

## HOMEOSTATIC MAINTENANCE OF PONDEROSA PINE GAS EXCHANGE IN RESPONSE TO STAND DENSITY CHANGES

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**Abstract.** Homeostatic maintenance of gas exchange optimizes carbon gain per water loss. Homeostasis is regulated by short-term physiological and long-term structural mechanisms, both of which may respond to changes in resource availability associated with competition. Therefore, stand density regulation via silvicultural manipulations may facilitate growth and survival through mechanisms operating at both short and long timescales. We investigated the responses of ponderosa pine (*Pinus ponderosa*) to stand basal area manipulations in Arizona, USA. Stand basal area was manipulated to seven replicated levels in 1962 and was maintained for four decades by decadal thinning. We measured basal area increment (BAI) to assess the response and sustainability of wood growth, carbon isotope discrimination ( $\Delta$ ) inferred from annual rings to assess the response of crown gas exchange, and ratios of leaf area to sapwood area ( $A_l:A_s$ ) to assess longer term structural acclimation. Basal area treatments increased soil water potential ( $r^2 = 0.99$ ) but did not affect photosynthetic capacity. BAI increased within two years of thinning, and the 40-year mean BAI was negatively correlated with stand basal area ( $r^2 = 0.98$ ).  $\Delta$  was negatively correlated with stand basal area for years 5 through 12 after thinning ( $r^2 = 0.90$ ). However,  $\Delta$  was relatively invariant with basal area for the period 13–40 years after initial thinning despite maintenance of treatment basal areas via repeated decadal thinnings. Independent gas exchange measurements verified that the ratio of photosynthesis to stomatal conductance was invariant with basal area, but absolute values of both were elevated at lower basal areas.  $A_l:A_s$  was negatively correlated with basal area ( $r^2 = 0.93$ ). We hypothesize that increased  $A_l:A_s$  is a homeostatic response to increased water availability that maximizes water-use efficiency and whole-tree carbon uptake. Elevated  $A_l:A_s$  of trees at low basal areas was associated with greater resilience to climate, i.e., greater absolute BAI during drought; however, trees with high  $A_l:A_s$  in low basal area stands also exhibited the greatest sensitivity to drought, i.e., greater relative decline in BAI.

**Key words:** Arizona; carbon isotope discrimination; ecological restoration; leaf area : sapwood area ratio; photosynthesis; *Pinus ponderosa*; productivity; stomatal conductance.

### INTRODUCTION

Ponderosa pine (*Pinus ponderosa*) is a widespread conifer in North America, with a range extending from southern Canada to central Mexico (Waring and Law 2001). This economically and ecologically valuable species is experiencing drastic constraints on survival and productivity in recent decades due largely to the policy of fire exclusion practiced since the late 1800s. Prior to this period, ponderosa pine forests typically were exposed to frequent surface fires that removed competing vegetation and maintained open, low-density stands (Cooper 1960, Covington and Moore 1994a, Moore et al. 1999, Swetnam et al. 1999). Fire exclusion has allowed heavy seedling regeneration within pine forests, which

has increased density and competition among trees (Agee 1993). These changes increase the risk of wildfires (Fulé et al. 2001, Allen et al. 2002, Pierce et al. 2004), bark beetle attacks (Waring and Pitman 1985, Kolb et al. 1998) and decrease individual tree productivity (Parsons and De Benedetti 1979, Biondi 1996). Scientists, land managers, and the public are concerned that unless intervention occurs, we may lose a large portion of North America's ponderosa pine forests.

Reducing stand density is an approach to restoring ecosystem resilience and reducing wildfire risk (Covington et al. 1997, Allen et al. 2002), and may be applicable as ecological restoration treatments to old-growth forests (Covington and Moore 1994b, Mast et al. 1999) or proactive application to younger forests (Skov et al. 2004). Although the ideal silvicultural prescriptions may vary between regions and even sites (Morgan et al. 1994, Fulé et al. 1997, Landres et al. 1999, Moore et al. 2003, Brown et al. 2004, Schoennagel et al. 2004), stand density reductions are likely to reduce forest susceptibility to disturbance and increase productivity of

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remaining trees (Fiddler et al. 1989, Feeney et al. 1998, Latham and Tappeiner 2002). Unfortunately, understanding of the physiological mechanisms underpinning the long-term relationship between the reduction in competition and the magnitude and sustainability of productivity response is lacking. Over the short term, it appears that increases in water availability are at least partly responsible for increased growth after thinning in semiarid forests where leaf area index (LAI) is low and light is not a strongly limiting factor (Sucoff and Hong 1974, Donner and Running 1986, Warren et al. 2001, McDowell et al. 2003). In such systems, increased water availability may increase photosynthesis ( $P_n$ ) via increased stomatal conductance ( $g$ ; Feeney et al. 1998, Kolb et al. 1998, McDowell et al. 2003, Skov et al. 2004). The duration of this physiological response over decadal timescales may be influenced by the response of LAI to reduced stand density via increased leaf area of the understory vegetation (Oren et al. 1987) or of the remaining trees; however, no longer-term investigation has been conducted to test the latter explanation.

A theoretical basis for the long-term regulation of productivity in response to stand basal area reductions can be derived from an individual tree-based application of the stand-level hydraulic model proposed by Jarvis (1975) and refined by Whitehead et al. (1984). This theory is based on Darcy's law and proposes that crown exchange of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  is regulated by a set of homeostatic relationships between structural and physiological parameters including the ratio of transpiring leaf area to sapwood area ( $A_l:A_s$ ) and the soil-to-leaf water potential gradient ( $\Psi_s-\Psi_l$ ):

$$g \approx \frac{A_s(\Psi_s - \Psi_l)}{A_l} \quad (1)$$

This version of the original equation grossly oversimplifies the hydraulic and metabolic system of trees; however, it is appropriate for a stand of trees of uniform age, in which we can expect that other factors such as water viscosity and density (Matzner and Comstock 2001), tree height (Schäfer et al. 2000), and xylem specific conductivity (Pothier et al. 1989) are relatively invariant. For more detailed versions of the model see Whitehead (1998), Schäfer et al. (2000), McDowell et al. (2002a), Phillips et al. (2002), and others. Importantly, Eq. 1 captures three critical parameters that may respond to stand basal area reductions: (1) a driving resource expected to change due to reduced stand-level transpiration,  $\Psi_s$ , (2) a structural response parameter,  $A_l:A_s$ , and (3) a physiological response parameter,  $g$ . As can be seen in Eq. 1, increases in soil moisture content ( $\Psi_s$ ) allow an increase in  $A_l:A_s$ ,  $g$ , or both.

Increasing  $A_l:A_s$  is an expected result of increasing soil moisture content because there is more water available to support transpiring surface area ( $A_l$ ), and likewise the importance of large  $A_s$  for water supply and capacitance is reduced (Waring et al. 1979, Mencuccini and Grace 1995, Maherali and DeLucia 2001). One benefit of

increasing  $A_l:A_s$  is the increased leaf area that can intercept light and conduct photosynthesis. Thus, even if the absolute rates of photosynthesis per unit leaf area remain unchanged after reductions in stand basal area, increased  $A_l:A_s$  should allow greater crown-scale  $P_n$ . However, shifts in aboveground architecture presumably take many years, even decades, to occur (Ishii and McDowell 2002). Therefore, understanding mechanisms regarding the long-term growth response of trees to reductions in stand-level competition requires assessment of  $A_l:A_s$  from long-term studies.

Increased  $g$  results from increased soil moisture because the greater supply of water enables increased transpiration at reduced risk of xylem cavitation (Tyree and Sperry 1988, Sperry et al. 1998). Increased  $g$  allows increased  $P_n$  due to increased  $\text{CO}_2$  diffusion to the mesophyll cells where photosynthesis occurs:

$$P \approx g \times (c_a - c_i) \quad (2)$$

In this representation of Fick's law,  $c_a$  and  $c_i$  are atmospheric and internal  $\text{CO}_2$  concentrations. Thus, thinning may result in increased  $P_n$  per unit leaf area (Kolb et al. 1998, McDowell et al. 2003).

We can retrospectively examine annual variation in crown-scale gas exchange metabolism using the carbon isotope ratio ( $\delta^{13}\text{C}$ ) of tree rings (Francey and Farquhar 1982, Walcroft et al. 1997). Photosynthesis by ponderosa pines discriminates against  $^{13}\text{CO}_2$  relative to  $^{12}\text{CO}_2$  because  $^{13}\text{CO}_2$  has a lower diffusivity through the stomatal pore and lower reactivity with the photosynthetic enzyme ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco). This discrimination ( $\Delta$ ) results in  $\delta^{13}\text{C}$  of the carbon within ponderosa pine tree rings to be ~15–25‰ below that of atmospheric  $\text{CO}_2$ . Discrimination can be expressed relative to  $c_i/c_a$  via the following simplified expression (Farquhar et al. 1989):

$$\Delta \approx a + (b - a) \times \frac{c_i}{c_a} \quad (3)$$

where  $a$  is the fractionation associated with diffusion in air (4.4‰),  $b$  is the net fractionation associated with carboxylation by Rubisco (27–29‰). See Eq. 4 later in this paper for details on how  $\Delta$  is calculated from  $\delta^{13}\text{C}$ . As can be seen from Eqs. 2 and 3, gas exchange parameters can be assessed using tree ring estimates of  $\Delta$ . The relative immobility of carbon within the tree rings allows us to examine the long-term, interannual  $\Delta$  patterns in response to stand basal area manipulations. In the three previous studies on *Pinus* tree ring  $\delta^{13}\text{C}$  or  $\Delta$  response to thinning, no response has been observed (Leavitt and Long 1986), increased discrimination has been observed and attributed to greater water availability (McDowell et al. 2003), and decreased discrimination has been observed and attributed to greater light and nutrient availability (Warren et al. 2001).

Tree ring estimates of  $\Delta$  can also allow us to determine if gas exchange is maintained at a homeostatic set point (Ehleringer 1993) after manipulation of stand basal area. The  $c_i$  value in Eqs. 2 and 3 is a result of the balance of

TABLE 1. Ponderosa pine stand treatment characteristics (standard errors in parentheses).

Treatment (m <sup>2</sup> /ha)†	Mean stem density (no./ha)	Mean dbh (cm)	Mean height (m)	Leaf area index (m <sup>2</sup> /m <sup>2</sup> )‡
7	70 (3.8)	47 (0.99)	19.5	1.32
14	145 (3.3)	40 (0.43)	18.6	1.72
18	245 (11.6)	34.8 (0.87)	18.9	2.02
23	366 (18.0)	31.7 (0.76)	18.9	1.59
28	471 (39.3)	30.4 (1.24)	16.9	1.92
35	789 (1.6)	25.5 (0.03)	15.9	1.50
45§	3160	13.4	11.1	1.26

† Treatments are presented as stand basal area (m<sup>2</sup>/ha) remaining after thinning.

‡ Leaf area index includes overstory and understory vegetation (N. G. McDowell, H. D. Adams, J. D. Bailey, and T. E. Kolb, *unpublished manuscript*).

§ The unthinned, 45 m<sup>2</sup>/ha treatment had only one plot; therefore no standard error values are provided.

CO<sub>2</sub> supply and demand ( $g$  and  $P_n$ ), such that shifts in the ratio of  $P_n/g$  cause direct changes in  $c_i$ . The ratio  $P_n/g$ , also known as intrinsic water-use efficiency (Ehleringer 1993), is optimized to maximize  $P_n$ . In semiarid conditions where  $g$  is low, this optimization results in relatively high values of  $P_n/g$  (Ehleringer 1993). However, plants with abundant moisture supply often have lower  $P_n/g$  but higher absolute rates of gas exchange. The decrease in  $P_n/g$  with increasing rates of gas exchange results because  $g$  increases more than  $P_n$  due to enzymatic and diffusional limitations on  $P_n$  (Cowan 1985, Meinzer et al. 1993, Buckley et al. 1999, McDowell et al. 2003). Despite interannual fluctuations in water availability, long-term studies often find that gas exchange maintains  $c_i/c_a$  at a homeostatic set point (Ehleringer 1993, but see Marshall and Monserud 1996). It remains to be seen how changes in stand basal area will affect gas exchange metabolism over the long term. In a 15-year retrospective study on the response to thinning in an Oregon ponderosa pine forest, McDowell et al. (2003) observed that reduced stand basal area resulted in higher absolute rates of  $P_n$  and  $g$  and a decline in the ratio  $P_n/g$ . However, shifts in  $P_n/g$  may not be maintained over decades if  $A_i:A_s$  changes or if competing vegetation becomes reestablished (Oren et al. 1987, McDowell et al. 2003). Therefore, the influence of stand basal area on homeostatic maintenance of gas exchange remains unclear.

The long-term homeostasis between crown-scale physiological and whole-tree structural behavior is critical to understanding the sustainability of tree productivity in response to ecological restoration treatments. The goal of our study was to examine the interaction between physiological and structural mechanisms of response to competition using a long-term, replicated study of ponderosa pine response to thinning in which basal area was manipulated to seven different levels. In particular, we sought to determine the long-term pattern of growth, crown-scale gas exchange metabolism, and  $A_i:A_s$  of ponderosa pine trees in

response to changes in competition. Using Eqs. 1 and 2 and previous observations from a similar study (McDowell et al. 2003) as our basis for hypotheses, we predicted that: (1) during the first decade after stand basal area reductions,  $\Delta$  would increase in response to stand basal area reduction, (2) over the long term,  $A_i:A_s$  would increase in response to stand basal area reductions, and (3) long-term homeostatic adjustments would hold  $\Delta$  constant across all stand densities after the first decade.

## METHODS

### Study site

The experimental site is the Taylor Woods portion of the Fort Valley Experimental Station (35°16'11" N, 111°44'30" W) located within the Coconino National Forest ~15 km northwest of Flagstaff, Arizona, USA. The stand is ~35.6 ha in area (Ronco et al. 1985), and is dominated by ponderosa pine (*Pinus ponderosa* var. *scopulorum*) that regenerated naturally ca. 1919 (Ronco et al. 1985, Savage et al. 1996). The trees were ~84 years old during the time of our field experiment (summer 2003). Overstory and total (overstory and understory) leaf area index for the stands is not correlated with stand density, and averages 1.52 and 1.62 m<sup>2</sup>/m<sup>2</sup> ground area, respectively (N. G. McDowell, H. D. Adams, J. D. Bailey, and T. E. Kolb, *unpublished manuscript*; Table 1). The leaf area of understory grasses and forbs increased exponentially with declining stand density, to a maximum leaf area index of 0.25 m<sup>2</sup>/m<sup>2</sup> ground area (N. G. McDowell, H. D. Adams, J. D. Bailey, and T. E. Kolb, *unpublished manuscript*). The stand has flat topography and is located at 2266 m elevation. The soils are classified as a montmorillonitic complex of frigid Typic Argiborolls and Argiboralfs (Wollum and Schubert 1975, Ronco et al. 1985). Mean annual temperature from 1909 to 1990 near the study site was 6.0°C and mean annual precipitation was 56.4 cm, with approximately half of this amount falling as snow (Schubert 1974, NOAA 1990). This region experiences a monsoonal climate typical of the southwest United States, with precipitation distributed in a bimodal pattern that peaks in the winter (November–March) and late summer (July–August), and a pronounced drought during May and June.

### Experimental design

We utilized a replicated set of stand basal area treatments to test our hypotheses regarding physiological and structural responses to changes in stand basal area. The initial experiment was designed by the USDA Forest Service to determine the effects of stand basal area on ponderosa pine growth (Myers 1967, Ronco et al. 1985). The forest was thinned originally in October 1962 to generate three replicated plots of each treatment basal area, where the residual basal areas of the seven treatment densities were 45 m<sup>2</sup>/ha (the uncut control), 34, 28, 23, 18, 14, and 7 m<sup>2</sup>/ha. It is worth noting that basal area of southwestern ponderosa pine forests in the

early 1900s (8 m<sup>2</sup>/ha; Moore et al. 2003) was similar to our lowest density treatment. The residual basal area was maintained by rethinning each plot once per decade, resulting in removal of trees in 1972, 1982, 1992, and during the last half of our two-week experimental phase in June 2003. The plots are about 0.4 ha in size, and have 0–10 m buffers. Data for tree density, diameter, height, and leaf area index for each basal area level are shown in Table 1. Although the unthinned plots have experienced some mortality resulting from self-thinning, no recent mortality has occurred in any of the plots as a result of bark beetle infestation.

Basal area increment (BAI, in square centimeters per year) was measured on three interior trees per plot, three plots per treatment. For  $\Delta$  and  $A_i:A_s$  we measured five interior trees per plot in one plot for each treatment. This was done to minimize the workload and costs to achievable levels for the  $A_i:A_s$  and isotopic measurements. Basal area increment was statistically indistinguishable between the intensive plots and the replicated plots (ANOVA  $P = 0.71$ ); therefore the  $\Delta$  and  $A_i:A_s$  values from these plots should be representative of each treatment. The plots are referred to as *intensive* and *replicated* plots throughout the remainder of the paper, where intensive indicates that a large assortment of measurements were made on one plot per treatment, and replicated indicates that BAI was measured. Thus, BAI was the only measurement that was truly replicated over three plots per treatment. Five trees were harvested from each of the intensive plots between 9 and 13 June 2003, as part of the decadal thinnings to maintain treatment basal area. Additionally, three or more trees were harvested and sampled for growth from all remaining plots in November 2003. We attempted to utilize trees that were of average size (height and diameter) for each treatment. Stem diameter at breast height (1.3 m, dbh) of the harvested trees tended to be slightly less (8%) than the plot average as measured by the regression slope of stand mean diameter at breast height (dbh) vs. harvested trees dbh (slope = 0.92,  $r^2 = 0.98$ ,  $P < 0.01$ ). Both the intensive and replicated plots were used for measurements of soil water availability and photosynthesis in an earlier study in 1994 (Kolb et al. 1998). Leaf gas exchange and water potential data were measured biweekly on eight dates between May and September 1994, on 3–5 trees per plot in two plots per treatment (Kolb et al. 1998). Also, we measured photosynthetic capacity in 2003 (see *Photosynthetic capacity*). As in any retrospective study that mixes data sets collected during disparate times, it is essential to remember that measurements from recent years may not be indicative of behavior during earlier years. Therefore, we consider measurements of water potential, gas exchange, and tree structure that were conducted in the 1990s and 2000s as representative of those times, and urge caution when extending these results to interpret isotope and growth data from the 1960s, 1970s, and 1980s.

### Productivity

We assessed aboveground productivity from tree ring analysis of BAI. After trees were felled we removed stemwood cross sections from a height of ~1.3 m from each stump with chainsaws. Cross sections were subsequently air dried for three months prior to further analysis. We sanded the cross sections using successively finer sandpaper of FEPA (Federation of European Producers of Abrasives, Paris, France) 100, 220, and 320 grit (162, 68, and 44.7–47.7  $\mu\text{m}$ , respectively; Orvis and Grissino-Mayer 2002) using a belt sander (Makita USA, La Mirada, California, USA). When necessary we also used FEPA 400 grit sandpaper (33.5–36.5  $\mu\text{m}$ , Orvis and Grissino-Mayer 2002). We measured ring widths using a Microcode II banister measuring system (Boeckler Instruments, Tucson, Arizona) attached to a PC running the Measure J2X software (*available online*).<sup>5</sup> Cores were cross-dated visually using narrow marker years from tree ring chronologies collected at local sites for ponderosa pine (Adams and Kolb 2004). We checked measurements for accuracy using skeleton plots (Stokes and Smiley 1968) and the COFECHA software program (Holmes et al. 1986, Grissino-Mayer 2001, International Tree Ring Data Bank program library). Ring widths were converted to BAI from 1950 to 2001 using tree-specific cross-sectional radii (inside bark) and assuming concentric circularity. Missing rings were rare except for 1999 through 2002 in trees from the unthinned treatment. We stopped measurement at 2001 because 2002 was a year of severe drought and most trees did not form rings that year except for trees in the lowest density treatment (7 m<sup>2</sup>/ha). BAI results are presented at the individual plot level and entire treatment (basal area) level.

### Carbon isotope discrimination

We measured  $\delta^{13}\text{C}$  of tree rings and related this to  $\Delta$  (Farquhar et al. 1982):

$$\Delta \approx \frac{\delta^{13}\text{C} - \delta^{13}\text{C}_a}{1 + \delta^{13}\text{C}/1000}. \quad (4)$$

We obtained annual atmospheric stable carbon isotope ratios ( $\delta^{13}\text{C}_a$ ) from the Institute for Arctic and Alpine Research (INSTAAR) at the University of Colorado and the National Oceanic and Atmospheric Administration (NOAA), Climate Monitoring and Diagnostics Laboratory (CMDL). Eq. 4 corrects for annual depletion of  $\delta^{13}\text{C}_a$  associated with fossil fuel emissions of  $\text{CO}_2$  depleted in  $\delta^{13}\text{C}$  (Leavitt and Long 1988a, Keeling et al. 1989). This correction is necessary because a change in the  $\delta^{13}\text{C}$  of  $\text{CO}_2$  used as the substrate for photosynthesis causes a physiologically independent change in the  $\delta^{13}\text{C}$  of plant material.

The stable isotope composition of tree rings was assessed in two data sets: (1) a short-term assessment of the response of  $\Delta$  to the 1962 thinning for each

<sup>5</sup> [www.voortech.com/projectj2x/tringMainV2.html](http://www.voortech.com/projectj2x/tringMainV2.html)

treatment, and (2) a long-term assessment of the  $\Delta$  pattern in relation to thinning over four decades. For the short-term assessment we determined  $\Delta$  for five trees from each of the intensive plots for the 15 years bracketing the 1962 thinning (1958–1972). For the long-term assessment we determined  $\Delta$  for the years 1952–2001 (49 years) for the 45, 28, 14, and 7 m<sup>2</sup>/ha intensive plots. The long-term assessment used a single pooled sample of five trees (i.e., rings) per plot and per year. The short-term assessment provides the estimate of within-plot  $\Delta$  variance, and the long-term assessment is used to determine the long-term  $\Delta$  response to thinning. To allow a statistical test of the long-term patterns, we also ran samples from a nondrought year (1992) and a drought year (2000) for the 45 and 7 m<sup>2</sup>/ha plots using five trees per plot.

After the stemwood cross sections of the five trees from each of the intensive plots had been cross-dated and measured we removed fine-grain particles of wood from all rings using a Dremel tool (Robert Bosch Tool Corporation, Mount Prospect, Illinois, USA) with a 2.38 mm (3/32 inch) diameter diamond bit. We removed wood from a 3–10 cm circumferential path along the ring, starting at a location where the ring was sufficiently wide to ensure no cross-year contamination. The path along the ring should have reduced  $\delta^{13}\text{C}$  variability due to circumferential variation (Leavitt and Long 1984, 1988b). We did not attempt to separate early from late wood (Livingston and Spittlehouse 1996, Leavitt and Wright 2002) because our objective was to examine the response of  $\Delta$  to stand basal area at the annual timestep. We were able to remove wood successfully from individual rings without contamination from neighboring rings except in the case of some rings from the uncut control plot (45 m<sup>2</sup>/ha) where the rings were often smaller than the finest point of the diamond bit. We estimate that the annual estimates of  $\Delta$  for the control plot may be up to 5% contaminated by neighboring rings; thus the control plot time series of  $\Delta$  may appear smoother than reality. We did not extract cellulose prior to measurement of  $\delta^{13}\text{C}$  because: (1) numerous studies have reported constant relationships between cellulose and whole-wood  $\delta^{13}\text{C}$  for sapwood (Livingston and Spittlehouse 1996, Marshall and Monserud 1996, Macfarlane et al. 1999, Loader et al. 2003), (2) most cross-ring contamination is associated with carbon movement from the sapwood into the heartwood (S. Leavitt, *personal communication*) and all of our sample rings were located within the sapwood, and (3) Eqs. 2–4 were designed for foliar gas exchange, and whole wood has undergone less metabolic processing postassimilation than cellulose per se (Hill et al. 1995). The fine dust collected from each ring was analyzed on a Eurovector Elemental Analyzer (Eurovector S.P.A., Milan, Italy) coupled to a Micromass Isoprime isotope ratio mass spectrometer (GV Instruments, Manchester, UK) operated in continuous flow mode at Los Alamos National Laboratory's Stable

Isotope Laboratory in Los Alamos, New Mexico, USA. Nitrous oxide was removed by gas chromatography and corrections for  $^{17}\text{O}$  (Craig 1957) were done for all runs. A total of 297 tree ring samples were run and overall precision for  $\delta^{13}\text{C}$  was 0.05‰ ( $n = 103$ ).

#### *Leaf area : sapwood area ratio*

We capitalized on the thinning in June 2003 to collect samples for calculating whole-tree leaf area : sapwood area ratio ( $A_l:A_s$ , m<sup>2</sup>/cm<sup>2</sup>). Whole-tree leaf area was estimated by scaling branch estimates of leaf area to the canopy (Maguire and Batista 1996, Monserud and Marshall 1999, McDowell et al. 2002b). Branch-scale allometric equations were developed through branch harvest and analysis for five trees from each of the intensive plots. We harvested branches immediately after each tree was felled to prevent any needle loss due to desiccation. Nine branches were harvested from throughout the height continuum of the crown for each of five trees per plot. Branches were harvested from all aspects, although previous research found no effect of aspect (McDowell et al. 2002b). The entire foliage mass for each branch ( $M_b$ ) was collected in industrial-size paper bags and transported back to the laboratory. In the laboratory, foliage from each branch was randomly subsampled to determine specific leaf area ( $S$ , cm<sup>2</sup>/g). Projected leaf area was determined using a video image recorder and AgVision software (Decagon Devices, Pullman, Washington, USA). The remaining foliage was dried at 65°C until the mass had stabilized and then weighed. Because of the small stature of the trees in the uncut control plot, we measured whole-tree leaf area for four of the five sampled trees, and used the branch regression approach for the fifth, largest, tree. Foliage was processed identically to the methods described earlier.

Based on previous results (Hubbard et al. 1999, Fischer et al. 2002, McDowell et al. 2002b), we used branch diameter ( $d$ ) to estimate  $M_b$ . Scatterplots of  $M_b$  vs.  $d$  revealed that variance in  $M_b$  did not consistently increase with larger values of  $d$  and the relationships were linear; therefore we used standard linear regression rather than weighted regression (Monserud and Marshall 1999, McDowell et al. 2002b). The  $d$  vs.  $M_b$  regressions had a mean  $r^2$  of 0.56,  $P < 0.01$ , when averaged across all sample trees ( $n = 31$ ). Mean slopes and intercepts for the regressions from each treatment are presented in Table 2. We used tree-specific  $d$  vs.  $M_b$  regressions to scale  $M_b$  up to the entire crown for each of the sample trees. This scaling was done using measurements of  $d$  collected on every live branch for every tree immediately after the tree was felled. Branch diameter  $d$  was measured with calipers 20 mm proximal to the main stem in two perpendicular directions for all branches.

Specific leaf area ( $S$ ) exhibited a weak but consistent increase with increasing distance from the tree tops for all plots ( $r^2$  ranged from 0.19 to 0.42). Because of this

TABLE 2. Stand and individual tree structural regressions were used to predict branch leaf mass ( $M_b$ ) from branch diameter ( $d$ ), and specific leaf area ( $S$ ) from the distance to the top of the tree.

Treatment (m <sup>2</sup> /ha)	$M_b$ vs. $d$ regressions				$S$ regressions			
	Slope	Intercept	$r^2$	$P$	Slope	Intercept	$r^2$	$P$
7	666	543	0.73	<0.01	0.61	26.7	0.24	<0.01
14	447	241	0.60	<0.01	1.14	28.3	0.39	<0.01
18	197	0†	0.42	<0.01	0.80	28.8	0.27	<0.01
23	322	79	0.43	<0.01	0.60	24.8	0.20	0.03
28	480	260	0.70	<0.01	1.2	27.8	0.42	<0.01
35	384	171	0.48	<0.01	1.56	24.6	0.34	<0.01
45‡	358				31.86			

Notes: The original units for branch diameter ( $d$ ) are centimeters, those for branch leaf mass ( $M_b$ ) are grams, and those for specific leaf area ( $S$ ) are square centimeters.

† The 18 m<sup>2</sup>/ha treatment regression had a slightly negative but still unrealistic intercept, so we fit the line through a zero intercept. There was no detectable change in the fit statistics.

‡ Four of the five sample trees in the 45 m<sup>2</sup>/ha treatment were entirely harvested and measured, so only the plot mean leaf mass and  $S$  are presented.

consistent trend of increasing  $S$  with increasing distance from the tree top (or increasing proximity to the ground), we applied plot-specific  $S$  – branch height corrections prior to multiplying  $S$  to  $M_b$  for estimating whole-branch leaf area. The treatment-specific slopes and intercepts for  $S$  – branch height regressions are presented in Table 2. Occasionally the predictions of branch leaf area were negative when branches had extremely small diameters. Negative leaf areas for these branches were set to zero.

Sapwood area was estimated from the stemwood cross sections for each tree. The sapwood–heartwood boundary was usually clear; however, we applied bromocresol green stain (Kutscha and Sachs 1962) to verify all visual estimates. On each cross section, sapwood depth was measured for four cambium-to-heartwood transects located at right angles to each other, with a random start location for the first transect. Sapwood depths were averaged and sapwood area was estimated assuming concentric circularity.

#### Photosynthetic capacity

Photosynthetic capacity can influence  $\Delta$  by increasing or decreasing  $P_n$  and subsequently causing an inverse change in  $c_i/c_a$  (Eq. 3). We examined photosynthetic capacity using response curves of photosynthetic assimilation to internal [CO<sub>2</sub>] ( $A$  vs.  $C_i$  curves). The  $A$  vs.  $C_i$  curves were measured on four trees in the 7 m<sup>2</sup>/ha intensive plot, five trees in the 23 m<sup>2</sup>/ha intensive plot, and eight trees in the 45 m<sup>2</sup>/ha intensive plot. The sample sizes varied because it became apparent during our field measurements that the 45 m<sup>2</sup>/ha plot had greater intertree variability than the other two plots. We made the measurements from 0700 to 1200 in the morning on two consecutive sunny, cloudless days (4 and 5 June 2003). Foliage from the upper 10% of the canopy was measured in situ using a moveable 20-m boom lift (Sunstate Rentals, Flagstaff, Arizona, USA). The  $A$  vs.  $C_i$  curves were measured with a LI-COR 6400 portable photosynthesis system (LI-COR, Lincoln, Nebraska, USA). The cuvette irradiance was main-

tained at 1400  $\mu\text{mol}$  of photons·m<sup>-2</sup>·s<sup>-1</sup> using a blue-red light source, well above photosynthetic light saturation for ponderosa pine (800  $\mu\text{mol}$  of photons·m<sup>-2</sup>·s<sup>-1</sup>, Hadley 1969, Kolb and Roberrecht 1996).  $A$  vs.  $C_i$  curves were generated by changing the cuvette CO<sub>2</sub> in the following order: 400, 300, 200, 100, 400, 600, 800, and 1200  $\mu\text{mol}/\text{mol}$ . We did not expose the foliage to higher CO<sub>2</sub> partial pressures because our goal was only to ascertain the maximum catalytic activity of Rubisco ( $V_{\text{cmax}}$ ). After each exposure to a new CO<sub>2</sub> level, net photosynthesis was allowed to reach steady state (cuvette CO<sub>2</sub> coefficient of variation <2%) prior to measurement. Three measurements were made per sample per CO<sub>2</sub> level over a 60-second period after steady state had been reached.  $V_{\text{cmax}}$  was calculated from the  $A$  vs.  $C_i$  curves using nonlinear, least squares regression to fit the values of these parameters to the equations of the Farquhar et al. (1980) photosynthesis model (Harley et al. 1992). Parameters were temperature corrected to 25°C using the equations of Leuning (1997), and the activation energies from Harley et al. (1992). Calculation of  $V_{\text{cmax}}$  was typically done using  $C_i$  values <300  $\mu\text{mol}/\text{mol}$  when the slope was quasilinear (Wullschlegel 1993).

#### Water potential

Predawn foliage water potential from overstory trees provides an index of soil water potential ( $\Psi_s$ ) within the rooting zone if nocturnal transpiration is consistent between treatments or is negligible (Donovan et al. 2001, Bucci et al. 2004). The parameter  $\Psi_s$  was measured twice a month from May to September 1994 from the 45, 28, 18, and 7 m<sup>2</sup>/ha treatments (Kolb et al. 1998). Kolb et al. measured predawn foliage water potential from 5 to 10 trees per treatment and from the lower and upper portions of the canopy, but did not correct these values for the hydrostatic gradient (0.01 MPa/m). We corrected their values for the hydrostatic gradient based on branch height above the ground. The corrected values were then averaged and used to assess the response of  $\Psi_s$  to stand basal area. Midday leaf water potential ( $\Psi_l$ ) was also

measured in 1994 on the same trees as the  $\Psi_s$  measurements. We have summarized these for the entire summer, averaged by treatment; in addition we calculated treatment mean  $\Psi_s - \Psi_1$  (Eq. 1). Other details on sampling procedure are given in Kolb et al. (1998).

#### *Ancillary gas exchange data*

In conjunction with the 1994  $\Psi_s$  measurements, Kolb et al. (1998) also measured leaf-level gas exchange twice a month from May to September 1994 from the 45, 28, 18, and 7 m<sup>2</sup>/ha treatments. The Kolb et al. measurements were conducted between 1000 and 1300 each day. They measured  $P_n$  and  $g$  from three to seven trees per treatment from the lower and upper crowns under ambient humidity and temperature and with light incident on the foliage  $> 1000 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . They did not find a significant difference in gas exchange with crown position, so we have averaged the values to provide crown mean rates of gas exchange. In the current study we used the gas exchange data to: (1) investigate the absolute rates of  $P_n$  and  $g$  and their ratio (Eq. 3) for a single summer within our inference period, and (2) examine the relationship between gas exchange,  $\Psi_s$ , and BAI.

#### *Climatic response*

We were curious if stand basal area treatments would cause differential dependency of growth on drought. To assess this question, we examined relationships between BAI and Palmer Drought Severity Index (PDSI) for each treatment in the 40 years following the initial stand basal area manipulations. PDSI is a measure of meteorological drought calculated from precipitation, temperature, and potential evapotranspiration (Palmer 1965, Alley 1984). We used annually averaged instrumental PDSI data for Region 2 of Arizona, available from the National Climatic Data Center (*available online*).<sup>6</sup> PDSI was used as the independent variable in regression analysis with BAI and with basal area normalized BAI (BAI/BA). Normalization was done to account for the inherent differences in tree size that occurred in the decades following the stand basal area treatments, allowing us to examine the relative responses of trees to drought.

#### *Statistics*

We tested the hypotheses that BAI and  $\Delta$  varied among stand basal area levels using regression analysis of values averaged from 1962 to 2001 to account for interannual variability due to climate or decadal harvests. We did a similar regression analysis with  $A_1:A_s$  measured in 2003 as the dependent factor. To assess the time period of significant responses we used blocked repeated measures analysis of variance for BAI and  $\Delta$  in which the blocks represent different basal area treat-

ments. Differences in  $V_{\text{cmax}}$ ,  $\Psi_s$ , and leaf-level  $P_n$  and  $g$  among stand basal area treatments were tested using analysis of variance. Unless otherwise specified, the regression results presented are the best statistical fit of a variety of regression forms tested. We conducted all tests with SYSTAT 11.0 (SYSTAT 2004).

## RESULTS

### *Overall response to stand basal area reductions*

Average tree BAI increased in response to stand basal area reductions (Fig. 1). Pre-thinning BAI did not differ between any of the plots except the 45 m<sup>2</sup>/ha treatment, which had lower BAI ( $P < 0.01$ ). This difference is probably due to our sample selection criteria, which was to harvest the "average" tree based on height and diameter. The average tree in the 45 m<sup>2</sup>/ha plot in 2003 was small; however, similar small trees in the other treatments were probably removed by the 1962 thinning. Post-thinning BAI differed among plots ( $P < 0.01$ ). The magnitude of BAI response to thinning was a negative function of residual stand basal area (Fig. 2). When calculated as a percentage of BAI of the 45 m<sup>2</sup>/ha treatment, the mean growth increase for the 7, 14, 18, 23, 28, and 34 m<sup>2</sup>/ha treatments over 40 years was 1770, 947, 808, 597, 570, and 371%, respectively.

Carbon isotope discrimination also responded to stand basal area reductions (Fig. 3). Prior to thinning (1958–1961),  $\Delta$  was not statistically different among plots ( $P = 0.11$ , Fig. 3A); however, there was a difference of almost 1.0‰ across treatments. In order to equitably compare responses without the interference of pretreatment variation, we calculated normalized  $\Delta$  that accounts for within-plot, pretreatment differences using the equation:  $Y = \Delta(\text{year } X) - \text{mean } \Delta(1958-1961)$  (see Carpenter et al. 1989 and Fig. 3B). Again there was no difference in normalized  $\Delta$  prior to thinning ( $P = 0.16$ , Fig. 3B). This normalization does not account for climatic variation from year to year. Therefore, to clearly test for the effects of stand basal area without interference of climate, we standardized the pre-thinning normalized data for each year (Fig. 3B) based on the normalized data from the control, unthinned stand (45 m<sup>2</sup>/ha). Using  $Y$  from the equation presented above for pre-thin normalization, the equation for normalization by the control stand is:  $Y_{\text{trt } X} - Y_{\text{ctl}}$ . In this normalization, control plot mean  $\Delta$  is used as an index of climatic variation that is free of thinning effects. Using this final normalized  $\Delta$ , we again observed no pre-thin differences ( $P = 0.61$ ). Normalized  $\Delta$  (Fig. 3C) was similar among basal area levels for four years following treatment ( $P = 0.45$ ), but significant differences occurred for years 5–12 after the initial thinning in 1962 ( $P < 0.01$ ). Normalized  $\Delta$ , 5–12 years after the initial thinning, was negatively related to stand basal area (Fig. 4). In other words,  $\Delta$  declined with increasing stand basal area during the period 5–12 years after thinning.

The long-term trend in  $\Delta$  from the 45, 28, 14, and 7 m<sup>2</sup>/ha intensive plots shown in Fig. 5 exhibits some

<sup>6</sup> [www.cdc.noaa.gov/Timeseries/](http://www.cdc.noaa.gov/Timeseries/)

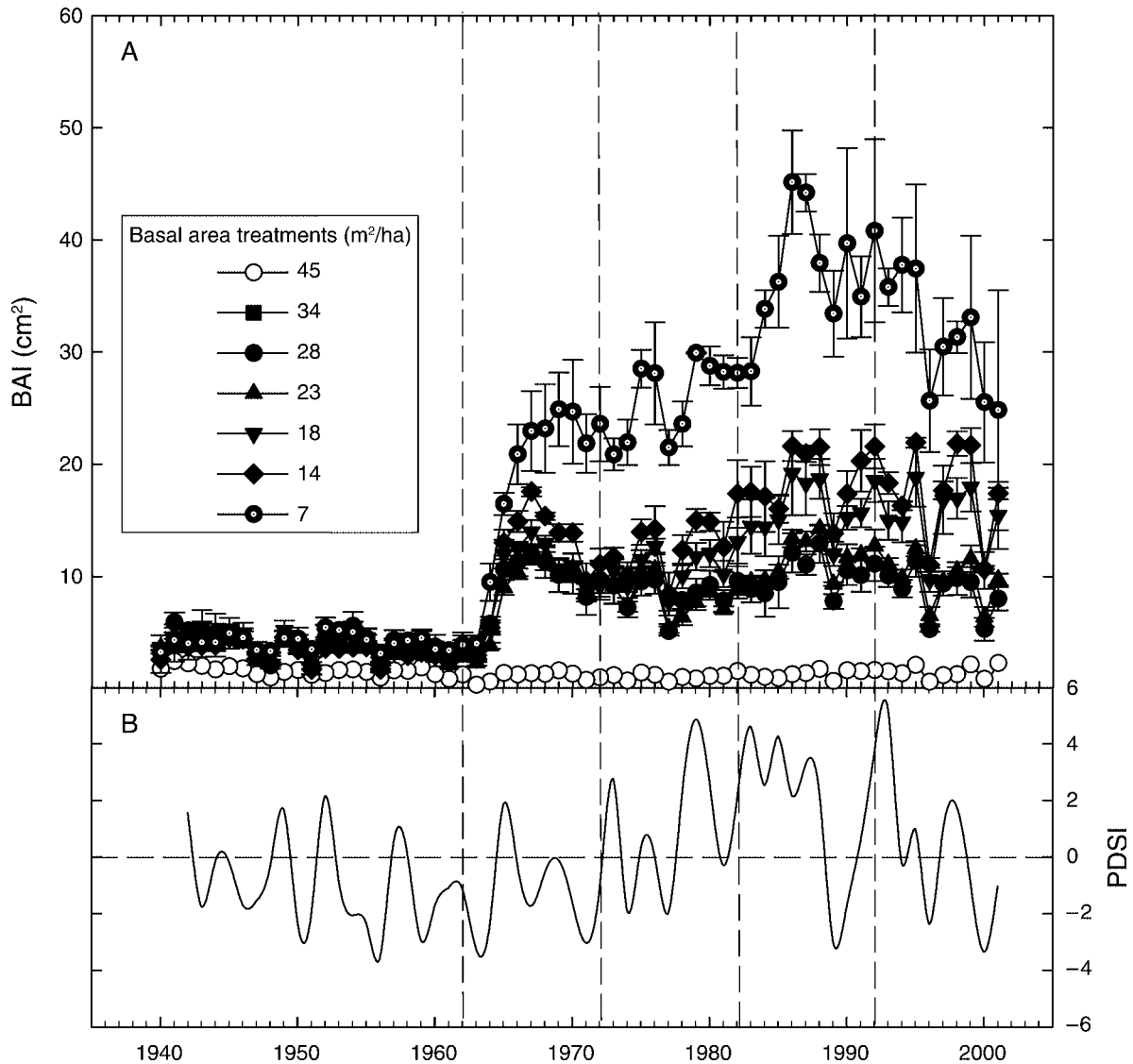


FIG. 1. (A) BAI (basal area increments) vs. stand basal area remaining after thinning for seven basal area (BA) treatments (7–45 m<sup>2</sup>/ha). Data are averaged for three plots per treatment with the exception of the 45 m<sup>2</sup>/ha control treatment (no thinning), which had a single plot. Bars represent  $\pm$ SE. The initial thinning treatment (1962) and subsequent thinning treatments (1972, 1982, 1992) are indicated by the vertical dashed lines. (B) Annual PDSI for Region 2 of Arizona (NCDC–NOAA). Negative PDSI values represent drought, and positive PDSI values represent wet periods.

interesting patterns. Fig. 5 (B,C) was calculated using the same normalization schemes as in Fig. 3 (B,C). Similar to Fig. 3A, the 45 m<sup>2</sup>/ha treatment had a slightly above-average  $\Delta$  prior to thinning and below-average  $\Delta$  for years 5–12 after the initial thinning in 1962 (Fig. 5A). After correction for pre-thinning differences (Fig. 5B), the 45 m<sup>2</sup>/ha treatment had the lowest  $\Delta$  for years 5–12 after the initial thinning; however, this difference disappeared in subsequent years with the exception of 1983–1985. After standardizing  $\Delta$  from the three thinned plots by the unthinned 45 m<sup>2</sup>/ha plot to account for year-to-year climatic variation, it appears that  $\Delta$  was not different from the control plot for the first four years

after the initial thinning, and then was substantially different for approximately years 5–12 after thinning. This result is similar to the pattern observed using the replicated data set (Fig. 3C). Notably, there was no apparent variation in normalized  $\Delta$  with stand basal area during the remaining decades except during an unusually wet period in the mid 1980s, when  $\Delta$  was lowest for the control plot, and an unusually dry period in the 1990s, when  $\Delta$  was highest for the control plot.

Statistical comparisons between the intensive plots were not conducted because only one single, pooled sample was analyzed per treatment per year. However, the patterns that emerged from the long-term data set



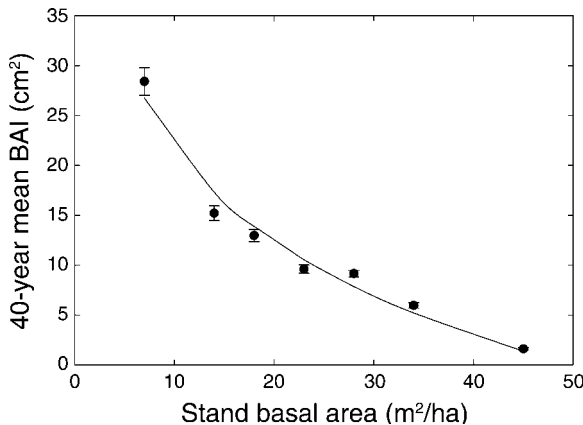


FIG. 2. Forty-year mean BAI (1963–2002) vs. stand basal area. Bars represent  $\pm$ SE. The regression equation is: 40-year mean BAI =  $-13.64 \ln(\text{basal area}) + 53.3$ ,  $r^2 = 0.97$ ,  $P < 0.01$ .

were confirmed with larger samples sizes for two years (1992 and 2000) for the 7 and 45  $\text{m}^2/\text{ha}$  treatments. The values for five trees per plot in the 7 and 45  $\text{m}^2/\text{ha}$  treatments (mean and standard error) were  $17.80 \pm 0.04\%$  and  $17.79 \pm 0.06\%$  during the nondrought year of 1992 ( $t$  test,  $P = 0.83$ ), and  $16.1 \pm 0.08\%$  and  $17.6 \pm 0.07\%$  during the drought year of 2000 ( $t$  test,  $P < 0.001$ ). These values are within 0.05% of the pooled sample values from those same years and treatments.

The relationship between long-term BAI from Fig. 1 and pre-thin normalized  $\Delta$  from Fig. 5B differed among basal area treatments (Fig. 6). Although the regressions are weak ( $r^2 = 0.16$ – $0.31$ ), the slopes are significantly different among treatments ( $P < 0.001$ ). The slope of BAI vs. normalized  $\Delta$  was negatively related to stand basal area; as stand basal area declined, BAI was more strongly related to incremental changes in normalized  $\Delta$ .

#### Leaf area : sapwood area

Whole-tree leaf area and sapwood area both declined with stand basal area. The regression equation describing the decline for leaf area is:  $A_l = -82.55 \times \ln(\text{basal area}) + 308.6$  ( $r^2 = 0.99$ ,  $P < 0.01$ ). The regression equation describing the decline for sapwood area is:  $A_s = -519.2 \times \ln(\text{basal area}) + 2086$  ( $r^2 = 0.97$ ,  $P < 0.01$ ). Leaf area and sapwood area exhibited different responses to stand basal area, however, resulting in a strong negative correlation between  $A_l:A_s$  and stand basal area ( $r^2 = 0.93$ ,  $P < 0.01$ ; Fig. 7). Mean  $A_l:A_s$  ranged from a minimum of  $0.04 \text{ m}^2/\text{cm}^2$  in the 45  $\text{m}^2/\text{ha}$  stand to a maximum of  $0.14 \text{ m}^2/\text{cm}^2$  in the 7  $\text{m}^2/\text{ha}$  stand.

#### Photosynthetic capacity, water potential, and in situ gas exchange

Photosynthetic capacity assessed using  $V_{\text{cmax}}$  calculated from  $A$  vs.  $C_i$  curves did not vary with stand basal area ( $P = 0.61$ , data not shown). The values for the 7, 28, and 45  $\text{m}^2/\text{ha}$  intensive plots (mean and standard error)

were  $59.7 \pm 9.0$ ,  $49.6 \pm 2.3$ , and  $62.1 \pm 11.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , respectively.

Net photosynthetic rate and  $\Psi_s$  during the summer of 1994 clearly varied with stand basal area. Both  $P_n$  and  $\Psi_s$  were greatest in the 7  $\text{m}^2/\text{ha}$  intensive plot and declined significantly as basal area increased ( $r^2 = 0.99$ ,  $P = 0.01$  for both, Fig. 8A, B). We also plotted BAI from 1994 for comparison (Fig. 8C), which showed a decline consistent with the overall trend shown in Fig. 2. Stomatal conductance showed a similar, but weaker pattern with stand basal area as  $P_n$  ( $r^2 = 0.80$ ,  $P = 0.09$ , data not shown). There was a positive, nonlinear relationship between BAI and  $\Psi_s$  (Fig. 9A), and a positive linear relationship between BAI and  $P_n$  (Fig. 9B). Despite large differences in the absolute rates of gas exchange among treatments, intrinsic water use efficiency ( $P_n/g$ ) exhibited no trend with stand basal area ( $P = 0.17$ , data not shown).

Midday  $\Psi$  averaged over the entire summer of 1994 for the 45, 28, 18, and 7  $\text{m}^2/\text{ha}$  intensive plots was (mean  $\pm$  SE)  $-1.68 \pm 0.06$ ,  $-1.62 \pm 0.07$ ,  $-1.65 \pm 0.09$ , and  $-1.51 \pm 0.09$  MPa, respectively. For the 7  $\text{m}^2/\text{ha}$  treatment,  $\Psi_1$  was significantly less negative than the other treatments ( $P < 0.01$ ). For the 45, 28, 18, and 7  $\text{m}^2/\text{ha}$  intensive plots,  $\Psi_s - \Psi_1$  averaged  $0.79 \pm 0.09$ ,  $0.95 \pm 0.08$ ,  $1.02 \pm 0.13$ , and  $1.01 \pm 0.11$  MPa, respectively. For the 45  $\text{m}^2/\text{ha}$  treatment,  $\Psi_s - \Psi_1$  was significantly smaller than for the other treatments ( $P = 0.015$ ).

#### Climatic response

PDSI varied from  $-3.34$  to  $5.26$  over the 40-year period from 1962 to 2001. Negative PDSI values represent drought and positive PDSI values represent wet periods. There was no relationship between PDSI and BAI for positive PDSI years, and when all years were combined the relationships were weak (data not shown). However, for negative PDSI years, BAI was positively correlated with PDSI for all treatments (Table 3). The slopes of BAI vs. PDSI (using the negative PDSI years only) were negatively correlated with stand basal area (Fig. 10A). This pattern remained after normalizing BAI by tree basal area (BAI/BA, Table 3 and Fig. 10B). Regressions of long-term  $\Delta$  data from Fig. 5B vs. PDSI consistently showed weak, positive relationships. The slopes and correlation coefficients ( $r^2$ ) for the 45, 28, 14, and 7  $\text{m}^2/\text{ha}$  intensive plots were: 0.9 (0.26), 0.12 (0.17), 0.17 (0.45), and 0.08 (0.11), respectively. There was no relationship between the slope of  $\Delta$ /PDSI and basal area ( $P = 0.71$ ).

#### DISCUSSION

Our results demonstrate that variation in stand basal area has long-term effects on the growth (Figs. 1, 2, and 6), physiology (Figs. 3–5, 8, and 9), and structure (Fig. 7) of ponderosa pine. The results are consistent with the hypothesis that gas exchange homeostasis is achieved through a balance of leaf- and whole-crown adjustments to changes in  $\Psi_s$  (Eq. 1). Crown-scale  $\Delta$  inferred from

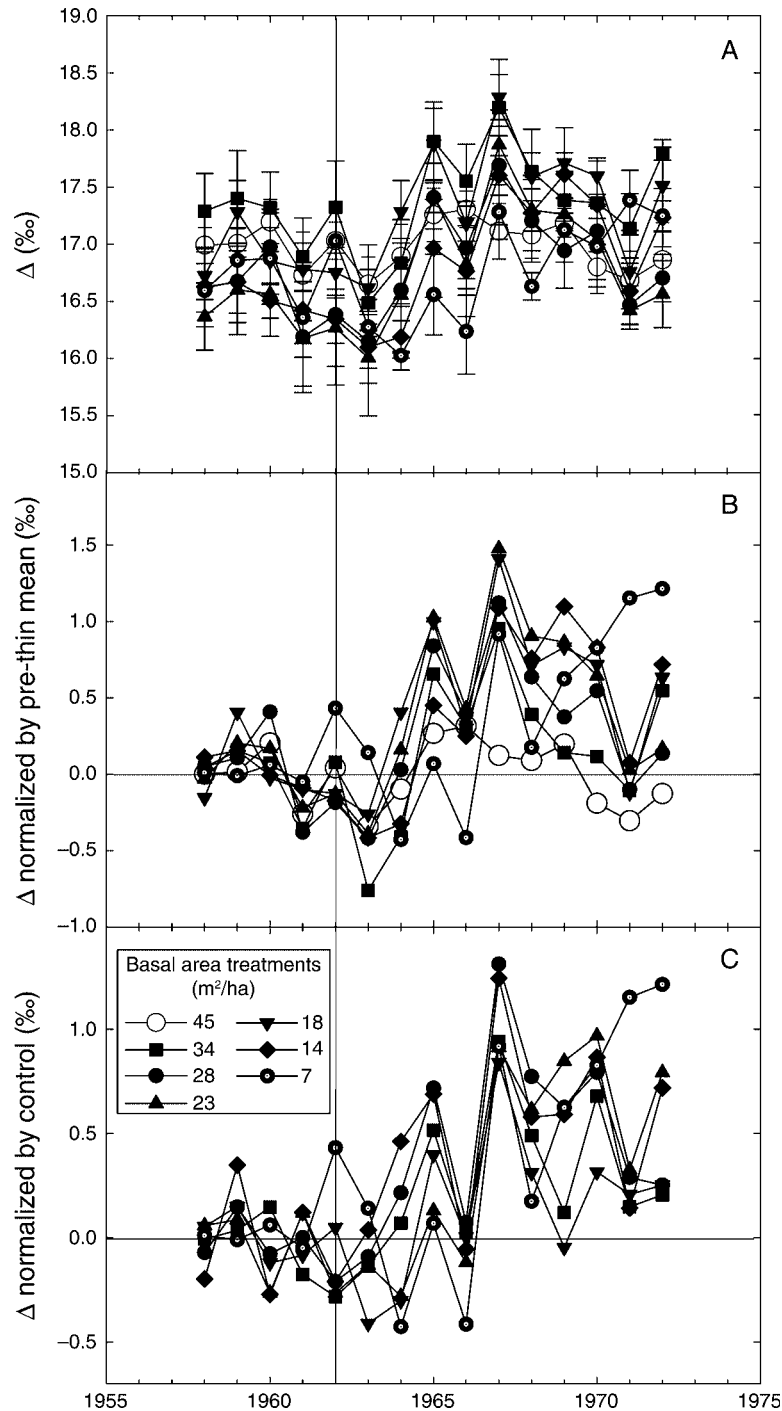


FIG. 3. (A) Carbon isotope discrimination ( $\Delta$ ; ‰) vs. year for seven BA treatments (7–45 m<sup>2</sup>/ha). Data are plot means for one plot per treatment, three trees per plot. Bars represent  $\pm$ SE. The year of initial thinning (1962) is indicated by a solid vertical line. (B) Data from panel A normalized by the plot-specific, pre-thinning mean  $\Delta$ :  $Y = \Delta(\text{year } X) - \text{mean } \Delta(1958\text{--}1961)$ . This normalizes for plot-specific differences (e.g., pre-thin density or microsite differences). Error bars are omitted from panels B and C for clarity. (C) Data from panel B normalized by  $\Delta$  of the control plot. The normalization equation is  $Y_{\text{trt } X} - Y_{\text{ctl}}$ , where “trt  $X$ ” in the subscript represents treatment  $X$  and “ctl” represents control. This calculation provides a  $\Delta$  response relative to the controls and therefore accounts for interannual climate variability.

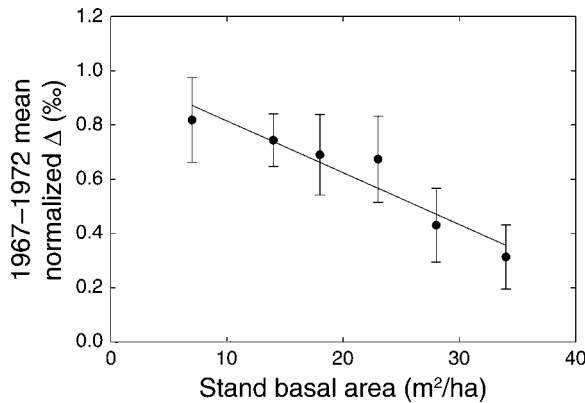


FIG. 4. Mean normalized carbon isotope discrimination ( $\Delta$ ) from 1967 to 1972 (period of significant response) from Fig. 3C vs. stand basal area. Bars represent  $\pm$ SE. The regression is: normalized  $\Delta = -0.019(\text{basal area}) + 1.01$ ,  $r^2 = 0.90$ ,  $P < 0.01$ . Regressions of different forms were not as strong or significant as linear regression.

tree rings increased during the first decade after reductions in stand basal area, indicating reduced water use efficiency (Figs. 3 and 4), but after 12 years  $\Delta$  returned to values similar to the trees in the unthinned treatment, suggesting that  $\Delta$  was maintained near a “set point” (Fig. 5; Ehleringer 1993, Ehleringer and Cerling 1995).  $A_1:A_s$ , in contrast, showed a significant long-term response to reduced stand basal area (Fig. 7). This shift in  $A_1:A_s$  is consistent with maintenance of  $\Delta$  near the observed set point. We presume that other physiological and architectural shifts may also have occurred (e.g., belowground); however, the observed shifts are consistent with homeostatic theory at the whole-tree (Whitehead and Jarvis 1981) and leaf level (Ehleringer 1993). Further, the results observed here have implications for future research and application of thinning and ecological restoration treatments.

#### Growth response

Changes in both leaf-level  $P_n$  and  $A_1$  likely contributed to the large and sustained response of BAI to stand basal area reductions. Regarding leaf-level  $P_n$ , the increased  $\Delta$  during years 5–12 after the initial thinning (Figs. 3 and 4) indicates a substantial increase in  $c_i/c_a$ , which probably resulted from increased  $g$ . Given the increased  $\text{CO}_2$  diffusion to the outer walls of the mesophyll cells facilitated by elevated  $g$ , it is almost certain that  $P_n$  increased during this period as well (Cowan 1985, Meinzer et al. 1993, Buckley et al. 1999, McDowell et al. 2003). It is possible that photosynthetic capacity also increased in the first few years after the thinning due to elevated soil nitrogen availability (Feeney et al. 1998, Kaye and Hart 1998), which would act to enhance  $P_n$  above and beyond the increase due to elevated  $g$ . Although the  $\Delta$  response largely diminished 12 years after the initial thinning, the absolute rates of  $P_n$  and  $g$  continued to be elevated in low basal area

treatments 32 years later (Figs. 8 and 9). Therefore, at least a portion of the sustained BAI increase after thinning resulted from elevated  $P_n$  per unit leaf area.

The sustained BAI response to stand basal area reductions was also a response to increased  $A_1:A_s$  (Fig. 7). Density dependence of  $A_1:A_s$  has been observed previously (Keane and Weetman 1987, Long and Smith 1988). Increased  $A_1:A_s$  allows greater light interception per unit respiratory carbon loss from sapwood respiration (Ryan et al. 1995, Magnani et al. 2000). The advantage of greater light interception per tree offered by elevated  $A_1:A_s$  is probably particularly manifest during wetter years when  $g$  is less of a constraint on  $A$  and hence the role of light interception in whole-tree carbon gain is greater. This is consistent with the higher slope of BAI vs.  $\Delta$  in low basal area treatments (Fig. 6), i.e., individual crown light interception could become a large driver of productivity during nondrought years so that larger crowns facilitate greater carbon gain per unit shift in  $\Delta$ .

We cannot partition the importance of increased  $P_n$  per unit leaf area vs. increased total leaf area per tree on total carbon gain in this study. Additionally, carbon allocation may have changed in response to thinning that resulted in enhanced BAI, such as reduced below-ground carbon allocation (Haynes and Gower 1995, McDowell et al. 2001, Ryan et al. 2004) or increased carbon allocation to defenses (Kolb et al. 1998, Wallin et al. 2004). Nonetheless, we suspect that greater rates of  $P_n$  per unit leaf area and the greater leaf area per tree and per sapwood area all facilitated greater whole-crown  $P_n$  and BAI in the low-density treatments.

#### Homeostatic theory

Homeostatic maintenance of whole-tree gas exchange results from a balance between biochemical capacity of foliage to conduct photosynthesis and hydraulic constraints imposed by soil water availability and the conducting properties of tree vascular systems (Whitehead and Jarvis 1981, Sperry et al. 1998, Whitehead 1998, Brodribb and Holbrook 2003, Katul et al. 2003). Little variation in photosynthetic capacity occurred among basal area treatments in our study, which is consistent with other long-term studies on ponderosa pine response to thinning (McDowell et al. 2003, Sala et al. 2005). However, the variation observed in  $A_1:A_s$  and  $\Psi_s - \Psi_1$  across the continuum of stand densities is consistent with the concept of maximizing transpiration per unit leaf area while minimizing the safety margin for xylem cavitation (Tyree and Sperry 1988, Sperry et al. 1998). Hydraulic theory suggests that trees balance factors in Eq. 1 along with properties such as root development and sapwood porosity to maximize  $\Psi_s - \Psi_1$  such that maximum water uptake from the soil is achieved while minimizing the risk of catastrophic xylem embolism were  $\Psi_1$  to become too negative (Sperry et al. 1998, Ewers et al. 1999, 2000). Data from the summer of 1994 showed that trees in the thinned treatments had

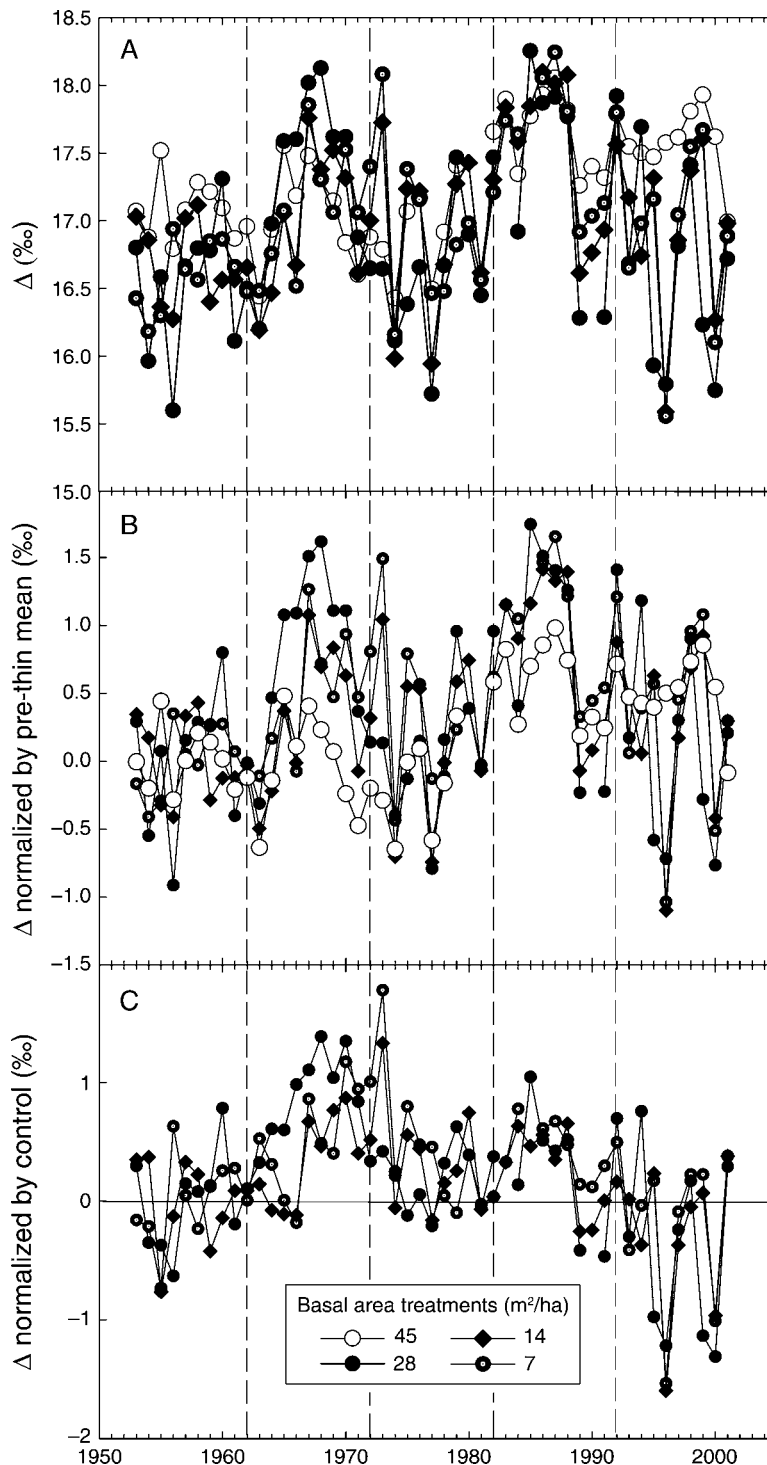


FIG. 5. (A) Carbon isotope discrimination ( $\Delta$ ), (B) pre-1962 normalized  $\Delta$ , and (C) control normalized  $\Delta$  from the 45, 28, 14, and 7 m<sup>2</sup>/ha intensive plots for the period 1952–2001. Panels A–C are calculated identically to Fig. 3 A–C. Each point represents a plot mean value obtained by pooling five trees per plot into a single sample. Hence there are no estimates of variance within each plot. The reader is referred to Fig. 3A and Fig. 4 for graphical representation of variance. The initial thinning treatment (1962) and subsequent thinning treatments (1972, 1982, 1992) are indicated by the vertical dashed lines.

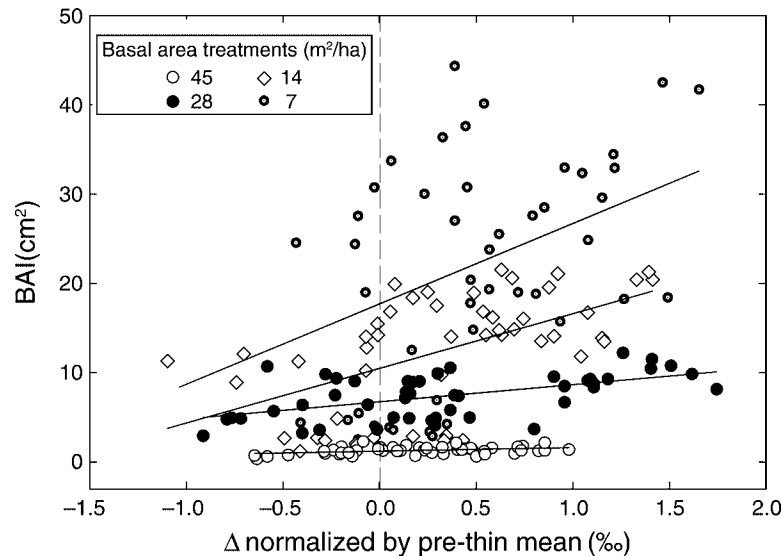


FIG. 6. BAI vs. the pre-thin normalized  $\Delta$  (from Fig. 5B) from the 45, 28, 14, and 7  $\text{m}^2/\text{ha}$  intensive plots for the period 1952–2001. Plots using data from Fig. 5A and 5C were similar to those shown here. The regression equations are of the form, treatment  $\text{BAI} = m(\text{normalized } \Delta) + b$ , where  $m = \text{BAI}/\Delta$  and  $b = \text{BAI}$ . Regression values for  $m$ ,  $b$ , and  $r^2$  are: for 45  $\text{m}^2/\text{ha}$ ,  $m = 0.39$ ,  $b = 1.2$ ,  $r^2 = 0.16$ ; for 28  $\text{m}^2/\text{ha}$ ,  $m = 1.9$ ,  $b = 6.7$ ,  $r^2 = 0.29$ ; for 14  $\text{m}^2/\text{ha}$ ,  $m = 6.1$ ,  $b = 10.5$ ,  $r^2 = 0.31$ ; and for 7  $\text{m}^2/\text{ha}$ ,  $m = 9.0$ ,  $b = 17.7$ ,  $r^2 = 0.16$ . The vertical dashed line represents the zero value of pre-thin normalized  $\Delta$ .

significantly greater  $\Psi_s - \Psi_l$  than trees within the unthinned, 45  $\text{m}^2/\text{ha}$  treatment (1.01 vs. 0.79 MPa,  $P < 0.01$ ). Greater  $\Psi_s - \Psi_l$  facilitates water extraction from the soil, thereby maintaining  $g$  for greater cumulative amounts of transpiration. Trees within the 45  $\text{m}^2/\text{ha}$  treatment, in contrast, probably initiated stomatal closure to prevent cavitation at lower transpiration rates, thereby limiting  $P_n$ . Therefore, it appears that as stand density decreased, less total soil water was used and, as a consequence,  $\Psi_s$  became less negative, allowing trees to experience increased  $\Psi_s - \Psi_l$  and presumably  $g$  and  $P_n$ . Furthermore, as stand density decreased, individual tree leaf area increased, and this, with increased  $g$ , increased total individual tree water use. Notably, the more positive midday  $\Psi_l$  in the 7  $\text{m}^2/\text{ha}$  treatment suggests that trees in the low basal area treatments have a greater safety margin from cavitation (Tyree and Sperry 1988), which may explain why these trees were the only ones that grew rings in 2002 (a year of particularly severe drought). This increased margin of safety may confer an advantage to trees at this low basal area during drought years. Similar increases in  $\Psi_s$  and  $\Psi_l$  after thinning have been observed (Sucoff and Hong 1974, Donner and Running 1986, Skov et al. 2004, Wallin et al. 2004, Simonin et al. 2006), but not in all studies (Cregg et al. 1990, Schmid et al. 1991).

The results of our study also support the concept that the homeostatic gas exchange set point, or the parameter that is regulated to stay constant regardless of changes in resource availability, is  $c_i/c_a$  (Ehleringer 1993, Ehleringer and Cerling 1995). We calculated  $c_i/c_a$ ,  $c_i$ , and  $c_a - c_i$  from our 40-year  $\delta^{13}\text{C}$  data set and Eqs. 3–4 (data not shown). Treatment differences were the same as those

shown in Figs. 3 and 5, including a decrease in  $c_a - c_i$  and an increase in  $c_i$  and  $c_i/c_a$  for only the period 5–12 years after the initial thinning. Over the 40-year period,  $c_i$  for all treatments rose from a minimum of  $\sim 170$  to  $\sim 200$   $\mu\text{mol}/\text{mol}$ , and  $c_a - c_i$  rose from a minimum of  $\sim 130$  to  $\sim 170$   $\mu\text{mol}/\text{mol}$ . In contrast,  $c_i/c_a$  oscillated between 0.50 and 0.60 over the same period, but exhibited no trend with time. Similar results have been reported using foliage  $\delta^{13}\text{C}$  in ponderosa pine thinning studies in Northern Arizona (Skov et al. 2004, Wallin et al. 2004). The exact reason for maintaining  $c_i/c_a$  constant is not clear. However, it can be seen from Eq. 4 that  $c_a - c_i = P_n/g$ , which at constant vapor pressure deficit equals  $P_n/E$ , where  $E$  is transpiration. Therefore,  $P_n/g$  increased over the four decades for all stand densities. It may be more appropriate to consider that plants in water-limited environments operate to maximize  $P_n/E$  (Cowan 1982, Ehleringer et al. 1992) rather than hold  $c_i/c_a$  constant per se. The rise in  $P_n/g$  over time in our study may be driven by reduced hydraulic conductance associated with increasing tree size, which forces a reduction in  $g$  (Yoder et al. 1994, Hubbard et al. 1999, Kolb and Stone 2000, Monserud and Marshall 2001, McDowell et al. 2002a). When tree size is held constant over time by sampling the young, inner rings of variously aged trees, no increase in  $P_n/g$  occurs over time (Marshall and Monserud 1996).

#### *Climatic sensitivity and forest sustainability*

The impacts of drought on forest growth and survival are a significant international concern, particularly in the southwestern United States where drought has initiated widespread limitations to photosynthetic gas

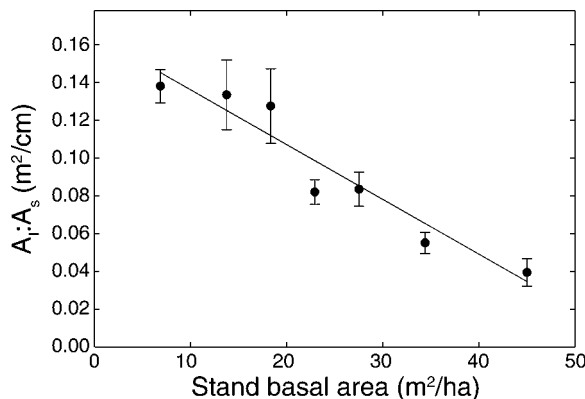


FIG. 7. Whole-tree leaf area : sapwood area ratio ( $A_l:A_s$ ) vs. residual stand basal area. Data were collected in 2003. Bars represent  $\pm$ SE. The regression equation is:  $A_l:A_s = -0.0029 \times \text{basal area} + 0.165$ ,  $r^2 = 0.93$ ,  $P < 0.01$ .

exchange of ponderosa pine (Feeny et al. 1998, Leavitt and Wright 2002, Skov et al. 2004), and has severely impacted growth and survival of ponderosa and piñon pine (*Pinus edulis*) (Allen and Breashers 1998, Ogle et al. 2000, Adams and Kolb 2004). High stand densities in contemporary forests may be exacerbating the effects of drought on these forests (Skov et al. 2004; N. G. McDowell and D. A. Falk, *unpublished data*; but see Zausen et al. 2005) because of the particularly extreme competition for water in high basal area stands (Fig. 8). We speculated that one benefit of thinning would be to reduce the negative effect of drought on growth. If this hypothesis were true, then reductions in stand density may be a proactive method to alleviate the negative impacts of climate change on tree growth.

The results of this study show that tree growth in low basal area treatments is more resilient to drought than growth in high basal area treatments, e.g., 1989, 1996, and 2000 (Fig. 1). This higher minimum BAI is presumably a result of the numerous advantages that the larger trees in the low basal area treatments have, such as larger root systems (Dawson 1996), a greater margin of safety from cavitation because of less xylem tension (i.e., higher  $\Psi_l$ ), and greater  $\Psi_s - \Psi_l$ . Therefore, it is reasonable to predict that as periodic droughts continue into the future, ponderosa pine trees will have greater growth and potentially greater survival in forests where stand basal area has been reduced toward presettlement levels.

Although BAI of low basal area treatments is more resilient to drought than BAI of high basal area treatments, the low basal area treatments were also more sensitive to drought (Figs. 5, 6, and 10, Table 2). Fig. 10A and Table 2 clearly show that the response of BAI to incremental changes in PDSI increased with decreasing stand basal area. Even after normalizing the BAI data for the inherent growth differences associated with tree size (e.g., relative growth rate), growth of trees from low basal area treatments remained more sensitive

to PDSI than growth of trees from high basal area treatments (Fig. 10B, Table 2). While trees in stands with low basal area have numerous hydraulic advantages mentioned previously, they may also be predisposed to greater variation in gas exchange associated with variation in water availability. There are numerous lines of evidence in support of this idea. First,  $\Delta$  of the thinned treatments was elevated above  $\Delta$  of the unthinned treatment during the particularly wet years of 1983–1988 (average PDSI 3.2), and was lower during

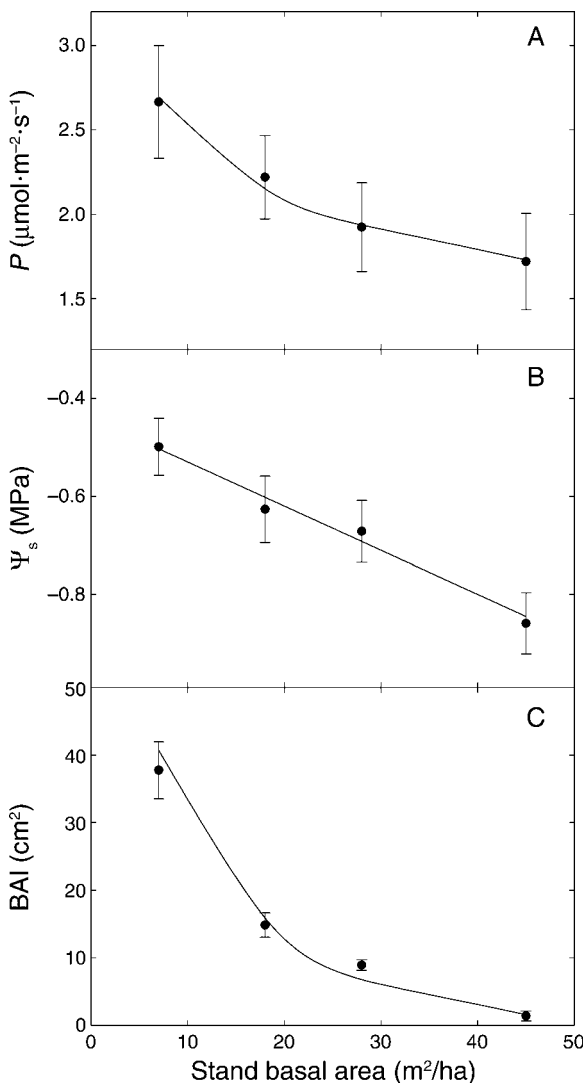


FIG. 8. (A) Leaf-level photosynthesis  $P_n$  based on all-sided leaf area averaged from May to September 1994 vs. stand basal area. (B) Soil water potential  $\Psi_s$  averaged from May to September 1994 vs. stand basal area. (C) 1994 BAI averaged for three plots per treatment vs. stand basal area.  $P_n$  and  $\Psi_s$  are recalculated from the raw data files used in Kolb et al. (1998), and are the averages of 3–7 trees per treatment. Bars represent  $\pm$ SE. Regression lines are provided for reference: (A)  $P_n = 4.28 \times (\text{basal area})^{-0.24}$ ,  $r^2 = 0.99$ ,  $P = 0.02$ ; (B)  $\Psi_s = -0.009 \times (\text{basal area}) - 0.44$ ,  $r^2 = 0.99$ ,  $P = 0.02$ ; and (C)  $\text{BAI} = 74.08 \times \exp[-0.086(\text{basal area})]$ ,  $r^2 = 0.99$ ,  $P = 0.01$ .

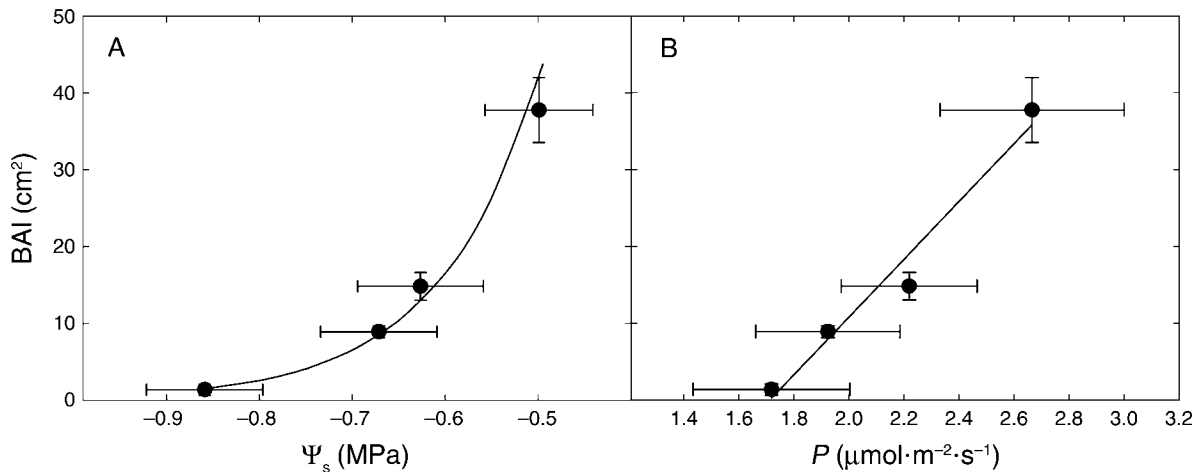


FIG. 9. (A) Average BAI vs.  $\Psi_s$  averaged over eight measurement dates (May–September) in 1994. (B) Average BAI vs.  $P_n$  based on all-sided leaf area from 1994. Data for both panels A and B are from the 1994 values presented in Fig. 8. Bars represent  $\pm$ SE. The regression equations are: (A)  $\text{BAI} = 4409.7 \exp(9.31 \times \text{basal area})$ ,  $r^2 = 0.99$ ,  $P = 0.01$ ; and (B)  $\text{BAI} = 37.6 \times \text{basal area} - 64.41$ ,  $r^2 = 0.97$ ,  $P = 0.03$ .

the particularly dry years of 1996 and 2000 ( $\text{PDSI} = -2.4$  and  $-3.3$ , respectively, Figs. 1B and 5B, C). This finding suggests that gas exchange is more variable for thinned than nonthinned treatments in response to drought. Second, the range of  $\Delta$  values is larger for thinned than unthinned treatments (see  $X$  axis, Fig. 6). Third, the response of growth to changes in gas exchange ( $\text{BAI}/\Delta$ ) was steeper for lower basal area treatments, indicating that incremental changes in gas exchange result in increasingly larger changes in BAI with decreasing stand basal area (Fig. 6). The reason for this greater gas exchange and growth sensitivity to drought in the low basal area treatments may be associated with the larger leaf area per tree. During wet years, the positive gas exchange response was distributed over a large leaf area, allowing greater whole-tree photosynthesis and hence greater BAI than trees with low leaf area. However, during dry years, these large leaf areas may have burdened the trees with a large transpirational demand. In accordance with Eq. 1, large leaf area can cause reduced  $g$  if soil water availability is limited. This balance between transpiring leaf area and  $g$  has been demonstrated over short times scales (Whitehead et al.

1996). In other words, trees in the high basal area treatments were relatively unable to take advantage of climatically wet years due to structural limitations (e.g., small root systems, low sapwood permeability), and likewise, they were already so severely water stressed due to competition that drought had little further effect on gas exchange.

#### CONCLUSIONS

Reductions in stand basal area in semiarid forests are likely to facilitate greater photosynthesis and growth of trees above those of trees growing at high basal areas. A primary driver of this response is the increased availability of soil water; however, the proximate cause is at least partially a result of a homeostatic balance of gas exchange at the leaf- and whole-crown levels. Short-term shifts in the ratio of photosynthesis to stomatal conductance ( $\Delta$ ) were balanced via changes in above-ground architecture ( $A_l:A_s$ ) that resulted over the long term in greater leaf- and crown-scale photosynthesis. These results are consistent with established theory regarding the homeostatic maintenance of gas exchange at the leaf and whole-plant levels. Notably, both the

TABLE 3. Regressions of basal area increments (BAI) and BAI/BA (basal area) vs. Palmer drought severity index (PDSI) using data from all plots for the negative PDSI years between 1962 and 2001.

Treatment (m <sup>2</sup> /ha)	BAI†				BAI/BA			
	Slope	Intercept	$r^2$	$P$	Slope	Intercept	$r^2$	$P$
7	2.26	27.14	0.06	0.29	0.0117	0.078	0.17	0.07
14	2.13	15.54	0.22	0.04	0.0111	0.063	0.22	0.04
18	1.45	12.79	0.17	0.07	0.0071	0.046	0.22	0.04
23	1.28	10.34	0.21	0.05	0.0078	0.049	0.19	0.06
28	1.38	10.29	0.31	0.01	0.0064	0.042	0.19	0.06
35	0.97	6.70	0.34	<0.01	0.0061	0.0061	0.18	0.07
45	0.29	1.57	0.48	<0.01	0.0048	0.0245	0.54	<0.01

† BAI has original units of square centimeters.

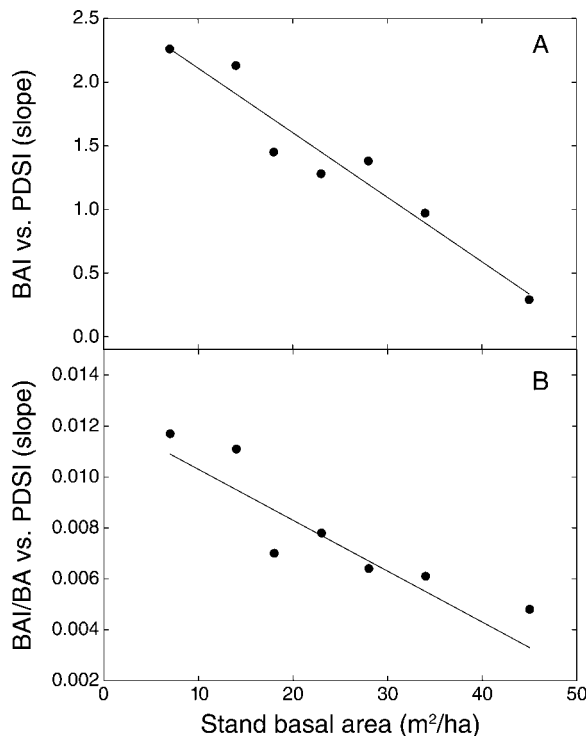


FIG. 10. (A) Treatment-specific slopes of BAI vs. PDSI using all plots per treatment, negative PDSI years from 1962 to 2001. (B) Treatment-specific slopes of basal-area-normalized BAI (BAI/BA) vs. PDSI for all plots per treatment, negative PDSI years from 1962 to 2001. Normalizing BAI by basal area accounts for variation in growth due inherently to tree size. The regression equations are: (A)  $\text{BAI:PDSI} = -0.051 \times \text{basal area} + 2.62$ ,  $r^2 = 0.93$ ,  $P < 0.01$ ; (B)  $(\text{BAI/BA}):PDSI = -0.0002 \times \text{basal area} + 0.012$ ,  $r^2 = 0.81$ ,  $P < 0.01$ .

resiliency and the sensitivity of growth to climate was greater in the lower basal area treatments, so ecological restoration treatments are likely to cause higher growth rates (on an individual tree basis) but also greater growth variability.

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