Tradeoffs in Overstory and Understory Aboveground Net Primary Productivity in Southwestern Ponderosa Pine Stands

Kyla E. Sabo, Stephen C. Hart, Carolyn Hull Sieg, and John Duff Bailey

Abstract: Previous studies in ponderosa pine forests have quantified the relationship between overstory stand characteristics and understory production using tree measurements such as basal area. We built on these past studies by evaluating the tradeoff between overstory and understory aboveground net primary productivity (ANPP) in southwestern ponderosa pine forests at the landscape level and over a gradient of stand structural types and burn histories. We measured overstory and understory attributes in 2004 and 2005 in four stand structural types (unmanaged, thinned, thinned and burned, and low basal area thinned and burned) relative to a stand-replacing wildfire site. Thinning alone and with prescribed burning reduced stand-level wood and total tree production relative to unmanaged stands. Understory (herbaceous) ANPP was highest in wildfire stands and low basal area thinned and burned plots but did not differ among the other stand structural types, apparently because of high residual basal area and relatively uniform tree spacing. Contemporary ponderosa pine forests are low productivity ecosystems that exhibit a threshold response between reductions in tree density and increases in understory production at ~5.9 m^2 ha. We calculated the slope of the relationship between tree and herbaceous ANPP to be −0.14, which was lower than the values we estimated from other, more productive savanna ecosystems. Our results suggest that to maintain more fire-resistant and hence sustainable southwestern ponderosa pine ecosystems, tree densities need to be substantially reduced from contemporary levels. Large, landscape-level reductions in tree density will decrease total ecosystem production of this forest type, but this reduction will probably be small relative to ecosystem production losses after widespread, stand-replacing wildfires. FOR. SCI. 54(4):408–416.

Keywords: aboveground tree production, aboveground understory production, basal area, thinning and prescribed burning, northern Arizona

STRUCTURAL AND FUNCTIONAL COMPONENTS of ponderosa pine (*Pinus ponderosa* P.C. Lawson var. *scopulorum* Engelm.) forests in the American Southwest have changed significantly owing to the introduction of livestock grazing, selective logging, and exclusion of frequent surface fires (Cooper 1960, Waltz et al. 2003, Fulé et al. 2005). Consequences of these anthropogenic influences include reduced understory cover and production under more homogeneous and denser pine stands dominated by a younger cohort of trees (Arnold 1950, Covington and Sackett 1992, Savage et al. 1996). Current tree densities (trees/ha) in this region have been estimated to be 40–50 times greater than before European settlement (Covington and Moore 1994, Covington et al. 1997). This increase in tree density has contributed to decreased understory productivity owing to lower light levels and reduced below-ground resource availability (Moore and Deiter 1992, Uresk and Severson 1998, Naumburg and DeWald 1999). Understory vegetation has been replaced by dense mats of slowly decomposing pine needles that have relatively low quality litter (high lignin concentration and high carbon to nitrogen mass ratio), which results in low rates of carbon and nitrogen cycling (Allen et al. 2002, Hart et al. 2006).

Although previous studies have shown concomitant relationships between aboveground tree (i.e., overstory) measurements and herbaceous (i.e., understory) productivity, few studies have assessed tradeoffs in productivity between overstory and understory components or measured the aggregate productivity of both these components under contrasting stand structural types that result from varying management histories. Previous research has generally used overstory measurements such as basal area, canopy cover, and stand density index as predictive variables of understory productivity (Moore and Deiter 1992, Uresk and Severson 1998, Peek et al. 2001). Even in those studies in which overstory and understory productivity both were measured, the researchers did not evaluate the tradeoffs in productivity but rather how the aggregate productivity (i.e., overstory plus understory) is influenced by abiotic factors and stand age (Grier et al. 1981, Comeau and Kimmins 1989, Coble et

Kyla E. Sabo, School of Forestry, PO Box 15018, Northern Arizona University, Flagstaff, AZ 86011-5018—Phone: (510) 299-3737; Fax: (928) 556-2130 c/o Carolyn Hull Sieg; Rhea10@aol.com. Stephen C. Hart, School of Forestry and Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011—Steve.Hart@nau.edu. Carolyn Hull Sieg, US Forest Service, Rocky Mountain Experiment Station, 2500 S. Pine Knoll Dr., Flagstaff, AZ 86011; csieg@fs.fed.us. John Duff Bailey, Department of Forest Resources, Peavy Hall 235, Oregon State University, Corvallis, OR 97331-5703John.Bailey@oregonstate.edu.

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al. 2001). Historically in southwestern ponderosa pine forests, the relationship between overstory and understory productivity favored grass-dominated meadows interspersed with patches of trees (Pearson 1950, Cooper 1960). The productive understory supported low-intensity surface fires every 2–20 years (Pyne et al. 1996), and the higher quality of understory litter (lower lignin concentration and lower carbon to nitrogen ratio) than pine litter stimulated decomposition and nutrient release for plant growth (Hart et al. 2005). Present day forests support dense stands of ponderosa pine with small fragmented patches of grass openings that have resulted in decreased rates of litter decomposition and greater risk of stand-replacing wildfires (Covington et al. 1997, Allen et al. 2002, Kaye et al. 2005).

Southwestern ponderosa pine ecosystems have evolved with fire as a natural disturbance agent, and past fires affected the relationship between overstory and understory (Covington et al. 1997, Hart et al. 2005). Thinning in combination with prescribed fire is being used currently to both reduce tree density in dense forests and restore a natural disturbance regimen to these forests. Desired indirect effects of these treatments include increased cover and productivity of herbaceous understory vegetation to levels approaching that of pre-European settlement (White et al. 1991). Prescribed burning in stands with a high tree basal area of >40 m^2 ha has led to either no change or small increases (i.e., 14 kg ha) in herbage production that can be sustained for only a few years after burning; however, prescribed burning in stands with basal areas approaching presettlement levels (<15 m^2 ha) generally has lead to much greater increases in understory productivity (Harris and Covington 1983, Andariese and Covington 1986, Wienk et al. 2004). In contrast to low-intensity prescribed fires, stand-replacing wildfires greatly enhance understory productivity, especially in the first few years after fire, owing to shifting tree-dominated ecosystems to grass-and shrub-dominated ecosystems (Merrill et al. 1980, Covington et al. 1997, Keeley et al. 2003, Wang and Kemball 2005).

The Stand Treatment Impacts on Forest Health (STIFH) study was designed to quantify current and future conditions of ponderosa pine forests varying in stand structure and burn history across northern Arizona (Bailey et al. 2000). The study design includes four stand structural types: unmanaged (range of basal area 23–89 m^2 ha), commercially thinned (11–30 m^2 ha), thinned and burned (5–36 m^2 ha), and stand-replacing wildfire (0 m^2 ha). The objectives of our study were to quantify tradeoffs in overstory and understory production under these contrasting stand structural types, and to compare these production responses to those from treatments designed specifically to restore the structure and function of ponderosa pine forests to presettlement conditions (Kaye et al. 2005). We hypothesized that tree aboveground net primary productivity (ANPP) would not be significantly different in treated stands than in unmanaged stands because of the low amount of basal area removed during the thinning treatments that generally occurred in these and other southwestern ponderosa pine stands before the initiation of more "restoration-driven" treatments (Covington et al. 1997). Furthermore, we hypothesized that differences in herbaceous ANPP between thinning or thinning and burning stands and unmanaged stands would also not be significantly different given the modest decreases in tree basal area resulting from these treatments; however, we predicted large increases in herbaceous ANPP in the wildfire sites because of the complete elimination of competition for resources with trees (Campbell et al. 1977, Uresk and Severson 1989, Crawford et al. 2001).

Methods

Study Sites and Design

Our study sites were located near Flagstaff, Arizona, USA (35.12°N, 111.39°W) in Coconino National Forest (Figure 1), at elevations ranging from 2,160 to 2,440 m. Most soils are basalt derived and classified as either Typic Argiborolls or Mollic Eutroboralfs (Miller et al. 1995). Part of one stand in the thinned and burned stand structural type was on soil that was derived from a limestone parent material, but limestone soils were only 30% of the total stand area and measures of soil nitrogen availability were similar in this stand to those in comparable stands on basalt-only parent materials (Grady and Hart 2006). Mean annual precipitation is 57 cm, most of which is received as late summer rain and winter snow (Western Regional Climate Center 2006). Total annual precipitation in the years of study was 40 cm for October 2003 to September 2004 (hereafter referred to as 2004), and 84 cm for October 2004 to September 2005 (hereafter referred to as 2005) (Figure 2).

The study stands were 20–80 ha in size and were established in 1998 to represent four common stand structural types with varying management histories (Bailey et al. 2000). Unmanaged stands had not been managed with either thinning or prescribed burning for 30 years. Commercially thinned and thinned and burned stands were mechanically

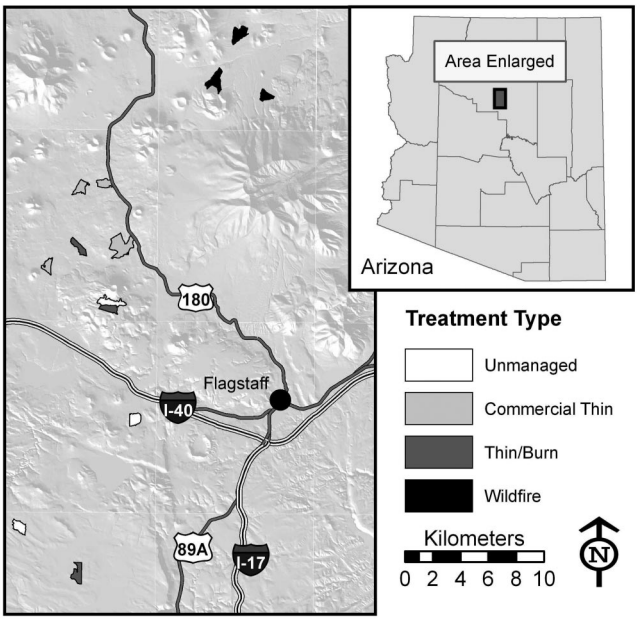

Figure 1. Locations of the unmanaged, commercially thinned, thinned and burned, and wildfire stand structural types in the Coconino National Forest near Flagstaff, Arizona, USA.

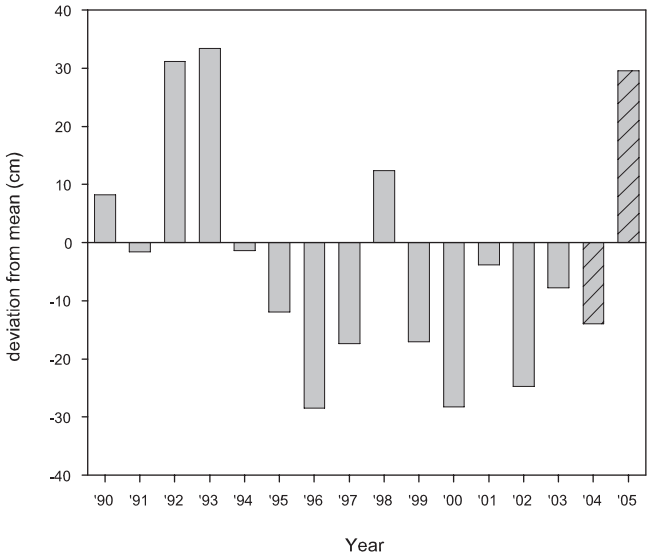

Figure 2. The deviation from mean annual precipitation during the 2 study years (hatched marks) and previous 14 years, based on data collected at the Flagstaff Airport from 1950 to 2005 (Western Regional Climate Center, 2006).

thinned from below followed by a broadcast burn of scattered logging slash and ground fuels between September and November by the US Forest Service. Flame heights were no greater than 40 cm. Commercially thinned stands were thinned between 1988 and 1992, thinned and burned stands were thinned between 1991 and 1995 and burned between 1993 and 1999, and wildfire stands were selected in areas severely burned in a 1996 wildfire that burned 5,000 hectares (Crawford et al. 2001). These high-severity wildfire stands were included in this study because they exemplify the eventual state that these forest ecosystems will reach if stand density and fuel loads are not greatly reduced (Grady and Hart 2006). This project was designed using a retrospective approach to quantify long-term effects of these silvicultural treatments distributed over a large area by randomly selecting stands treated by silvicultural methods and exposed to wildfire before initiation of our research (750 km^2) (Figure 1). In 2004, we randomly selected a subset of 16 stands that represented the four structural types. Within each of these 16 stands, 10 permanent 20-m $\times$ 20-m overstory tree plots were established on a 150- or 200-m grid, for a total of 160 plots of all stand structural types. We selected 13 of these 16 stands for sampling understory attributes to minimize variability in basal area across stands and established between two and six understory plots, 20 m $\times$ 50 m in size, that overlapped existing permanent overstory plots. A total of 28 plots were established, which were accessible to livestock and native ungulate grazing during the study.

In 2005, we added 12 additional understory plots (20 m $\times$ 50 m) in areas with low overstory basal area to capture stand densities between those of the common moderate-to-high basal area of traditionally thinned stands and complete lack of overstory on wildfire sites (Table 1). These low basal area plots were established within two of the thinned and burned stands and had a mean basal area of 5.9 m^2 ha (ranged from 2.4 to 13.1 m^2 ha). The 20-m $\times$ 50-m plots were randomly selected from a larger pool of 24 potential plots that fell within this basal area range, and we maintained the same 150- to 200-m distance between plots as in the other stand structural types. These plots were also accessible to livestock and native ungulate grazing.

Aboveground Tree Productivity

We remeasured the diameter of each tree >7.6 cm in dbh (1.4 m height) within the 20-m $\times$ 20-m plots and used these trees to calculate basal area and tree density (Bailey et al. 2000). Trees <7.6 cm in diameter were not considered because the allometric equations we used for estimating aboveground biomass were not developed for trees in this size class and they underestimate stemwood by >50% (Kaye et al. 2005). Trees with diameters <7.6 cm comprised only 0.09% of the biomass in our study and therefore have a limited effect on overall stand biomass and ANPP estimates. Trees were initially measured between 1998 and 2001, and were measured again in 2004. Allometric equations were used to calculate aboveground tree biomass for initial measurements (1998–2001) and the remeasurement (2004). These equations relate dbh to biomass of various tree components (stem wood, stem bark, live and dead branch wood and bark, and foliage) and were developed locally (Kaye et al. 2005).

Tree litterfall was collected from June 2003 to June 2004. Each plot had one randomly placed litter trap (0.065 m^2). Litter samples were collected twice per year over a 2-year period, and contents were dried for 48 h at 70°C and weighed. Foliar productivity was calculated as the sum of the increase in live foliar biomass plus nonwoody tree litterfall. ANPP of trees was calculated from the allometric equations by determining changes in total aboveground biomass over time from the two separate biomass estimates plus these measurements of tree nonwoody litterfall (Kaye et al. 2005). Woody litterfall was excluded from ANPP estimates because wood turnover was accounted for in the allometric equations (Kaye et al. 2005). Additionally, we calculated net aboveground production per tree to quantify

Table 1. Basal area, tree density, and tree diameter for each southwestern ponderosa pine stand structural type

Stand type	Basal area (m^2/ha)	Tree density (trees/ha)	Tree diameter (cm)
Unmanaged	34.9 (2.2) c	814.9 (77.7) c	20.7 (5.4) a
Commercially Thinned	24.5 (2.6) b	391.2 (70.5) bc	27.0 (5.6) ab
Thinned and Burned	14.2 (1.1) a	214.9 (13.5) bc	27.9 (4.1) b
Low Basal Area Thinned and Burned	5.9 (0.7) a	68.8 (14.6) a	32.1 (5.8) b

Data are mean (SE). Numbers within the same column followed by similar letters did not differ significantly ($P = 0.05$).

the mean tree growth, calculated by dividing ANPP per plot by the number of trees in the plot.

The low basal area thinned and burned plots added in 2005 did not have initial dbh measurements from 1998, so we estimated tree radial growth from increment cores taken in 2005. We extracted three short cores oriented north and 120° apart at dbh from each tree in the 20-m × 20-m plots. We verified the accuracy of this technique with a comparison sample of such cores from 10 trees each of the other structural types. These short cores were mounted and surfaced; annual radial growth from 1998 to 2004 was recorded to the nearest 0.01 mm on an incremental measuring stage (Kaye et al. 2005). We found biomass equations and increment cores for estimating diameter increment to be highly correlated (linear regression: $R^2 = 0.99$, $P < 0.001$, $n = 30$). Similarly, litterfall was also not collected on these low basal area thinned and burned plots. We therefore estimated litterfall in these plots using a linear relationship between stand basal area and annual litterfall from the other stands ($R^2 = 0.56$, $P < 0.001$, $n = 2$).

Aboveground Understory Productivity

Aboveground herbaceous productivity was estimated by sampling aboveground herbaceous tissue at peak standing crop in August of 2004 and 2005 in the original 28 plots and in 2005 in the low basal area thin and burn plots (Bonham 1989). Two 50-m transects were established along the outside of each plot. Total biomass of herbaceous species was estimated by clipping plants to ground level in 10 0.25-m^2 circular frames randomly located within a 2-m wide strip outside each plot. Herbaceous biomass was clipped on the outside of the plot so as not to compromise the herbaceous cover and richness estimates that were being made inside the plot as part of a different study (Sabo 2006). Herbaceous vegetation clipped in 2004 was avoided in 2005. The clippings were sorted by species in the field, and then dried in an oven at 70°C for 48 hours and weighed.

Statistical Analyses

Data were tested for normality and homogeneous variance assumptions for analysis of variance (ANOVA) and linear regression using JMP 5.1.2 statistical software (SAS 2002–2004). Homogeneous variances were evaluated using Levine's test (Neter et al. 1996). We used ANOVA to test for significant differences ($P = 0.05$) in aboveground tree productivity, productivity of total tree foliage and wood, and aboveground productivity per tree among the three stand structural types with overstories (unmanaged, commercially thinned, and thinned and burned stands). When significant differences among stand structural types were indicated, we used Tukey's multiple comparison to separate response variable means among stand structural types. We also used ANOVA to test for differences in aboveground herbaceous productivity among all four stand structural types, followed by Tukey's test. Simple linear regression analysis was used to examine the relationship between 2-year (2004 and 2005) mean aboveground herbaceous productivity and tree productivity across unmanaged, commercially thinned, thinned and burned, and wildfire stand structural types. However, because we added the low basal area plots in 2005, we compared aboveground tree productivity to aboveground herbaceous productivity using only 2005 herbaceous productivity data when including these plots in our analyses. Normality of the residuals was evaluated using a Shapiro-Wilks test, which showed no significant deviation from normality.

Results

Foliar productivity was 50% higher in unmanaged stands than in thinned stands ($P = 0.04$) but did not differ between commercially thinned and thinned and burned stands (Table 2). Mean foliar productivity ranged from 1,506 kg ha^{-1} $year^{-1}$ in unmanaged stands to 1,034 kg ha^{-1} $year^{-1}$ in commercially thinned stands to 833 kg ha^{-1} $year^{-1}$ in thinned and burned stands. There was no significant effect of stand structural type on wood ($P = 0.18$) (Table 2) or aboveground tree productivity (i.e., foliar plus wood; $P = 0.51$). Mean wood productivity ranged from 1,895 kg ha^{-1} $year^{-1}$ in unmanaged stands to 2,376 kg ha^{-1} $year^{-1}$ in thinned and burned stands. Mean aboveground tree productivity ranged from 3,514 kg ha^{-1} $year^{-1}$ in commercially thinned stands to 3,210 kg ha^{-1} $year^{-1}$ in thinned and burned stands (Table 2).

The ratio of wood to aboveground tree productivity differed ($P = 0.02$) among stand structural types (Table 2). Wood productivity/aboveground tree productivity was lower in unmanaged stands than in commercially thinned and thinned and burned stands, but there was no difference between commercially thinned and thinned and burned stands. Wood productivity averaged 55% of the aboveground tree productivity in unmanaged stands and averaged 72 and 73% in commercially thinned and thinned and burned stands, respectively.

Foliar production per tree was similar among stand structural types ($P = 0.18$) (Table 3). In contrast, wood and

Table 2. Foliar, wood, and total aboveground (i.e., foliar plus wood) overstory tree productivity in each southwestern ponderosa pine stand structural type

Stand type	Foliar productivity	Bole wood productivity	Wood productivity	Aboveground productivity	Ratio of wood to to total productivity (%)
			(kg/ha/yr)		
Unmanaged	1506 (203) b	1481 (167) b	1895 (212) a	3402 (364) a	55% (10) a
Commercially Thinned	1034 (98) ab	1930 (119) ab	2481 (151) a	3514 (182) a	72% (8) b
Thinned and Burned	833 (156) a	1850 (88) a	2376 (110) a	3210 (139) a	73% (9) b

Data are mean (SE). Numbers within the same column followed by similar letters did not differ significantly ($P = 0.05$).

Table 3. Foliar, wood, and total aboveground tree production per tree in each southwestern ponderosa pine stand structural type

Stand Type	Foliar production	Bole wood production	Wood production	Aboveground tree production
	(kg/tree/yr)			
Unmanaged	2.8 (0.3) a	2.4 (0.4) a	3.0 (0.5) a	5.5 (0.4) a
Commercially Thinned	4.0 (0.4) a	6.5 (1.0) b	8.4 (1.3) b	12.4 (1.5) ab
Thinned and Burned	8.1 (2.9) a	11.0 (0.8) c	13.5 (1.1) c	20.8 (3.7) b

Data are mean (SE). Numbers within the same column followed by similar letters did not differ significantly ($P = 0.05$).

aboveground (i.e., foliar plus wood) production per tree differed significantly among stand structural types ($P < 0.001$) (Table 3). Thinned and burned stands had 60% higher wood production per tree than unmanaged stands, with thinned stands having wood production statistically similar to that in thinned and burned and unmanaged stands (Table 3). In addition, thinned and burned stands had significantly higher total productivity per tree than unmanaged stands ($P < 0.01$), with that in thinned stands being statistically similar to that in unmanaged and thinned and burned stands (Table 3).

Aboveground understory productivity ranged from 72.3 to 255.8 kg ha^{-1} year^{-1} and was similar among unmanaged, commercially thinned, and thinned and burned stand structural types but was more than 2-fold greater in wildfire stands (mean 552.1 kg ha^{-1} year^{-1}, $P = 0.003$) (Figure 3). The ratio of aboveground herbaceous productivity to total ANPP (herbaceous plus tree productivity) was highest in wildfire stands because there was no tree productivity. Aboveground understory productivity constituted between 1 and 9% of total ANPP in unmanaged, commercially thinned, and thinned and burned stands and did not differ significantly among these stand structural types. Two-year mean aboveground understory productivity was negatively correlated with aboveground tree productivity measured over several years across these three stand structures ($R^2 = 0.71$, $P < 0.001$).

In 2005, aboveground understory productivity was higher in the low basal area thinned and burned plots (525.6 kg ha^{-1} year^{-1}, mean basal area 5.9 m^2 ha) (Table 1) than in unmanaged and commercially thinned stands ($P < 0.001$) but was similar to productivity in wildfire sites. Aboveground herbaceous productivity in 2005 across all stand structural types, including the low basal area thinned and burned plots, was negatively correlated with aboveground tree productivity measured over multiple years ($R^2 = 0.90$, $P < 0.001$) (Figure 4).

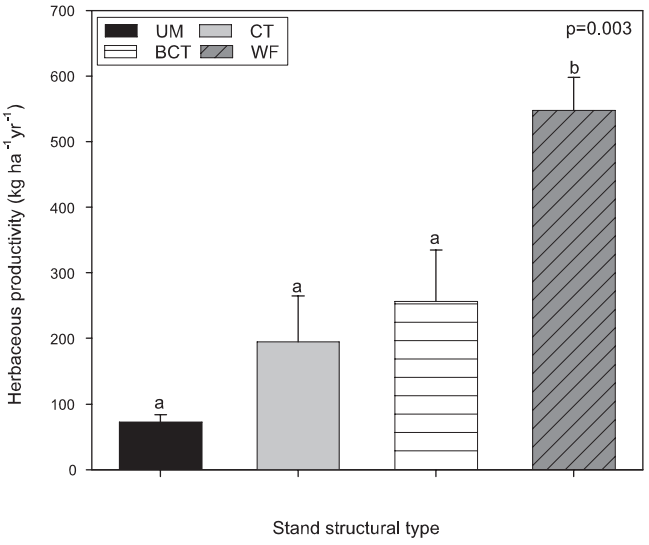

Figure 3. Mean aboveground herbaceous productivity across southwestern ponderosa pine stand structural types (UM, unmanaged; CT, commercially thinned; BCT, thinned and burned; WF, wildfire). Vertical lines denote 1 SEM. Means with different letters differed statistically ($P = 0.05$).

Discussion

Tree and herbaceous understory productivities have been affected by historical management of southwestern ponderosa pine forests, resulting in dense forests that fall outside the historical range of natural variability (Swetnam et al. 1999, Moore et al. 2006). Commercial thinning operations, either alone or in combination with prescribed fire, in this forest type up until the early 1990s generally resulted in small decreases in stand basal area and tree density, characteristic of the stands we studied. More recently, restoration-driven treatments have been implemented that involve much greater reductions in stand basal areas and tree density and are designed with the objective of restoring stand structure and function to approximate pre-EuroAmerican settlement conditions (Covington et al. 1997).

Despite reductions in basal area and prescribed burning

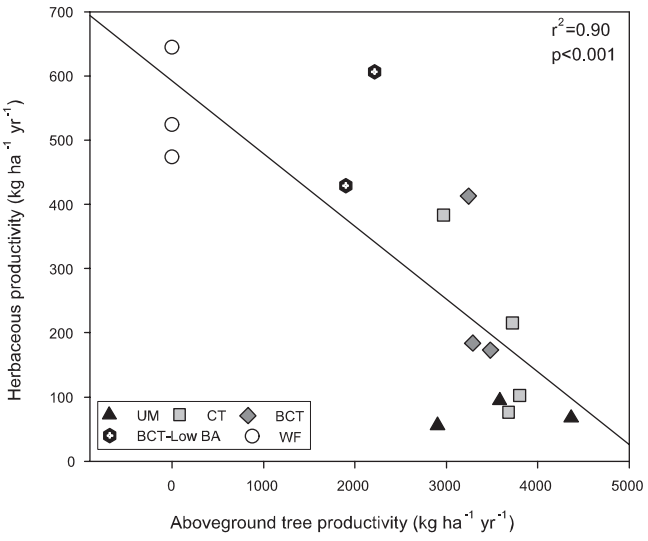

Figure 4. Relationship between 2005 aboveground herbaceous productivity and mean aboveground tree productivity across southwestern ponderosa pine stand structural types (UM, unmanaged; CT, commercially thinned; BCT, thinned and burned; BCT-Low BA, low basal area thinned and burned; WF, wildfire.

within our sites, there was no significant difference in stand ANPP between treated (both commercially thinned and thinned and burned) and unmanaged stands. Even though treated stands were producing two to more than four times more wood and total aboveground production per tree than in unmanaged stands, substantially higher tree densities in the unmanaged stands resulted in similar stand-level wood productivity and ANPP among the stand structural types. In contrast, foliar productivity was 50% higher in unmanaged stands than in thinned and burned stands, with commercially thinned stand having intermediate values; foliar productivity per tree was nevertheless similar among stand structural types. Apparently, ponderosa pine trees have much greater plasticity in wood production than foliar production across a fairly broad range in stand densities and diameters. Such plasticity in wood production may help explain the ability of even old-growth ponderosa pine trees to increase diameter growth after tree thinning (Kolb et al. 2007).

The lack of stand-level increases in tree ANPP in our retrospective study was not surprising, given that some previous studies have found either no significant increase or a decrease in tree ANPP after thinning of southwestern ponderosa pine stands in experimental settings. For instance, Kaye et al. (2005) reported no significant difference in tree ANPP 2–3 years after heavy ("restoration") thinning in ponderosa pine stands near our study sites. In their study, basal area was reduced to a degree similar to that in our study, but tree density was reduced to a much greater degree (from about 4,100 to about 150 trees ha). In contrast, Hart et al. (2006) recently reported about a 50% decrease in tree ANPP 7 years after an operational restoration thinning treatment in a ponderosa pine stand also near our study area. In that study, stand basal area was reduced by almost 80% (39.7 to 8.5 m^2 ha), and tree density was reduced to a greater degree than in the present study (800 to 91 trees ha).

Two consistent patterns emerge from these thinning studies in southwestern ponderosa pine. First, residual trees of the stand, regardless of age, increase their individual rates of ANPP in response to the thinning treatment (Kolb et al. 1997, Hart et al. 2006). Whether the stand-level ANPP response is increased, decreased, or unchanged depends on numerous factors including the intensity and type (tree sizes removed) of thinning, as well as the time period over which the response has been observed. Second, the ratio of wood to total tree aboveground productivity increases after thinning. We found that >70% of the total tree ANPP was due to wood production in our treated stands compared with only 55% in the unmanaged stands. Similar increases have been found in the previous studies noted above (i.e., 9 to 19% and 24 to 33% in unmanaged and restored stands, respectively [Kaye et al. 2005] and 31% and 42% in unmanaged and restored stands, respectively [Hart et al. 2006]). Greater wood productivity relative to ANPP in thinned stands suggests increases in growth efficiencies (Waring and Schlesinger 1985) of residual trees, apparently attributable to increases in resource availability to individual trees (e.g., light, water, and nutrients) (Ronco et al. 1985, Waring and Schlesinger 1985, Kolb et al. 1997, 2007, Kaye et al. 2005, Hart et al. 2006).

We hypothesized that understory (herbaceous) ANPP would not be significantly higher in treated stands than in unmanaged stands because of the relatively modest reductions in tree basal area from these treatments. Consistent with this hypothesis, we found no significant difference in herbaceous ANPP among unmanaged and treated stands. We also predicted large increases in herbaceous ANPP in the wildfire sites because of the complete elimination of competition for resources with trees. In support of that prediction, we found that aboveground herbaceous productivity was more than two-fold higher on wildfire sites than in the other stand structural types. This increase may be due to elevated levels of soil nitrogen availability in these wildfire sites compared with the other stand structural types, as well as increased light and soil water availabilities (Grady and Hart 2006). Apparently, tree basal area needs to be reduced to <5.9 m^2 ha (the mean value for the low basal area thinned and burned stands) before a significant increase in herbaceous productivity can occur. Our findings that herbaceous ANPP in the low basal area thinned and burned plots was similar to that on the wildfire sites and significantly higher than that in the unmanaged and commercially thinned stands are consistent with this speculation. Furthermore, previous studies in ponderosa pine ecosystems have only shown differences in herbaceous ANPP among unmanaged, thinned, and thinned and burned stands when tree basal area was reduced to similar levels (14 m^2 ha [Uresk and Severson 1998] and 12 m^2/ha [Wienk et al. 2004]).

The spatial pattern of the residual trees in treated stands may also be an important factor controlling herbaceous growth response to overstory removal (Pase 1958, Anderson et al. 1969, Mitchell and Bartling 1991). For instance, Naumburg and DeWald (1999) found higher herbaceous productivity in stands in which ponderosa pine trees were spatially aggregated than in stands with more spatially homogeneous stand structures such as those used in our study. Historically in northern Arizona, ponderosa pine stands supported few large-diameter trees (>37 cm) that were aggregated into small groupings of 3n44 stems within areas ranging between 0.02 and 0.28 hectare, with large grass openings in between (Covington and Moore 1994). However, the impacts of selective large-diameter tree removal in the early 1900s and the more recent, light, mechanical-type thinning frequently applied to these stands, have resulted in dense stands of small-diameter trees with a fairly even spatial distribution. Hence, the lack of difference in herbaceous ANPP in our study between treated and unmanaged stands may be due to both a higher basal area and a more homogeneous tree cover in the stands we studied than in those studied previously.

Restoring southwestern ponderosa pine stands to pre-EuroAmerican settlement structure with higher herbaceous production probably will result in overall decreases in total ecosystem production (Kaye et al. 2005). Consistent with this hypothesis is our result that herbaceous ANPP constituted only 1 to 9% of the total ANPP (herbaceous + tree) in unmanaged, commercially thinned, and thinned and burned stands, and these values did not differ significantly among these stand structural types. Similar small proportions of

herbaceous to total ecosystem productivity have been reported in other southwestern ponderosa pine forests, even when belowground net primary productivity is also considered (e.g., Kaye et al. 2005). We examined the tradeoff in ANPP between the herbaceous understory and the tree overstory by regressing the 2-year mean herbaceous ANPP with the tree ANPP measured over several years. In this analysis, we included the wildfire sites as one of the end members of the tree-grass continuum. We found that these two components were strongly and negatively correlated. When we added the low basal area thinned and burned plots to our analysis (which forced us to compare only 2005 herbaceous ANPP to tree ANPP averaged over multiple years), we found an even stronger negative correlation. Analysis of the slope of this regression indicates that only about 140 g of aboveground herbaceous production is gained for every kg of aboveground tree production lost (ratio of understory ANPP to overstory ANPP = 0.14). Although previous studies have discussed this tradeoff in production in ponderosa pine forests, these other studies have used a surrogate of tree production (e.g., stand basal area or tree canopy cover), and hence a quantification of the tradeoff in ANPP between the two plant functional groups was not possible (Hart et al. 2005).

We analyzed data published from studies in other types of savanna-like forests to evaluate the generality of this plant functional group tradeoff in ANPP. Using data from longleaf pine (*Pinus palustris* Mill.)-wiregrass (*Aristida stricta* Michx.) savannas in the southeastern United States growing along a soil moisture gradient (Mitchell et al. 1999), we calculated a ratio of the understory (mostly herbaceous) ANPP to the tree overstory ANPP of approximately 0.38 (from Figure 4 in the publication). Similarly, using data from a chronosequence of fire-return frequencies (Reich et al. 2001) in oak-savannas in Minnesota, we calculated a ratio of herbaceous understory ANPP to woody plant ANPP (mostly *Quercus* spp. in the overstory, but also including some woody shrubs) of about 0.20 (from Figure 3 in the publication). In all three ecosystem types, the ratio is much less than 1, suggesting that overstory (woody) plants are better at utilizing site resources than herbaceous plants in the understory (Chapin et al. 2002). The ratio from southwestern ponderosa pine forests is lower (greater tradeoff in production) than that in these other more productive savannas, perhaps indicating that as resource availability increases the relative functional capacity of the understory vegetation for capturing site resources increases. Unknown differences in herbivory of both understory and overstory components among these ecosystems may influence this relationship, but typically grazing consumes only a relatively small proportion ($\sim$10–20%) of ecosystem ANPP (Cyr and Pace 1993, Cebrian 1999). This tradeoff in production affects many other ecosystem processes besides the distribution and total amount of ecosystem productivity, including nitrogen cycling rates and ecosystem water balance (Hart et al. 2005). Furthermore, it affects the presence, abundance, and distribution of understory species in these forests, which has restoration and conservation implications (Moore et al. 2006).

Conclusions

Contemporary ponderosa pine stands have low ANPP relative to that of other forest types (Hart et al. 2006) and exhibit a strong tradeoff between herbaceous and tree production. In addition, current ponderosa pine forests have uncharacteristically high tree densities and low understory productivity, which has led to an accumulation of fuels and a homogenization of canopy cover as well as an increase in the likelihood of large, stand-replacing wildfires (Covington and Moore 1994, Swetnam et al. 1999, Brown et al. 2004). This contemporary fire regimen contrasts greatly with the frequent, low-severity surface fire regimen that occurred pre-EuroAmerican (Covington and Moore 1994, Covington et al. 1997). Wildfires greatly reduce ecosystem ANPP both immediately after the fire and for decades, if not centuries, to come because of slow rates of reestablishment and inherently low net primary productivity of these ecosystems (Hart et al. 2005, 2006, Dore et al. 2008).

The long-term sustainability of high basal area stands is questionable, especially across large landscapes, because of their susceptibility to stand-replacing fires and other forest health concerns (Covington et al. 1997). Low basal area stands are characterized by lower ANPP compared with high basal area stands but support understory productivity equal to wildfire plots and are likely to be more resistant to stand-replacing wildfires. The low intensity of the thinning and thinning and burning treatments investigated in our study might have enhanced the resistance of treated stands to passive or active crown fires by removing ladder fuels and some coarse woody debris within the stands (Brown et al. 2003, Fulé et al. 2004). However, the treated stands remain especially susceptible to conditional crown fires that spread into the stands from adjacent stands, owing to the continuous overstory canopy cover and interlocking tree crowns (Agee et al. 2000); therefore, both of these treatments remain at a higher risk of stand-replacing wildfire than the more open low basal area stands that have discontinuous overstory canopies.

Our study supports previous research suggesting that there is a threshold, rather than a continuous response of understory production to overstory removal in southwestern ponderosa pine forests. Our data suggest that basal area reductions to $\leq$5.9 m^2 ha are needed to enhance understory productivity substantially while sustaining a significant amount of overstory production with a high growth efficiency (Hart et al. 2005). If the goal is to maintain both the productivity and sustainability of ponderosa pine ecosystems in this region, the best approach may be to provide a mix of stand structural types across the landscape.

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