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Long-term impacts of stand management on ponderosa pine physiology and bark beetle abundance in northern Arizona: A replicated landscape study

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Abstract

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests in northern Arizona have degraded due to overgrazing, logging, and fire suppression that accompanied Euro-American settlement in the late 1800s. Overstocked stands of suppressed trees with low structural diversity dominate the landscape. These conditions create high risk of catastrophic fires and insect outbreaks. We investigated long-term effects (8–16 years post-treatment) of thinning and thinning + prescribed burning on ponderosa pine water stress, leaf carbon isotope discrimination and nitrogen concentration, oleoresin exudation flow, phloem thickness, radial growth, and bark beetle abundance relative to unmanaged control stands over 2 years of measurement in 12 stands replicated across the landscape. Predawn water potential in late June, phloem thickness, and basal area increment were lower in unmanaged than managed stands. Oleoresin exudation flow in July was greater in unmanaged and thinned + burned stands than thinned stands, and greater in a warm year than a cooler year. Leaf nitrogen concentration differed between years, but not among treatments. Tree competition and water stress were positively correlated, and tree competition was negatively correlated with radial growth and phloem thickness. Pheromone-baited trap catches of *Dendroctonus* spp. (*D. brevicomis* Leconte pooled with *D. frontalis* Zimmerman) were higher in unmanaged than managed stands, whereas catches of *Ips* spp. did not differ among treatments. We conclude that thinning with and without prescribed burning can have long-term effects on ponderosa pine water stress, growth, phloem thickness, resin flow, and bark beetle abundance. Low levels of tree mortality from bark beetles at our study sites suggest remarkable resistance of ponderosa pine in mid-elevation forests in northern Arizona, even at high tree densities.

Keywords: Competition; *Dendroctonus brevicomis*; *Dendroctonus frontalis*; Fire; *Ips pini*; *Pinus ponderosa*; Prescribed burning; Resin defense; Thinning

1. Introduction

Many experts agree that current forest conditions in northern Arizona are unsustainable due to increases in

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tree density that have occurred since Euro-American settlement in the late 1800s (Covington et al., 1997; Dahms and Geils, 1997; Allen et al., 2002). Current, undesirable conditions include overstocked stands of suppressed trees, high fuel loads, low understory diversity, and homogeneity of tree size and age classes (Covington and Moore, 1994a; Covington et al., 1997; Stone et al., 1999). With these conditions come high risk of epidemic insect outbreaks and catastrophic wildfire (Olsen et al., 1996; Feeney et al., 1998; Kolb et al., 1998; Fulé et al., 2001; Sanchez-Martinez and Wagner, 2002). The current state of the Arizona ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forest is a result of overgrazing, logging, and fire suppression that accompanied Euro-American settlement, in addition to favorable conditions for tree establishment in the early 20th century (Cooper, 1960; Covington and Moore, 1994b; Savage et al., 1996). These factors promoted a pulse of tree regeneration resulting in an almost even-aged cohort of trees growing at high density across the landscape (Savage et al., 1996).

Managers and researchers have implemented thinning and prescribed burning treatments to decrease risk of wildfires and improve ponderosa pine forest condition in northern Arizona. Thinning of these forests is effective in increasing individual tree growth (Ronco et al., 1985; Feeney et al., 1998; Skov et al., 2005), decreasing tree water stress (Kolb et al., 1998; Skov et al., 2004; Wallin et al., 2004), increasing tree defense against bark beetles through increased resin production (Kolb et al., 1998), and increasing leaf nitrogen concentration and hence photosynthetic capacity in some cases (Feeney et al., 1998; Wallin et al., 2004). The few long-term studies of prescribed burning in Arizona ponderosa pine forests suggest that frequent burning can impact tree nitrogen and water relations, and growth. For example, Wallin et al. (2004) reported higher predawn water potentials of old-growth ponderosa pine in thinned plots burned twice at 4-year intervals compared to thinned-only plots and decreased leaf nitrogen concentration in thinned + burned plots compared to thinned-only plots. Similarly, Wright and Hart (1997) found that repeated burning over 20 years depleted soil nitrogen in a ponderosa pine stand. Peterson et al. (1994) reported that prescribed burning at 4–6-year intervals increased ponderosa pine growth rate compared with longer or shorter burn intervals. In contrast to these findings in Arizona, ponderosa pines in thinned and thinned + burned treatments in western Montana had similar physiological characteristics 8 and 9 years after treatment (Sala et al., 2005).

Bark beetle populations in northern Arizona region were endemic prior to 2002 for almost a century (Sanchez-Martinez and Wagner, 2002). However, mortality of ponderosa pine from drought and bark beetles in this region increased dramatically between 2000 and 2003 (http://www.fs.fed.us/r3/resources/health/beetle/index.shtml). Biotic and abiotic stresses such as high inter-tree competition, defoliation, drought, lightning strikes, and fire damage are thought to influence tree susceptibility to bark beetle attack (Berryman, 1976; Christiansen et al., 1987; Ruel et al., 1998; Bradley and Tueller, 2001; Wallin et al., 2003). Thinned stands of several pine species have been reported to be less susceptible to tree-killing bark beetles (e.g., Sartwell and Stevens, 1975; Mitchell et al., 1983; Brown et al., 1987; Amman et al., 1988; Schowalter and Turchin, 1993). Research in northern Arizona has suggested greater ponderosa pine resistance to bark beetles, based on higher resin flow, in thinned or thinned + burned stands compared to unthinned stands (Feeney et al., 1998; Kolb et al., 1998; Wallin et al., 2004). Higher resin flow in thinned stands may result from greater tree resource uptake and greater carbon allocation to constituitive, or preformed resin, and increased resin flow has been associated with an induced resin synthesis response to stem tissue damage from fire or physical wounding, or inoculation by blue stain fungi (Feeney et al., 1998; Ruel et al., 1998; Klepzig et al., 2005). In contrast, severe defoliation because of crown scorch during fire decreases ponderosa pine resin production and increases bark beetle attacks and success (Wallin et al., 2003). In loblolly pine (*Pinus taeda* L.) moderate water stress has been shown to increase carbon allocation to resin production (Lorio, 1986; Lorio et al., 1995; Reeve et al., 1995), but the influence of water stress on resin defenses of other pines is poorly understood.

Our objectives were to compare ponderosa pine water and carbon relations, growth, resin defenses, and bark beetle occurrence among different forest conditions produced by silvicultural treatments in northern Arizona. The conditions are unmanaged stands, stands thinned 8–16 years ago, and similarly thinned stands that were broadcast burned after thinning. Our study is unique in addressing longer-term impacts of operational silvicultural treatments on tree physiological characteristics, growth, and bark beetle occurrence in ponderosa pine forests with treatment stands replicated across a large landscape.

2. Methods

2.1. Study area

We randomly selected a subset of four stands in each of three stand conditions from a group of 44 research sites in the Coconino National Forest near Flagstaff, Arizona (Fig. 1). Research sites are part of the Stand Treatment Impacts on Forest Health (STIFH) study to assess impacts of past operational forest management on ponderosa pine forest condition in northern Arizona (Bailey et al., 2001). STIFH sites cover a range of disturbance intensities from unmanaged controls to areas burned by stand-replacing fire. Our study included stands in unmanaged (UN), thinned (TH), and thinned and broadcast burned (TB) treatments. The size of selected stands ranged between 50 and 180 ha. The UN treatment consists of dense stands with greater than 90% crown closure that have not been treated by thinning or prescribed burning in the last 30 years. The TH treatment consists of stands thinned to remove greater than 30% of basal area between 1988 and 1995. The percent of basal area removed in the TH stands ranged between 32 and 59% and averaged 40%. TB stands had similar thinning (percent basal area removal between 33 and 70%, mean of 57%) and were followed by a broadcast burn of scattered logging slash and naturally occurring ground fuels within 8 years. Thinnings in both TH and TB stands were even-spaced improvement thinnings from below to reach a target basal area of about 17 m^2/ha. Density of mature, presettlement trees (dbh > 54 cm) in all stands is currently low (less than 10 trees/ha).

We used four stands of each treatment and treated them as replicates. There is variation in the dates of thinning and burning among stands within a treatment (Table 1) and stand attributes such as basal area (Table 2). For example, year of thinning varied by 4 years among stands for both the TH and TB treatments and year of first burning varied by 7 years (Table 1). The average and range in basal area (BA) among stands were lowest in the TB treatment, intermediate in the TH treatment, and highest in the UN treatment (Table 2). This variation was acceptable in our study because it represents the variation that occurs within stand treatment groups across the landscape.

Table 1
Years of thinning and prescribed burning for the eight treated stands (TH = thinned, TB = thinned + broadcast burned)

Stand	Treatment	Year thinned	Year burned
Aspen	TH	1992	
Malpais	TH	1992	
Walker Hill	TH	1991	
Grand Canyon	TH	1988	
South Wing	TB	1991	1999
Moore 1	TB	1991	1993
Moore 3	TB	1991	1992 + 2000
Cinder Pit	TB	1995	1995

Soils on all 12 stands are basalt-derived, mainly Typic Argiborolls, Typic Eutroboralfs, and Mollic Eutroboralfs composed of fine, smectitic residiums of basalt cinders, and clayey—skeletal and loamy skeletal composites (Miller et al., 1995). Mean annual precipitation for this region is 57 cm, most of which comes from winter snow and late summer rain (Western Regional Climatic Center; http://www.wrcc.dri.edu/index.html). Elevation across all stands ranges from 2160 to 2440 m.

2.2. Measurement trees

At each of the 12 stands, we selected 10 trees for physiological measurements ($n = 120$). Out of 10 plots

Table 2
Mean and range ($n = 4$ stands per treatment) for competition index and local basal area for unmanaged (UN), thinned (TH), and thinned + broadcast burned (TB) stands

Treatment	Competition index		Basal area (m^2/ha)	
	Mean	Range	Mean	Range
UN	5.61	4.93–6.11	20.60	16.00–23.00
TH	2.41	1.22–4.67	11.50	8.70–14.00
TB	1.72	1.16–1.99	8.70	8.30–9.20

Competition index was calculated following Lorimer (1983); see Section 2 for details. Basal area was measured locally around each measurement tree ($n = 40$ trees per treatment).

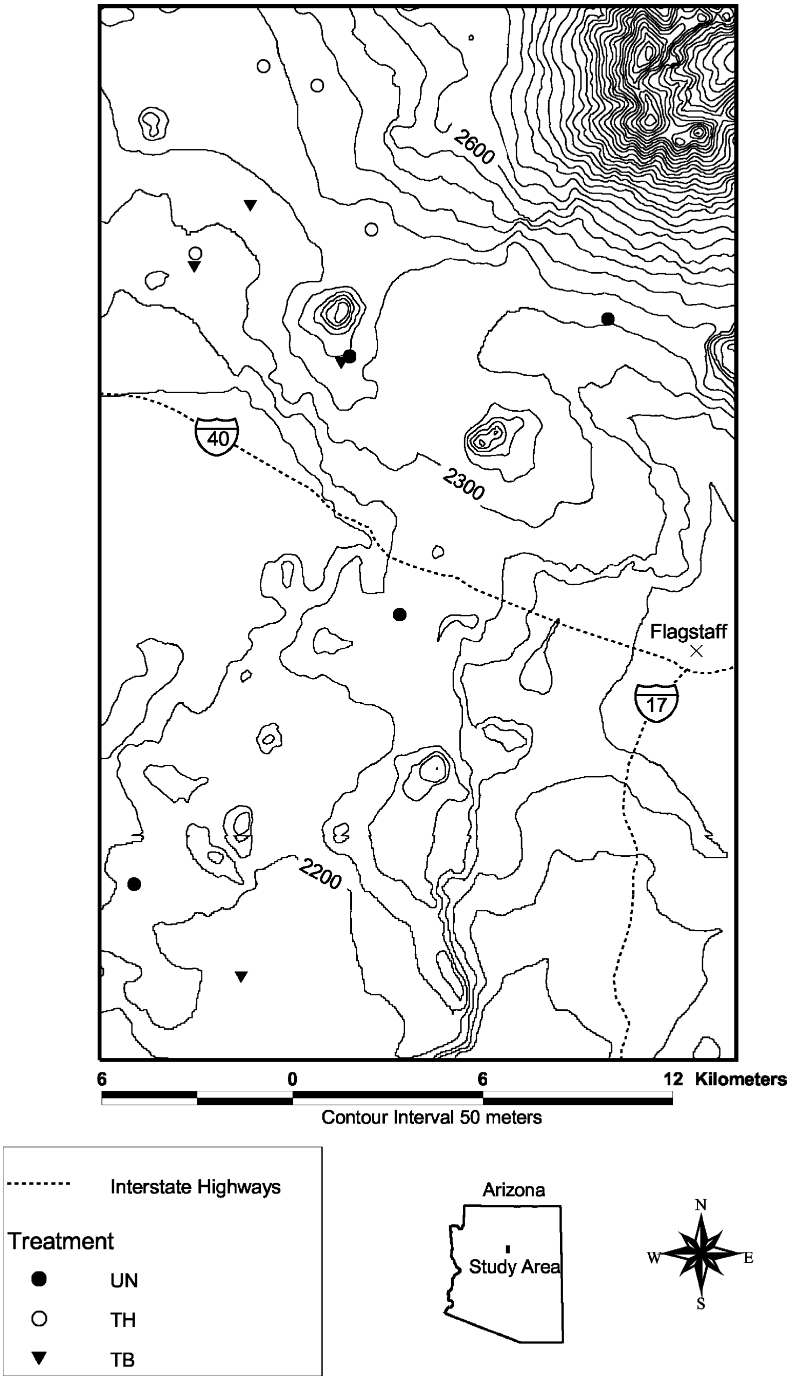

Fig. 1. Locations of four unmanaged (UN), four thinned (TH), and four thinned + broadcast burned (TB) stands in the Coconino National Forest near Flagstaff, Arizona.

laid out in a systematic grid (Bailey et al., 2001), we chose four plots nearest to the center of each stand and selected two or three trees per plot. Plots were located 150 or 200 m apart. We selected the first two or three trees per plot located east of the plot center with a dbh between 27 and 33 cm. We chose the largest tree dbh that was common across all treatments because *Dendroctonus brevicomis* LeConte prefers larger trees (Olsen et al., 1996). Trees with dwarf mistletoe or obvious physical or insect damage were excluded.

2.3. Predawn water potential

We measured leaf predawn water potential (Ψ_p) during the driest season to compare tree water stress among treatments. Measurements were made during the last week of June in 2003 and 2004 at the end of the spring–early summer dry period that typically occurs in the Southwestern U.S. In each year, we measured Ψ_p at all 12 stands over 5 consecutive days. To compensate for potential differences among sample dates, one stand of each treatment was measured within a 2-day period. Data were obtained by two separate crews that received identical training and used identical procedures. Each crew obtained data from two of the four stands per treatment in each year. Weather conditions were dry each year throughout the measurement period. We sampled 10 trees per stand prior to sunrise (about 05:00 h). We used pole pruners to remove one branch per tree from the mid-canopy (6–14 m above ground, depending on tree height) to obtain several fascicles of 1-year-old needles, which were sealed in a plastic bag with a slightly damp paper towel and stored in a dark cooler on ice. We then transported the samples to the lab and measured Ψ_p with a pressure chamber (Model 1000, PMS Instruments, Corvallis, OR) within 2 h after removal from the tree. This procedure of measuring Ψ_p produces similar values to those obtained by measurements immediately after needle excision from the tree (Kaufmann and Thor, 1982), and has been used in several studies of ponderosa pine (Feeney et al., 1998; Kolb et al., 1998; Skov et al., 2004). We measured Ψ_p of several needles of each tree and averaged the first three values that were within 0.1 MPa of each other as the mean for the tree.

2.4. Foliar carbon isotope discrimination and nitrogen concentration

We sampled leaves for measurement of leaf carbon isotope discrimination (δ^{13}C) and nitrogen concentration (*N*) during the first week in September of 2003 and 2004 following full needle development. Leaf δ^{13}C is a measure of leaf internal CO_2 concentration and the balance between uptake of CO_2 in photosynthesis and supply via stomatal conductance during assimilation of carbon used for leaf construction (Farquhar and Lloyd, 1993; Pate, 2001). ^{13}C-enriched leaf tissue suggests that development occurred under conditions that reduced leaf internal CO_2 concentration and stomatal conductance, such as water stress (Farquhar and Lloyd, 1993; Pate, 2001). Leaf *N* is an indicator of photosynthetic capacity and levels of the carboxylating enzyme Rubisco (Field and Mooney, 1986).

To obtain samples we removed branch-tips using pole pruners from fully sunlit portion of the upper third of the canopy (9–18 m above ground, depending on tree height) and collected three to four fascicles of green needles formed in the current year. Needles were transported to the lab in a cooler and then oven dried at 70 °C for 48 h. Once dry, whole-tissue samples were ground using a Wiley Mill (3383-L10 series, Thomas Scientific, Swedesboro, NJ) to 40 mesh. Ground samples were oven dried again at 70 °C for 24 h to remove any residual moisture, placed in a dessicator, and weighed following sample preparation guidelines of the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University (http://www4.nau.edu/cpsil). Samples were analyzed by this laboratory for δ^{13}C and *N* with an Elemental Analyzer-Continuous Flow Isotope Ratio Mass Spectrometer (Finnigan *Delta^{plus} Advantage*).

2.5. Oleoresin exudation flow

We measured oleoresin exudation flow (OEF) following phloem wounding in July of 2003 and 2004. We chose July to coincide with bark beetle flights. We measured OEF on the same trees used for Ψ_p, δ^{13}C, and *N* measurements. We created a flat surface on the tree bark using a draw knife and drove a 2.54 cm diameter Osborne arch punch (Model 149, King Bearing Co., Flagstaff, AZ) through the bark, phloem, and cambium to the xylem surface without wounding the xylem (Lorio et al., 1990). Two wounds were made on opposite sides of each tree at 1.3 m above ground. We funneled resin into vials using aluminum funnels in 2003 and using silicon caulking in 2004 and measured resin volume after 24 h. We measured phloem thickness from the portion extracted during wounding using a digital micrometer. Phloem thickness was measured at three locations 120° apart around the circumference of the extracted portion, and averaged for each tree.

2.6. Tree growth

We calculated basal area increment (BAI) of all trees using the most recent 5 years of growth (years 2000–2004). We took two xylem cores at breast height from opposite sides of each tree in November 2004 using an increment borer. Once dry, the cores were mounted and sanded using standard procedures (Stokes and Smiley, 1968). We measured ring widths to the nearest 0.01 mm using a Microcode II measuring banister system (Boeckler Instruments, Tucson, AZ) connected to a digital output system. Care was taken to cross-date measurements because 2002 was often a missing ring due to a severe drought that year. Average yearly growth increments were converted into average yearly BAI based on dbh of previous years estimated from growth increments and assuming no change in bark thickness over the 5-year period (Avery and Burkhart, 1983). BAI was averaged over the two cores for each tree.

2.7. Competition index

To evaluate the competitive status of trees used for physiology measurements we used the diameter-distance competition index (CI) described by Lorimer (1983). CI was calculated based on the sum of ratios of the diameters at breast height of each *i*th subject tree and its *j*th neighboring trees, weighted by the distances between the i and j trees:

$$\mathrm{CI}=\sum_{j=1}^{n}\left[\frac{(\mathrm{dbh}_j/\mathrm{dbh}_i)}{\mathrm{distances}_{ij}}\right]$$

All trees within 40 times the dbh of the subject tree (e.g., for a 0.3 m dbh tree, competition radius = 12 m) were considered competitors (Sutherland et al., 1991). We measured distance of each competing tree within the competition radius using a digital hypsometer (Vertex III and transponder T3, HAGLÖF Sweden AB) and recorded dbh. We also estimated local basal area (BA) around each measurement tree using a 10-factor basal area prism (Shiver and Borders, 1996) with the subject tree as the center of the variable–radius plot.

2.8. Bark beetle abundance

We installed four 12-unit Lindgren funnel traps (Phero Tech., Delta, BC, Canada) at each stand ($n = 48$) and baited two with a *D. brevicomis* lure (composed of frontalin, exobrevicomin, and myrcene terpenes) and two with an *Ips pini* lure (Ipsdienol +3/−97 and lanierone) (Phero Tech., Delta, BC, Canada). We placed each trap in a different quadrant within each stand. We hung funnel traps one meter above ground from a bent 2 cm metal conduit anchored with rebar stakes in the center of each quadrant, at least 50 m from any measurement trees and at least 200 m away from other traps. Pest strips were placed in collection buckets to kill all trapped insects and eliminate bark beetle predation. Traps were baited in June or early July and monitored for 4 or 5 weeks in 2003 and 2004. The trapping periods overlapped with the Ψ_p and OEF measurements so we could quantify tree resistance during the trapping periods. Trap buckets were emptied weekly and bark beetles were counted and identified in the lab.

Our target species for the *D. brevicomis* lure was *D. brevicomis*, but we expected to also capture *D. frontalis* Zimmermann with this lure as has been reported in other studies in northern Arizona (Sanchez-Martinez and Wagner, 2002; Gaylord et al., in press). In northern Arizona, *D. brevicomis* and *D. frontalis* have similar flight times, numbers of flights, and attractiveness to chemical attractants (Sanchez-Martinez and Wagner, 2002; Gaylord et al., in press), and both species can co-occur in the same bole section of ponderosa pine (Breece and Kolb, unpublished). The *D. brevicomis* lure, we used is more attractive to *D. frontalis* in northern Arizona than the commercially available lure for *D. frontalis* containing only frontalin (Gaylord et al., in press). For insects captured with the *D. brevicomis* lure, we counted the number of *D. brevicomis* and *D. frontalis* pooled over species, and refer to these captures as *Dendroctonus* spp. Our target species for the *I. pini* lure was *I. pini* Say, but we expected to also capture other *Ips* species, such as *I. latidens* LeConte and *I. lecontei* Swaine, based on previous studies in northern Arizona with the *I. pini* lure containing Ipsdienol +3/−97 and lanierone (Gaylord et al., in press). For insects captured with the *I. pini* lure, we counted the number of all *Ips* beetles pooled over species and refer to these captures as *Ips* spp.

2.9. Stand level tree mortality

During the fall of 2004, we assessed recent tree mortality at all stands. All trees on 10, 20 m × 20 m permanent plots systematically located in each stand were observed ($N = 2322$ trees over all stands) and mortality associated with bark beetles was noted. Tree death was associated with bark beetles, if there was evidence of bark beetle infestation such as pitch tubes, frass, or flaking of bark by woodpeckers.

2.10. Statistical analysis

Stand means ($n = 4$ per treatment) were used as the experimental unit and were compared among treatments using analysis of variance (ANOVA or MANOVA). We analyzed all tree physiological parameters measured in 2003 and 2004 using a repeated measures MANOVA design. Sources of variation in the MANOVA were treatment (d.f. = 2), year (d.f. = 1), and the year × treatment interaction (d.f. = 2). We analyzed the total number of captures of each bark beetle genera (*Dendroctonus*, *Ips*) pooled over collection dates in each year using one-way ANOVA with treatment as a factor. Normality and equal variance assumptions for bark beetle abundance data were not met, but nonparametric data analysis and ANOVA on transformed data resulted in similar results and *p*-values, thus we present the results of the non-transformed data. Tree BAI, CI, phloem thickness, and mortality were analyzed using one-way ANOVA with treatment as a factor followed by Tukey–Kramer HSD mean comparisons. We used correlation analysis to identify relationships between tree physiological and growth characteristics and competition. The threshold *p*-value for statistical significance was 0.05, and all analyses were conducted with JMP 5 (SAS Institute Inc., 2002).

3. Results

3.1. Predawn water potential

Predawn water potential was significantly greater ($p = 0.03$) in managed (TH and TB) compared to unmanaged (UN) stands during late June in 2003 and 2004 (Fig. 2). There were no significant year ($p = 0.36$) or year × treatment interaction ($p = 0.83$) effects on Ψ_p.

3.1.1. Foliar carbon isotope discrimination and nitrogen concentration

Leaf $\delta^{13}C$ did not differ significantly among treatments ($p = 0.09$) or years ($p = 0.83$), and the year × treatment interaction was not significant ($p = 0.21$; Fig. 3a). Leaf *N* did not differ among treatments ($p = 0.60$), but was significantly ($p < 0.0001$) lower in 2004 compared to 2003 (Fig. 3b). The interaction between year and treatment for *N* was not significant ($p = 0.93$).

3.1.2. Oleoresin exudation flow

Mean 24 h OEF in July differed significantly among treatments ($p = 0.007$) and years ($p = 0.01$), and the interaction between year and treatment

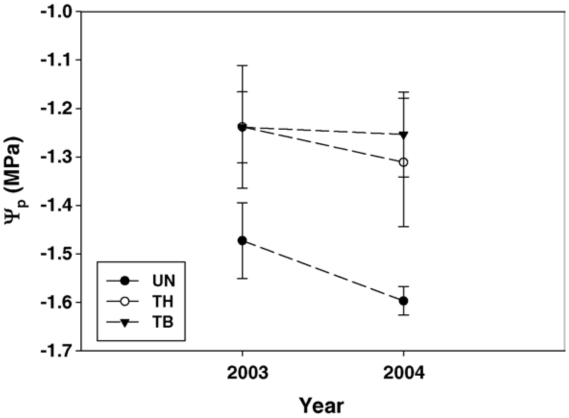

Fig. 2. Mean predawn water potential (Ψ_p) in late June of 2003 and 2004 for unmanaged (UN), thinned (TH), and thinned + broadcast burned (TB) stands. The bars show ±1 S.E. Mean Ψ_p of UN stands in both years was significantly lower than Ψ_p of both TH and TB stands (MANOVA, $p = 0.03$).

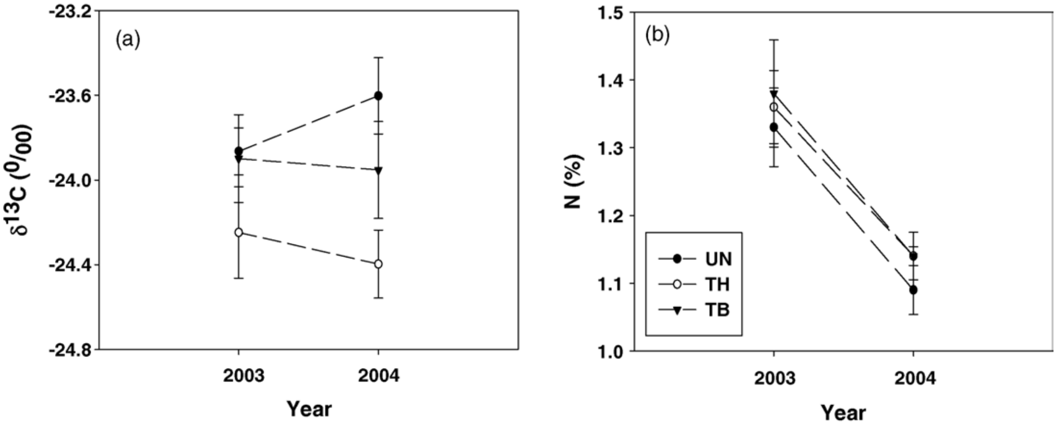

Fig. 3. Leaf carbon isotope discrimination ($\delta^{13}C$) (a) and leaf nitrogen concentration (N) (b) in 2003 and 2004 for unmanaged (UN), thinned (TH), and thinned + broadcast burned (TB) stands. The bars show ±1 S.E. $\delta^{13}C$ was similar among stands (MANOVA, $p = 0.09$) and years ($p = 0.83$). Leaf N was higher in 2003 than 2004 (MANOVA, $p < 0.001$), and was similar among stands ($p = 0.60$).

was not significant ($p = 0.63$). OEF was greater ($p = 0.002$) for trees in UN stands than TH stands (Fig. 4). OEF in TB stands was similar to OEF in UN stands ($p = 0.18$), and higher than OEF in TH stands ($p = 0.02$). OEF was lower in 2004 compared to 2003 for all treatments (Fig. 4).

3.2. Tree growth and phloem thickness

Mean BAI was significantly ($p = 0.007$) greater in TB than UN stands. BAI of TH stands was intermediate, and did not differ significantly from BAI of the other two treatments (Fig. 5). Similarly, phloem thickness was significantly ($p = 0.037$) greater in TB than UN stands, and phloem thickness for TH stands did not differ from the other two treatments (Fig. 6).

3.3. Relationships among tree growth and physiological characteristics and competition

We found significant negative correlations between stand-mean BAI and basal area ($r = -0.76$, Fig. 7a)

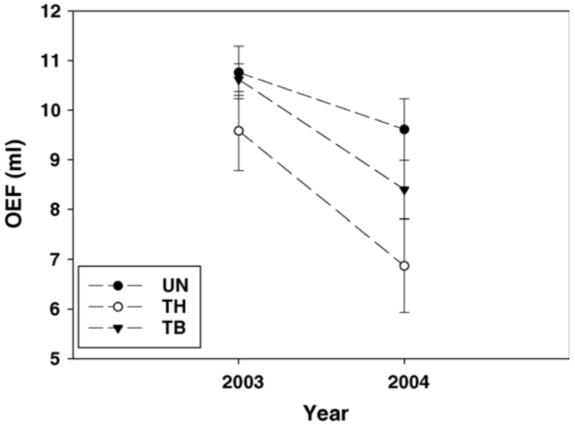

Fig. 4. Mean 24 h oleoresin exudation flow (OEF) in July of 2003 and 2004 for unmanaged (UN), thinned (TH), and thinned + broadcast burned (TB) stands. The bars show ±1 SE. OEF was greatest in UN stands, intermediate in TB stands, and lowest in TH stands (MANOVA, $p = 0.007$), and was greater in 2003 than 2004 ($p = 0.01$).

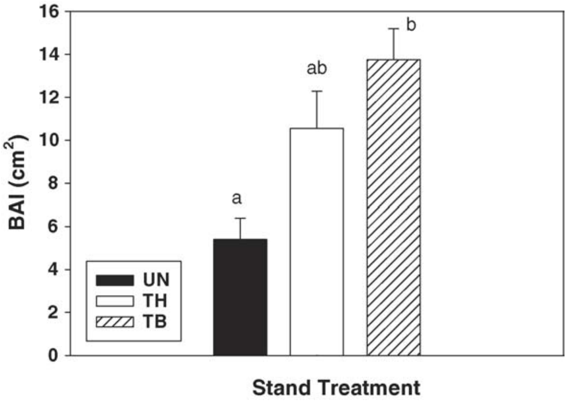

Fig. 5. Mean basal area increment (BAI) of the most recent 5 years of growth (2000–2004) for unmanaged (UN), thinned (TH), and thinned + broadcast burned (TB) stands. The lines show +1 S.E. and bars with the same letter do not differ significantly ($p \leq 0.05$, Tukey–Kramer HSD pairwise comparison). TB stands had greater BAI than UN stands. BAI for TH was not different from the other two treatments.

and CI ($r = -0.87$, Fig. 7b). Mean CI for UN stands was significantly ($p = 0.0007$) greater than TH and TB stands (Table 2). Stand-mean basal area was negatively correlated with phloem thickness ($r = -0.66$, Fig. 7c), and stand-mean BAI was positively correlated with phloem thickness ($r = 0.90$, Fig. 7d).

We also examined relationships between tree growth, physiological characteristics, and competition with individual-tree data pooled over all treatments (Table 3). Overall, relationships for individual-tree data were similar to relationships for stand-level data (Fig. 7). Significant relationships occurred between CI and BAI ($r = -0.71$), phloem thickness and BAI ($r = 0.52$), CI and phloem thickness ($r = -0.49$), and phloem thickness and leaf N ($r = 0.24$). CI and Ψ_p were negatively correlated in both years ($r = -0.51$ for 2003, $r = -0.39$ for 2004), whereas phloem thickness and Ψ_p were positively correlated in both years ($r = 0.36$ for 2003, $r = 0.30$ for 2004).

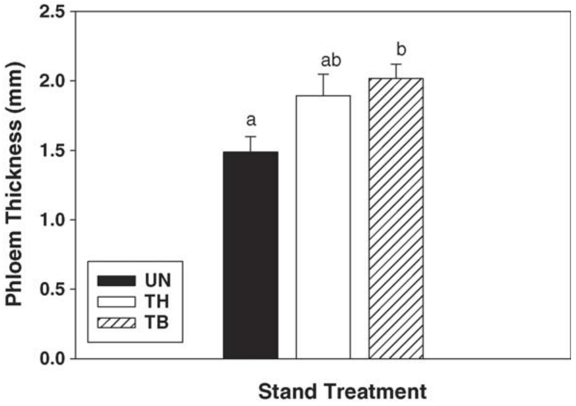

Fig. 6. Mean phloem thickness for unmanaged (UN), thinned (TH), and thinned + broadcast burned (TB) stands. The lines show +1 S.E. and bars with the same letter do not differ significantly ($p \leq 0.05$, Tukey–Kramer HSD pairwise comparison). TB stands had thicker phloem than UN stands. Phloem thickness for TH was not significantly different from the other two treatments.

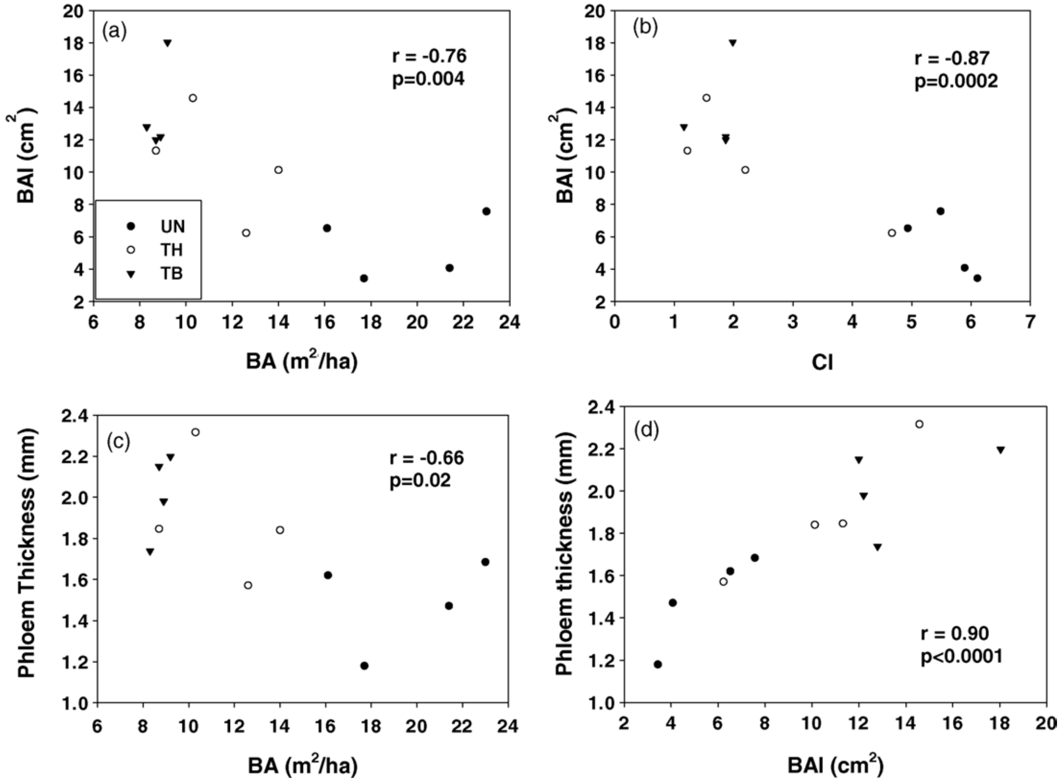

Fig. 7. Correlations between local basal area (BA) and basal area increment (BAI) (a), competition index (CI) and BAI (b), BA and phloem thickness (c), and BAI and phloem thickness (d) for unmanaged (UN), thinned (TH), thinned + broadcast burned (TB) stands. Each point is the mean from one study site ($n = 12$).

Table 3
Correlation coefficients (r) between tree physiological and growth parameters in 2003 and 2004 using individual-tree data (n = 120 in each year)

2003	Competition index	Phloem thickness	**2004**	Competition index	Phloem thickness
Ψp	**−0.51**	**0.36**	Ψp	**−0.39**	**0.30**
OEF	0.00	−0.03	OEF	0.17	−0.10
δ^{13}C	0.10	−0.04	δ^{13}C	0.17	−0.17
N	−0.10	**0.24**	N	−0.10	0.09
BAI	**−0.71**	**0.52**	Phloem thickness	**−0.49**	

Significant correlations ($p \leq 0.05$) are indicated in bold. Competition index, basal area increment (BAI), and phloem thickness were measured once and all other variables (Ψ_p = leaf predawn water potential, OEF = oleoresin exudation flow, δ^{13}C = leaf carbon isotope discrimination, N = leaf nitrogen concentration) were measured in both years.

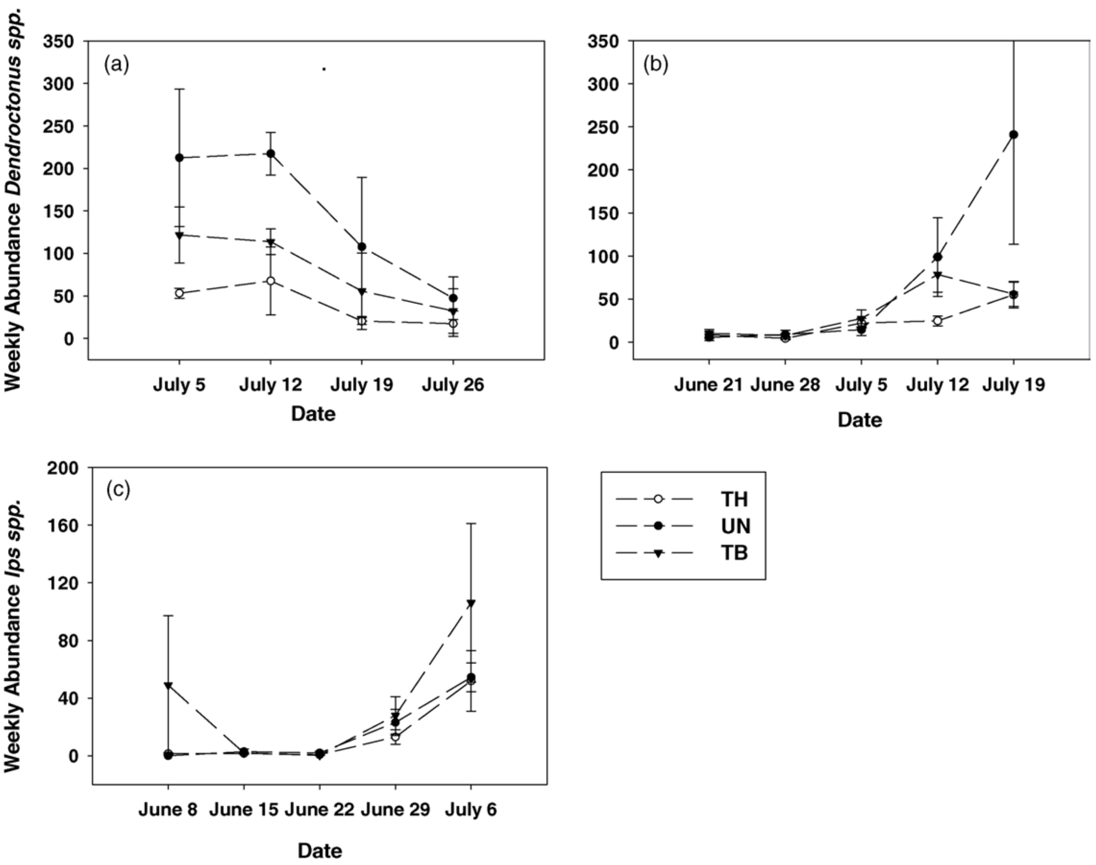

Fig. 8. Mean weekly abundance of *Dendroctonus* spp. in July 2003 (a) and June–July 2004 (b), and *Ips* spp. in June–July 2003 (c) for unmanaged (UN), thinned (TH), and thinned + broadcast burned (TB) stands. The bars show ±1 S.E. Each point represents the average capture from eight pheromone-baited traps (two per each of four stands). Abundance of *Dendroctonus* spp. totaled over dates in 2003 was greater in UN compared to TH stands (ANOVA, p = 0.04). Total abundance of *Dendroctonus* spp. in 2004 and *Ips* spp. in 2003 and 2004 did not differ among treatments ($p > 0.05$). *Ips* spp. abundance in 2004 is not shown because few beetles were caught in all treatments.

3.4. Bark beetle abundance

In 2003 catches of *Dendroctonus* spp. were higher ($p = 0.04$) in UN than TH stands (Fig. 8a). Catches in TB stands were intermediate and did not differ significantly from the other treatments. Average catches of *Dendroctonus* spp. over all dates in 2004 did not differ significantly among treatments (Fig. 8b), although catches were highest in UN stands in July when captures increased across all treatments. *Ips* spp. catches did not differ among treatments in 2003 (Fig. 8c) or 2004 (data not shown due to low numbers of beetles).

3.5. Stand level tree mortality

Tree mortality associated with bark beetles was low in all stands and did not differ among treatments ($p = 0.78$). Less than 0.1% of all trees surveyed ($n = 2322$) in each treatment had died recently.

4. Discussion

Thinning stands to lower tree densities (with and without ensuing prescribed fire treatments) decreased ponderosa pine water stress as indicated by higher Ψ_p during the peak of the dry season (late June) 8–16 years after thinning and 3–10 years after the most recent prescribed burn, compared with unmanaged stands in northern Arizona. Similar findings have been reported previously in northern Arizona (Feeney et al., 1998; Kolb et al., 1998; Skov et al., 2004) and western Montana (Sala et al., 2005). These results can be attributed to increased water availability to trees resulting from decreased tree competition in thinned stands. In 2004, greater tree water stress in UN stands persisted throughout the period of leaf development (May–July), based on the UN stands having the highest leaf δ^{13}C of all stands. Leaf δ^{13}C can vary due to factors that change leaf internal CO_2 concentration, such as a change in the balance between uptake via photosynthesis and supply via stomatal conductance (Farquhar and Lloyd, 1993; Pate, 2001). Maximum photosynthetic capacity was likely similar among treatments in our study, as evidenced by similar leaf *N* (Field and Mooney, 1986). The most likely explanation for higher δ^{13}C in UN stands is lower leaf internal CO_2 caused by reduction of stomatal aperture in response to water stress during leaf development.

Contrary to our expectation, thinning decreased resin flow. OEF in July was greatest in UN stands, intermediate in TB stands, and least in TH stands. This result is the opposite of a previous report of greater ponderosa pine OEF in thinned compared with unthinned stands in northern Arizona (Kolb et al., 1998). The difference between our results and Kolb et al. (1998) may be due to the standardization of tree dbh to 27–33 cm across all treatments and the shorter duration and lower intensity of thinnings in our study. In Kolb et al. (1998), an initial heavy thinning in 1962 followed by additional thinnings every decade over 35 years to maintain constant stand basal area created large differences in tree growth rate and dbh; OEF was negatively related to stand basal area between 6.9 and 78.2 m^2/ha, and positively related to differences in dbh among stands between 10.7 and 40.9 cm. In contrast, the management treatments in our study created stands with a lower range in basal area (8.7–20.6 m^2/ha based on measurements around study trees), and the thinnings were conducted only once in each stand 8–16 years prior to our measurements. Our results and Kolb et al. (1998) suggest that effects of thinning on OEF of ponderosa pine in northern Arizona cannot be generalized without consideration of tree size and the intensity and duration of thinnings.

Our results are consistent with the growth differentiation–balance hypothesis, which predicts that trees allocate more carbon for growth under optimum conditions, but more carbon for defense, e.g., resin synthesis, under moderately stressful conditions such as seasonal water deficits that limit growth (Lorio and Sommers, 1986; Lorio et al., 1990). Our Ψ_p results show that trees in UN stands were under greater water stress just prior to measurement of OEF. Trees in UN stands also had less diameter growth than trees in managed stands. Decreased Ψ_p and BAI in UN compared to managed stands, yet greater OEF in UN stands, supports the hypothesis of greater carbon allocation to secondary metabolic processes rather than growth under stressed conditions such as those produced by heavy competition in unmanaged stands of ponderosa pine in northern Arizona. A similar tradeoff between growth and oleoresin production was reported for ponderosa pine in northern Arizona for 2 years that differed in water stress (Feeney et al., 1998).

Prescribed burning increased OEF in thinned stands. A similar result for OEF measured in late June was reported for old-growth ponderosa pines 2, 3, and 7 years after implementation of restoration treatments in northern Arizona (Feeney et al., 1998; Wallin et al., 2004). The difference in OEF between TB and TH stands in our study was not clearly related to tree competition, as correlations between OEF and various measures of tree competition and physiological status were low for stand-level and individual-tree data (e.g., Table 3). The mechanism by which prescribed fire stimulates constituitive resin defenses in ponderosa pine is not known, but may involve an increase of resin production in response to wounding of the cambium or phloem (e.g., Ruel et al., 1998), or greater rates of resin flow in response to higher bole temperature (e.g., Ruel et al., 1998) associated with lower tree density in burned stands. The latter explanation is supported in our study by lower basal area and competition index for trees in TB than TH stands (Table 2).

OEF in July was less in 2004 than 2003 for all treatments. Differences in temperature between years may have affected resin viscosity and flow rate, as OEF is known to be positively associated with temperature during short-term measurements (Ruel et al., 1998). July mean air temperature at a weather station located near our study sites (Fort Valley, Arizona, http://cdo.ncdc.noaa.gov/ancsum) was 1.2 °C lower in 2004 (17.4 °C) when resin flow was low, than in 2003 (18.6 °C) when resin flow was higher.

Phloem thickness, a measure of food resources to bark beetles (Amman and Pasek, 1986), was influenced by forest management treatments. Phloem thickness was positively and strongly correlated with BAI (Fig. 7d), indicating that faster growing trees had thicker phloem than slower growing trees of the same dbh. Similar results were reported for lodgepole pine in British Columbia, Canada (Shrimpton and Thomson, 1985). This relationship could have important management implications regarding tree suitability for bark beetles. Managed stands may have a higher percentage of suitable host trees due to increased phloem thickness because thinning stimulates radial growth.

The effects of prescribed fire on tree growth in our study were negligible or indistinguishable from effects of thinning. Our regression analyses (Fig. 7; Table 3) strongly suggest that differences in tree growth among stand treatments can be largely explained by effects of thinning on tree competitive status. Sutherland et al. (1991) reported an initial decrease in ponderosa pine growth for 2 years after a prescribed burn followed by a return to growth rates similar to control trees. Such short-term effects may have occurred following the prescribed burns in our study, but were not detected in our measurements 3–10 years after the last burn treatment.

Past forest management influenced abundance of *Dendroctonus* spp. (*D. brevicomis* pooled with *D. frontalis*) as measured by pheromone-mediated trap catches. We trapped high numbers of these beetles in all stands in July 2003, and catches were greater in UN than managed stands. In 2004, this same trend occurred in late July as abundance of *Dendroctonus* spp. increased. Sanchez-Martinez and Wagner (2002) used pheromone-baited traps to attract these beetles in the same stands in 1999 and found no differences in abundance among stands. Total trap catches in 1999 reported by Sanchez-Martinez and Wagner (2002) were much lower than our totals for 2003 and 2004 suggesting that there was an increase in populations of *Dendroctonus* spp. in these stands prior to our study. During our trapping periods, bark beetles in UN stands may have been flying more than populations in managed stands. This explanation is unlikely because emergence of tree-killing bark beetles is often synchronized for populations in the same region (Berryman, 1982).

A possible explanation for greater capture of *Dendroctonus* spp. in unthinned than thinned stands is that the pheromone plume was more concentrated in unthinned stands because of lower windspeed and less mixing of the pheromone plume (Thistle et al., 2004). A more concentrated pheromone plume with greater directional consistency may be more favorable for long-range detection of pheromones by bark beetles. Also, *Dendroctonus* spp. may prefer unthinned stands because higher tree density provides greater availability of hosts at shorter flying distances. Moreover, habitat suitability may be better in dense, unthinned stands due to decreased bark temperature (Schmid et al., 1991).

In contrast to *Dendroctonus* spp., past forest management did not influence trap catches of *Ips* spp. Sanchez-Martinez and Wagner (2002) reported similar results for *I. pini* in these stands in 1999. In 2004 catches of *Ips* spp. from June 17–July 20 were near zero in all treatments. This result may indicate emigration of the local population or that this genus was not flying during the trapping period. We conclude that *Ips* spp. shows no specific preference for the range of stand conditions included in our study.

We were surprised to find that bark beetle impact on tree mortality at our 12 study sites on the Coconino National Forest was minimal during our study considering the widespread reports of ponderosa pine mortality from bark beetles in this region between 2000 and 2003 (http://www.fs.fed.us/r3/resources/health/beetle/index.shtml). Ponderosa pine forests located near the lower extent of their elevational range in Arizona (~2000 m) appear to have been impacted more by the 2002 drought and bark beetle outbreak than our study sites at higher elevations (2160–2440 m). Because we observed little mortality from bark beetles in our study stands, our trap catch results cannot be interpreted as abundance at outbreak levels of beetles that cause high tree mortality.

Our study is the first in northern Arizona to assess long-term responses of both bark beetles and host–tree physiology and resin defenses to operational forest treatments across the landscape using replicated stands. We conclude that thinning treatments that remove 30–50% of stand basal area, with or without prescribed fire, decrease water stress of dominant and co-dominant ponderosa pines 27–33 cm dbh during the dry season 8–16 years after treatment. Treatment differences in tree water stress likely develop earlier based on previous research and may persist for many years. Contrary to our expectation, lower tree water stress in thinned stands was associated with lower constituitive resin defenses of ponderosa pine against bark beetles. Food resources available to bark beetles on a per tree basis were greater in managed stands because thinning increased phloem thickness, yet populations of *Dendronctonus* spp. were lower in managed than unmanaged stands. Despite these effects of stand management on bark beetles and host tree physiology, negligible tree mortality in all stand conditions after several years of drought suggest remarkable resistance of ponderosa pine to bark beetles in mid-elevation stands in the Coconino National Forest, or other unknown factors that limit bark beetle success.

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