Forest Ecology and Management 429 (2018) 124–132

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

A comparison of coarse woody debris volume and variety between old-growth and secondary longleaf pine forests in the southeastern United States

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ARTICLE INFO

Keywords:
Fire-adapted
Primary forests
Reference conditions
Virgin forests

ABSTRACT

Few efforts have been made to quantify the amount and variety of deadwood in frequently burned ecosystems, particularly the longleaf pine (*Pinus palustris* Mill.) ecosystem of the southeastern United States. Moreover, comparisons of coarse woody debris between old-growth and secondary longleaf pine forests are lacking despite the widely recognized value of deadwood to biodiversity in many forest types. We measured standing and fallen deadwood in three old-growth and four mature (100–125 years-old) secondary forests in two landscapes characterized by either sandy or clayey soils within the historic range of *P. palustris*. Downed coarse woody debris volume was variable at the old-growth locations, ranging from 2.51 ± 0.79 to 29.10 ± 14.55 m^3 per ha, which includes perhaps the lowest values ever reported from any old-growth forest. Factors likely contributing to these low volumes include frequent fire, the low basal area characteristic of this forest type, subtropical climatic conditions of the southeastern Coastal Plain, and large termite populations. The high variability observed among the three old-growth locations probably reflect interactions between fire and other disturbances (e.g., wind damage). The old-growth location on sandy soils had significantly higher coarse woody debris volume and deadwood variety (e.g., diameter increments, posture, tree genera and decay classes) than secondary forests sampled nearby. Highly resinous heartwood is a significant indicator of old-growth conditions relative to secondary locations, appearing to accumulate as a persistent fraction of the deadwood pool over time.

1. Introduction

Because deadwood supports a large fraction of forest biodiversity (Stokland et al., 2012; Ulyshen, 2018) and plays an important role in carbon sequestration, there is great interest among forest ecologists in better understanding how it varies in amount and variety (i.e., defined by the number of wood species, postures, diameter classes, decay classes, etc.) among forest types and management histories. Old-growth remnants provide an opportunity to collect baseline information about the characteristics of deadwood pools under relatively undisturbed conditions (e.g., Spetich et al., 1999). Such information is critical to understanding deadwood dynamics in a particular ecosystem and can help develop general guidelines for restoration as well as silvicultural recommendations for promoting valued old-growth features and associated organisms (White and Lloyd, 1995; Bauhus et al., 2009). Input and loss rates of deadwood vary greatly as influenced by a large number of interacting factors. These include climatic conditions such as temperature and humidity, site productivity, tree species composition, stand density, insect activity and fire frequency (Cornwell et al., 2009).

The volume of downed deadwood typical of old-growth forests varies widely among different regions and forest types, ranging from > 300 m^3 per ha in temperate rainforests that are characterized by high productivity and low rates of decomposition (Spies et al., 1988; Lindenmayer et al., 1999) to < 20 m^3 per ha in xeric conifer forests that experience frequent fires (Robertson and Bowser, 1999). Forests growing in cooler latitudes or elevations are generally thought to have larger accumulations of wood than those that experience warmer conditions due to differences in decay rates (Muller and Liu, 1991). Most previous studies indicate that coarse woody debris volume increases with forest age and that old-growth forests contain significantly more downed and standing deadwood than secondary forests (Sturtevant et al., 1997; Kirby et al., 1998; Robertson and Bowser, 1999; Siitonen et al., 2000). There are exceptions to these patterns, however, with published examples of mature secondary forests having comparable amounts of deadwood as old-growth stands (Lindenmayer et al., 1999) and large amounts of legacy wood in young stands growing on recently-

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https://doi.org/10.1016/j.foreco.2018.07.017
Received 19 May 2018; Received in revised form 4 July 2018; Accepted 6 July 2018
0378-1127/ Published by Elsevier B.V.

Table 1
Study location information.

Region	Location	Coordinates	Age	Stand size (ha)[a]	% basal area pine[b]	Forest age (years)[c]	Fire frequency (return interval, years)[d]
Eglin AFB	Patterson Natural Area	30.487154–86.741373	Old-growth	375–2031[e]	99.5	400 +	2
	E-24	30.540883–86.875927	Secondary	~650	93.6	125	2.5
	F-22	30.596333–86.706026	Secondary	~500	100	125	2
Red Hills	Wade Tract	30.758367–83.999040	Old-growth	83	99.0	350 +	2
	Tall Timbers	30.651599–84.226949	Secondary	~150	75.7	125	1.5
	Greenwood Secondary	30.836033–84.018704	Secondary	~250	95.4	100	2
	Greenwood Big Woods	30.844923–84.017743	Old-growth	200	94.4	300 +	2

[a] Old-growth stand sizes were taken from Varner and Kush (2004).
[b] Based on data collected in this study.
[c] Approximate age of the living trees.
[d] Based on the ten year period from 2008 to 2017.
[e] The extent of the old-growth forest at Patterson Natural Area remains uncertain.

harvested sites (Spies et al., 1988; Spetich et al., 1999).

A number of studies have quantified the amount of deadwood in the forests of the southeastern United States. Reported coarse woody debris volumes vary by forest type, ranging from $< 5\,m^3$ per ha in pine-dominated forests to over $100\,m^3$ per ha in mixed hardwood forests (McMinn and Hardt, 1996). Compared to western North America, there are few old-growth forests remaining in the southeastern United States (White and Lloyd, 1995; Landers and Boyer, 1999; Bragg, 2002; Varner and Kush, 2004; Mitchell et al., 2009). Although a few studies have characterized dead wood in particular old-growth remnants in the region (Muller and Liu, 1991), we are not aware of any efforts to specifically compare the amount and variety of deadwood between old-growth and regenerating forests in the southeastern United States. It thus remains almost entirely unknown whether characteristics of the deadwood pool can be used as indicators of old-growth conditions. Although differences in the total amount of wood can be anticipated from work done in other regions, the amount of specific substrates or decay classes may be even more informative in some cases. This is especially true for the pine-dominated forests of the region which are known to slowly produce heartwood as they age (Demmon, 1936; Conner et al., 1994; Schultz, 1997). Because heartwood is much more resistant to decay than sapwood, the presence of large amounts of heartwood on the forest floor may suggest a forest is both old and relatively undisturbed.

One of the most biodiverse and imperiled forest types in the southeastern U.S. is the longleaf pine (*Pinus palustris* L.) ecosystem (Kirkman et al., 2004). Longleaf pine historically dominated the Atlantic and Gulf Coastal Plains of the southeastern United States and extended into the Piedmont and mountains of Alabama in Georgia (Stambaugh et al., 2017) where it was maintained by frequent fires initiated by lightning strikes and later by Native Americans. These forests are commonly referred to as savannas as they are characterized by low basal area (~12–35 m^2/ha when undisturbed) of widely-spaced longleaf pine in the overstory and extremely diverse herbaceous plant communities (Platt et al., 1988b; Platt and Rathbun, 1993 ; Varner and Kush, 2004). The longleaf pine ecosystem has been lost over much of its former range, being replaced by other land uses, including the planting of other pine species, or lost as a consequence of fire suppression. Today, longleaf pine covers only about 776,000 ha (~2% of its historic range) with 5100 ha of remaining old-growth forests (~0.01% of its historic range) (Means, 1996; Varner and Kush, 2004; Mitchell et al., 2009). Longleaf pine ecosystems have been intensively studied with respect to their plant communities (Platt et al., 1988a; Provencher et al., 2001; Hiers et al., 2007; Kirkman et al., 2013) and their value to endangered vertebrates such as the red-cockaded woodpecker (Engstrom et al., 1984; Walters et al., 2002; Rudolph et al., 2007; Mitchell et al., 2009; Steen et al., 2013). Despite recent efforts to inventory and restore old-growth forests in the region (Means, 1996; Landers and Boyer, 1999; Varner and Kush, 2004; Johnson et al., 2018), few efforts have been made to characterize deadwood in this ecosystem. Although a number of studies have quantified the number of snags present in longleaf pine forests (Landers and Boyer, 1999; Blanc and Walters, 2008a; Blanc and Walters, 2008b; Mitchell et al., 2009), there is very little published information about the amount of fallen deadwood on the forest floor. This absence of information may be a reflection of CWD being a perceived as an uncommon feature of the forest floor in the longleaf pine ecosystem (Landers and Boyer, 1999). Indeed, in one of the few studies to investigate this question, Hanula et al. (2012) reported a mean CWD volume of only $2.09 \pm 0.59\,m^3$ per ha from even-aged ~90 year-old longleaf pine stands with some history of salvage logging in Florida. Major mortality events from fire and hurricanes are common to the region (Glitzenstein et al., 1995; Pederson et al., 2008; Grissino-Mayer et al., 2010), however, and can be expected to result in occasional large inputs of deadwood. Moreover, the prevalence of highly resinous heart pine in older forests (Mitchell et al., 2006; Rother et al., 2018) create the potential for different patterns of CWD accumulation in old-growth vs. secondary forests.

The purpose of this study was to characterize the amount and variety of deadwood in three of the largest remnant old-growth longleaf pine forests and neighboring secondary pine forests in two regions within the historic range of longleaf pine. We also consider the role frequent fire plays in affecting these patterns and present our findings within the context of other investigated forest types. Because most previous research on coarse woody debris has been conducted in boreal or temperate forests that rarely experience fire, this study offers a relatively unique perspective on deadwood dynamics in forested ecosystems.

2. Methods

2.1. Locations and design

This study was conducted in seven forests within the historic range of longleaf pine (*Pinus palustris* Mill.) on the coastal plain of the southeastern United States, including three large old-growth remnants (Table 1). Our locations were divided between Eglin Air Force Base (AFB) on the western end of the Florida panhandle (Okaloosa and Santa Rosa counties) and the Red Hills region surrounding Thomasville Georgia. While the Eglin AFB locations are characterized by xeric sandy soil (typic Quartzipsamments of the Lakeland series) with a mean depth to water table of 2 m (Overing et al., 1995), the Red Hills region is characterized by clayey soils (ultisols) of the Tifton Uplands. Based on records from neighboring towns (Thomasville, Georgia and Niceville, Florida), the Red Hills and Eglin AFB have mean annual temperatures of 19.6 and 18.7 C and mean annual rainfall of 134.9 and 180.2 cm, respectively (usclimatedata.com, accessed 26 April 2018). Site productivity within the Red Hills region is substantially greater than Eglin AFB due to differences in soil quality (Means, 1996; Craul et al., 2005).