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Stand density and age affect tree-level structural and functional characteristics of young, postfire lodgepole pine in Yellowstone National Park

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ABSTRACT

More frequent fire activity associated with climate warming is expected to increase the extent of young forest stands in fire-prone landscapes, yet growth rates and biomass allocation patterns in young forests that regenerated naturally following stand-replacing fire have not been well studied. We assessed the structural and functional characteristics of young, postfire lodgepole pine (*Pinus contorta* var. *latifolia*) trees across the Yellowstone subalpine plateaus to understand the influence of postfire stand density and age on tree-level aboveground biomass (AB), component biomass (bole, branch, foliage), partitioning to components, tree-level aboveground net primary productivity (ANPP) and leaf area (LA). Sixty 24-year-old lodgepole pine trees were harvested from 21 sites ranging from 500 to 74,667 stems·ha⁻¹ for development of allometric equations to predict biomass, ANPP and LA. All traits increased nonlinearly with increasing tree basal diameter. Tree-level total AB and component biomass decreased with increasing stand density and increased with age when compared with measurements from 11-year-old trees. Bole partitioning increased with stand density, while foliage and branch wood partitioning declined. Tree-level ANPP and LA decreased significantly with stand density and age. Overall, our results indicate that stand density and age explain much of the variation in tree characteristics and that 24 years after fire, the initial postfire regeneration density is still exerting significant influence on the structure and function of individual trees.

1. Introduction

Expected climate-driven changes in disturbance regimes are likely to increase the frequency and severity of major disturbance events throughout the 21st century, thus increasing the importance of disturbance as a key determinant of ecosystem structure and function (Flannigan et al., 2009; Turner et al., 2013). Disturbances have large-scale impacts on ecosystem processes and exert significant influence on developmental trajectories (Attiwill, 1994; Turner et al., 2004; Kashian et al., 2006). Sustained alterations of disturbance frequencies have the power to shift ecosystems to qualitatively different states, characterized by substantial heterogeneity in structure and function (Bormann and Likens, 1979; Turner, 2005). Thus, understanding how disturbance patterns affect structural and functional characteristics of post-disturbance

ecosystems is critical to understanding changing ecosystem conditions.

In forested ecosystems in particular, warming temperatures and earlier snowmelt have lengthened fire seasons, leading to an increase in the frequency and severity of forest fires (Westerling et al., 2006; Bowman et al., 2009; Girardin et al., 2009; Qui, 2009). Fire regimes in boreal and subalpine forests are driven by climate, suggesting that changes in regional fire regimes and the accompanying vegetation shifts are likely to be sustained (Bessie and Johnson, 1995; Schoennagel et al., 2004; Littell et al., 2009). If inter-fire periods are shortened as predicted, young, fire-origin stands will increase in extent and importance.

Substantial variation in regenerating stand density (stems·ha⁻¹) following stand-replacing fire is a well-documented phenomenon and drives variation in patterns of biomass accumulation, partitioning, and productivity in fire-origin trees of the same age (Blevins et al., 2005; Jiménez et al., 2011; De las Heras et al., 2013). Increasing stand density has been shown to lead to reduced productivity, aboveground biomass, and leaf area of fire-origin trees (Reid et al., 2004; Blevins et al., 2005; Jiménez et al., 2011;

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De las Heras et al., 2013), and may also drive increased partitioning of biomass to bole wood relative to foliage and branch wood (Burkes et al., 2003; Blevins, 2004; Ares and Brauer, 2005). These trends suggest that trees in high density stands may demonstrate accelerated development relative to sparser stands, and that stand density may interact with stand age to influence tree-level characteristics. Trees regenerating on disturbed sites typically exhibit a rapid growth rate that eventually declines with age (Long and Smith, 1984; Gower et al., 1996). At the stand-level, the timing of the growth decline largely coincides with canopy closure and self-thinning. For individual trees, the timing of the decline in biomass accumulation may vary with canopy position and density (Smith and Long, 2001) but has generally not been well described. Additional data is needed to evaluate the long-term effects of variable stand density and age on tree development and to explain variation in development trajectories.

In this study, we investigate the effects of stand density and age on tree-level aboveground biomass, biomass partitioning and allocation, LA and ANPP of 24-year-old postfire lodgepole pine trees across the Yellowstone subalpine plateaus. The Yellowstone ecosystem experienced a series of large, stand-replacing fires during the summer of 1988 that created heterogeneous landscape patterns of regenerating lodgepole pine (*Pinus contorta* var. *latifolia*) forests (Turner et al., 1997, 2004). As a result of variation in prefire serotiny and burn severity, initial stem density in regenerating stands spanned six orders of magnitude and has led to substantial diversity in stand biomass and productivity (Kashian et al., 2004; Turner et al., 2004). To investigate patterns of tree-level structure and function related to stand density and age, we combine recent measurements with an extensive long-term data set of regenerating lodgepole pine stands in Yellowstone that have been observed since stand initiation following the 1988 fires (Turner et al., 2004). In addition to identifying trends in structural and functional characteristics related to age and stand density, we develop new, site-specific allometric equations to more accurately estimate tree-level total aboveground biomass (AB), component biomass, ANPP and LA of these 24-year-old trees. Finally, we compare the variation in structural and functional characteristics 11 years postfire with recent measurements (24 years postfire) to gain insight in to the long-term effects of regeneration density on tree-level structural and functional characteristics.

2. Methods

2.1. Study site

Yellowstone National Park (YNP) encompasses approximately 9000 km² primarily in the northwest corner of Wyoming, with portions of the park extending into Idaho and Montana. Over 80% of the park is dominated by lodgepole pine forests (*Pinus contorta* var. *latifolia* [Engelm. Ex Wats.] Critchfield) (Renkin and Despain, 1992). Our study area was focused on the forested portions of the Yellowstone subalpine plateaus that burned during the summer of 1988. The subalpine plateaus cover 15% of the park at elevations that range from roughly 2000–2700 m (Romme and Despain, 1989). Of the 252,900 ha of forests burned in 1988, 174,000 ha were located on the subalpine plateaus (Renkin and Despain, 1992; Turner et al., 2004). Climate across the plateaus is fairly consistent and is characterized by a short growing season and low mean temperatures. Mean annual temperature reported for the plateaus ranges from –7.6 to 9.6 °C and mean precipitation averages 61.7 cm with 548.4 cm of snowfall (Powell and Hansen, 2007). Plateau soils are primarily volcanic-origin rhyolites, characterized by low calcium and a sandy texture (Despain, 1990; Powell and Hansen, 2007). A smaller portion of the plateaus is underlain by andesite, a volcanic-origin soil dominated by clay (Despain, 1990).

Our harvest sites were selected from a series of 90 plots across the burned region that were first established in 1999. Biomass, LA, ANPP and stand density were initially estimated in all plots in 1999 and again in subsequent years for several subsets of plots (Turner et al., 2004). We utilized a subset of 21 of these plots in an effort to extend previous data sets and investigate changes in tree characteristics over time.

2.2. Field sampling

A total of 60 trees were harvested for the construction of allometric equations from 21 sites during the summer of 2012 (Table 1). Sites were selected to represent the range of post-fire stem densities across the Yellowstone plateaus and were separated into five density classes based on 1999 stem density (<1000 stems·ha⁻¹; 1000–5000 stems·ha⁻¹; 5000–10,000 stems·ha⁻¹; 10,000–30,000 stems·ha⁻¹; >30,000 stems·ha⁻¹). Four sites were included from each density class and were all located on similar substrate and at comparable elevations.

At each sampling location, plot center was located by previously-established GPS coordinates and the plot was delineated by three 50 m transects oriented in a north-south direction and spaced 25 m apart. Stand density was estimated by counting the number of stems within a 1-m belt along either side of each transect. These numbers were extrapolated to the entire 0.25 hectare plot to estimate stems·ha⁻¹. Three trees were then selected for harvest immediately outside of the plot to represent the smallest, intermediate and largest diameter trees in each stand. Basal diameter ranged from 1.60 to 20.5 cm with a mean of 6.74 cm (SD = 3.98, SE = 0.51) and a median of 5.70 cm. The basal diameter sampling distribution from harvested trees was consistent with that of a larger sample of trees measured for morphometry data (0.10–23.40 cm, *n* = 1123), and therefore likely representative of the range of diameters encountered in the postfire region. Trees were harvested at the root collar to capture all aboveground biomass. Basal diameter, DBH, total tree height and crown length were measured prior to division of components for subsampling (Table 2). The crown was then divided into equal thirds and the remaining basal bole weighed separately. All branches were

Table 1

Site characteristics for all 21 sites on the Yellowstone subalpine plateaus from which trees were harvested to develop allometric equations. Stand density (stems·ha⁻¹) is based on 2012 measurements, except for two sites for which stand densities are estimated from 1999 measurements (Turner et al., unpublished data). Across all other sites, stand density changed little from 1999 to 2012.

Stems·ha ⁻¹	Elevation (m)	Substrate	UTM coordinates
500	2535	rhyolite	526394 E 4899299 N
533	2433	rhyolite	528200 E 4910400 N
2433	2499	rhyolite	537625 E 4953870 N
2467	2469	rhyolite	538949 E 4954217 N
3167	2515	rhyolite	517063 E 4924840 N
3467	2384	rhyolite	534502 E 4915509 N
5333	2383	rhyolite	530886 E 4904678 N
6100	2423	rhyolite	535624 E 4914380 N
8167	2442	rhyolite	533157 E 4911736 N
9833	2440	rhyolite	559062 E 4931975 N
11167	2377	rhyolite	527329 E 4896594 N
12333	2427	rhyolite	528850 E 4909800 N
12933	2495	andesite	543993 E 4965097 N
13367	2399	rhyolite	532435 E 4907853 N
16467	2374	rhyolite	514809 E 4920611 N
18133	2490	rhyolite	536876 E 4951781 N
23000	2144	rhyolite	511621 E 4942311 N
51300	2487	rhyolite	536876 E 4951792 N
52800	2089	rhyolite	501643 E 4946704 N
56733	2065	rhyolite	501130 E 4948061 N
74667	2050	rhyolite	498928 E 4943590 N

Table 2
Attributes of 60 trees harvested for construction of allometric equations.

	Mean	Min	Max	SD
BD (cm)	6.7	1.6	20.5	3.9
DBH (cm)	4.7	0.4	14.0	3.0
Height (m)	3.6	1.2	6.7	1.3
Crown Length (m)	2.8	0.6	6.0	1.3
Crown width (m)	1.1	0.44	2.6	0.5

removed from each portion of the bole and a total weight for all branches associated with each crown third was obtained to the nearest 0.01 kg using Salter Brecknell ElectroSamson 10 kg (Model no. 816965000586) and 45 kg (Model no. 816965000609) hanging scales (Avery Weigh-Tronix, LLC). Each additional bole section was also weighed in the field. Foliage attached to the bole was removed from each bole portion and weighed separately.

Both 2012 and 2011 top growth were removed and weighed separately to aid in estimations of annual increment. A disk was cut from the base of each bole section (basal, lower third, mid third, upper third) as a subsample. Branch subsamples were obtained by selecting a single branch from each of the crown thirds that appeared representative of average branch size. After being weighed in the field, branch and bole subsamples, 2012 top wood and foliage, 2011 top wood and foliage and bole foliage associated with each third were enclosed in paper bags and transported back to the lab for processing.

2.3. Aboveground biomass, ANPP and LA

While still fresh, branch and top growth subsamples were separated into 2012 foliage, 2012 branch wood, 2011 foliage, 2011 branch wood, remaining foliage, remaining fine wood (<¼ inch in diameter) and all remaining wood greater than ¼ inch in diameter. Wet weights were taken for each component to the nearest 0.01 g. All samples were then dried to a constant mass at 65 °C in a So-Low 750F Laboratory Oven (Model no. OF275-5A) and dry weights were used to develop dry weight to wet weight ratios for each subsample. These ratios were applied to component wet masses to estimate total biomass of bole, branch wood and foliage for each crown third. Biomass values were subsequently summed to estimate total aboveground tree biomass, total bole biomass, total branch wood biomass and total foliage biomass.

Because current year (2012) growth was collected before the end of the growing season, the previous year's (2011) growth was used to estimate annual growth increment. The 2011 growth consisted of all stem wood, branch wood and foliage above the 2011 branch whorl and below the most recent branch whorl, all branch wood and associated foliage beyond the 2011 bud scars and before the 2012 bud scars, all bole wood after the 2010 and through the 2011 late wood and all radial wood growth on branches produced before 2011. To estimate bole wood contribution, we used calipers to measure diameter through the 2010 annual ring and diameter through the 2011 annual ring on each bole subsample (basal, lower third, mid third, upper third, base of last year's top wood). These values were used to estimate the volume of two tapered cylinders: one with a radius through the 2010 annual ring and a second cylinder with a radius through the 2011 annual ring. The volume of the smaller cylinder was subtracted from the volume of the larger cylinder to estimate the volume of bole wood produced during the 2011 growing season. This value was then used to estimate the proportion of total bole volume accounted for by 2011 growth. We applied this proportion to bole biomass and to all branch wood biomass produced before 2011 to estimate biomass of 2011 radial growth.

Because estimates of ANPP only considered annual increment and failed to account for losses to herbivory or litterfall, the values presented here are likely underestimates. However, previous work in this system suggests that losses to herbivory are minimal in young lodgepole pine and thus likely constitute a negligible portion of ANPP (Turner et al., 2004).

We calculated leaf area by measuring the width, length and mass of a sample of needle fascicles. Forty-five fascicles from each density class were selected to represent each crown third and each year of foliage production (2012, 2011 and remaining foliage; $n = 225$). Each needle within the fascicle was assumed to represent a sector in cross section with radius r . Total needle surface area was calculated following the equation for the surface area of a sector, as applied to pine needles by Johnson (1984):

$$SA = \left(2r + \frac{2\pi r}{n}\right)l \quad (1)$$

where r is equal to the width of the needle divided by two, n corresponds to the number of needles in each fascicle (two), and l is equal to the length of a needle. Total needle surface area was divided by two and reported as projected (one-sided) surface area.

Average fascicle weight for each crown third and year was then used to estimate the number of fascicles in each category for each tree. Total fascicle number was multiplied by average fascicle surface area for each crown third and year and summed to estimate projected leaf area for a given tree.

2.4. Allometric equation construction

Allometric equations for lodgepole pine have been developed for both mature (Pearson et al., 1984) and very young (Turner et al., 2004) trees, but these equations likely do not apply to 24-year-old trees. We constructed new, age-specific allometric equations by regressing our estimates of total tree-level aboveground biomass, component biomass, ANPP and LA against basal diameter, DBH and height. Predictors were selected using the best subsets method. To test the effect of stand density on allometric relationships, we also considered absolute stand density as a predictor. Stand density was not significant in any of the models, and was thus eliminated from further allometric equation development. Nonlinear equations were fit to untransformed data using a power function form. We also fit linear equations to log-transformed data to determine whether the multiplicative error associated with back-transformation of linear log-log equations would better characterize the variance in our data than the additive error assumed by power functions (Kerkhoff and Enquist, 2009).

All predictor variables were highly correlated, so a single predictor was selected for each model to eliminate multicollinearity. The best single predictor model was selected to correspond with the highest coefficient of determination (r^2). Goodness of fit for all models was evaluated based on a comparison of p -values and mean square of errors (MSE).

2.5. Statistical analysis

All statistical analyses were completed using Minitab 16© (Minitab Inc., 2010) and Program R (R Core Team, 2013). We used Akaike's Information Criterion (AIC) to compare the fit of power functions fit to untransformed data and functions fit to log-transformed data. To determine how our equations differ from those developed for 11-year-old lodgepole saplings (Turner et al., 2004) and mature lodgepole pines (Pearson et al., 1984), young and mature tree equations were applied to 24-year-old trees and model fit was compared using AIC. Mature tree equations were only available for bole, branch and foliage biomass, so not all of

Table 3

Summary statistics for all biomass, ANPP, LA, and partitioning estimates derived from sixty 24-year old lodgepole pine trees in Yellowstone National Park.

Component	Min	Max	Mean	SE	SD	CV
Aboveground biomass (g)	131	37412	5771	1007	7862	1.36
Bole biomass (g)	57	21637	3279	542	4230	1.29
Branch biomass (g)	6	9657	1131	254	1986	1.76
Foliage biomass (g)	28	9262	1361	241	1881	1.38
ANPP (g·year ⁻¹)	45	7050	1004	181	1321	1.32
LA (m ²)	0.54	18.55	2.97	0.54	3.98	1.34
Bole percent mass	28.26	84.92	63.88	1.64	12.79	0.20
Branch percent mass	2.59	37.26	13.46	1.01	7.89	0.59
Foliage percent mass	11.41	41.28	22.62	0.82	6.40	0.28

our equations could be compared with those developed for mature trees.

We used simple linear regression (SLR) to analyze the relationship between stand density and tree-level biomass, ANPP and LA. ANPP, LA, total aboveground and component biomass, and percent of biomass partitioned to aboveground components were regressed against \log_{10} (density) to identify density-driven trends. We also considered the effect of elevation, a weakly significant predictor. However, elevation is known to be highly correlated with postfire regeneration density (Tinker et al., 1993) and elevation effect was not determined to be different from the effect of stand density. Thus, elevation as a predictor was eliminated from further analyses.

In order to explore the relationship between aboveground biomass, ANPP, LA and stand age, one-way Analysis of Variance (ANOVA) was employed to test for differences between mean tree-level values for 11-year-old trees (Turner et al., 2004) and current values for 24-year-old trees. We also used ANOVA to test for differences in biomass allocation and partitioning to various tree components between 11-year-old and 24-year-old trees.

3. Results

3.1. Measured biomass, ANPP, LA and biomass partitioning

Total aboveground biomass and biomass of all tree components showed a wide range of values for all harvested trees, with all Coefficients of Variation > 1 (Table 3). The distributions for all variables were heavily skewed right (total AB $G = 2.37$, bole $G = 2.45$, branch $G = 2.69$, foliage $G = 2.47$, ANPP $G = 2.70$, LA $G = 2.32$). Branch biomass was the most variable measurement, followed by foliage biomass, total aboveground biomass and bole biomass. Tree-level ANPP and LA also spanned a broad range of values, reflecting the variation in structural characteristics (Table 3).

Partitioning of biomass was also variable among trees (Table 3). Bole wood represented the greatest portion of aboveground biomass. Foliage comprised the next largest portion of total AB, and branch wood was, on average, the smallest biomass component. Bole biomass also made up the largest portion of 2011 ANPP ($\bar{x} = 55.73\%$, $SE = 2.01$), followed by foliage biomass ($\bar{x} = 26.38\%$, $SE = 1.39$) and branch biomass ($\bar{x} = 17.90\%$, $SE = 0.92$).

3.2. Allometric equations

Basal diameter was the strongest single predictor for all allometric equations ($p < 0.0001$) and was significantly correlated with other measured variables, including DBH (Pearson $r = 0.96$, $p < 0.0001$), tree height (Pearson $r = 0.86$, $p < 0.0001$) and stand density (Pearson $r = -0.46$, $p < 0.0001$). Thus, inclusion of additional predictors both reduced the significance of the equations and introduced multicollinearity. Untransformed field measurements of all tree biomass components increase nonlinearly with

tree basal diameter, as do ANPP and LA (Fig. 1). Equations predict a 5-fold increase in total tree aboveground biomass as basal diameter is doubled and an approximately 4-fold increase in bole biomass, an 8-fold increase in branch biomass, a 5-fold increase in foliage biomass, a 4-fold increase in ANPP and a 5-fold increase in LA with each doubling of basal diameter (Table 4).

Power functions built from untransformed data fit measured data best when compared with back-transformed functions built from log-transformed data and equations built for 11-year-old saplings (Turner et al., 2004) and for mature trees (Pearson et al., 1984; Fig. 2). These functions minimized the AIC in all cases when compared to alternative equations, although differences between power functions fit to untransformed data and back-transformed functions fit to log-transformed data were minimal. Analysis of AIC values for allometrics developed for young and mature lodgepole pines demonstrate the improved fit provided by our equations (Table 5). 11-year-old sapling equations generally overpredicted total AB, branch biomass, foliage biomass and ANPP and underpredicted bole biomass. Mature tree allometrics greatly overpredicted bole and foliage biomass. However, mature tree equations (Pearson et al., 1984) fit branch biomass data relatively equally to the branch biomass equation developed in this study and mature tree equations better fit branch biomass of 24-year-old trees than do 11-year-old tree equations (Turner et al., 2004).

3.3. Structural and functional relationships with stand density

Tree-level total aboveground biomass and biomass of all aboveground components decreased significantly with increasing stand density (SLR: $p < 0.001$, Fig. 3). Bole biomass showed the weakest relationship with stand density (adj. $r^2 = 0.33$), decreasing by an average of 787 g with a doubling of stand density. Similarly, mean total aboveground biomass decreased by 1777 g (adj. $r^2 = 0.56$), foliage biomass by 478 g (adj. $r^2 = 0.56$) and branch biomass by 378 g (adj. $r^2 = 0.51$) for each doubling of stand density.

Partitioning of biomass to tree components showed clear density-driven trends (Fig. 4). Foliage and branch biomass partitioning decreased with increasing stand density by an average of 1.7% of foliage biomass for each doubling of stand density (SLR: $p = 0.002$, adj. $r^2 = 0.43$) and 1.8% of branch biomass ($p = 0.002$, adj. $r^2 = 0.43$). The similar relationships between foliage partitioning and density and branch partitioning and density highlight the significant positive correlation between branch and foliage partitioning (Pearson $r = 0.581$, $p < 0.0001$). The decrease in partitioning to branch wood and foliage was matched by an increase in partitioning to bole wood. On average, bole partitioning increased by 3.3% for each doubling of stand density ($p = 0.002$, adj. $r^2 = 0.48$).

As expected, tree-level ANPP and LA were highly correlated (Pearson $r = 0.96$, $p < 0.0001$) and showed similar relationships with stand density (Fig. 5). A doubling of stand density is associated with a 250 g decrease in mean ANPP ($p = 0.014$, adj. $r^2 = 0.28$) and a 0.8m² decrease in mean LA ($p = 0.004$, adj. $r^2 = 0.37$).

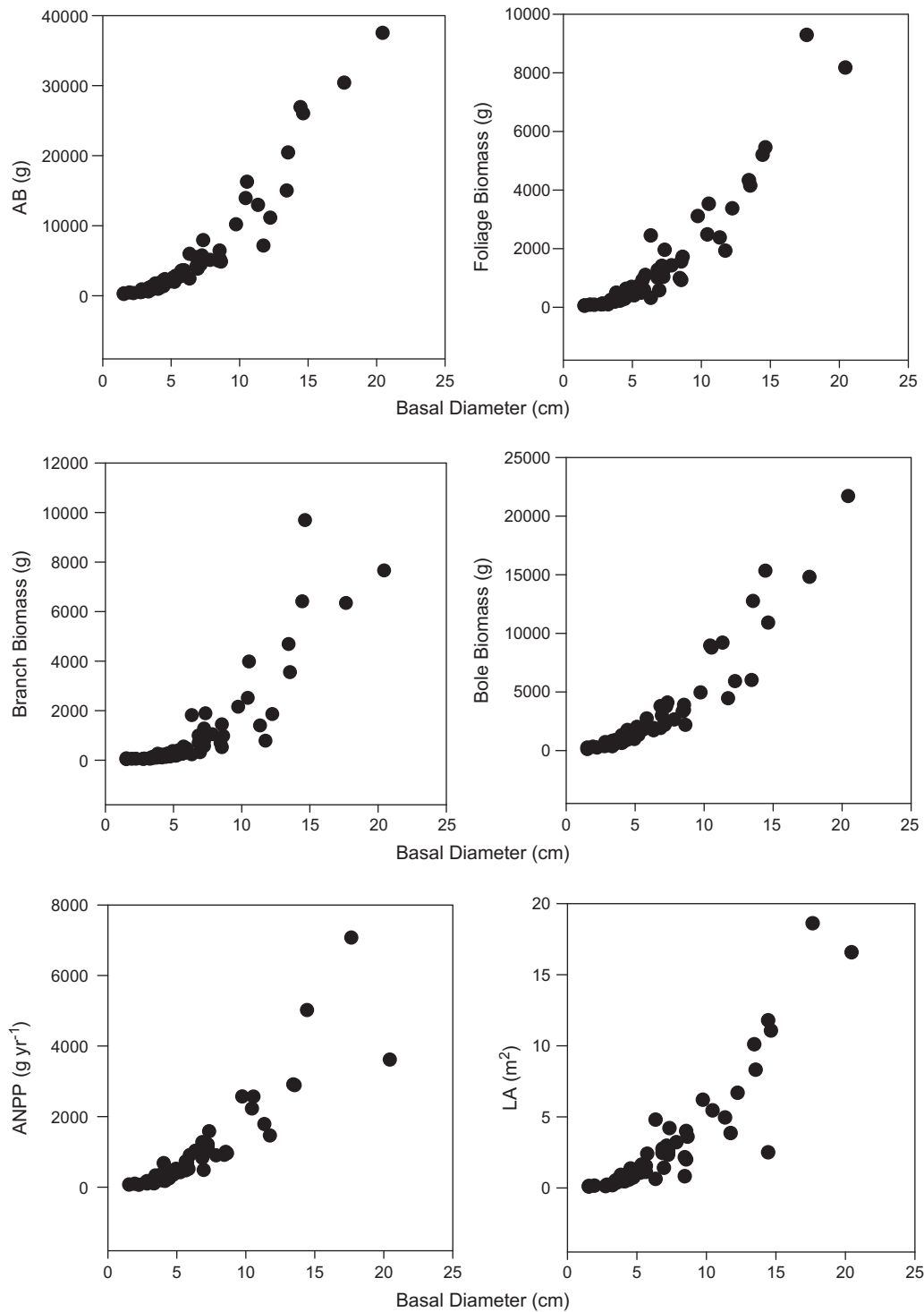


Fig. 1. Untransformed relationship between basal diameter and total aboveground and component biomass for sixty 24-year-old lodgepole pine trees in Yellowstone National Park.

3.4. Structural and functional relationships with tree age

Mean tree-level ANPP, LA, total aboveground biomass, and biomass of all components increased with tree age, and variation in the structural characteristics among trees changed little (Table 6). Total aboveground biomass per tree increased significantly with tree age (one-way ANOVA: $F = 59.40$, $p < 0.0001$), spanned a broader range of values among 24-year-old than 11-year-old trees and was similar in variation among both age groups. Foliage biomass

was both significantly greater (one-way ANOVA: $F = 52.78$, $p < 0.0001$) and slightly more variable among 24-year-old than 11-year-old trees. Mean branch biomass increased with tree age (one-way ANOVA: $F = 35.83$, $p < 0.0001$) and decreased in variation. Mean bole biomass increased significantly from 11-year-old to 24-year-old trees (one-way ANOVA: $F = 68.53$, $p < 0.0001$) and showed similar variation among both age groups. Mean tree-level ANPP increased significantly with tree age (one-way ANOVA: $F = 52.68$, $p < 0.0001$). Variation in ANPP estimates was similar

Table 4

Summary of tree-level allometric equations built from 24-year-old lodgepole pine trees harvested from a range of stand densities across the Yellowstone subalpine plateaus^a.

Dependent variable	<i>n</i>	<i>a</i>	<i>b</i>	MSE	F-ratio	<i>p</i>
Total aboveground biomass	60	98.85	1.99	3742767	6.7	<0.0001
Foliage biomass	60	22.90	2.00	270457	1.5	<0.0001
Branch biomass	60	14.44	2.14	854592	6.8	<0.0001
Bole biomass	60	65.26	1.99	1537053	6.3	<0.0001
ANPP	53	38.90	1.66	360453	13.4	<0.0001
Leaf area	55	0.02	2.34	3	0.4	<0.0001
1 h branchwood (<1/4" diam.)	60	4.74	2.16	49603	2.6	0.035

^a All equations are of the form $Y = aX^b$ where X = basal diameter in cm. Biomass is predicted in grams, ANPP in grams-year⁻¹ and LA in m².

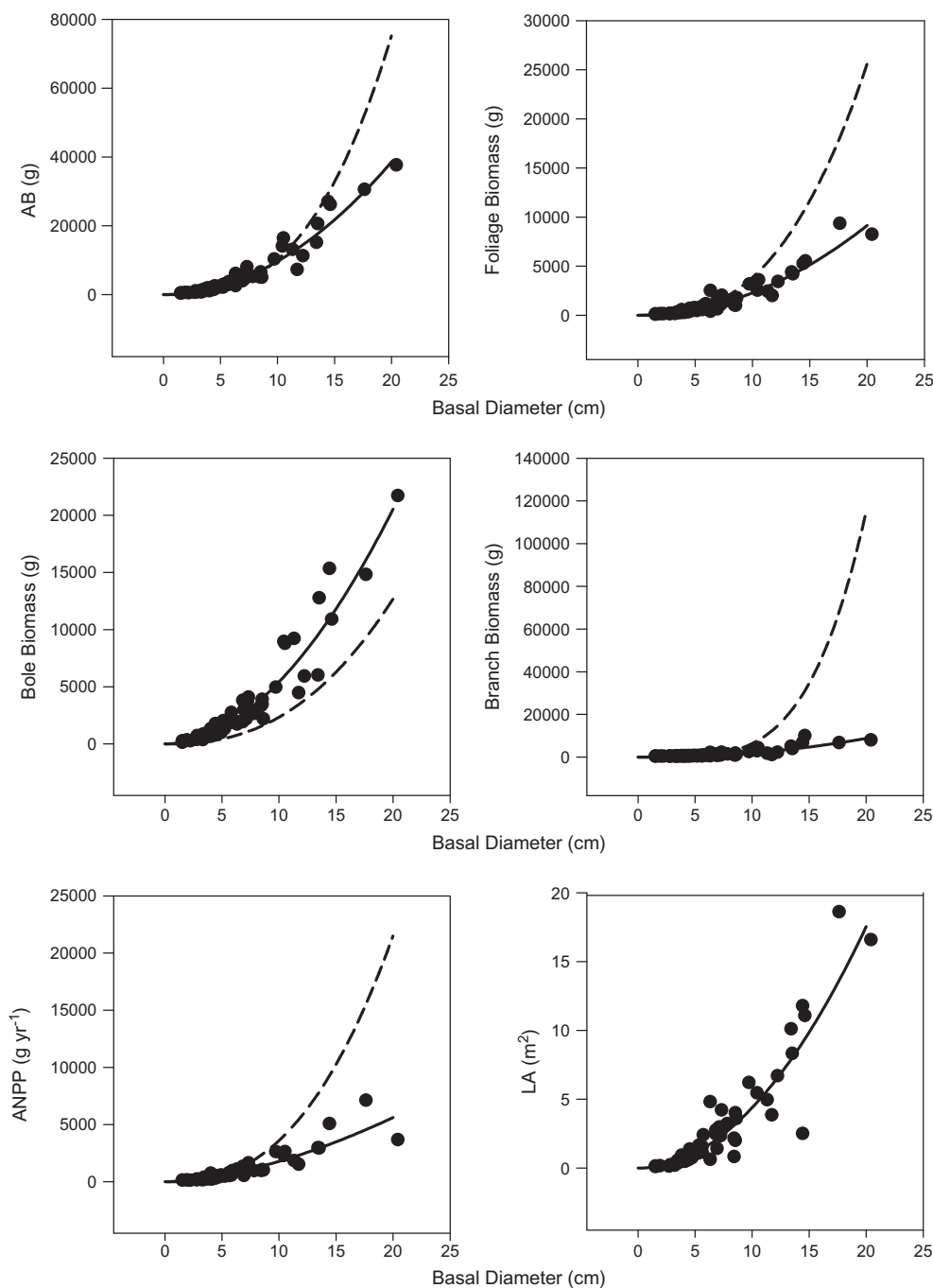


Fig. 2. Trend lines representing predicted values for total biomass, all biomass components, ANPP and LA of postfire lodgepole pine trees from allometric equations developed for 24-year-old trees (solid line), and equations built for 11-year-old saplings (dashed line; [Turner et al., 2004](#)). Because a different variable was used to predict LA for 11-year-old trees, leaf area equations could not be directly compared. Additionally, equations developed for mature trees ([Pearson et al., 1984](#)) could not be visually compared due to a different predicting variable.

Table 5
AIC values comparing model fit to measured data for allometric equations developed for 24-year-old lodgepole pines, and equations developed for 11-year-old (Turner et al., 2004) and mature lodgepole pines (Pearson et al., 1984) fit to 24-year-old tree data.

Component	This study	Turner et al., 2004	Pearson et al., 1984
Aboveground biomass	17.1	19.6	–
Bole biomass	16.2	17.9	25.2
Branch biomass	15.7	21.6	16.8
Foliage biomass	14.5	18.1	20.3
ANPP	14.5	18.2	–
LA	2.9	–	–

among both age groups. Mean tree-level LA also increased significantly with tree age (one-way ANOVA: $F = 43.18$, $p < 0.0001$) and variation changed little.

Aboveground biomass partitioning trends changed substantially with tree age (Table 6). Analysis of Variance on biomass partitioning showed a clear trend of increased partitioning to bole wood with age ($F = 119.32$, $p < 0.0001$), coupled with significant decreases in partitioning to foliage ($F = 176.56$, $p < 0.0001$) and branch wood ($F = 4.59$, $p < 0.034$). Partitioning to branch wood showed the smallest decrease between age groups yet variation in branch wood partitioning was much greater among 11-year-old than 24-year-old trees. Bole wood partitioning increased with tree age and decreased in variation. The increase in bole wood partitioning was largely accounted for by the decreased

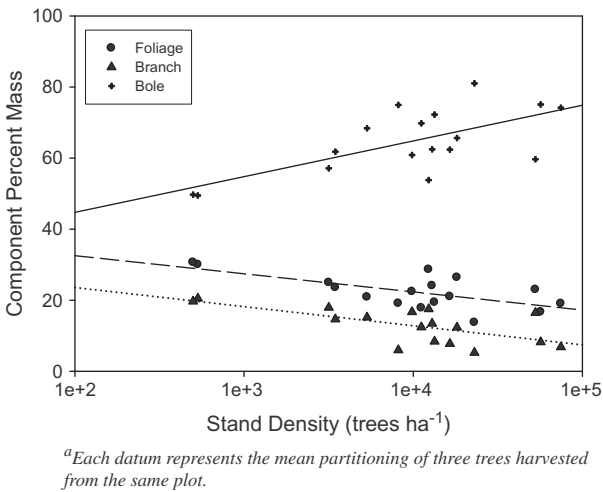


Fig. 4. Relationship between biomass partitioning to bole, branch and foliage and stand density for sixty 24-year-old lodgepole pine trees across 21 plots in Yellowstone National Park^a.

partitioning to foliage with tree age. Variation in foliage percent mass was low and did not appear to change with tree age.

4. Discussion

Our results demonstrate that stand density and age explain much of the variation in aboveground tree biomass and patterns

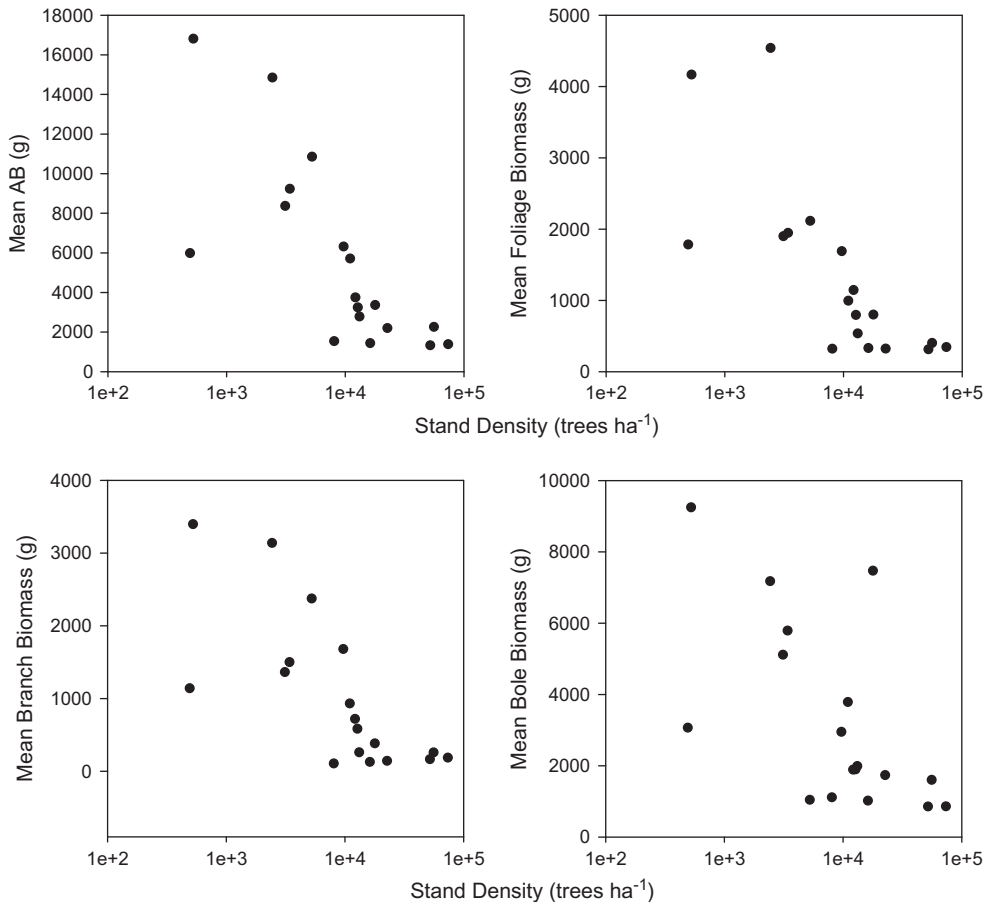
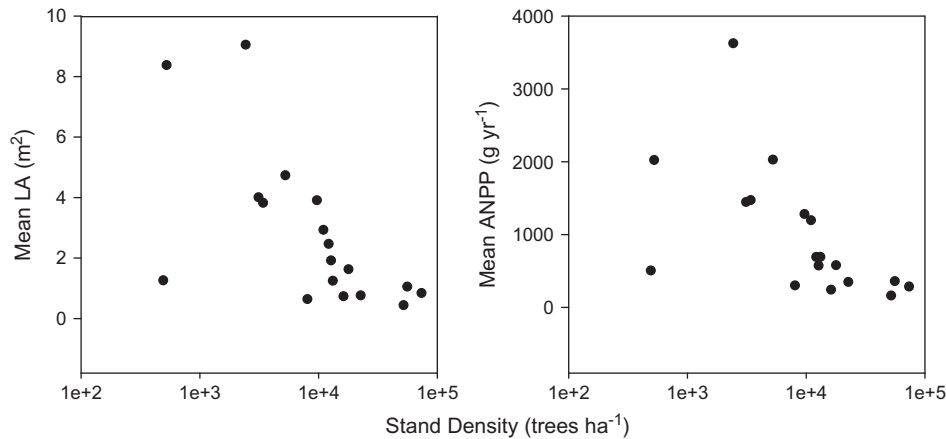


Fig. 3. Relationship between total and component biomass and stand density from sixty 24-year-old lodgepole pine trees across 21 plots in Yellowstone National Park^a.



^aEach datum represents the mean ANPP and LA of three trees harvested in the same plot

Fig. 5. Relationship between tree-level LA (m²), ANPP (g·year⁻¹) and stand density (stems·ha⁻¹) for 24-year-old postfire lodgepole pine trees^a.

in tree-level biomass partitioning, ANPP and LA in young postfire lodgepole pine stands in YNP. The importance of density and age in tree morphometry was recognized by [Johnstone \(1970\)](#) in his predictive equations for mature lodgepole biomass and was subsequently confirmed by [Pearson et al. \(1984\)](#), [Ares and Brauer \(2005\)](#), [Peichl and Arain \(2007\)](#) and, more recently, by [Kashian et al. \(2013\)](#) in their assessment of carbon storage dynamics across postfire lodgepole pine stands. We have also demonstrated that partitioning of biomass to various tree components is strongly dependent on density and age, even in young, developing stands.

4.1. Allometric relationships

For all biomass equations, basal diameter was a stronger predictor than DBH or tree height, and combining predictors did not significantly improve the fit of the equations. Diameter measurements have been consistently shown to be the strongest predictors of aboveground tree biomass across a range of species and stand conditions ([Pearson et al., 1984](#); [Turner et al., 2004](#); [Chave et al., 2005](#); [Konôpka et al., 2010](#)), and are particularly robust when predicting across varying stand conditions, including nutrient, density, and moisture gradients ([Blevins et al., 2005](#); [Peichl and Arain, 2007](#); [Jiménez et al., 2013](#)). Our models demonstrate similar robustness, as they were not significantly influenced by the inclusion of stand density.

The relationships between tree morphometry (basal diameter) and biomass, ANPP and LA identified in our study differ from those documented in very young (11-yr old; [Turner et al., 2004](#)) and mature ([Pearson et al., 1984](#)) lodgepole pine stands. Equations developed by [Turner et al. \(2004\)](#) for the same landscape in 1999 produced significantly greater slope parameters, demonstrating that these relationships have changed substantially over the past 13 years of stand development. Equations developed for 11-year-old trees were fitted to harvested trees ranging from 0.3 to 6.0 cm in basal diameter, while the equations developed on this study were fitted to trees ranging from 1.60 to 20.5 cm. Additional model comparisons reveal that the 11-year-old tree equations do a poor job at predicting total and component biomass for larger trees, but are generally adequate for the smaller trees used in this study. Among trees greater than 6.0 cm basal diameter, the 11-year-old tree equations overpredict total AB, foliage biomass, branch biomass and ANPP. However, for trees less than 6.0 cm in basal diameter, the 11-year-old tree equations fit total AB, foliage biomass, branch biomass and ANPP data just as well as equations for 24-year-old trees (AIC difference < 1). Surprisingly, both equations adequately predict bole biomass for trees greater than 6 cm

basal diameter, but the 11-year-old tree equations underpredict bole biomass for small trees.

When compared to equations developed for mature lodgepole pine trees in Wyoming ([Pearson et al., 1984](#)), our equations generally showed a much stronger fit to measured biomass components. Mature tree equations overpredict bole and foliage biomass but predict branch biomass relatively equally to our equations. The differences in model fit among equations developed for 11-year-old, 24-year-old and mature trees are likely related to changes in biomass partitioning over time. We have shown that trees partition more biomass to the bole and less to foliage and branch wood as they age. This may explain why equations for young trees generally underpredict bole biomass and overpredict foliage and branch biomass, while mature tree equations overpredict bole biomass. Other differences between our equations and those developed for mature trees are more difficult to explain, but are likely tied to site differences that influence morphometry and development. These results highlight the importance of our new equations in providing accurate estimates of current biomass and ANPP relationships and also emphasize the importance of stand age in morphometry and tree-growth trends.

4.2. Biomass, ANPP, LAI and relationships with stand density

Our results show that, for stands of the same age, greater stand density is associated with lower total and component aboveground biomass, increased partitioning to bole wood, and decreased partitioning to foliage and branch wood. Our findings are consistent with trends documented for a range of young, fire-origin conifer species including lodgepole pine ([Reid et al., 2004](#); [Blevins et al., 2005](#)), Aleppo pine ([De las Heras et al., 2013](#)), and maritime pine ([Jiménez et al., 2011](#)). Higher total and component biomass of individual trees in sparser stands has been attributed to a similar amount of resources being shared among fewer individuals ([Long and Smith, 1984](#); [Blevins et al., 2005](#); [Jiménez et al., 2011](#)). While we did not directly measure site fertility, our data suggests that differences in stand density, and not soil fertility, largely determine the amount of resources available to individual trees. Trees grown on more fertile sites typically show a disproportionate increase in foliage biomass relative to other aboveground components when compared to trees grown on less fertile sites ([Albaugh et al., 2004](#); [Blevins et al., 2005](#)), yet in this study stand density affected all biomass components similarly ([Fig. 3](#)). Additionally, across the Yellowstone plateaus, soil moisture and Nitrogen availability have been shown to decline as stand density increases ([Litton et al.,](#)

Table 6

Comparison of tree-level biomass, partitioning, ANPP and LA for 11-year-old (Turner et al., 2004) and 24-year-old postfire lodgepole pine trees. Asterisks (*) denote significant differences between 11- and 24-year-old mean values at a significance level of 0.05.

Component	11-Year-old			24-Year-old		
	Mean	SE	CV	Mean	SE	CV
Aboveground Biomass (g)	244.8*	30.7	1.37	5771*	1007	1.36
Bole Biomass (g)	88.6*	10.2	1.27	3279*	542	1.29
Branch Biomass (g)	46.6*	8.0	1.89	1131*	254	1.76
Foliage Biomass (g)	109.7*	13.2	1.31	1361*	241	1.38
ANPP (g.tree ⁻¹ .year ⁻¹)	118.6*	13.8	1.27	1004*	181	1.32
LA (m ²)	0.5*	0.1	1.31	2.966*	0.537	1.34
Bole Percent Mass	41.8*	1.2	0.31	63.88*	1.64	0.2
Branch percent mass	15.6*	0.5	0.36	13.46*	1.01	0.59
Foliage percent mass	42.6*	1.0	0.25	22.66*	0.819	0.28

2003) despite consistency among substrate types, suggesting that resource availability is largely determined by stand density.

Tree physiology may interact with resource availability to affect tree growth across gradients of stand density. Jiménez et al. (2008) documented higher soil water availability in thinned postfire maritime pine stands than in dense, control stands and related this to measurements of higher sap flow density and growth rates in thinned stands. The increase in biomass associated with declining stand density in this study may be the result of greater sapwood area and higher sap flow density in sparser stands. In postfire lodgepole pine, reduced competition for water has been related to improved water relations due to greater sapwood volume per unit leaf area (Reid et al., 2004, 2006). Across our plots, leaf area and biomass declined with increasing stand density. Suppression of growth in dense stands may be explained by limited hydraulic supply capacity due to lower leaf area and growth efficiency interacting with water and nutrient limitation (Reid et al., 2004; Blevins et al., 2005).

The decline in leaf area with increasing stand density was also correlated with a decline in tree-level ANPP. ANPP and LA have been well-documented to increase with tree size and to be highly correlated (Smith and Long, 2001; Turner et al., 2004). For the young trees measured in this study, foliage biomass is a significant component of ANPP. LA is closely tied to foliage biomass, and, in addition to being related to resource availability and hydraulic capacity, is a reflection of the growing space available to an individual tree (Reid et al., 2004; De las Heras et al., 2013). In crowded, resource-limited dense stands, LA is reduced, which is accompanied by a reduction in foliage biomass, photosynthetic activity, and ANPP. Crowding in dense stands may also explain reduced partitioning of biomass to branches due to limitation of lateral growth (Zhao et al., 2011).

4.3. Relationships with tree age

Mean total aboveground biomass, component biomass, LA and ANPP all showed marked increases over the past 13 years. This is not surprising, given that much of ANPP can be explained by variation in biomass (Gower et al., 2001). The high rate of increase suggests that stands are still in an early stage of development and may continue to increase in productivity for some time. Across a range of conifer forests, ANPP has been shown to increase until 40–150 years after stand initiation (Chen et al., 2002; Litton et al., 2004; Kashian et al., 2013). Comparing our estimates of mean tree ANPP with estimates from a number of other studies of lodgepole pine trees in the Rocky Mountains suggests that, at the tree level, our postfire lodgepole pine trees may continue to increase in ANPP for up to 100 years (Fig. 6). However, in a chronosequence of stands across the Yellowstone plateaus, Kashian et al. (2013) found that stand-level ANPP reached a maximum in stands

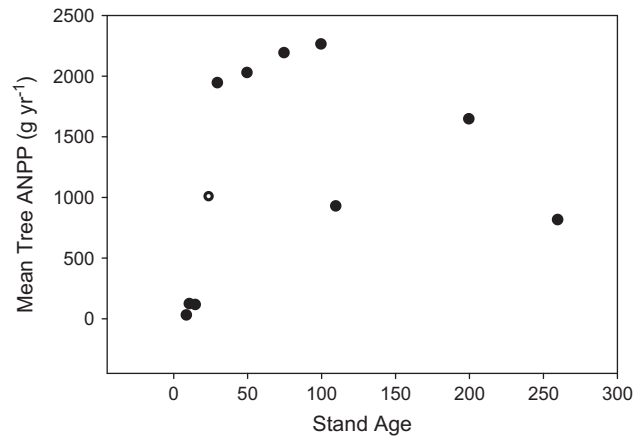


Fig. 6. Tree-level ANPP estimates from lodgepole pine stands in the Rocky Mountains ranging from 9 to 260 years of age. Tree-level values have been estimated from stand-level values reported by Pearson et al., 1987; Olsson et al., 1997; Reed et al., 1998; Smith and Resh, 1999 and Turner et al., 2004. Mean tree-level ANPP from this study is demonstrated by an open point.

24–46 years old and declined thereafter. The substantial variation we have noted in tree-level ANPP values along with variation in stand density may result in diverse patterns of stand development across the Yellowstone landscape. Therefore, it is difficult to predict when ANPP and LA will begin to decline, but it is likely that the age of maximum ANPP and LA will vary with stand density (Smith and Long, 2001). Because tree growth is largely controlled by factors related to stand density, it is possible that maximum values may be reached by trees in dense stands much earlier than in sparse stands (Gower et al., 1996; Reed et al., 1998; Litton et al., 2004).

As our postfire stands have aged, individual trees have partitioned less biomass to branches and foliage and more to bole wood. Bole biomass has been well documented to increase relative to other tree components as trees age (Ryan and Waring, 1992; Gower et al., 1996; Peichl and Arain, 2007). This may reflect increasing nutrient limitation, which favors carbon-rich woody growth over nitrogen-rich foliage (Chen et al., 2002). Additionally, foliage has higher respiratory costs than woody components, and this demand becomes more significant as biomass increases (Gower et al., 1996). As respiratory demand increases, trees must increasingly allocate resources to tissues that minimize this demand. However, we measured relatively high foliage allocation in our stands, suggesting that stand resources are still sufficient to support high growth rates (Peichl and Arain, 2007).

Despite substantial changes in biomass, ANPP and LA over time, variation in these characteristics across all trees has changed little. This is consistent with the findings of Binkley et al. (2006) who postulated that the absence of a strong growth dominance phase in lodgepole pine stands was due to early relative differences in tree sizes that were either maintained or decreased over the course of stand development. If the model presented for growth dominance in lodgepole pine holds true in our stands, we can expect variation in tree biomass to either be maintained or decrease with the onset of self-thinning across all stand densities.

5. Summary and conclusions

Taken as a whole, our results demonstrate that stand density and age explain much of the variation in aboveground tree biomass and patterns in tree-level biomass partitioning, ANPP and LA in young, postfire lodgepole pine stands in YNP. As stand density increases across the study site, individual tree biomass, LA and ANPP

decline and trees allocate a greater proportion of biomass to bole wood and less to branches and foliage. These trends are likely driven by resource availability and physiology. Over the last 13 years of stand development, tree-level total and component biomass, LA, ANPP and partitioning of biomass to bole wood have increased, while partitioning to branches and foliage has declined.

The trends reported in this study demonstrate the long-term effects of postfire regeneration patterns on structural and functional characteristics of individual trees. Variation in tree characteristics associated with stand density has changed little in the past 13 years of stand development, suggesting that structural and functional variation among postfire trees may be retained for some time.

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