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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 km$^2$ 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 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 |