometric model that considers the fascicle as a dissected cylinder (Svenson & Davies 1992).

Leaf Nitrogen and δ^{13}C

We collected current-year, 1-, and 2-year-old needles adjacent to those used for water potential measurements for nutrient analysis. Needles were oven dried at 70°C for 48 hr and were ground in a Thomas-Wiley mill (3383-L10 series, Thomas Scientific, Swedesboro, NJ, U.S.A.) to pass through a 20-mesh screen. Ground samples were analyzed for total foliar nitrogen and carbon stable isotope content (δ^{13}C) with a continuous-flow mass spectrometer (Ceinstrument NC2100 and Delta Plus XL, Finnigan, MAT, San Jose, CA, U.S.A.) at the Colorado Plateau Stable Isotope Facility at Northern Arizona University. Nitrogen concentration was expressed on a leaf area (g/m^2) and leaf mass basis (mg/g).

Insect-Resistance Characteristics

We measured resin flow and phloem thickness of the pre-settlement trees in late June and early August 2000. We removed the outer bark and phloem tissue using a 2.5 cm diameter Osborne arch punch (Model 149, King Bearing Co., Flagstaff, Arizona, U.S.A.). Directly below the wound we attached metal funnels, which directed resin into 15-ml vials. We collected resin 24 hr after wounding. We measured phloem thickness of the removed phloem disk with an electronic digital caliper (Model CD-6″ BS, Mitutoya Corp.) by averaging two measurements taken 90° apart for each disk.

We measured leaf toughness on the same trees used for leaf water potential measurements in June and August 2000. Excised needles were stored in sealed plastic bags in a dark cooler until the measurements were conducted. Leaf toughness was measured in the laboratory on the day of collection as the amount of pressure required to penetrate the needle with a penetrometer (TA-XT2 Texture Analyzer, Texture Technologies Corp., Scarsdale, NY, U.S.A.). A constant penetration depth (1 mm), needle velocity, and needle surface area were used for all measurements. Therefore leaf toughness was expressed as units of mass (g). We calculated average leaf toughness for each tree by averaging three measurements on each of five needles from different fascicles.

Data Analysis

We compared the differences in response variables among the thinned and thinned-and-burned treatments and the control using fixed effects analysis of variance on plot means ($n = 5$ per treatment). Sources of variation were block, treatment, sample date, and the interaction between treatment and date. Blocks ($n = 5$) in the analyses

consisted of three spatially adjacent plots (one of each treatment), and all measurements were performed by block. This is the same model used in analyses of 1995 and 1996 data from this experiment (Feeney et al. 1998). We explored the use of path length for water movement from soil to leaf (estimated stem height above ground plus branch length to the sampled leaf) as a covariate in our analysis of $\delta^{13}C$ to adjust for variation that may have been caused by differences in cumulative resistance to water flow among trees (Warren & Adams 2000). However $\delta^{13}C$ was not significantly correlated with path length for any leaf age class; hence no covariate was used in analysis of $\delta^{13}C$.

Variances were homogeneous among treatments and dates for all variables as indicated by Hartley's test (Sokal & Roalf 1995), except for P_n, resin flow, and leaf N concentration on a mass basis. We log transformed P_n, square-root (sqrt) transformed resin flow, and 1/sqrt transformed N data to homogenize variances. Two outliers in leaf nitrogen data were tested, removed, and replaced using methods described by Sokal and Roalf (1995). As reported by Feeney et al. (1998), mean comparisons among treatments were performed with Fisher's LSD, and a threshold probability value of 0.10 was used in all tests because of the inherent large variability of a population of old trees. This p value also was chosen to maintain consistency with previous studies at the GPNA (Feeney et al. 1998; Kaye & Hart 1998*a*, 1998*b*; Kaye et al. 1999). All statistical analyses were conducted using the SAS JMP statistical package (SAS Institute Inc., Cary, NC, U.S.A.) (SAS 1996).

Results

Leaf Water Relations

Tree PWP differed significantly among treatments. It was highest in the thinned-and-burned treatment, intermediate in the thinned treatment, and lowest in the control (Tables 1 & 2). Average PWP was significantly lower in June than August, and differences among treatments were consistent between months (Table 1). MMWP and MWP of trees did not differ among treatments, and the interaction between month and treatment was not significant (Table 1).

Leaf Gas Exchange

Net photosynthetic rate (P_n) of 1-year-old foliage did not differ significantly among restoration treatments or between months (Tables 1 & 2). Leaf g_s differed significantly among treatments (Table 1) and was highest in the thinned treatment, intermediate in the thinned and burned treatment, and lowest in the control (Table 2). In addition g_s was significantly lower in June (mean = 27.0, SE = 3.4 mmol m^{-2} s^{-1}) than August (mean = 32.2, SE = 2.5 mmol m^{-2} s^{-1}) (Table 1). Average leaf C_i was

Table 1. Probability values from analysis of variance on pre-dawn (PWP), mid-morning (MMWP), and mid-day (MWP) leaf water potential, photosynthetic rate (P_n), stomatal conductance (g_s), leaf internal CO_2 concentration (C_i), leaf toughness, resin volume, and phloem thickness of pre-settlement ponderosa pines at the Gus Pearson Natural Area.

	Block	Month	Treatment	Month × Treatment
df	4	1	2	2
PWP	0.001	0.001	0.001	0.32
MMWP	0.08	0.2	0.35	0.4
MWP	0.07	0.11	0.24	0.2
P_n	0.8	0.15	0.57	0.97
g_s	0.05	0.07	0.008	0.9
C_i	0.56	0.21	0.07	0.04
Leaf toughness	0.34	0.14	0.001	0.42
Resin volume	0.32	0.009	0.003	0.42
Phloem thickness	0.67	0.45	0.22	0.33

Factors in the analysis were block, month (June and August 2000), and restoration treatment (control, thinned, and thinned-and-burned).

significantly greater in the control treatment than the thinned and thinned-and-burned treatments (Tables 1 & 2), and differences among treatments depended on month (Table 1). Leaf C_i was similar among treatments in June, but C_i in August was greater in the control (mean = 253.0, SE = 23.4) than in both thinned treatments (thinned: mean = 136.0, 1 SE = 30.9; thinned-and-burned: mean = 114.0, SE = 30.1).

Leaf Nitrogen and $\delta^{13}C$

Leaf N_{tarea} differed significantly among leaves formed in different years and treatments, and the year–treatment interaction was also significant (Table 3). For current-year (2000) and 2-year-old foliage (1998), N_{tarea} was highest in the thinned treatment, intermediate in the thinned and burned treatment, and lowest in the control (Fig. 1b). Leaf N_{tarea} of 1-year-old foliage was lower in the control compared with both thinned treatments (Fig. 1b). The pattern of differences among treatments and years was similar for N_{tmass} as for N_{tarea} (Table 3; Fig. 1a & 1b), except for 2-year-old leaves (1998) in which N_{tmass} was not significantly different among treatments.

Leaf $\delta^{13}C$ was greater in foliage formed in 2000 compared with 1999 and 1998 (Table 3; Fig. 2). Leaf $\delta^{13}C$ was not significantly influenced by treatments for any foliage age class (Table 3; Fig. 2).

Insect-Resistance Characteristics

Resin volume differed significantly among treatments and months (Tables 1 & 2), and was significantly greater across all treatments in August than June (Fig. 3). In June resin volume was greater from trees in the thinned and burned treatment than trees in the control or thinned treatment (Fig. 3). However in August, resin volume was greatest from trees in the control, intermediate in the thinned-

Table 2. Mean (one standard error of the mean) for pre-dawn (PWP), mid-morning (MMWP), and mid-day (MWP) leaf water potential, photosynthetic rate (P_n), stomatal conductance (g_s), leaf internal CO_2 concentration (C_i), leaf toughness, and resin volume of pre-settlement ponderosa pines at the Gus Pearson Natural Area.

	Control	*Thinned*	*Thinned-and-Burned*
PWP (MPa)	−1.7 (0.07)[a]	−1.5 (0.05)[b]	−1.2 (0.03)[c]
MMWP (MPa)	−2.3 (0.04)[a]	−2.0 (0.05)[a]	−2.2 (0.03)[a]
MWP (MPa)	−2.2 (0.05)[a]	−2.0 (0.04)[a]	−2.1 (0.04)[a]
P_n (μmol m^{-2} s^{-1})	4.1 (1.4)[a]	5.8 (1.4)[a]	4.2 (1.3)[a]
g_s (mmol m^{-2} s^{-1})	23.1 (1.7)[a]	34.1 (1.5)[b]	30.0 (1.6)[c]
C_i (p.p.m.)	184.5 (22.4)[a]	132.11 (20.0)[b]	130.3 (21.7)[b]
Leaf toughness (g)	64.2 (0.56)[a]	72.3 (0.9)[b]	70.3 (0.81)[c]
Resin volume (ml)	3.4 (0.9)[a]	3.0 (0.7)[a]	6.9 (1)[c]
Phloem thickness (mm)	2.5 (1.0)[a]	2.7 (1.2)[a]	2.5 (1.2)[a]

Factors in the analysis were block, month (June and August 2000), and restoration treatment (control, thinned, and thinned-and-burned). Different superscript letters in the same row indicate significant differences at $p < 0.1$.

and-burned treatment, and least in the thinned treatment (Fig. 3). Tree phloem thickness did not differ significantly among treatments or months (Tables 1 & 2).

Leaf toughness varied significantly among treatments but not months (Tables 1 & 2). Leaf toughness was greatest in the thinned treatment, intermediate in the thinned-and-burned treatment, and lowest in the control (Table 2).

Discussion

A major objective of this continuing study was to understand the effects of restoration treatments on pre-settlement ponderosa pines at GPNA 7 years after initial treatment. We compared physiological responses of pre-settlement trees between earlier studies conducted in 1994–1996 (Feeney et al. 1998; Stone et al. 1999) and our study in 2000, 7 years after thinning. Of the years included in earlier studies, 1996 was most comparable to 2000 because both were characterized by significant drought. Precipitation between January and June near the study site was 60% lower than the long-term average in 1996 and 73% lower in 2000.

PWP of pre-settlement trees at the GPNA was consistently lower in the control compared with the thinned and thinned-and-burned treatments in 1996, 3 years after thinning (Feeney et al. 1998). This was also true in our study in

2000. These findings indicate that the 1993 thinning, which removed over 90% of post-settlement trees, continued to increase water uptake of pre-settlement trees 7 years after thinning despite a large increase of herbaceous plants within the thinned plots (Covington et al. 1997, M.M. Moore, School of Forestry, Northern Arizona

Table 3. Probability values from analysis of variance on leaf nitrogen concentration on a leaf mass basis (N_{tmass}), and leaf area basis (N_{tarea}), and carbon isotope ratio ($\delta^{13}C$) of leaves formed in different years 2000, 1999, and 1998 for pre-settlement ponderosa pines at Gus Pearson Natural Area exposed to three restoration treatments (control, thinned, and thinned-and-burned).

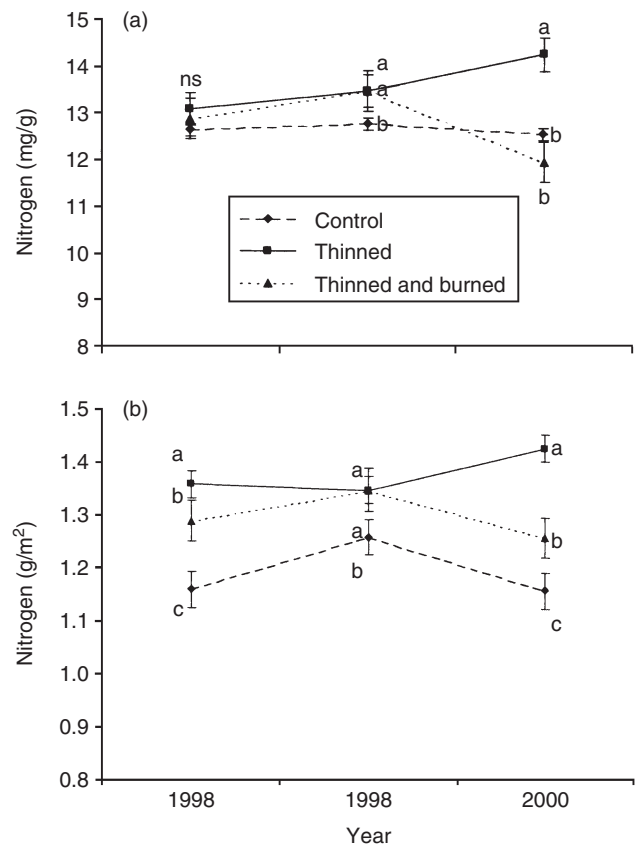|	*Year*	*Treatment*	*Year × Treatment*
df	2	2	4
N_{tmass} (mg /g)	0.25	0.003	0.26
N_{tarea} (g/m^2)	0.05	0.007	0.06
$\delta^{13}C$	0.001	0.26	0.66

Figure 1. Effects of restoration treatments on leaf nitrogen concentration (a) per leaf mass and (b) per leaf area for current (2000), 1- (1999), and 2- (1998) year-old foliage. Different letters indicate significant treatment differences within years ($p < 0.1$).
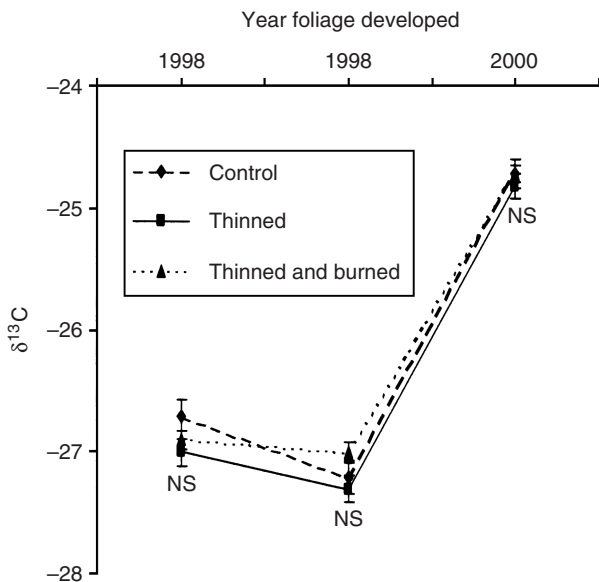
Year foliage developed

Figure 2. Effects of restoration treatments on δ^{13}C of current (2000), 1- (1999), and 2- (1998) year-old foliage. NS denotes no significant differences among treatments.

University, unpublished data). Stomatal conductance often varies with PWP of pre-settlement ponderosa pines in northern Arizona (Kolb & Stone 2000). However stomatal conductance did not differ significantly among treatments in 1996 (Feeney et al. 1998), whereas it was consistently greater in both the thinned treatments compared with
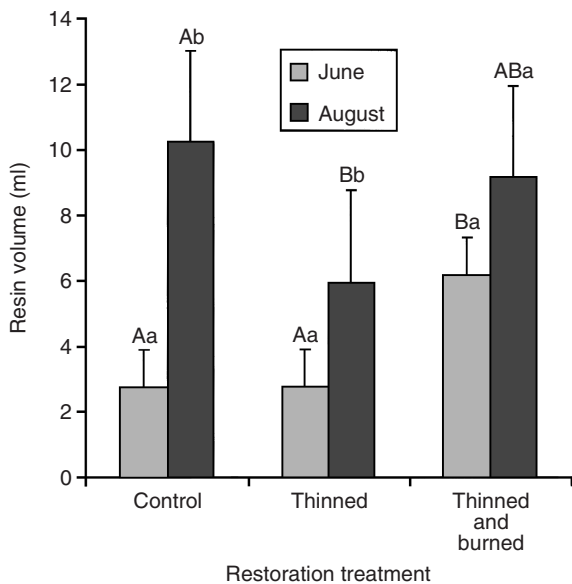

Figure 3. Effects of restoration treatments on resin volume (ml) collected in June and August 2000. Different capital letters indicate significant differences ($p < 0.1$) among treatments within months. Different lower case letters indicate significant differences ($p < 0.1$) between months. Means and one standard error are shown.

the control in 2000. Thus effects of the thinning treatments on stomatal aperture of pre-settlement trees at GPNA appear to be greater 7 years after treatment compared with 3 years after treatment.

In 1996 foliar nitrogen concentration on a leaf area basis was lower for 1-year-old leaves of pre-settlement trees in the control compared with both the thinned treatments, and nitrogen concentration on a leaf mass basis was similar among treatments (Feeney et al. 1998). In 2000 leaf nitrogen concentration on a leaf area basis was lower in the control compared with the thinned treatments for current-year, 1-, and 2-year-old leaves. Current and 1-year-old leaves in 2000 in the control plots also had lower leaf nitrogen concentration on a mass basis than trees in the thinned treatments. Thus the 1993 thinning of post-settlement trees continued to increase nitrogen concentration in leaves of pre-settlement trees 7 years after treatment.

Differences in leaf nitrogen concentration between thinned and thinned-and-burned treatments occurred in both 1996 and 2000, but in a different pattern. In 1996, the second growing season after the first prescribed fire, leaf nitrogen concentration on a mass basis was greater in the thinned-and-burned treatment than in thinned treatment; concentrations were similar on a leaf area basis (Feeney et al. 1998). In 2000, the second growing season after the second prescribed fire, leaf nitrogen concentration was greater in the thinned treatment than the thinned-and-burned treatment based on both mass and area. There are several factors that may have influenced the change in rank of leaf nitrogen concentration between burned and unburned thinned treatments between 1996 and 2000. First the 1994 prescribed fire was the first fire in the GPNA since 1876. Trees in the thinned-and-burned treatment may have been especially responsive to the pulse of plant-available nitrogen produced by the 1994 fire (Covington & Sackett 1986, 1992) considering the slow rate of nitrogen cycling that characterized the GPNA in the absence of ecological restoration treatments (Kaye & Hart 1998a). This pulse may have been short, as Kaye and Hart (1998a) reported no effect of the 1994 fire at GPNA on nitrogen mineralization between May and October 1995. Second the negative impact of the 1998 prescribed fire on leaf nitrogen concentration of pre-settlement trees compared with the thinned-only treatment may reflect losses of nitrogen from the site due to volatilization. Repeated prescribed burning of ponderosa pine forests can negatively influence nitrogen cycling (Wright & Hart 1997). Alternatively nitrogen transformation rates at our study site are positively associated with grass cover (Kaye & Hart 1998a), and there is evidence of less grass cover in thinned-and-burned compared with thinned plots at our study site (Covington et al. 1997; M. M. Moore, School of Forestry, Northern Arizona University, unpublished data). Thus differences in grass cover between burned and unburned thinned treatments may have indirectly affected leaf nitrogen concentration of pre-settlement trees at GPNA in 2000.

Net photosynthetic rate of pre-settlement trees in 1996 was lower in the control compared with both thinned treatments in May and June when water stress was most severe, whereas rates were similar among treatments at other times of the growing season (Feeney et al. 1998). Lower leaf nitrogen concentration in 2000 of pre-settlement trees in the control compared with both thinned treatments suggests lower photosynthetic capacity of trees in the control, as leaf nitrogen concentration is a good indicator of maximum photosynthetic rate (Field & Mooney 1986). However our measurements of mid-day net photosynthetic rate on two dates in 2000 (June and August) failed to show such a difference. Evidence from other measurements suggests lower net photosynthetic rate in the control than in the thinned treatments in 2000. For example, leaf internal CO_2 concentration was lower for pre-settlement trees in the thinned treatments compared with the control despite higher supply of CO_2 into the stomatal cavity, as indicated by greater stomatal conductance in the thinned treatments. We speculate that the lower leaf internal CO_2 concentration in the thinned treatments was caused by greater net photosynthetic rate driven by higher concentrations of photosynthetic enzymes, as implied by higher leaf nitrogen concentration (Field & Mooney 1986) in the thinned treatments. The leaf $\delta^{13}C$ results also are consistent with this explanation. Leaf $\delta^{13}C$, a time-integrated measure of the ratio between photosynthesis and stomatal conductance (Ehleringer et al. 1993), did not differ among treatments in any year (1998–2000). However stomatal conductance was higher in both thinned treatments than the control in both June and August 2000. An explanation for these results is that both photosynthesis and stomatal conductance were greater in the thinned treatments than the control over major portions of the 2000 growing season, which resulted in a similar ratio of photosynthesis to stomatal conductance and thus similar $\delta^{13}C$ for all treatments.

If the above explanation is correct, why did our measurements of mid-day net photosynthetic rate not differ among treatments in 2000? MMWP and MWP of pre-settlement trees in June and August 2000 in all treatments were between about −2.0 and −2.4 MPa, which is below the threshold value of about −1.8 MPa reported to reduce stomatal conductance and net photosynthetic rate of pre-settlement age ponderosa pine in northern Arizona (Kolb & Stone 2000). In contrast, mid-day tree water potential was greater than −2.0 MPa for pre-settlement trees in all treatments in 1996 when significant differences in June net photosynthetic rate were reported (Feeney et al. 1998). Interestingly, leaf $\delta^{13}C$ was much greater in 2000 than 1999 and 1998, suggesting low stomatal conductance integrated over the growing season in 2000. Thus severe water stress in 2000 likely reduced our ability to detect treatment effects on net photosynthetic rate measured at mid-day.

Resin flow in response to wounding, a key defense of conifers against bark beetles (Smith 1975; Raffa & Berryman 1982, 1983; Wallin & Raffa 2001), was higher in June

1996 in pre-settlement trees in the thinned-and-burned treatment compared with both the thinned treatment and the control (Feeney et al. 1998). The factors causing higher resin flow in the thinned-and-burned treatment in 1996 are not completely understood, but may include stimulation of resin production in response to wounding of cambium or phloem by the fire (Ruel et al. 1998), or differences in resource availability or carbon allocation to resin production among treatments. Treatment differences in resin flow in June 2000 followed the same pattern as reported for June 1996. In contrast the pattern of treatment differences in resin flow in August 2000 differed from June 2000. Resin flow in the control was lowest among treatments in June, but was highest among all treatments in August. The relationship between growth and defense (Lorio 1986; Herms & Mattson 1992; Wallin & Raffa 2001) may explain this result. Radial growth of pre-settlement trees at the GPNA was slower in the control compared with the thinned and thinned-and-burned treatments (Feeney et al. 1998). Radial growth of ponderosa pine in northern Arizona typically peaks in June and declines from July to September (Pearson 1924; Schubert 1974). Lower use of carbon for diameter growth later in the season may account for the increase in carbon available for resin production in August in all treatments, and especially in the control where carbon use for radial growth is low.

Our finding that resin volume of pre-settlement trees in the control can be as great as volume of trees in the thinned treatments suggests that temporal variation in the effects of restoration treatments on resin defenses should be considered regarding tree susceptibility to bark beetles. Given that resin flow is considered an important component of tree susceptibility to bark beetles (Smith 1975; Raffa & Berryman 1982, 1983), our results suggest that trees in the control were more susceptible in June, but less susceptible in August, relative to trees in the thinned-and-burned treatment. Further research on effects of forest restoration and management treatments on ponderosa pine susceptibility to bark beetles should include temporal variation in resin defenses, as well as better information on temporal variation in bark beetle flights which is virtually unknown in northern Arizona.

Our results for leaf toughness, a measure of ponderosa pine resistance against sawflies (McMillin & Wagner 1993; Wagner & Zhang 1993), were similar in 1996 (Feeney et al. 1998) and 2000. In both years, toughness of pre-settlement trees was lowest in the control, intermediate in the thinned-and-burned treatment, and highest in the thinned treatment (Feeney et al. 1998). Thus treatment effects on leaf toughness have not changed between 3 and 7 years after thinning.

In summary several beneficial effects of thinning restoration treatments (higher PWP, higher stomatal conductance, higher leaf nitrogen concentration, and tougher foliage) on pre-settlement trees at the GPNA continue to be expressed 7 years after thinning under drought conditions in 2000. We found no clear evidence to support a

change in the magnitude of these effects between 3 (1996) and 7 (2000) years after thinning. Thus increased use of soil resources by herbaceous plants in thinned treatments (Covington et al. 1997; M. M. Moore, School of Forestry, Northern Arizona University, unpublished data) does not appear to be having strong negative effects on resource availability to pre-settlement trees. However we did find evidence that two low-intensity prescribed burns 4 years apart in thinned plots reduced leaf nitrogen concentration, indicating that burning effects on soil nitrogen transformations and plant uptake should be studied further in restoration experiments. Finally responses of resin defenses of pre-settlement trees at GPNA to restoration treatments were not consistent between early- and late-summer measurements, which raises the possibility that treatment effects on tree susceptibility to bark beetles are more complex than suggested by earlier research (Feeney et al. 1998).

Acknowledgments

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