

# The role of stand density on growth efficiency, leaf area index, and resin flow in southwestern ponderosa pine forests

Nate G. McDowell, Henry D. Adams, John D. Bailey, and Thomas E. Kolb

**Abstract:** We examined the response of growth efficiency (GE), leaf area index (LAI), and resin flow (RF) to stand density manipulations in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests of northern Arizona, USA. The study used a 40 year stand density experiment including seven replicated basal area (BA) treatments ranging from 7 to 45 m<sup>2</sup>·ha<sup>-1</sup>. Results were extended to the larger region using published and unpublished datasets on ponderosa pine RF. GE was quantified using basal area increment (BAI), stemwood production (NPP<sub>s</sub>), or volume increment (VI) per leaf area (A<sub>l</sub>) or sapwood area (A<sub>s</sub>). GE per A<sub>l</sub> was positively correlated with BA, regardless of numerator (BAI/A<sub>l</sub>, NPP<sub>s</sub>/A<sub>l</sub>, and VI/A<sub>l</sub>; r<sup>2</sup> = 0.84, 0.95, and 0.96, respectively). GE per A<sub>s</sub> exhibited variable responses to BA. Understory LAI increased with decreasing BA; however, total (understory plus overstory) LAI was not correlated with BA, GE, or RF. Opposite of the original research on this subject, resin flow was negatively related to GE per A<sub>l</sub> because A<sub>l</sub>/A<sub>s</sub> ratios decline with increasing BA. BAI, and to a lesser degree BA, predicted RF better than growth efficiency, suggesting that the simplest measurement with the fewest assumptions (BAI) is also the best approach for predicting RF.

**Résumé :** Nous avons étudié la réaction de peuplements de pin ponderosa (*Pinus ponderosa* Dougl. ex Laws.) à des manipulations de leur densité en termes d'efficacité de croissance, d'indice de surface foliaire et d'écoulement de résine dans le nord de l'Arizona, aux États-Unis. Pour réaliser cette étude, nous avons eu recours à une expérience vieille de 40 ans sur la densité des peuplements. Le dispositif incluait sept répétitions de traitements faisant varier la surface terrière de 7 à 45 m<sup>2</sup>·ha<sup>-1</sup>. Les résultats ont été étendus à une plus grande région à l'aide de fichiers de données publiés et non publiés sur l'écoulement de résine chez le pin ponderosa. L'efficacité de croissance a été quantifiée à partir de l'accroissement en surface terrière, de la production de bois de la tige ou de l'accroissement en volume par unité de surface foliaire ou de surface d'aubier. L'efficacité de croissance par unité de surface foliaire était positivement corrélée à la surface terrière, peu importe la variable utilisée comme numérateur (r<sup>2</sup> = 0,84, 0,95 et 0,96 respectivement pour l'accroissement en surface terrière, la production de bois de la tige ou l'accroissement en volume comme numérateur). La réaction de l'efficacité de croissance par unité de surface d'aubier à la surface terrière était variable. L'indice de surface foliaire du sous-étage a augmenté avec une diminution de la surface terrière. Cependant, l'indice de surface foliaire total (sous-étage et étage dominant) n'était pas corrélé avec la surface terrière, l'efficacité de croissance ou l'écoulement de résine. Contrairement aux résultats des premiers travaux de recherche sur ce sujet, l'écoulement de résine était négativement relié à l'efficacité de croissance par unité de surface foliaire parce que le rapport entre la surface foliaire et la surface d'aubier diminuait avec une augmentation de la surface terrière. L'accroissement en surface terrière, et dans une moindre mesure la surface terrière, avaient la capacité de mieux prédire l'écoulement de résine que l'efficacité de croissance, ce qui indique que la mesure la plus simple qui comporte le moins d'hypothèses (l'accroissement en surface terrière) est aussi la meilleure approche pour prédire l'écoulement de résine.

[Traduit par la Rédaction]

## Introduction

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) is an ecologically and economically important conifer found throughout North America, with a range extending from

southern Canada to central Mexico (Waring and Law 2001). Prior to Euro-American settlement, many ponderosa pine forests were subjected to frequent ground fires that removed competing vegetation and maintained low-density stands (Cooper 1960; Swetnam et al. 1999). Since the policy of

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fire exclusion was implemented in the late 1800s, heavy seedling regeneration within pine forests (Savage et al. 1996) has increased stand basal areas (BAs) above values that existed prior to 1900 (Covington and Moore 1994; Moore et al. 2003). High stand density increases the risk of catastrophic wildfires (Fulé et al. 2001; Pierce et al. 2004) and bark beetle attacks (Waring and Pitman 1985; Negrón 1997) and decreases individual tree productivity (Parsons and DeBenedetti 1979; Biondi 1996).

Selective thinning that favours larger trees is a silvicultural technique introduced to restore stand densities to historic levels (Allen et al. 2002) and may be applied to either old-growth forests (Covington and Moore 1994; Mast et al. 1999) or to younger forests (Skov et al. 2004). The ideal silvicultural prescriptions may vary between regions and even sites (Brown et al. 2004, Schoennagel et al. 2004); however, if successful, remaining trees should increase growth and may be less susceptible to bark beetles and fire (Allen et al. 2002; McDowell et al. 2003).

One method by which stand density reductions may facilitate tree resistance to insect attack is via increased growth efficiency (GE) (Waring and Pitman 1985; Coyea and Margolis 1994). GE is commonly defined as stemwood production (volume, mass, or basal area increment) per unit BA, sapwood area, or leaf area (Waring et al. 1980; Waring 1983) or per crown projected area (Assman 1970). Although not a true thermodynamic efficiency (e.g., net primary production per gross photosynthesis; Ryan et al. 1997a), GE has been associated with tree susceptibility to attack. In particular, thinning studies during the 1970s and 1980s reported that stand density reductions increased tree GE and decreased susceptibility to bark beetle attacks (Larsson et al. 1983; Mitchell et al. 1983), perhaps because of greater resource allocation to tree resin defenses (Christiansen et al. 1987).

However, the relationship between stand density, GE, and bark beetle resistance is not as clear as it was in the early 1980s. Recent studies have found that GE increases rather than decreases with increasing stand density (e.g., Smith and Long 1989; Reid et al. 2004). Increased GE with increasing stand density has been attributed to increased efficiency of growth and resource use of small and suppressed trees (Binkley et al. 2004; Long et al. 2004). The difference between the studies that found increases versus decreases in GE (based on leaf area) with stand density may reside in different approaches used to estimate leaf area. Studies that used stand density-specific allometrics (e.g., Long and Smith 1990; Reid et al. 2004) or stand leaf area index (e.g., Smith and Long 1989) found increasing GE with stand density, and studies that used nondensity-specific allometrics found decreasing GE with stand density (e.g., Mitchell et al. 1983; Larsson et al. 1983). This pattern may result because the assumption of constant leaf area per unit sapwood area across a continuum of stand densities is false (Brix and Mitchell 1983; Keane and Weetman 1987; Long and Smith 1988; McDowell et al. 2006). In this study, we quantified GE using site- and treatment-based measurements of leaf area and sapwood area so that GE could be calculated a variety of ways.

Measurements of bark beetle resistance have rarely been included in studies that calculated GE using stand-level

measurements or stand density-specific allometrics. It has been observed that resin flow (RF) declined with increasing stand BA in a ponderosa pine spacing trial (Kolb et al. 1998), but not in a recent ponderosa pine study that held tree diameter constant across a range of stand densities (Zausen et al. 2005). Given these observations, we speculate that, if RF increases with decreasing stand density (when tree size varies) and if GE declines with decreasing stand density (Long et al. 2004), then GE may be inversely correlated with RF.

Another critical component of forest response to stand density management is leaf area index (LAI), or the square metres of projected foliage area per square metre of ground area. LAI regulates ecosystem-scale light interception, carbon uptake, and transpiration and is a critical component in models of forest production (Landsberg and Gower 1997). LAI may also directly or indirectly regulate GE and RF because greater LAI may indicate more competition for resources (Oren et al. 1987; Waring 1987). LAI is initially reduced by forest thinning because of partial removal of the overstory. The long-term response of LAI to thinning in pine forests of the Pacific Northwest is regulated by both the regrowth of overstory foliage and the response of shrub foliage production, which together may allow LAI to return to prethinning levels (Oren et al. 1987). To our knowledge, no study has investigated the long-term response of LAI to thinning in ponderosa pine forests of the southwestern United States where there are few shrubs but an abundance of understory grasses and forbs that may contribute to LAI after thinning (Moore and Deiter 1992; Moore et al. 2006).

The objective of our study was to examine the relationship between GE, RF, and LAI in ponderosa pine ecosystems in northern Arizona, USA. We conducted this analysis using a two-pronged approach. First, we used a new data set on leaf area and sapwood area allometrics that was collected across a continuum of stand densities to calculate the long-term response of GE and LAI to density manipulations at a site where density was maintained at seven replicated levels for 40 years (McDowell et al. 2006). Second, we examined the relationships between growth efficiency, LAI and RF for ponderosa pine forests across the larger region using five data sets from northern Arizona (Kolb et al. 1998, 2006; Zausen et al. 2005; Gaylord et al. 2007; T.E. Kolb and N. Guerard, unpublished data). Our primary hypotheses were (i) GE increases with increasing stand density; (ii) LAI in thinned stands rebounds to the level in unthinned stands via both increased overstory and understory leaf area; (iii) because of the invariance in LAI with stand BA, GE will show no relationship with LAI; (iv) GE is inversely correlated with RF; and (v) because of the invariance in LAI with stand BA, no relationship will exist between LAI and RF.

## Methods

### Study site

Our primary 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 approximately 15 km northwest of Flagstaff, Arizona. The stand is 35.6 ha in area (Ronco et al. 1985) and is domi-

nated by ponderosa pine (*P. ponderosa* var. *scopulorum*) that regenerated naturally in approximately 1919 (Ronco et al. 1985). The trees were approximately 84 years old during the time of our field experiment (summer 2003). A sparse understory of grasses and forbs was present. 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 (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. This region experiences a monsoonal climate typical of the southwestern 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

Our experimental design included a focused analysis at the experimental site and an extended analysis throughout the region. For the focused analyses, we used a replicated set of stand BA treatments at Taylor Woods to test our hypotheses regarding GE, LAI, and RF responses to changes in stand BA. The initial experiment was designed by the USDA Forest Service to determine the effects of stand BA on ponderosa pine growth (Ronco et al. 1985). The forest was thinned originally in October 1962 to generate three replicated plots of each treatment BA, where the residual BAs of the six treatment densities were 34, 28, 23, 18, 14, and 7 m<sup>2</sup>·ha<sup>-1</sup> (790, 471, 367, 246, 145, and 68 trees·ha<sup>-1</sup>, respectively). The residual BA was maintained by rethinning each plot once per decade, resulting in removal of trees in 1972, 1982, 1992, and 2003. Stand characteristics are provided in McDowell et al. (2006) but are briefly summarized here. The mean diameters at breast height (DBHs) for the 45, 34, 28, 23, 18, 14, and 7 m<sup>2</sup>·ha<sup>-1</sup> treatments in 2003 were 13.4, 25.5, 30.4, 31.7, 34.8, 40.0, and 47.0 cm, respectively. For these same respective treatments, the mean tree heights were 11.1, 15.9, 16.9, 18.9, 18.9, 18.6, and 19.5 m (McDowell et al. 2006). The experiment also includes three replications of an uncut control that had a mean BA of 45 m<sup>2</sup>·ha<sup>-1</sup> (3200 trees·ha<sup>-1</sup>) in 2003. The plots are about 0.4 ha in size and have 0–10 m buffers. Although the unthinned plots have experienced some mortality likely resulting from self-thinning, no recent mortality has occurred in any of the plots as a result of bark beetle infestation.

Whole-tree harvests were conducted in 2003 as part of the decadal thinning practice, and in the case of the control treatment, five trees were also harvested. Trees harvested from plot interiors during this process were used for measurement of sapwood and leaf area. Stem diameter at 1.3 m height of the harvested trees tended to be slightly less (8%) than the plot mean as measured by the regression slope of stand mean DBH versus harvested trees DBH (slope = 0.92,  $r^2 = 0.98$ ,  $p < 0.01$ ). We measured radial growth and sapwood area ( $A_s$ ) of three trees per plot in three plots per treatment. On a single plot per treatment, we measured  $A_s$  and whole-tree leaf area ( $A_l$ ) on five trees (McDowell et al. 2006). Basal area increment (BAI, cm<sup>2</sup>·year<sup>-1</sup>) was statistically indistinguishable among the plots in which  $A_l$  was measured and the two other treatment replicates (McDowell

et al. 2006). Individual tree GE was calculated only from trees in which we had directly measured leaf area and so was limited to the five trees (single plot) per treatment. LAI and stand-level GE were calculated using measurements from all three plots per treatment.

### Growth efficiency

We assessed GE six ways: (i) BAI/ $A_s$ , (ii) BAI/ $A_l$ , (iii) NPP<sub>s</sub>/ $A_s$ , (iv) NPP<sub>s</sub>/ $A_l$ , (v) VI/ $A_s$ , and (vi) VI/ $A_l$ , where VI is volume increment (m<sup>3</sup>·tree<sup>-1</sup>·year<sup>-1</sup>) and NPP<sub>s</sub> is stemwood net primary production (g dry mass·tree<sup>-1</sup>·year<sup>-1</sup>). Five trees were harvested from each of the primary plots between 9 June and 13 June 2003 as part of the decadal thinnings to maintain treatment basal area. From these trees we measured diameter, BAI,  $A_s$ , and  $A_l$ . Details on cross-dating, ring widths,  $A_s$ , and  $A_l$  measurements can be found in McDowell et al. (2006) and are briefly summarized here. After trees were felled, we removed stemwood cross sections from a height of approximately 1.3 m from each stump with chainsaws. Cross sections were air-dried for 3 months prior to analysis. We sanded the cross sections using successively finer sandpaper of FEPA (Federation of European Producers of Abrasives) 100, 220, 320, and occasionally 400 grit (162, 68, 44.7–47.7, and 33.5–36.5 μm, respectively) using a belt sander (Makita USA, La Mirada, Calif.). We measured ring widths using a Microcode II banister measuring system (Boeckler Instruments, Tucson, Ariz.) attached to a PC running the Measure J2X software (<http://www.voortech.com/projectj2x/tringMainV2.html>). 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 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 using tree-specific cross-sectional radii (inside bark) and assuming concentric circularity. In this paper, annual values for ring widths and derived values such as NPP<sub>s</sub>, BAI, and VI were averaged for 1996–2001. We stopped measurement at 2001 because 2002 was a year of severe drought, and many trees did not form rings that year (Gaylord et al. 2007).

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.

We estimated NPP<sub>s</sub> using an allometric equation generated from harvested ponderosa pine within Fort Valley Experimental Station (Gholz et al. 1979) and estimated VI from a local ponderosa pine volume equation based on diameter and height (Hann and Bare 1978). Despite the necessary height correction, the volume equation still gave unrealistic predictions for trees within the 45 m<sup>2</sup>·ha<sup>-1</sup> plot because it was not developed for severely suppressed trees; therefore, we left data for that treatment out of all results that included VI.



Although our focus was on individual-tree responses to thinning treatments, we also examined stand-level responses of  $NPP_s$  ( $NPP_{stand}$ ) and GE. To obtain  $NPP_{stand}$ , we inventoried DBH for every live tree on each plot. We calculated stemwood mass for the average tree (quadratic mean) for each plot using the local stem mass equation from Gholz et al. (1979) and multiplied this value by stand density (trees per hectare) for inventory data collected in 1998 and 2002. The difference between stand-level stemwood mass in 2002 and 1998, divided by four, gives the 4 year mean stemwood NPP per year.

### Leaf area index

LAI was calculated by scaling tree-level  $A_s/A_1$  measurements to the stand with plot-level  $A_s$  data. To obtain plot-level  $A_s$ , we inventoried DBH for every live tree on each plot. We then calculated plot-level BA from DBH assuming concentric circularity. Plot-level  $A_s$  was then calculated using a  $BA/A_s$  relationship developed from direct measurements on the 11 trees harvested per treatment (5 trees for the control treatment) as described above (overall  $r^2 = 0.96$ ; McDowell et al. 2006). We then multiplied plot-level  $A_s$  by on-site, treatment-specific  $A_1/A_s$  data collected using the approach described in McDowell et al. (2006) and summarized here. Whole-tree  $A_1$  was estimated by scaling branch estimates of leaf area to the canopy (Maguire and Batista 1996; McDowell et al. 2002a). Branch-scale allometric equations were developed through branch harvest and analysis for five trees per treatment. Nine branches were harvested from throughout the height continuum over several aspects of the crown for each of five trees per plot. The entire foliage mass for each branch 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 ( $cm^2 \cdot g^{-1}$ ). Projected leaf area was determined using a video image recorder and AgVision software (Decagon Devices, Pullman, Wash.). 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  $A_1$  for four of the five sampled trees, and used the branch regression approach for the fifth tree. Foliage was processed identically to the methods described above.

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

Specific leaf area 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,  $p$  ranged from  $<0.01$  to 0.03). Be-

cause of this consistent trend, we applied plot specific branch height-specific leaf area corrections prior to multiplying specific leaf area by foliage mass for estimating whole-branch  $A_1$ .

Leaf area of understory grasses and forbs was measured in 1998 and 1999. Percent cover was ocularly estimated using three to five randomly located 0.5 m  $\times$  2.0 m rectangular sampling frames per plot during September of each year. Percent cover was estimated as the fraction of surface area covered by foliage. We converted percent cover directly to understory LAI, i.e., 20% cover equals 0.20  $m^2 \cdot m^{-2}$  LAI, by assuming that any overlapping foliage in the percent cover estimates are compensated by gaps between foliage. Understory LAI was averaged for 1998 and 1999. Palmer drought severity index (PDSI) in northern Arizona averaged 0.5 over these 2 years (2 and -1, respectively), indicating that our study may be representative of average or slightly wetter than normal years. Total stand LAI was calculated as overstory plus understory LAI.

### Regional analysis

We extended our analysis to include all of the regional studies on ponderosa pine that included a uniform data set from which to compare GE, LAI, and RF. The single uniform measurement of RF across all studies was the 7 day resin flow in response to artificial wounding of phloem at a height of 1–1.5 m aboveground. In most studies, wounding was induced on two sides (north and south) of each tree for at least five trees per site by hammering a 2.54 cm Osborne arch punch (Model 149, King Bearing Co., Flagstaff, Ariz.) through the bark, phloem, and cambium to the outside of the xylem. Resin was collected at 1 day or 2 day intervals over 7 days with funnels attached to test tubes. The only exception to this protocol was the study of Zausen et al. (2005) in which only 24 h RF was measured. We converted the 24 h values to 7 day values using a relationship between the two derived from ponderosa pine trees in northern Arizona (Gaylord 2003): 7 day RF = 1.39(24 h RF) + 1.24,  $p < 0.001$ ,  $r^2 = 0.86$ . RF is also strongly correlated with air temperature (Ruel et al. 1998; Gaylord et al. 2007). To minimize the impact of this potentially confounding factor, we only used RF data from each study that was collected in the month of June when temperatures are warm.

Stand characteristics of all of the regional sites are described in Table 1. GE was calculated as  $NPP_s/A_s$ ,  $BAI/A_s$ ,  $BAI/A_1$ , and  $NPP_s/A_1$  using tree-specific diameters and was corrected for stand density using the  $A_1/A_s$  relationships from McDowell et al. (2006) for data with homogenous diameter distributions (the intensive site; Zausen et al. 2005; Gaylord et al. 2007). For dense stands with heterogeneous diameter distributions (Kolb et al. 2006; T.E. Kolb, unpublished data) we used local ponderosa pine  $A_1/A_s$  relationships from Simonin et al. (2006). In all cases, we assumed that stem BA is 95% sapwood (McDowell et al. 2006). We did not have height increment data for the regional sites, so we did not calculate GE using VI. Overstory LAI was calculated for each site using the predicted leaf area values for the trees along with stand BA.

### Statistics

Regression analysis was used to test the following hypoth-

**Table 1.** Stand characteristics for each study within the regional analysis.

Study	Stand BA (m <sup>2</sup> ·ha <sup>-1</sup> )	DBH (cm)	Overstory LAI (m <sup>2</sup> ·m <sup>-2</sup> )	Treatment	Tree age (years)	Year of data collection
Kolb et al. 1998	7–45	10–41	1.1–2.0	TH, C	75	1994
Zausen et al. 2005	8–20	27–33	1.1–2.0	TH, TB, C	na	2003–2004
T.E. Kolb et al., unpublished data	32.1	9–59	1.9	C	38–160	2002
Gaylord et al. 2007	36.7	25–46	2.1	C	na	2002–2003
Kolb et al. 2006	43.6	8–54	2.1	C	21–203	2003

**Note:** The data of Kolb et al. (1998) are also derived from the Taylor Woods study site. LAI is overstory LAI only and does not include understory vegetation. Treatment codes are thinned (TH), thinned and burned (TB), and controls with no manipulation (C). na, not available.

eses: (i)  $NPP_s$  at the individual-tree or stand levels is dependent on stand BA, (ii) stemwood productivity (BAI,  $NPP_s$ , or VI) is dependent on  $A_1$  or  $A_s$ , (iii) growth efficiency is dependent on stand basal area or LAI, and (iv) resin flow is related to GE or LAI. We present results of the best regression fits based on  $pF$  value and  $r^2$ , and present the simplest regression if more than one regression presented similar fit statistics. We conducted all tests with Systat version 11.0 (Systat, San Jose, Calif.).

**Results**

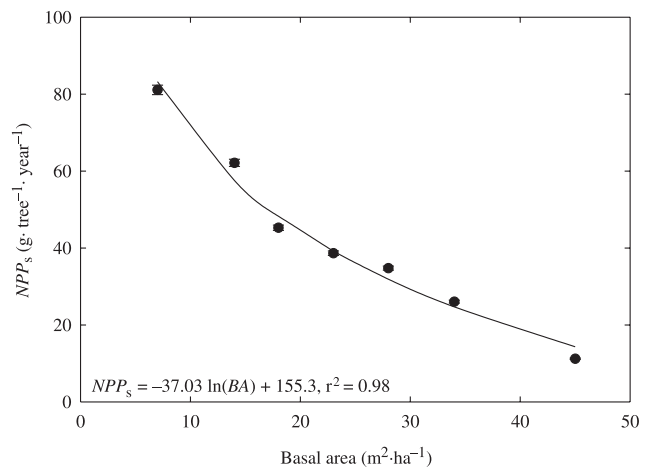
Aboveground productivity on an individual-tree basis measured as  $NPP_s$  increased with decreasing stand BA ( $p < 0.01$ ; Fig. 1). Similar relationships were observed between stand BA and BAI or VI (data not shown). BAI,  $NPP_s$ , and VI each increased strongly with increasing  $A_s$  ( $p < 0.01$  for each; Figs. 2A–2C). Likewise, BAI,  $NPP_s$ , and VI each increased strongly with increasing  $A_1$  ( $p < 0.01$  for each; Figs. 2D–2F).

The response of GE on an individual-tree basis to control of stand BA by thinning depended on how GE was calculated. GE calculated as  $BAI/A_s$  declined with increasing stand BA ( $p = 0.01$ ; Fig. 3A). In contrast, GE calculated as  $BAI/A_1$  increased with stand BA ( $p < 0.01$ ; Fig. 3B). GE calculated as  $NPP_s/A_s$  was not related to stand BA ( $p = 0.42$ ; Fig. 3C), whereas  $NPP_s/A_1$  increased with stand BA ( $p < 0.01$ ; Fig. 3D). GE calculated as  $VI/A_s$  and as  $VI/A_1$  increased with increasing stand BA ( $p < 0.01$  for both; Figs. 3E and 3F).

$NPP_{stand}$  increased with stand BA ( $p < 0.01$ , Fig. 4A). This response is the opposite of the individual tree response (Fig. 1). Stand-level GE, defined as  $NPP_{stand}/LAI$ , also increased with stand BA (Fig. 4B), similar to the individual tree response (Fig. 3D).

Individual-tree  $A_s$  was strongly and positively correlated with tree BA ( $A_s = 0.95(\text{individual tree BA})$ ,  $r^2 = 0.99$ ,  $p < 0.01$ ; data not shown). In contrast, individual-tree  $A_s$  exhibited a nonlinear decline with increasing stand BA ( $A_s = -0.052 \times \ln(\text{stand BA}) + 0.21$ ,  $r^2 = 0.97$ ,  $p < 0.01$ ; data not shown). Understory LAI increased with decreasing stand BA ( $p < 0.01$ ; Fig. 5A). The contribution of understory LAI to total stand LAI was greatest at low stand BA levels (Fig. 5B). Neither overstory nor total LAI exhibited a clear pattern with stand BA ( $r^2 = 0.02$ ,  $p = 0.71$ ; Fig. 5B). The low and high BA treatments had the lowest LAI values at 1.3 m<sup>2</sup>·m<sup>-2</sup>, and the maximum observed LAI was 2.04 m<sup>2</sup>·m<sup>-2</sup> for the 18 m<sup>2</sup>·ha<sup>-1</sup> BA treatment.

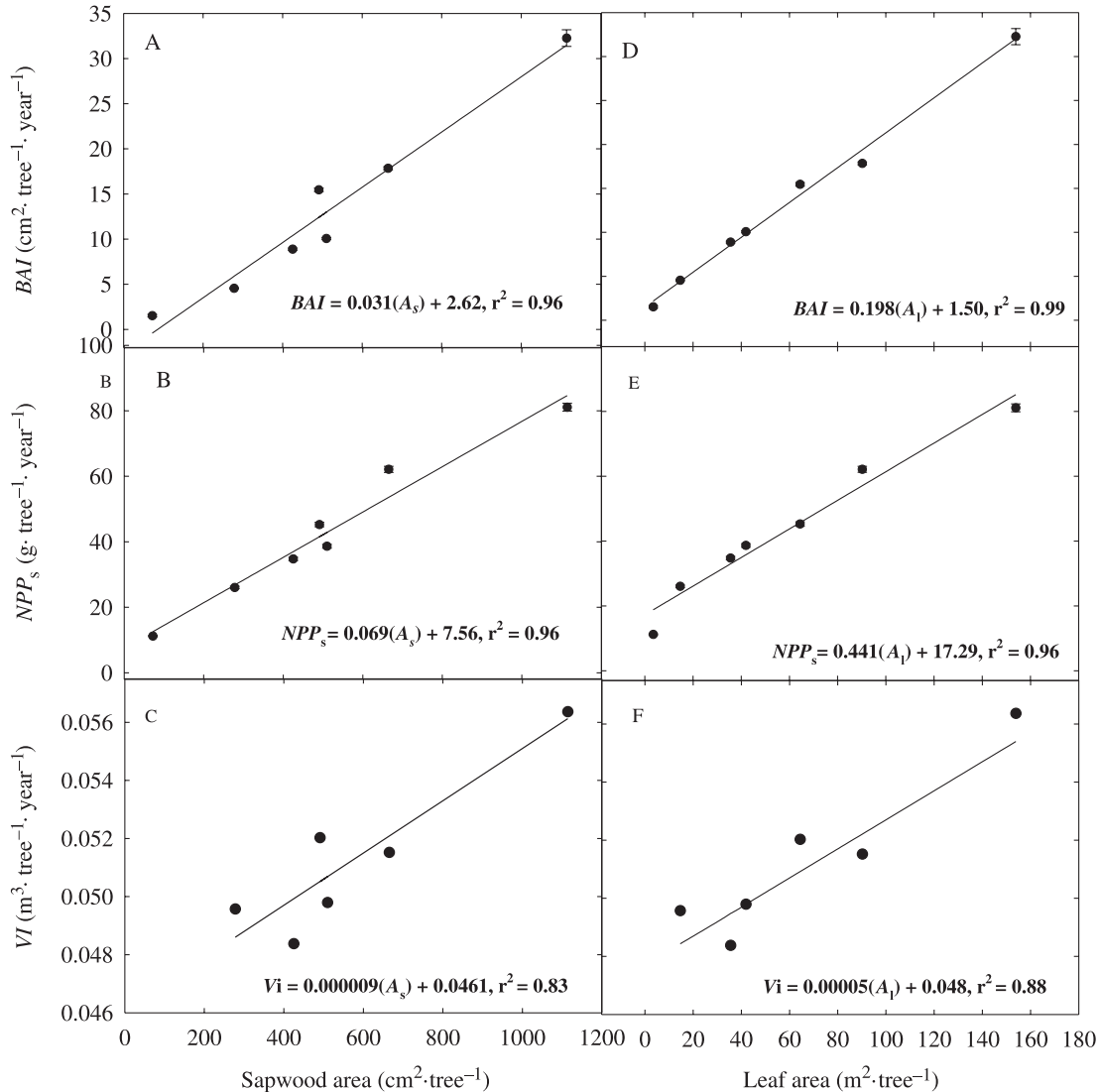
**Fig. 1.** Individual-tree stemwood net primary production ( $NPP_s$ ) versus stand basal area.  $NPP_s$  is calculated as the mean annual growth for the 5 year period of 1997–2001. Error bars are SEs.



GE, defined as  $NPP_s/A_1$ , did not show a clear pattern with total stand LAI (Fig. 6). The fit of the regression of  $NPP_s/A_1$  versus LAI was not significant ( $r^2 = 0.24$ ,  $p = 0.21$ ), primarily because of the low  $NPP_s/A_1$  of the stand with the lowest BA (circled point in Fig. 6). Similar nonsignificant patterns were observed using  $BAI/A_1$  and  $VI/A_1$  versus LAI ( $r^2 = 0.21$  and  $0.20$ ,  $p = 0.21$  and  $0.07$ , respectively; data not shown). We present previous results from ponderosa pine in the Pacific Northwest as a line in Fig. 6 for comparison with our results.

GE was negatively related to 7 day RF for both the intensive site and the extended regional analysis (Fig. 7). The only exception to this pattern was  $BAI/A_s$ , which had a positive but nonsignificant relationship (slope = 0.004,  $p = 0.53$ ,  $r^2 = 0.11$ ; data not shown). Figure 7 displays two examples of the relationship between GE and RF. There was no significant relationship between RF and  $NPP_s/A_1$  ( $p = 0.09$ ; Fig. 7A;), although RF appeared to increase at low  $NPP_s/A_1$ . The relationship between RF and  $BAI/A_1$  was marginally significant ( $r^2 = 0.25$ ,  $p = 0.051$ ; Fig. 7B). RF was negatively related to stand BA (Fig. 8A). The relationship between RF and stand BA is much stronger if three data points calculated from Zausen et al. (2005), in which 7 day RF was predicted from 24 h RF, are not included ( $RF = 0.55BA + 30.0$ ,  $r^2 = 0.84$ ,  $p = 0.01$ ; broken regression line in Fig. 8A). In contrast with all of the other relationships with RF, the relationship between RF and BAI was positive

**Fig. 2.** Growth (BAI,  $NPP_s$ , or VI) as a function of (A–C) whole-tree sapwood area or (D–F) whole-tree leaf area. All regressions were significant at  $p < 0.05$ .



and statistically strong (Fig. 8B). There was no significant relationship between RF and LAI ( $p = 0.43, r^2 = 0.09$ ; data not shown).

## Discussion

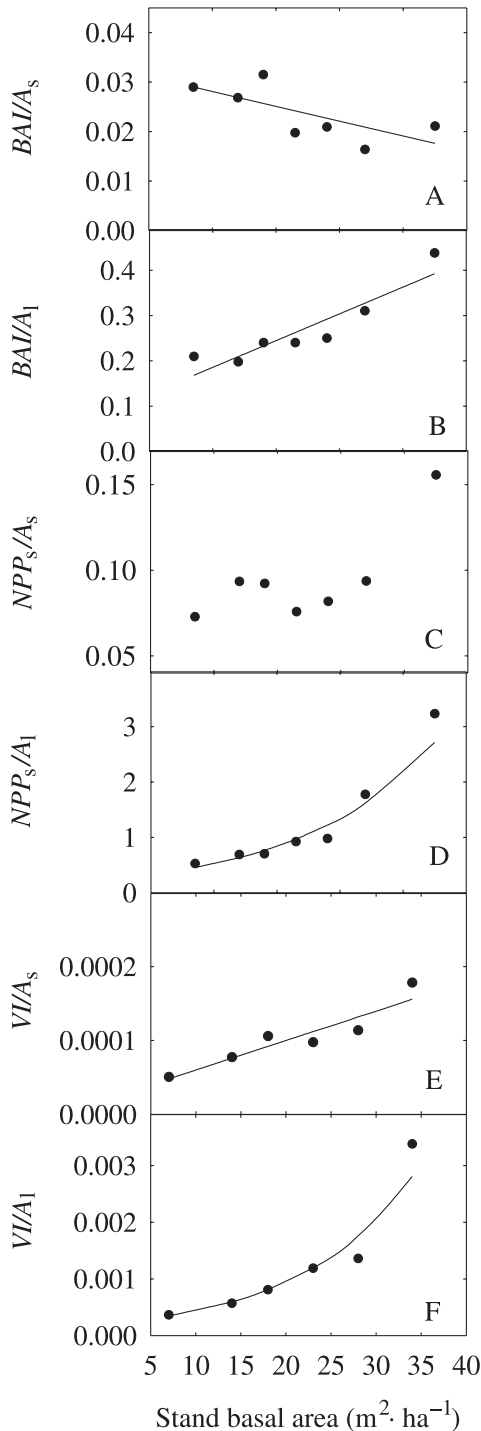
Forty years of stand density management resulted in large differences in growth (Figs. 1 and 4A), GE (Figs. 3 and 4B), and RF (Figs. 7 and 8). Growth per unit sapwood area was decoupled from growth per unit leaf area regardless of the measure of growth used (Fig. 3). The hypothesis that GE increases with increasing stand BA was supported when leaf area was the denominator for the GE calculations (Figs. 3B, 3D, and 3F). Understory LAI increased as stand density decreased (Fig. 5A); however, overstory and total LAI did not exhibit a clear pattern in relation to stand BA (Fig. 5B). Thus, our hypothesis that LAI is constant across all BA treatments because of increased overstory and understory LAI was not clearly supported nor refuted. We observed no clear pattern of stand-level GE in relation to LAI (Fig. 6).

This result was consistent with our hypothesis; however, the result was strongly influenced by a single treatment level (7 m<sup>2</sup>·ha<sup>-1</sup>), and the trend for the remaining treatments was consistent with previous results (Waring 1987). Therefore, with more samples, we may have seen a different result. Consistent with our fourth hypothesis, GE (per unit leaf area) was inversely correlated with RF, although not always significantly so. Perhaps more importantly, the simplest predictor, BAI, was well correlated with RF. Lastly, no significant relationship was apparent between stand LAI and RF.

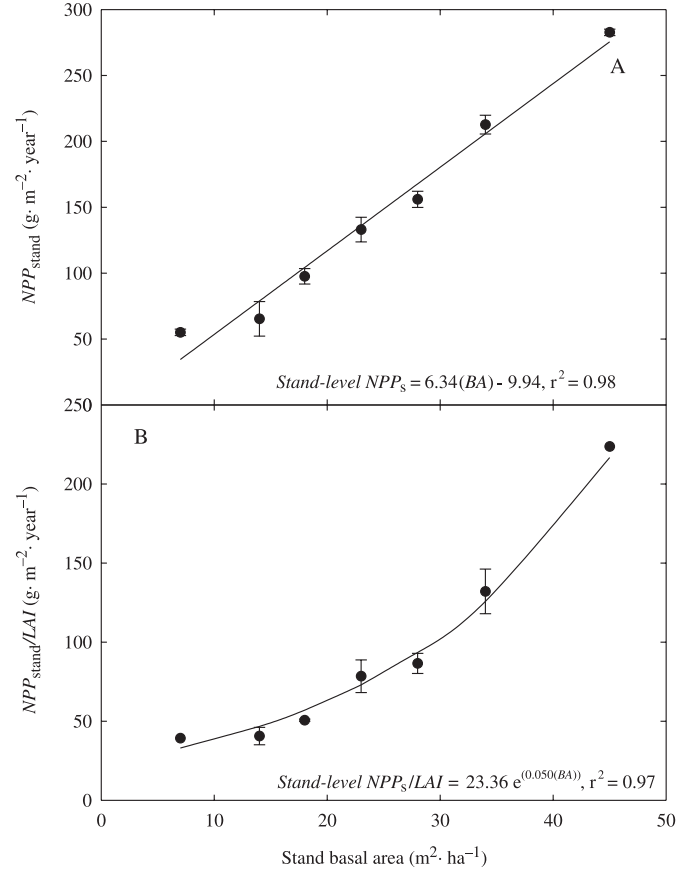
## Growth efficiency

We examined GE using two denominators,  $A_s$  and  $A_l$ , and three numerators, BAI,  $NPP_s$ , and VI, to determine the similarity among these different measures. When  $A_s$  was in the denominator, GE exhibited a decline with increasing stand BA ( $BAI/A_s$ ) (Fig. 3A), no relationship with stand BA ( $NPP_s/A_s$ ; Fig. 3C), or a positive relationship ( $VI/A_s$ ) (Fig. 3E). It is not clear why there were differences in the response of GE (per  $A_s$ ) to stand BA associated with the dif-

**Fig. 3.** Individual-tree growth efficiency versus stand BA. Panels and regression relationships are as follows: (A) BAI per unit sapwood area ( $BAI/A_s$ ,  $\text{cm}^2\text{-cm}^{-2} A_s\text{-year}^{-1}$ ) =  $-0.0003(BA) + 0.031$ ;  $r^2 = 0.51$ ,  $p < 0.01$ ; (B) BAI per unit leaf area ( $BAI/A_l$ ,  $\text{cm}^2\text{-m}^{-2} A_l\text{-year}^{-1}$ ) =  $0.006(BA) + 0.127$ ;  $r^2 = 0.84$ ,  $p < 0.01$ ; (C)  $NPP_s$  per unit sapwood area ( $NPP_s/A_s$ ,  $\text{g}\cdot\text{cm}^{-2} A_s\text{-year}^{-1}$ ), no significant relationship; (D)  $NPP_s$  per unit leaf area ( $NPP_s/A_l$ ,  $\text{g}\cdot\text{m}^{-2} A_l\text{-year}^{-1}$ ) =  $0.328 e^{0.048(BA)}$ ;  $r^2 = 0.95$ ,  $p < 0.01$ ; (E) VI per unit sapwood area ( $VI/A_s$ ,  $\text{m}^3\text{-cm}^{-2} A_s\text{-year}^{-1}$ ) =  $0.00005(BA) + 0.048$ ;  $r^2 = 0.88$ ,  $p < 0.01$ ; (F) VI per unit leaf area ( $VI/A_l$ ,  $\text{m}^3\text{-m}^{-2} A_l\text{-year}^{-1}$ ) =  $0.0002 e^{0.078(BA)}$ ;  $r^2 = 0.96$ ,  $p < 0.01$ .



**Fig. 4.** (A) Stand-level  $NPP_{stand}$  versus stand BA and (B) stand-level growth efficiency defined as  $NPP_{stand}/\text{total LAI}$  versus stand BA. Error bars are SEs.

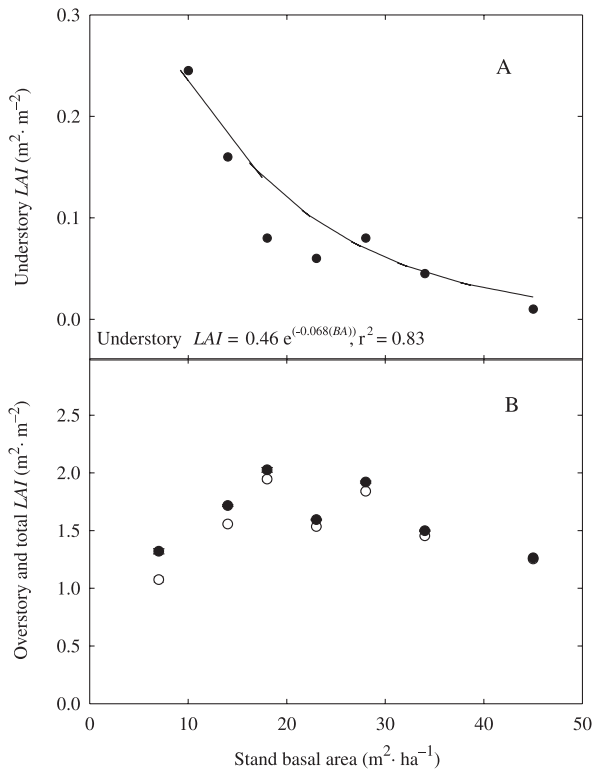


ferent numerators. BAI is a measure only of wood growth at the base of the tree, whereas  $NPP_s$  and VI are measures of total stemwood growth. Only VI includes a correction for tree height, potentially making it the most relevant measure of aboveground productivity. Regardless, it is clear that the choice of numerator (BAI,  $NPP_s$ , or VI) can have a large effect on conclusions regarding GE when using  $A_s$  for the denominator in southwestern ponderosa pine forests.

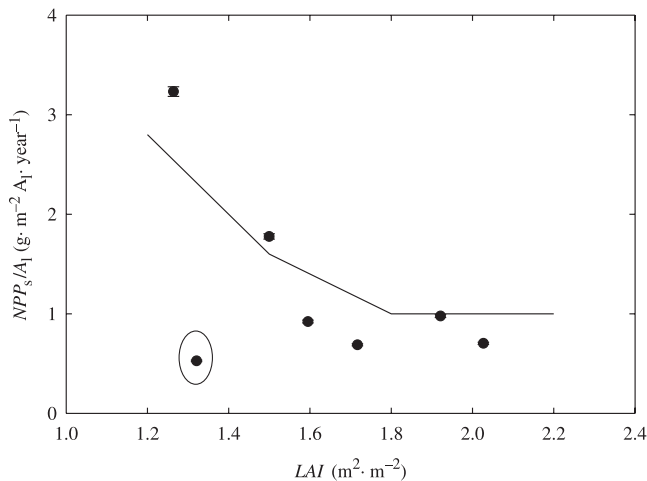
When  $A_l$  was in the denominator, GE increased with stand BA regardless of the numerator ( $BAI/A_l$ ,  $NPP_s/A_l$ , and  $VI/A_l$ ; Figs. 3B, 3D, and 3F, respectively). This result was expected based on the findings of Smith and Long (1989), Long and Smith (1990), Burkes et al. (2003), and Reid et al. (2004). Something held in common by these studies and ours is that they all used stand density-specific allometrics (e.g., Long and Smith 1990; Reid et al. 2004) or stand LAI (e.g., Smith and Long 1989) to calculate GE. Prior studies that found a negative relationship between GE and stand density used equations that did not account for decreases in  $A_l/A_s$  as density increases, likely causing errors in the estimate of  $A_l$  (e.g., Waring et al. 1980; Mitchell et al. 1983; Larsson et al. 1983; Waring and Pitman 1985; Stoneman and Whitford 1995). As is now well-known (but was not known in the late 1970s and early 1980s), the assumption of constant  $A_l/A_s$  across a continuum of stand densities is false (Brix and Mitchell 1983; Keane and Weetman 1987; Long and Smith 1988; McDowell et al. 2006). Variation in  $A_l/A_s$  with density



**Fig. 5.** (A) Understory LAI versus stand BA and (B) overstory (open symbols) and total (solid symbols) LAI versus stand BA.



**Fig. 6.**  $NPP_s/A_l$  versus stand LAI. The lowest, circled point is the  $7 \text{ m}^2\cdot\text{ha}^{-1}$  stand, and the highest point is the  $45 \text{ m}^2\cdot\text{ha}^{-1}$  stand. Error bars are SEs. The line is redrawn from Waring (1987).



may be due to homeostatic shifts to maximize gas exchange (McDowell et al. 2006) and may be associated with different rates of development along the continuum of the  $A_l/A_s$  versus stand density relationship (Coleman et al. 1994). In our study,  $A_l/A_s$  varied from  $0.04 \text{ m}^2\cdot\text{cm}^{-2}$  in the  $45 \text{ m}^2\cdot\text{ha}^{-1}$  stand to a maximum of  $0.14 \text{ m}^2\cdot\text{cm}^{-2}$  in the  $7 \text{ m}^2\cdot\text{ha}^{-1}$  stand (McDowell et al. 2006). This variation in  $A_l/A_s$  causes growth per unit sapwood area to be decoupled from growth per unit leaf area. Given the variation in  $A_l/A_s$  with stand density and with tree size (McDowell et al. 2002a; Simonin et al. 2006), it is clear that GE studies that use leaf area as

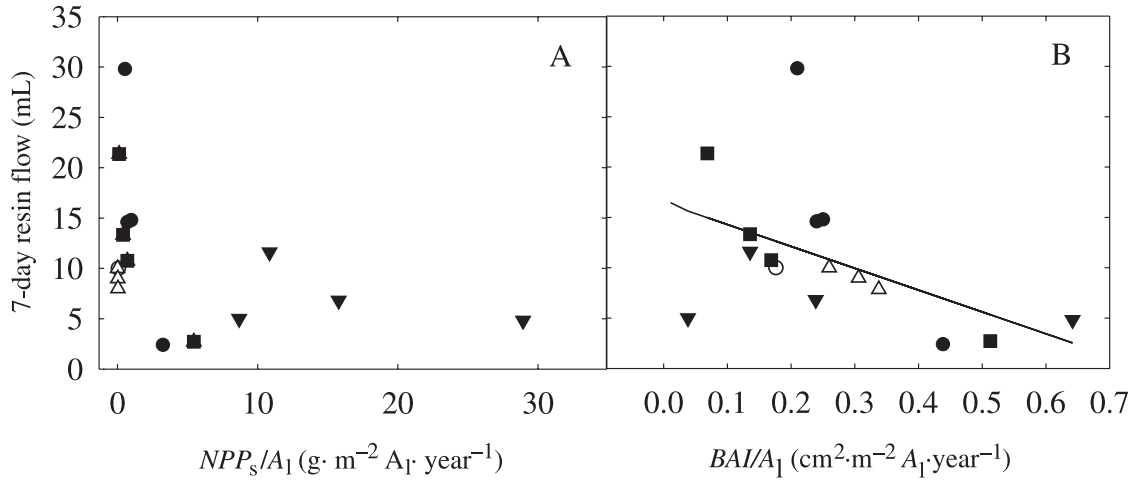
the denominator must make on site measurements or use allometric equations that account for influence of stand density and tree size.

Increased GE with increasing stand density has been attributed to increased efficiency of growth and resource use by small and suppressed trees (Binkley et al. 2004; Long et al. 2004; however, this is not always seen, e.g., Gersonde and O'Hara 2005). The exact physiological mechanism(s) for this response are not known. A traditional explanation has been that respiration costs increase disproportionately with tree size, but this explanation has been refuted in quantitative studies of respiration costs associated with tree size and stand density (Ryan et al. 2004). Reid et al. (2004) speculated that small lodgepole pine (*Pinus contorta* Dougl. ex Loud.) trees in high-density stands have higher GE because of higher photosynthetic capacity per unit leaf area and higher sapwood porosity per unit leaf area. We have no porosity data from our study; however, a study on mature (75-year-old) ponderosa pines at a nearby site in northern Arizona concluded that porosity was higher for trees in thinned compared with unthinned plots (Simonin et al. 2006), counter to the hypothesis proposed by Reid et al. (2004). Further, we observed no variation in photosynthetic capacity across stand-density treatments (McDowell et al. 2006). An explanation consistent with our results is that large trees in the more open stands may have reduced the fraction of assimilated carbon allocated to stemwood production and increased the fraction of carbon allocated belowground to structural roots to maintain stability in response to greater wind-loading on their larger crowns (McDowell et al. 2003). If carbon allocation belowground per tree was substantially higher in low BA treatments, then total (above and belowground) NPP per unit leaf area may not have declined with decreasing stand BA. This hypothesis is consistent with the age-related shifts in belowground allocation (Magnani et al. 2000), but it remains to be tested in stand-density experiments. Another likely explanation is a size-related constraint on GE. Many studies have observed a decline in GE with increasing tree size or leaf area (Long and Smith 1990; Coyea and Margolis 1994; Gilmore and Seymour 1996; Mencuccini and Grace 1996; Ryan et al. 1997b; McDowell et al. 2002b; Will et al. 2002; Mainwaring and Maguire 2004). Hydraulic and other constraints associated with large tree size have been implicated as the mechanisms of GE decline (Yoder et al. 1994; Gower et al. 1996; Mencuccini and Grace 1996; Ryan et al. 1997b; Magnani et al. 2000; McDowell et al. 2002b). In our study, tree size increased with decreasing stand BA (Ronco et al. 1985; McDowell et al. 2006); therefore, size-related growth constraints are a plausible hypothesis to explain the decline in GE with decreasing stand BA in our study.

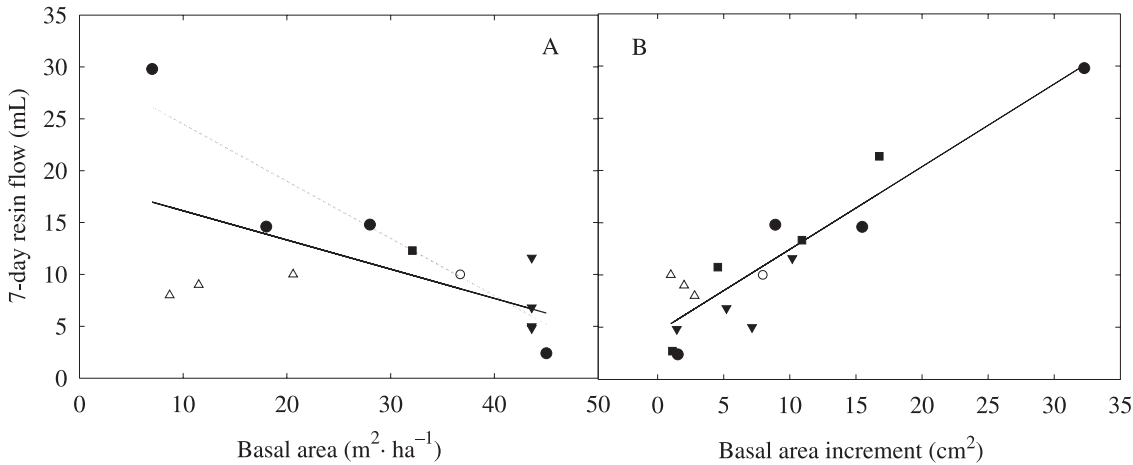
The stand-level response of  $NPP_{\text{stand}}$  to density manipulation (Fig. 4A) was consistent with previous productivity – stand density relationships (Oliver and Larson 1990). Although individual trees grow much faster after a site has been thinned (Fig. 1), NPP on a ground-area basis is typically highest in unthinned stands because the site is stocked to its maximum carrying capacity throughout the stem exclusion phase. GE at the stand level (Fig. 4B) showed a pattern similar to the individual-tree results. Notably, the exponent of the exponential regressions was similar for the



**Fig. 7.** Seven day resin flow (RF) versus (A)  $NPP_s/A_1$  and (B)  $BAI/A_1$ . Solid circles, this study and Kolb et al. (1998); open circles, Gaylord et al. (2007); open triangles, Zausen et al. (2005); solid squares, T.K. Kolb, unpublished data; solid triangles, Kolb et al. (2006). The regression for Fig. 7A was not significant; however, a significant regression is shown for Fig. 7B:  $RF = -21.2(BAI/A_1) + 16.4$ ;  $r^2 = 0.25$ ,  $p = 0.051$ .



**Fig. 8.** Seven day RF versus (A) stand basal area and (B) individual-tree BAI. The regression relationships are as follows:  $RF = -0.28(BA) + 18.9$  ( $r^2 = 0.36$ ,  $p = 0.03$ ) and  $RF = 0.79(BAI) + 4.5$  ( $r^2 = 0.84$ ,  $p = 0.01$ ). Symbols are as in Fig. 7. The broken line in Fig. 8A represents the relationship when the RF data that were converted from 24 h values to 7 day values (Zausen et al. 2005; see Methods) are excluded.



individual-tree GE response (0.048; Fig. 3D) and the stand-level response (0.050; Fig. 4B). This similarity is largely due to the fact that differences in LAI among BA levels were much less (twofold; Fig. 6B) than differences in  $NPP_{stand}$  (sevenfold; Fig. 4A).

**Leaf area index**

LAI of understory grasses and forbs responded to stand-density management as we expected based on earlier reports in the southwestern United States (Moore and Deiter 1992; Moore et al. 2006), with a large increase with decreasing stand BA (Fig. 5A). Oren et al. (1987) observed a similar response in ponderosa pine forests of Oregon, in which the understory shrub LAI increased with decreasing stand density. Controlled experiments with several grasses native to southwestern ponderosa pine forests have shown reduced net photosynthetic rate and whole-plant biomass in response to shading (Naumburg et al. 2001). Therefore, the observed

LAI response to BA is likely driven by the increased resource availability associated with less overstory competition. However, if light were the only limiting resource driving this response, then we would expect to see a correlation between understory LAI (Fig. 5A) and overstory LAI (Fig. 5B). However, no such correlation is apparent; thus, it is likely that increased water, nutrients, or another resource were also critical to the understory LAI response.

Overstory and total LAI exhibited little pattern with stand density (Fig. 5B). The lack of a distinct pattern of LAI with stand BA makes it impossible for us to disprove our original hypothesis that LAI would be constant across all BA levels. However, the relatively low LAI at the lowest (7  $m^2 \cdot ha^{-1}$ ) and highest (45  $m^2 \cdot ha^{-1}$ ) BA levels suggests that LAI may not be constant with stand density. Low LAI at the lowest BA level is due largely to the lack of overstory tree crowns, because trees in this treatment had the highest leaf area per tree of all the BA levels (McDowell et al. 2006). The low

LAI of the overstory was not compensated for by the understory LAI in this treatment. It appears that in this forest, reducing BA to 7 m<sup>2</sup>·ha<sup>-1</sup> results in underutilization of site resources for plant production and carbon sequestration.

GE did not respond to LAI (Fig. 6). However, as mentioned above, GE data for the 7 m<sup>2</sup>·ha<sup>-1</sup> BA level may be an outlier because stocking of the stand was so low and the understory foliage production was unable to compensate, resulting in the lowest LAI values of the entire study (Fig. 5B). If we ignore the 7 m<sup>2</sup>·ha<sup>-1</sup> stand, then GE declined with increasing LAI (Fig. 6). This result is surprising considering that we directly refuted the idea that GE of individual trees was lower in higher BA stands for most measures of GE (Fig. 3). The explanation lies in that stand BA and LAI were not correlated in this study. Importantly, the apparent decline in GE with increasing LAI is consistent with the decline observed for ponderosa pine trees in Oregon (Waring 1987) (Fig. 6). This result is plausible if we assume that the increased competition for water, nutrients, and light induced by greater LAI should result in decreased efficiency at the stand level. An alternate hypothesis was suggested by Binkley et al. (2004), who proposed that severe competition may result in a small number of large trees obtaining a disproportionate amount of the resources and using them efficiently, whereas the remaining suppressed trees use resources inefficiently. This is also referred to as asymmetric competition (Schwinning and Weiner 1998). It is possible that this phenomenon also occurred within our study because of variation in the ratio of dominant to suppressed trees among stand BA levels. However, the apparent relationship in Fig. 6 must remain speculative because (i) Waring (1987) assumed a constant  $A_l/A_s$  to calculate GE, whereas the ratio is not necessarily constant for ponderosa pine (McDowell et al. 2002a, 2006) and (ii) because an assumption underlying this comparison is that the 7 m<sup>2</sup>·ha<sup>-1</sup> stand is an outlier. Regardless of the mechanism, it is clear that individual-tree and stand-level GE (calculated as BAI, NPP<sub>s</sub>, and VI per unit leaf area) increases with stand BA in northern Arizona ponderosa pine forests, but it remains to be determined if there is a relationship between GE and LAI.

### Resin flow

RF was negatively related to GE in our regional analysis of five studies, counter to the expectations based on the traditional concept that increasing GE results in improved resistance against bark beetles. As noted earlier, this discrepancy is probably due to the false assumption of constant  $A_l/A_s$  when calculating GE in previous studies. However, a more important result is that the best predictor of constitutive RF in ponderosa pine stands of northern Arizona was simply BAI (Fig. 8B). BAI measures carbon allocation to stem tissue that contains resin ducts, such as new xylem and phloem, and hence, it is logical that this parameter should be well correlated with RF. For example, phloem thickness is strongly and directly correlated with BAI in ponderosa pine (Zausen et al. 2005). BAI is also a better parameter for predicting RF than GE because it is simple and fast to measure using only an increment core, ruler, and diameter tape, and thus, it is hard to measure incorrectly. GE, on the other hand, has assumptions associated with the utilization of allometric equations developed off site that may

not be entirely accurate for the sites of interest. Stand BA may also be a strong predictor of RF. The relationship between BA and RF is strong if we do not consider the RF data from Zausen et al. (2005) that we converted from 24 h RF collections to 7 day values (see Methods), a conversion that may have errors. Stand BA and BAI data exist from standard mensurational data collected on regionwide scales such as by timber producers or federal inventory (e.g., the USDA's Forest Inventory and Analysis Program). We recommend that forest managers and scientists interested in a simple and fast prediction of constitutive RF consider using BAI.

The similar methods of measuring RF in all five studies in the regional analysis allowed us to examine broad-scale relationships between RF and BAI that were not previously possible. The finding that RF increased strongly with BAI in the regional analysis is not consistent with another study of ponderosa pine (Zausen et al. 2005) that included a much smaller range in BAI and reported that trees with low BAI in unthinned stands had slightly greater RF than trees of similar size with higher BAI in lightly thinned stands. A possible explanation for the results in Zausen et al. (2005) is a trade-off in carbon allocation between growth (i.e., BAI) and defense (i.e., RF) whereby water stress in unthinned stands limits carbon allocation to growth more than defense (Dunn and Lorio 1993). Our analysis suggests that, although trade-offs in carbon allocation may cause small differences in ponderosa pine constitutive RF (see Fig. 8B, open triangles), the more important factor regulating RF regionally is carbon allocation to growth of tissues rich in resin ducts, such as phloem and new xylem. In other words, BAI is well correlated with RF in cases where a large range of BAI exists, such as in regional settings.

The lack of correlation between overstory LAI and RF is consistent with our observation that growth and GE were not correlated with LAI. It appears that site LAI is somewhat decoupled from growth or constitutive resin defense, presumably because LAI alone is not an ideal predictor of carbon assimilation or allocation (Smith and Long 1989). Again, actual measures of growth such as BAI are clearly a better index of RF than indirect parameters such as LAI because of the direct tie to carbon allocation to stemwood. Also noteworthy was the observation that RF was higher in lower density stands (Fig. 8A). This result is consistent with the notion that trees within lower density stands should have greater resources to allocate against insect attack (Christiansen et al. 1987) and empirical observations that probability of bark beetle attack increases with stand density for ponderosa pine (Negron 1997).

### Conclusions

Thinning treatments to reduce stand BA in southwestern ponderosa pine forests often increase growth per tree; however, they do not appear to increase growth per leaf area, or GE. Growth per unit leaf area at the individual-tree and stand levels declined with increasing BA regardless of the numerator used to estimate growth (BAI, stemwood NPP, or VI). LAI of understory grasses and forbes increased dramatically with decreasing stand BA. Total LAI (overstory plus understory) showed no clear pattern with stand BA; however, it does appear that the lowest BA stands were un-

able to support an LAI as high as the other treatments because of low overstory stocking and the inability of the understory vegetation to compensate for the low overstory LAI. RF was negatively correlated with GE, opposite the traditional concept of GE and insect resistance. Measuring leaf area of overstory trees directly, or by using leaf area/sapwood area allometrics developed across a range of stand densities, is necessary for accurate GE estimates in thinning trials. RF was negatively correlated with stand density, supporting the idea that thinning reduces the threat of bark beetle attack. Most importantly, RF was strongly correlated with BAI, allowing managers and scientists a simple, direct, and accurate index of constitutive resin defenses against bark beetles.

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