Tree Ecophysiology Research at Taylor Woods

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Abstract—*We summarize the key findings of tree ecophysiology studies performed at Taylor Woods, Fort Valley Experimental Forest, Arizona between 1994 and 2003 that provide unique insight on impacts of long-term stand density management in ponderosa pine forests on tree water relations, leaf gas exchange, radial growth, leaf area-to-sapwood-area ratio, growth efficiency, leaf area index, resin defenses, and stand-level above-ground carbon sequestration.*

Introduction

The stand density experiment initiated in 1962 at Taylor Woods, Fort Valley Experimental Forest, Arizona set the stage for a series of tree ecophysiology studies conducted between 1994 and 2003 that provide insight on effects of stand density management in ponderosa pine forests on tree and stand growth and physiology. Many of the questions addressed in these recent studies were not anticipated when the stand density experiment was started in 1962. Maintenance of the density experiment for over 40 years by Rocky Mountain Research Station staff, notably Carl Edminster, provided us with the opportunity to ask contemporary questions about impacts of long-term silvicultural thinning on a range of tree- and stand-level physiological characteristics that is not possible in short-term studies. Thus, Taylor Woods has proven to be one of the most important long-term forestry research sites in the southwestern United States.

This paper briefly describes results of our ecophysiology studies at Taylor Woods. For brevity, we introduce the study site and follow with major findings. Our methods have been described in detail elsewhere (Kolb et al. 1998, McDowell et al. 2006, McDowell et al. 2007).

Taylor Woods is in the Fort Valley Experimental Forest (35°16'11" N, 111°44'30" W) located within the Coconino National Forest approximately 15 km northwest of Flagstaff, Arizona, USA. The stand is approximately 35.6 ha and is dominated by ponderosa pine (*Pinus ponderosa* var. *scopulorum*) that regenerated naturally in

approximately 1919 (Ronco et al. 1985, Savage et al. 1996). A sparse understory of grasses and forbs is present. The stand has flat topography and is located at 2,266 m elevation. 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). The region has a monsoonal climate typical of the Southwest U.S. with precipitation distributed in a bimodal pattern that peaks in the winter and late summer, and a pronounced drought during May and June.

We utilized a replicated set of stand basal area treatments at Taylor Woods to obtain data about physiological and structural responses to changes in stand basal area (BA). The initial experiment was designed by the US Forest Service to determine effects of stand BA on ponderosa pine growth (Myers 1967, Ronco et al. 1985). The forest was first thinned in October 1962 to generate three replicated plots of each of six BA (34, 28, 23, 18, 14, 7 m^{-2} ha^{-1}) plus an unthinned control. The residual BA levels were maintained by re-thinning once per decade (1972, 1982, 1992, 2003). The plots are about 0.4 ha in size, and have 0-10 m buffers. Stand structural data for year 2003 are shown in Table 1.

Table 1. Stand characteristics in year 2003 for each basal area treatment at the Taylor Woods, Fort Valley Experimental Forest, Arizona. One standard error of the mean is shown in parentheses. The unthinned 45 m^2 ha^{-1} treatment had only one plot, therefore no standard errors are provided. Following McDowell et al. (2006).

Basal area treatment (m^2 ha^{-1})	Stem density (no. ha^{-1})	Mean DBH[a] (cm)	Mean height (m)
7	70 (3.8)	47 (0.99)	19.5
14	145 (3.3)	40 (0.43)	18.6
18	245 (11.6)	34.8 (0.87)	18.9
23	366 (18.0)	31.7 (0.76)	18.9
28	471 (39.3)	30.4 (1.24)	16.9
35	789 (1.6)	25.5 (0.03)	15.9
45	3160	13.4	11.1

[a] Diameter at breast height.

Major Findings

Direct measurements of leaf gas exchange in summer 1994 following the third thinning in 1992 show that thinning increased net photosynthetic rate (P_n; Fig. 1A). Increased P_n in response to thinning was highly correlated with leaf-level stomatal conductance (Kolb et al. 1998) and was not associated with increased leaf nitrogen concentration (Kolb et al. 1998) or a change in carboxylation efficiency (McDowell et al. 2006). Hence much of the positive effect of thinning on P_n was due to increased supply of carbon dioxide to chloroplasts due to higher stomatal conductance.

Data from 1994 (Kolb et al. 1998) show that thinning increased water availability to trees. Stand BA was inversely and linearly related to average growing-season leaf xylem predawn water potential (Fig. 1B). Thus, thinning can be used to reduce water stress on ponderosa pine in northern Arizona.
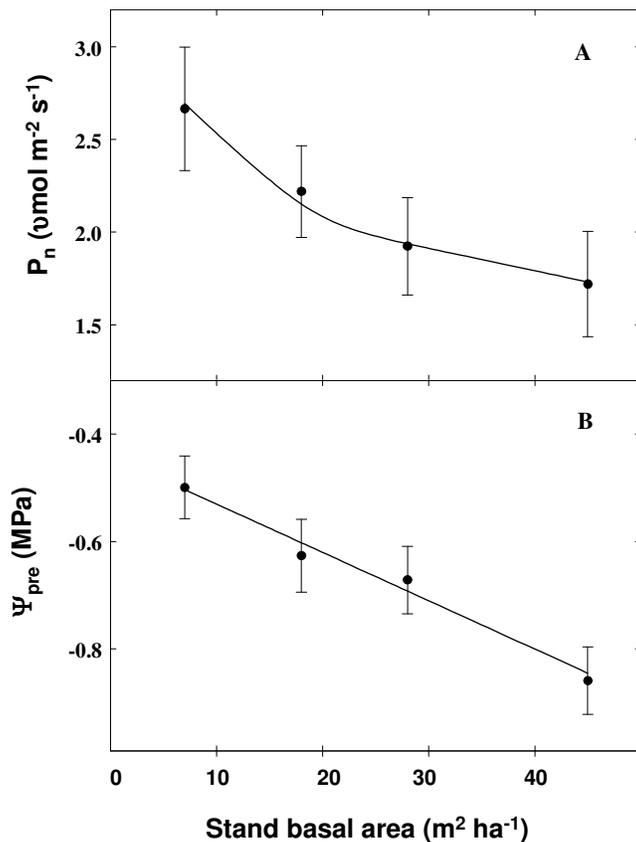
Figure 1. A) Leaf-level net photosynthetic rate (P_n) based on all-sided leaf area and averaged from May to September, 1994 vs. stand basal area (BA). B) Leaf xylem predawn water potential (Ψ_{pre}) averaged from May to September, 1994 vs. BA. Bars are +/- one standard error. Equations for the regression lines are A. $P_n = 4.28 \bullet BA \bullet^{(-0.24)}$, $r^2=0.99$, $p=0.02$, B. $\Psi_{pre} = -0.009 \bullet BA - 0.44$, $r^2=0.99$, $p=0.02$. Derived from Kolb et al. (1998) and McDowell et al. (2006).

A chronology of basal area increment (BAI) calculated from increment cores sampled at breast height shows that BAI increased at all BA levels starting two years after the onset of thinning. BAI was similar for all BA prior to thinning between 1940 and 1961 (Fig. 2A). The increase in BAI started in the second year after thinning (1964) for all treatments. BAI was consistently higher in all thinned plots compared with the control in all years between 1964 and 2002. BAI in the control was extremely low (between 0 and 2 cm^2 yr^{-1}) in all years. Thinning to a BA of 7 m^2 ha^{-1} caused the largest increase in BAI, followed by the 14 m^2 ha^{-1} and 18 m^2 ha^{-1} BA levels (Fig. 2A). Trees in the 23, 28, and 34 m^2 ha^{-1} BA levels had similar BAI in most years. Increases in BAI after the later thinnings (i.e., post 1962) were most pronounced in the 7 m^2 ha^{-1} BA. BAI decreased at all BA following the 1992 thinning (Figure 2A); this reduction was associated with drought between 1993 and 2000 (Fig. 2B). These results can be used by silviculturists to design treatments to control individual tree growth.

Comparison of the slope of the relationship between BAI and the Palmer drought severity index (PDSI) during drought years (negative PDSI, Fig. 2B) showed that the sensitivity of BAI to drought differed among BA (Fig. 3). The slope, and thus sensitivity of BAI to drought, was inversely and linearly related to BA (Fig. 3). BAI in low BA was more sensitive to drought than in high BA. In contrast, there was no significant relationship between sensitivity of BAI to PDSI when data from all years (i.e., positive and negative PSDI) were used in the comparison (McDowell et al. 2006). The results suggest that severe droughts will have greater relative (e.g., proportional) impacts on BAI of fast-growing trees at low BA than slow-growing trees at high BA.
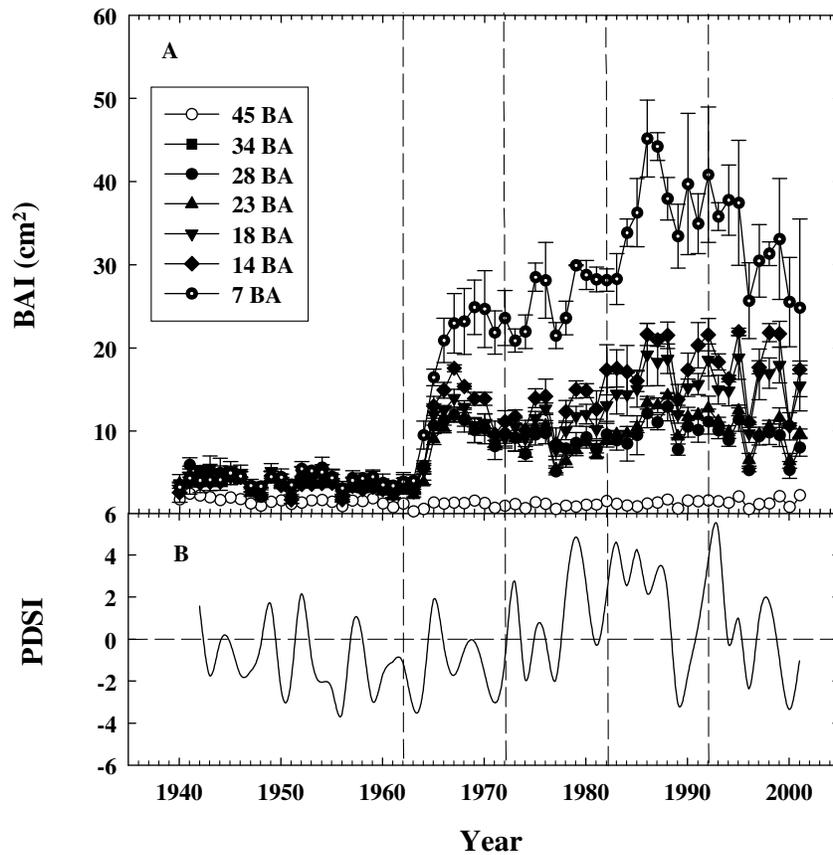
Figure 2. A) Basal area increment (BAI) for seven basal area (BA) treatments (7 to 45 m^2 ha^{-1}). Data are averaged for three plots per treatment with the exception of the 45 m^2 ha^{-1} control treatment (no thinning), which had a single plot. Bars are +/- one standard error. The initial thinning treatment (1962) and subsequent thinning treatments (1972, 1982, 1992) are indicated by the vertical lines. B) Annual Palmer drought severity index (PDSI) for Region 2 of Arizona. Negative PDSI values represent drought and positive PDSI values represent wet periods. From McDowell et al. (2006).
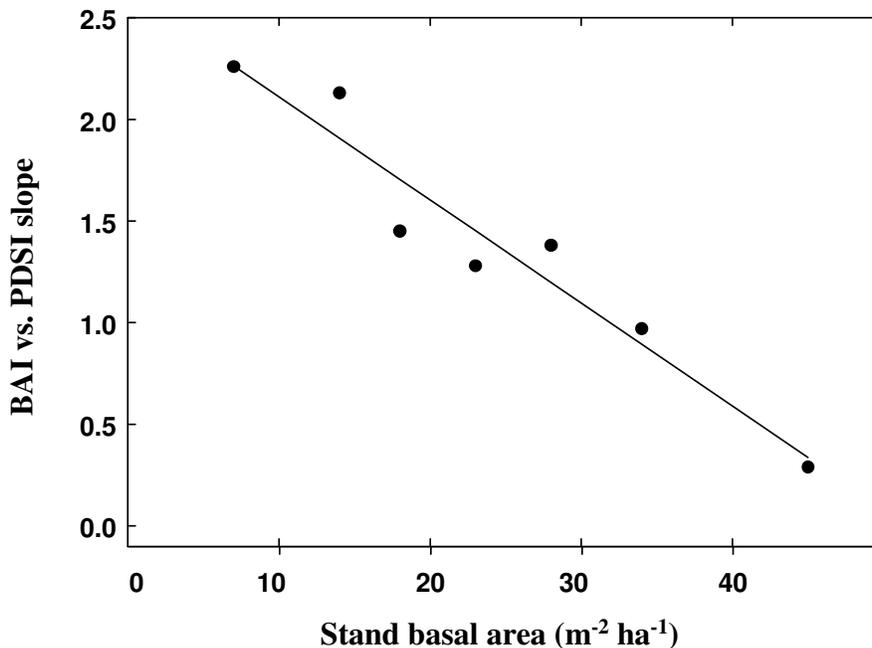

Figure 3. Treatment-specific slopes of basal area increment (BAI) versus annual Palmer drought severity index (PDSI) using all plots per treatment, and only the negative PDSI years from 1962 to 2001. The regression equation is: BAI:PDSI = -0.051•BA + 2.62, r^2=0.93, p<0.01. From McDowell et al. (2006).

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The chronosequence of carbon isotope discrimination (Δ) derived from tree rings and corrected for temporal changes in atmospheric carbon isotope ratio caused by fossil fuel emissions (McDowell et al. 2006) shows that thinning had a pronounced effect on the ratio of carbon dioxide concentration in the leaf mesophyll (C_i) to concentration in the atmosphere (C_a; Fig. 4). With no change in carboxylation efficiency as was shown for the thinning treatments at Taylor Woods (McDowell et al. 2006), and assuming similar C_a, vapor pressure deficit and light intensity, increased Δ results from increased C_i due to greater stomatal conductance. Normalization of Δ relative to Δ either prior to thinning (Fig. 4B) or relative to the unthinned control (Fig. 4C) provided a clearer signal of the effect of thinning than non-normalized data (Fig. 4A). Relative to the control (Fig. 4C), thinning increased Δ at all wide range of BA levels 5 and 12 years after treatment suggesting a large simulation in C_i and stomatal conductance. Interestingly, the second thinning increased Δ for only one post-thinning year (1973) and only at the lowest BA (7 and 14 m^2 ha^{-1}, Fig. 4B, C). Effects of the third thinning (1982) on Δ were similar to the first thinning with a general increase in Δ for all BA for several years after thinning (Figure 4C). The fourth thinning (1992) did not increase Δ in any BA relative to the control (Figure 4C).
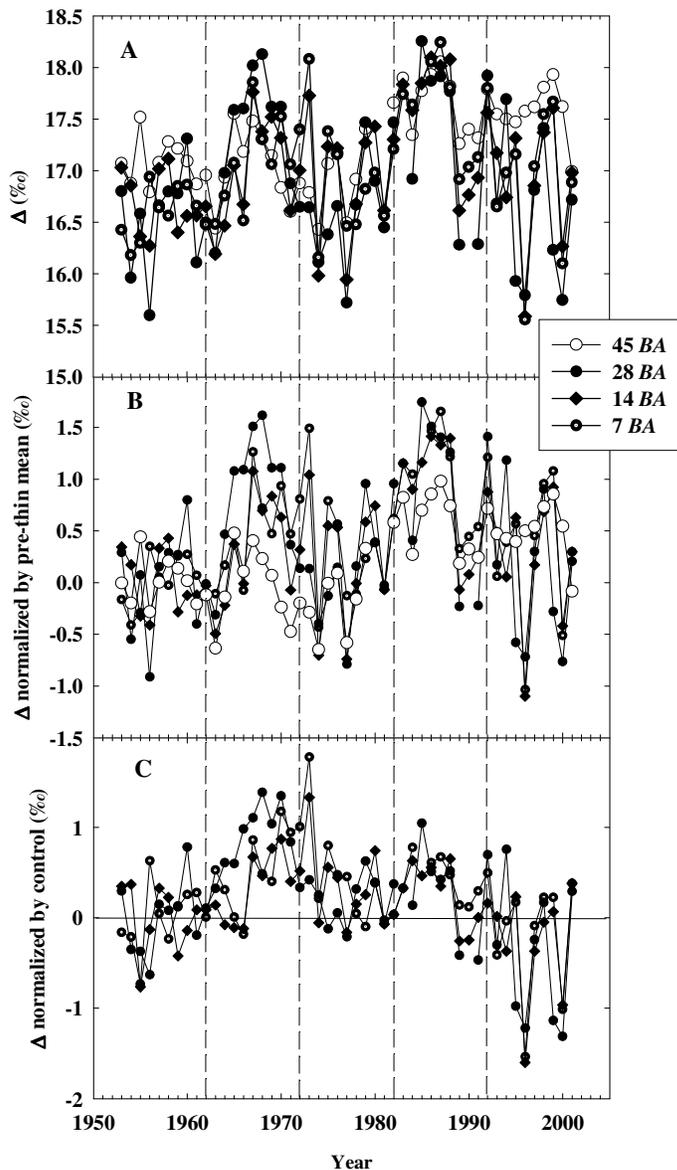

Figure 4. A) Carbon isotope discrimination (Δ), B) Δ nominalized to prethinning (1952-1961) Δ, and C) Δ normalized to the unthinned control for the 45, 28, 14 and 7 m^{-2} ha^{-1} basal area treatments for years 1952-2001. Each point represents a plot mean value obtained by pooling five trees per plot into a single sample. The initial thinning treatment (1962) and subsequent thinning treatments (1972, 1982, 1992) are indicated by the vertical dashed lines. From McDowell et al. (2006).

Thinning had unequal effects on whole-tree leaf area and sapwood area which changed the ratio of leaf area to sapwood area (McDowell et al. 2006). Reduction of BA by thinning increased both tree leaf area (Figure 5A) and sapwood area at breast height (Figure 5B) as would be expected due to a general stimulation of tree growth by thinning. The ratio of leaf area to sapwood area was inversely and linearly related to BA (Figure 5C); sapwood of trees growing at low BA supported more leaf area than trees at high BA. These results combined with the $\Delta\_$ results suggest that thinning increases tree BAI first by greatly increasing stomatal conductance, followed by a large increase in carbon allocation to leaf area.

Thinning altered growth efficiency, defined as yearly biomass production divided by either sapwood area or leaf area (Waring et al. 1980, Waring 1983). In four of six cases, growth efficiency decreased in response to reduction in BA (Figure 6B, D, E. F; McDowell et al. 2007). Growth efficiency increased with thinning intensity in only one case (Figure 6A). Thus, our results are not consistent with earlier hypotheses (Waring et al. 1980, Waring 1983) that thinning increases the "efficiency" of wood production using conventional measurements of growth efficiency.
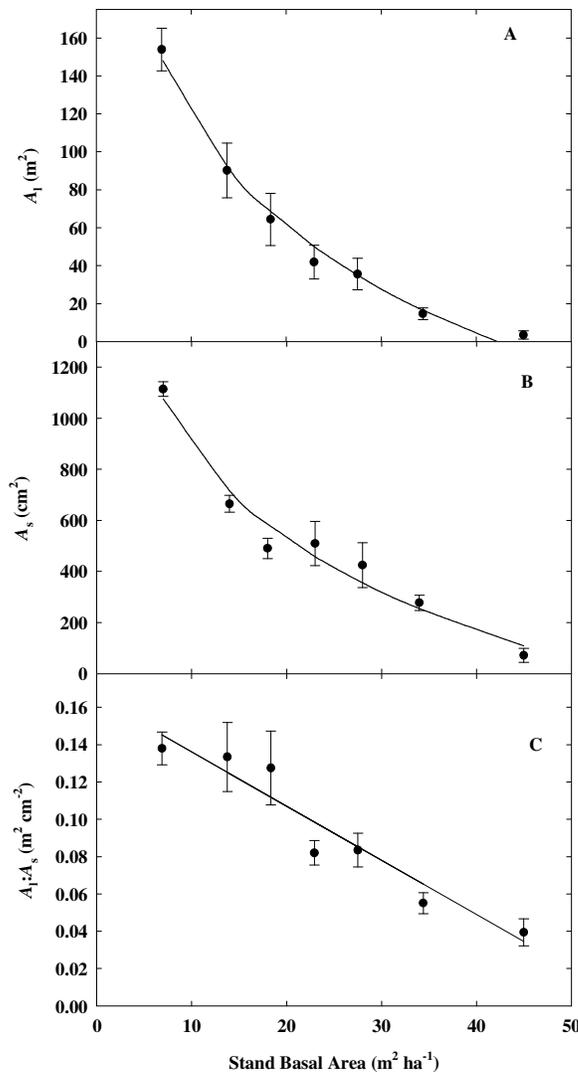

Figure 5. A) Whole tree leaf area (A_l), B) sapwood area (A_s) and C) leaf area:sapwood area ratio (A_l:A_s) versus stand basal area (BA). Bars are +/- one standard error. The regressions equations are: A) $A_l = -82.55 \cdot \ln (BA) + 308.6$, $r^2 = 0.99$, p<0.01, B) $A_s = -519.2 \cdot \ln (BA) + 2086$, $r^2 = 0.97$, p<0.01, and C) A_l:$A_s = -0.0029 \cdot BA + 0.165$, $r^2 = 0.92$, p<0.01. Derived from McDowell et al. (2006, 2007).

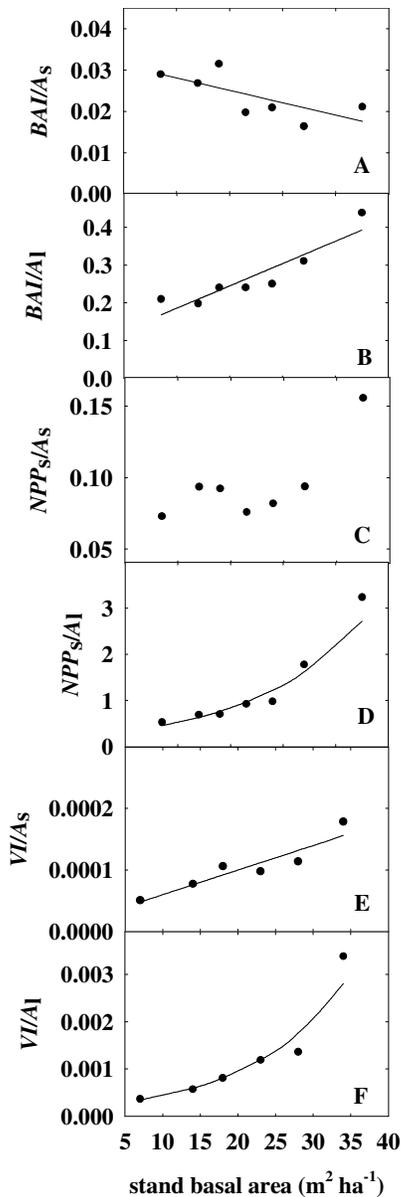USDA Forest Service RMRS-P-53CD. 2008.

Figure 6. Individual-tree growth efficiency versus stand basal area (BA). Panels and regression relationships are:

A) BAI per unit sapwood area (BAI/A_s, cm^2 cm^{-2} A_s y^{-1}) = -0.0003 * BA + 0.031, p<0.01, r^2=0.51,

B) BAI per unit leaf area (BAI/A_l, cm^2 m^{-2} A_l yr^{-1}) = 0.006 * BA + 0.127, p<0.01, r^2=0.84,

C) NPP$_s$ per unit sapwood area (NPP$_s$/A_s, g cm^{-2} A_s yr^{-1}), no significant relationship,

D) NPP$_s$ per unit leaf area (NPP$_s$/A_l, g m^{-2} A_l yr^{-1}) =0.328*e$^{(0.048*BA)}$, p<0.01, r^2=0.95,

E) VI per unit sapwood area (VI/A_s, m^3 cm^{-2} A_s yr^{-1}) = 0.00005 * BA + 0.048, p<0.01, r^2=0.88, and

F) VI per unit leaf area (VI/A_l, m^3 m^{-2} A_l yr^{-1}) = 0.0002 * e$^{(0.078*BA)}$, p<0.01, r^2=0.96.

From McDowell et al. (2007).

Thinning also affected leaf area index (LAI). Understory LAI, measured in 1998 and 1999, was more responsive to thinning than overstory or total stand LAI (Figure 7). Thinning increased understory LAI, and the largest increase occurred at low BA (Figure 7A). Understory LAI was a small proportion of total stand LAI at all BA (Figure 7B); the contribution of the understory to total LAI ranged from about 15% at the lowest BA (7 m^2 ha^{-1}) to about 0% at the highest (45 m^2 ha^{-1}) BA (Figure 7B). Overstory and total LAI were highest at intermediate BA, and were lowest at both the highest and lowest BA (Figure 7B). Peak total-stand projected-area LAI was about 2.0 m^2 m^{-2}. These results can be used to inform models of forest photosynthesis and transpiration and range production.
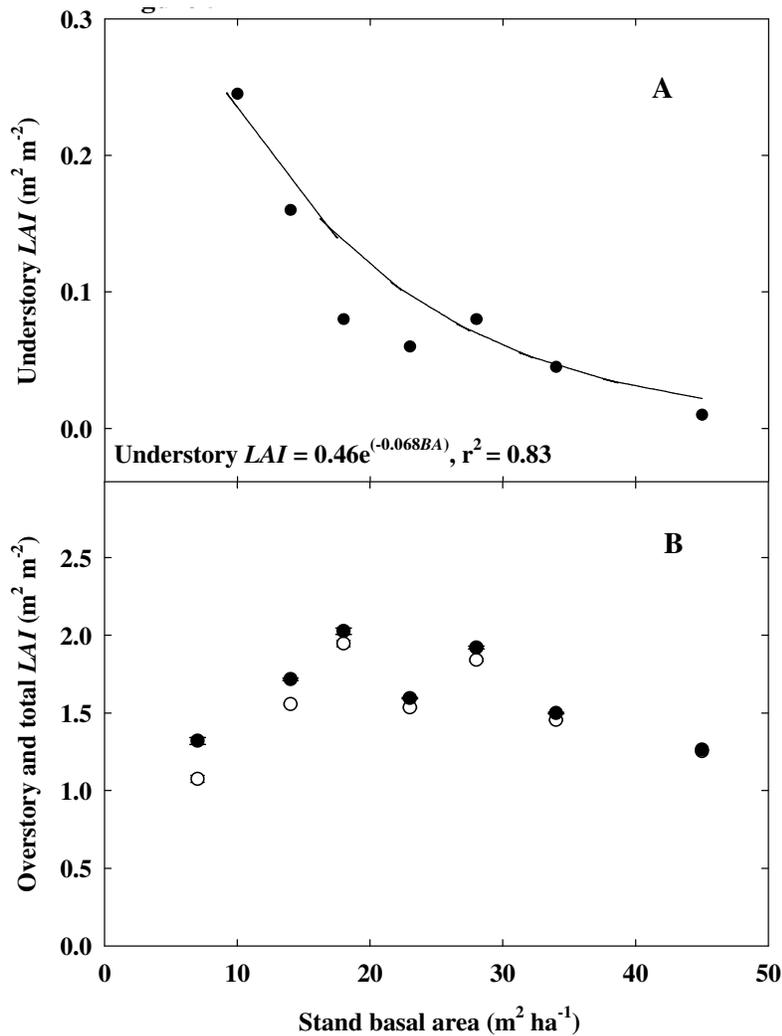
Figure 7. A) Understory leaf area index (LAI) versus stand basal area, and B) overstory (open symbols) and total (closed symbols) LAI verses stand basal area. From McDowell et al. (2007).

Understory $LAI = 0.46e^{(-0.068BA)}$, $r^2 = 0.83$

We pooled data on bole resin flow in response to phloem wounding over a range of BA at Taylor Woods in 1994 (Kolb et al. 1998) with data from four similar studies of ponderosa pine in northern AZ to address whether resin defense against bark beetles was related to stand basal area (McDowell et al. 2007). Resin flow was negatively related to BA for data from Taylor Woods and pooled over all studies (Figure 8A). Resin flow was positively related to tree BAI for data from Taylor Woods and pooled over all studies (Figure 8B). Silviculturists can use our results to design treatments that enhance tree resin defense against bark beetles.

Control of stand basal area by three and a half decades of repeated thinning strongly influenced stand-level above-ground carbon sequestration which was measured as above-ground net primary production (NPP_{stand}) in years 1996-2001 (McDowell et al. 2007). Net primary production decreased with stand basal area for non-normalized NPP_{stand} (Figure 9A) and for NPP_{stand} normalized by stand LAI (Figure 9B). Thus, greater NPP_{stand} at high BA occurred because the greater density of stems at high BA (Table 1) overcompensated for the lower growth rate of individual trees at high compared with low BA (e.g., Figure 2A).
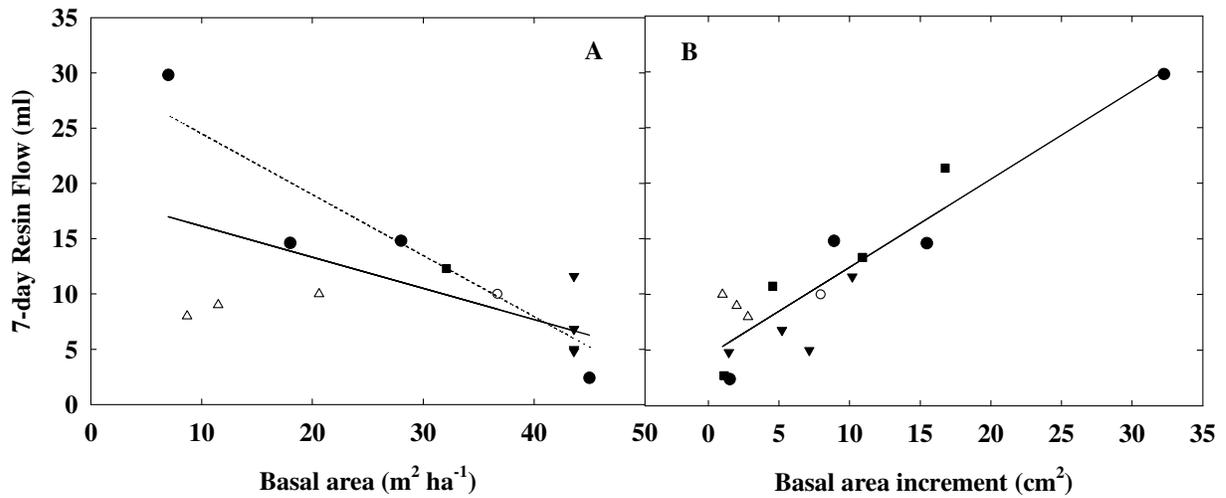
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Figure 8. Seven day resin flow after phloem wounding versus A) stand basal area (BA), and B) individual tree basal area increment (BAI). The regression relationships are: A) resin flow = -0.28*BA + 18.9 (p=0.03, r^2=0.36), and B) resin flow=0.79*BAI+ 4.5, (p=0.01, r^2=0.84). The symbols denote different studies (see McDowell et al. 2007 for details). The dashed line in A) represents the relationship when the resin flow data that was converted from 24-hour values to 7-day values (open triangles) is excluded.
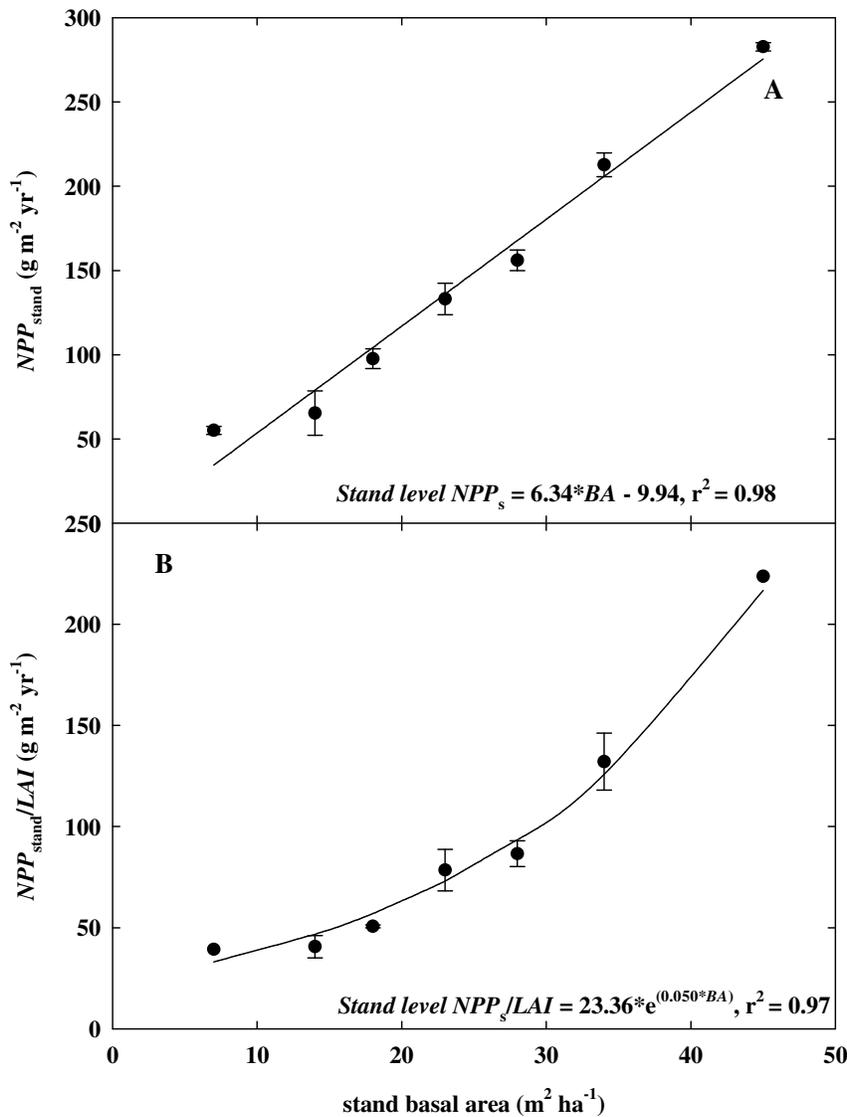

Figure 9. A) Stand-level primary production (NPP$_{stand}$; annual average for 1996-2001) verses stand basal area, and B) stand level growth efficiency defined as NPP$_{stand}$/total leaf area index (LAI) verses stand basal area. Bars are one standard error. From McDowell et al. (2007).

*Stand level NPP$_s$ = 6.34*BA - 9.94, r^2 = 0.98*

*Stand level NPP$_s$/LAI = 23.36*e$^{(0.050*BA)}$, r^2 = 0.97*

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