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
Available online 11 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 ± 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).

Eglin AFB and the Redhills are two of the most significant regions with respect to supporting old-growth longleaf pine remnants. Eglin alone supports at least 3650 ha which represents > 70% of the remaining old-growth forest area (Varner and Kush, 2004). We sampled in one of the largest old-growth tracts on the property, Patterson Natural Area, as well as two mature (~125 yrs-old) secondary sites (E-24 and F-22) (Table 1). Within the Red Hills region, we sampled two old-growth (The Wade Tract and Greenwood Big Woods) and two mature (100–125 yrs-old) secondary locations (Table 1). One Red Hills secondary forest was at Tall Timbers Research Station (Leon County, Florida), and the other was a site near the Big Woods owned by Greenwood Plantation. All seven locations except the stand at Tall Timbers were dominated by longleaf pine. At Tall Timbers, which was farmed through the late 19th Century, the overstory is characterized by loblolly (*P. taeda* L.) and shortleaf (*P. echinata* Mill.) pine. Eglin AFB location F22 was treated with herbicide for red-cockaded woodpecker management in 2008. The Greenwood Big Woods location experienced scattered wind damage in January 2017, several months before data were collected for this study.

All seven locations are managed using frequent prescribed fire, with return intervals ranging from 1.5 to 2.5 years (Table 1). All locations were burned in 2017, the same year our measurements were taken, and all but two locations (E-24 and F-22) were sampled following the burn. Due to access restrictions, both E-24 and F-22 were sampled prior to scheduled prescribed burns in 2017; thus, sampling at those locations took place 2 years since the last burn. We do not expect this to affect our general conclusions given the small amounts of wood present at both of those locations and the frequency at which all locations experience fire. All plots at each location were measured either before or after the burn so there were no inconsistencies among plots within a location.

To make our deadwood measurements, an approximately linear 700 m transect of eight sampling plots was established at each location, with a distance of 100 m between plots. All plots were at least 50 m from any forest boundary. Transects were directed parallel to tertiary forest roads at all locations. Plot positions were established from a random starting point to initiate each 700 m transect, and were not influenced by any prior knowledge or expectations about deadwood abundance or distribution.

2.2. Measurements

Measurements of living tree basal area, downed coarse woody debris and standing dead snags were made within the eight 0.1 ha circular plots along each 700-m plot transect from March-July 2017. To calculate the basal area of living trees, we measured the diameter (dbh) of all stems ≥10 cm. We defined CWD as any downed wood that measures ≥10 cm in width at any point along its length. For each piece of CWD, we measured the diameter at each end and the length. We also measured the thickness of flattened pieces. When a piece of CWD intersected the boundary of a plot, we measured the diameter at the boundary and excluded all material extending beyond the boundary from consideration. At the Greenwood Big Woods (old-growth) location, some salvage from individual dead pines is a common practice, and four trees within our plots had missing sections harvested from the main bole. Because the bottom-most section and crown remained on location, it was possible to correct for missing wood volume. When possible, we recorded the tree genus to which each piece of CWD belonged. We also assigned each piece of CWD to one of seven decay classes as outlined in Table 2 and shown in Fig. 1. This classification system recognizes that sapwood in southern pines generally decomposes soon after death whereas heartwood decays at a reduced rate as has been shown for other tree species (Schowalter et al., 1998). Unlike previous studies, we distinguish between wood with some highly decomposed sapwood remaining (decay class 5) from wood that consists entirely of heartwood (decay class 6). Working in Colorado *Pinus ponderosa* forests, Robertson and Bowser (1999) referred to similar heartwood remains as "skeleton wood" and encouraged future researchers to separate this kind of wood into a separate decay class. To further understand potential differences in old-growth and secondary forests, we also distinguish between apparently solid heartwood and obviously decomposing heartwood, assigning the latter to decay class 7.

We also recorded the diameter, height and decay class for all standing deadwood present within the plots, limited to stems ≥10 cm (Table 3). Stems less than or equal to 2 m tall were classified as stumps while stems exceeding this height were classified as snags. The basal diameter of snags was measured at 1.5 m whereas the diameter of stumps was measured at a position estimated to represent the average diameter along the length of the stump. As with downed wood, we distinguish between snags or stumps that were obviously still decomposing (decay classes 1–4) and those that were dried from sun exposure or charred by fire (decay class 5). Although only heartwood remained on many snags or stumps assigned to decay class 5, many were still to some degree covered with extremely dry and hardened sapwood.

2.3. Analysis

We calculated the volume of each downed CWD piece based on the equation for the volume of a truncated cone: $V = \pi\ h/3\ (r_1^2 + r_1 r_2 + r_2^2)$ where r_1 and r_2 are the radii of the two ends and h is the height or length. When pieces were flattened, volume was calculated by multiplying the average diameter of the two ends by the length and width of the piece. We summed the total volume of CWD measured in each plot and also calculated this for each decay class. We also calculated the total basal area of living trees (m^2/ha) as well as measured the basal area of snags per plot and the number of snags and stumps per plot. Although we did not take measurements to allow for an accurate estimate of downed wood mass per plot, this was roughly estimated using the density values for longleaf pine (660.0 kg/m^3) and oak (704.8 kg/m^3) provided by (Prichard et al., 2006).

Similar to Hekkala et al. (2016), we calculated deadwood variety per plot by counting the number of deadwood types based on posture (downed or standing), tree genus, decay class and diameter class. Diameter classes were based on 10-cm increments (e.g., > 10 cm and ≤20 cm; > 20 cm and ≤30 cm; etc.) according to basal diameter measurements. Snags, but not stumps, were included in the calculation of variety.

We analyzed plots from the two regions separately. ANOVA followed by Tukey's studentized range test was used to compare tree basal area, CWD volume, deadwood variety and stump number among locations. To satisfy normality assumptions, CWD volume was log(x + 1)-transformed while the square-root transformation was applied to wood variety and stump number prior to analysis. Snag basal area and snag number were compared among locations for each region separately using the Kruskal-Wallis test. Non-transformed data are presented in all figures and tables.

To assess how the composition of the downed woody debris pool differed among plots from old-growth and secondary forests, we performed nonmetric multidimensional scaling (NMS) using PC-ORD (McCune and Mefford, 2011). Only downed woody debris was used in this analysis because we did not measure snag volumes. Downed woody debris categories were based on decay class, wood species and diameter as described above for the calculation of deadwood variety. All downed wood categories recorded from fewer than three plots were excluded from analysis as were all plots for which there were no data. The final matrix consisted of 23 categories and 51 plots. No plots were outliers based on outlier analysis, i.e., no plot within the distance matrix was more than two standard deviations from the mean. NMS was performed using Bray-Curtis distance measurements on 250 runs each of real and randomized data.

To determine which categories of downed wood are most strongly associated with old-growth conditions, indicator species analysis (ISA) was also performed in PC-ORD, using the same dataset described for

Table 2
Decay class designations for downed coarse woody debris.

Characteristic	DC 1	DC 2	DC 3	DC 4	DC 5	DC 6	DC 7
Shape	Round	Round	Round	Round to oval	Oval	Round (heartwood only)	Oval (heartwood only)
Bark	Present, intact	Present, loose	Trace to absent	Trace to absent	Absent	Absent	Absent
Sapwood	Recently dead, original color	Mostly intact, partly soft in places	Partly soft	Crushes under foot but not powdery (termite damage severe)	Crushes in hand, powdery	Absent	Absent
Heartwood (if present)	Not visible	Not visible	Not visible	Not visible or beginning to become visible	Visible in places	Heartwood only, not decomposing	Heartwood only, decomposing

NMS analysis. Indicator values (IV) were calculated based on the following equation: $IV_{ij} = A_{ij} \times B_{ij} \times 100$ where A_{ij} is the mean abundance of category i in the sites of group j compared to all groups and B_{ij} is the relative frequency of occurrence of category i in the sites of group j (Dufrêne and Legendre, 1997). Indicator values range from 0 (no indication) to 100 (perfect indication) and give an indication of how abundant a particular category is in one group compared to other groups as well as the constancy of that species within a group. Significance was determined by a Monte Carlo randomization test with 4999 permutations.

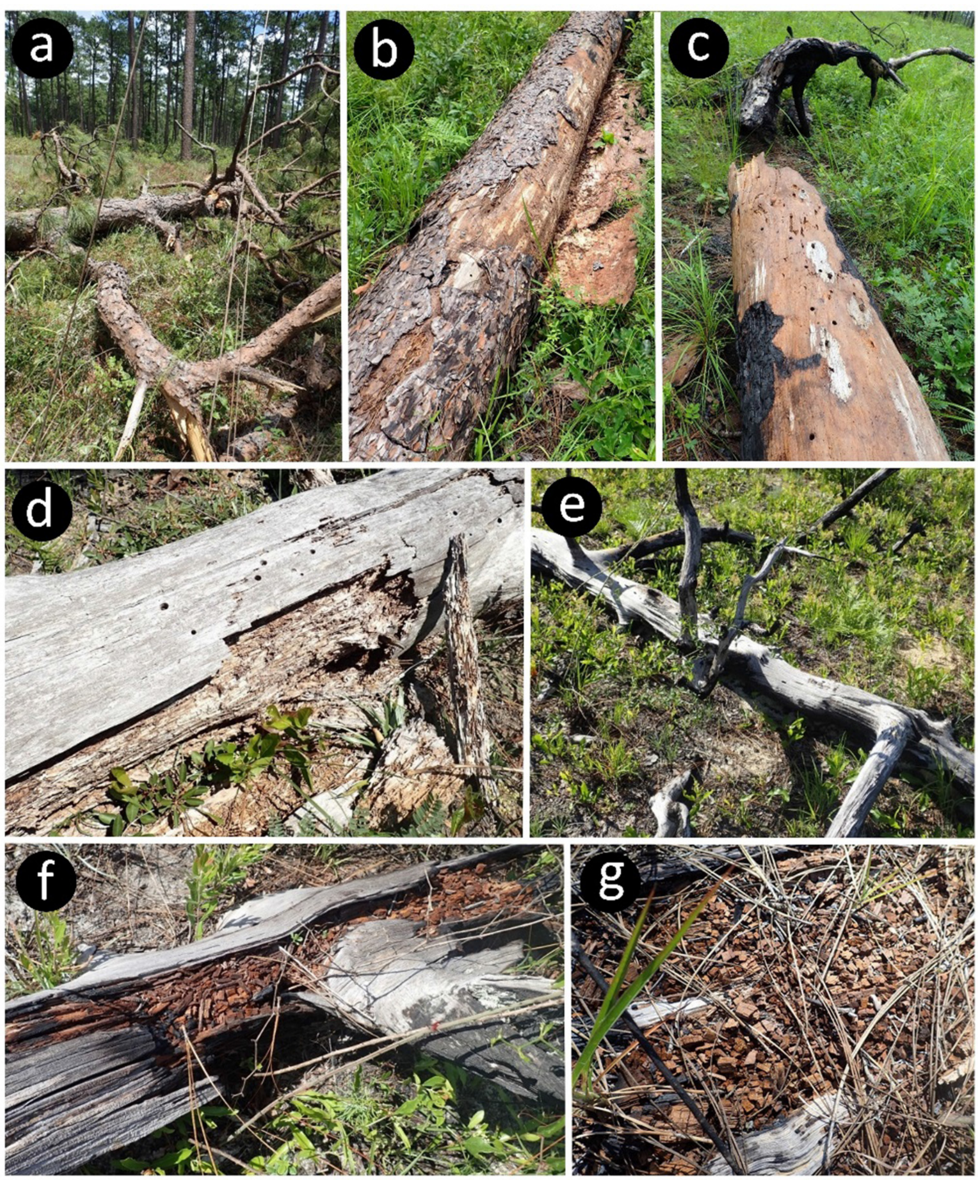

Fig. 1. Examples of decay classes 1 (a), 2 (b), 3 (c), 4 (d), 6 (e) and 7 (f-g) from Greenwood Big Woods (a), the Wade Tract (b and c) and Patterson Natural Area (d-g).

Table 3
Decay class designations for standing deadwood.

Characteristic	DC 1	DC 2	DC 3	DC 4	DC 5
Twigs < 3 cm	Present	Absent	Absent	Absent	Absent
Bark	Present	Loose and/or partly absent	Trace to absent	Trace to absent	Absent
Sapwood	Intact	Intact but soft in places	Present and soft but not ready to fall apart	Present but soft and ready to fall apart	Usually absent. If present, then sunbaked and extremely hard
Heartwood (if present)	Not visible	Not visible	Not visible	Often visible in places	Visible, extremely hard

3. Results

3.1. Stand composition and basal area

The basal area of living trees was low at all locations, ranging from about 5.3 m^2 per ha on the Patterson Natural Area to 14.2 m^2 per ha on the Wade Tract. Pine accounted for over 90% of the total basal area at all locations except for Tall Timbers where pine made up just 75.7% of the total basal area, with large oak trees accounting for the remainder (Table 1). Longleaf pine was by far the most abundant pine species at all locations except for Tall Timbers where loblolly pine dominated. The second most frequent and abundant tree genus was *Quercus* which was absent from just one of the seven locations. The Greenwood Big Woods plots had the highest tree diversity, with small numbers of *Liquidambar styraciflua* L. and *Magnolia virginiana* L. being present along an ephemeral stream margin in one plot.

3.2. Standing deadwood

Snags, defined here as standing dead trees at least 2 m tall, were rare at most locations, with plots having one or less on average at six of the seven locations (ranging from 1.25 to 10 per ha) (Fig. 2). Patterson Natural Area had the greatest number of snags, with an average of 4.75 per plot (47.5 per ha). The abundance of snags at Patterson Natural Area was largely driven by a single plot that contained 25 (18 of which were *Quercus laevis* Walt.), resulting in high variability among plots at this location (Fig. 2). We found the number and basal area of snags to differ significantly among Red Hills locations, with the highest number reported from the Greenwood Big Woods. Despite Patterson Natural Area having the highest mean values among the three Eglin AFB locations for both snag number and snag basal area, there were no significant differences among them due to high inter-plot variability (Fig. 2). ***Pinus*** snags accounted for the majority of the snag basal area at the seven locations and were the only snags represented at locations F22, Greenwood Secondary, Greenwood Big Woods and Tall Timbers (not including snags that could not be identified to genus). *Quercus* made up 8.2–46.5% of the snag basal area at the other three locations, being most prevalent at the Patterson Natural Area.

Stumps were more common than snags, with the number per plot ranging from ~1–5 (11.2–52.5 per ha). Among the Eglin AFB locations, there were significantly more stumps in Patterson Natural Area than in F-22 but there were no differences between E-24 and the other two locations. There were no significant differences in stump number among the Red Hills locations.

3.3. Downed coarse woody debris

Deadwood volume varied greatly among the plots, ranging from 0-2.1 m^3 (i.e., 0–21 m^3 per ha) at Eglin AFB and from 0 to 12.7 m^3 (i.e., 0–127 m^3 per ha) in the Red Hills. At Eglin AFB, Patterson Natural Area had significantly greater wood volume than the two secondary forest locations. There were no significant differences among locations in the Red Hills, by contrast, although the Wade Tract and Greenwood Big Woods had, on average, several times less and more wood volume than the other locations, respectively (Fig. 2). The lack of significance among the Red Hills locations underscores the high degree of variability observed among plots at each location. This was especially dramatic at the Greenwood Big Woods location where wood volume per plot ranged from 1.1 to 12.7 m^3, with the highest value being nearly three times greater than the second-highest value.

The three old-growth forests sampled in this study differed greatly in coarse woody debris volume. The Wade Tract had by far the lowest volume on average (2.51 ± 0.79 m^3 per ha), followed by Patterson Natural Area (10.59 ± 2.50 m^3 per ha). Greenwood Big Woods had the highest CWD volume, averaging 29.10 ± 14.55 m^3 per ha. Because we wanted our results from old-growth locations to reflect "undisturbed" amounts of wood as closely as possible, the wood volumes measured in four of the Greenwood Big Woods plots include estimated volumes of five sections of fallen trees that had been removed from the location. Without this correction, the volume of wood on the ground when our measurements were taken was 17.9 ± 7.3 m^3 per ha.

Wood assigned to decay classes 6 or 7 (i.e., classes consisting entirely of heartwood) dominated the coarse woody debris pools on Eglin AFB, making up between 74.8 and 88.2% of wood volume at the three locations (Table 4). These decay classes were also abundant, though less dominant, in the Red Hills, ranging from 13.3 to 54.2% of total wood volume at those locations (Table 4). Decay classes 1 and 2, by contrast, were entirely absent at the Eglin AFB locations and made up between 27.6 and 52.0% of wood volume in the Red Hills (Table 4).

Our rough estimates of downed wood mass varied from 0.5 ± 0.1 Mg/ha at F22 to 19.3 ± 9.6 Mg/ha at the Greenwood Big Woods, which are comparable to the values reported for pitch pine forests in North Carolina (McMinn and Hardt, 1996). Eglin values are as follows: E24: 0.9 ± 0.5; F22: 0.5 ± 0.1; and Patterson Natural Area: 7.1 ± 1.7. Red Hills values are: Greenwood Big Woods: 19.3 ± 9.6; Greenwood Secondary: 6.9 ± 3.5; Tall Timbers: 7.4 ± 3.9; the Wade Tract: 1.7 ± 0.5.

3.4. Deadwood variety

Deadwood variety, representing the variety of downed and standing deadwood based on species, diameter increments and decay classes, varied greatly among locations. At Eglin AFB, deadwood variety was significantly greater on average at the Patterson Natural Area than at the other two locations (Fig. 2). There were no differences in deadwood variety among the Red Hills locations but the values for the Wade Tract were the lowest while those for Greenwood Big Woods were highest.

3.5. Deadwood composition

Nonmetric multidimensional scaling yielded a two-dimensional solution with a final stress of 18.2. Axes 1 and 2 explained 32.5 and 19.4% of the variation, respectively. There is considerable overlap in the spaces occupied by the old-growth and secondary plots in the ordination (Fig. 3). Total heartwood volume was negatively correlated with axis 1 (r = -0.5). Based on indicator species analysis, nine of the 23 downed wood categories assessed were significantly associated with old-growth forests and none was an indicator of secondary forests. Two of the old-growth indicator categories were pine belonging to decay class 4 (≤10 cm (IV = 27.8, P = 0.04) and 10–20 cm (IV = 40.3,

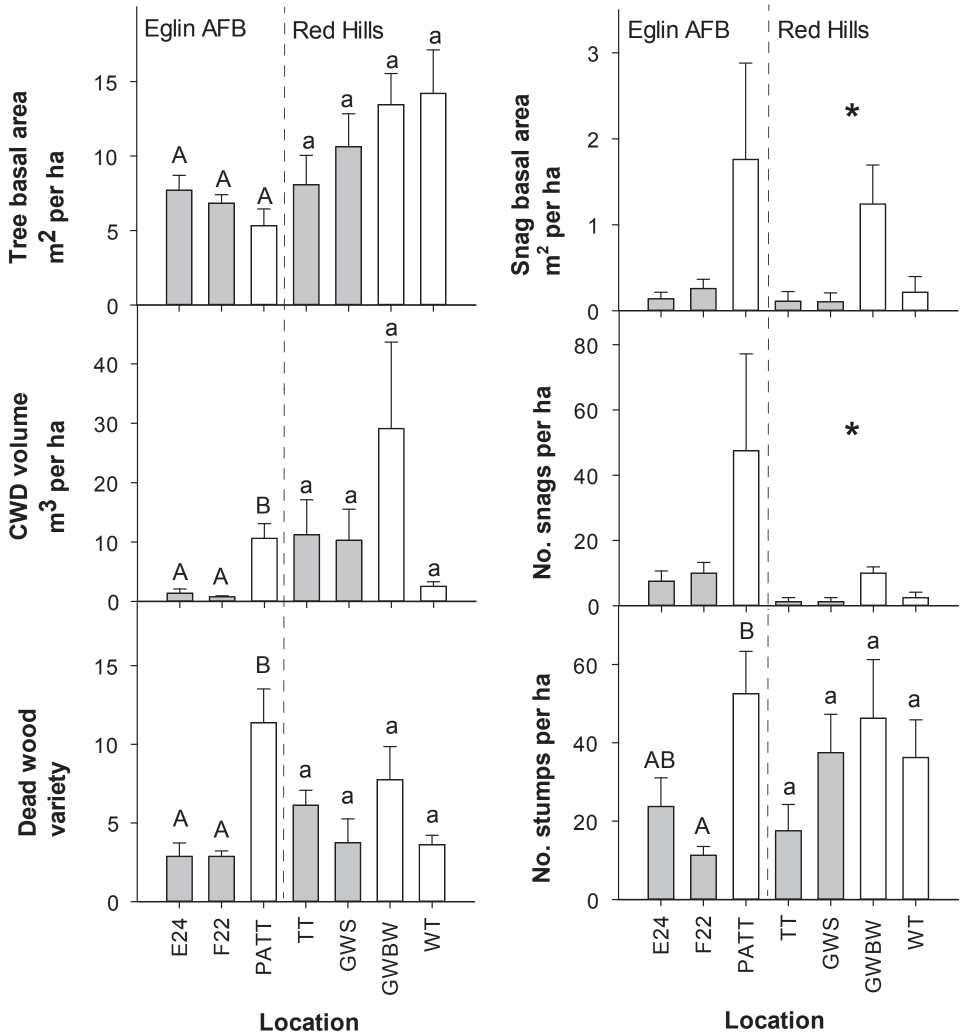

Fig. 2. Mean ± SE (n = 8) living basal area, snag basal area, downed CWD volume, number of snags, deadwood variety and number of stumps at each of the seven locations (Abbreviations are as follows: PATT = Patterson Natural Area; TT = Tall Timbers; GWS = Greenwood Secondary; GWBW = Greenwood Big Woods and WT = Wade Tract). For each region (Eglin AFB and Red Hills), bars with different letters above them are significantly different based on Tukey's studentized range test. For the graphs showing snag basal area and number of snags, asterisks are used to indicate when there were significant differences among locations within a particular region according to the Kruskal-Wallis test. Shaded and empty bars represent secondary and old-growth locations, respectively.

P = 0.02)), three were pine belonging to decay class 6 (≤10 cm (IV = 79.2, P = 0.0008); 20–30 cm (IV = 48.7, P = 0.003) and 30–40 cm (IV = 20.2, P = 0.04)), two were pine belonging to decay class 7 (≤10 cm (IV = 21.4, P = 0.03) and 10–20 cm (IV = 30.3, P = 0.004)), one was oak belonging to decay class 3 (10–20 cm (IV = 21.9, P = 0.01)) and one was oak belonging to decay class 4 (10–20 cm (IV = 28.5, P = 0.01)).

4. Discussion

The wood volumes reported in this study for old-growth longleaf pine forests are among the lowest values ever reported from old-growth

Table 4
Mean ± SE (n = 8) CWD volume by decay class (DC) and location. Percentages for each location are given in parentheses. Abbreviations are as follows: PATT = Patterson Natural Area; TT = Tall Timbers; GWS = Greenwood Secondary; GWBW = Greenwood Big Woods and WT = Wade Tract.

	Eglin AFB			Red Hills			
DC	E24	F22	PATT	TT	GWS	GWBW	WT
1	0 ± 0 (0)	0 ± 0 (0)	0 ± 0 (0)	5.27 ± 5.27 (47.08)	0.02 ± 0.02 (0.23)	1.19 ± 1.16 (4.09)	0 ± 0 (0)
2	0 ± 0 (0)	0 ± 0 (0)	0 ± 0 (0)	0.55 ± 0.40 (4.89)	2.81 ± 2.04 (27.37)	9.38 ± 6.81 (32.22)	0.91 ± 0.52 (36.11)
3	0.27 ± 0.26 (19.3)	0 ± 0 (0)	0.79 ± 0.60 (7.43)	0.03 ± 0.03 (0.31)	0.02 ± 0.02 (0.15)	9.19 ± 7.50 (31.59)	0.20 ± 0.20 (8.06)
4	0.01 ± 0.01 (0.85)	0.09 ± 0.09 (11.77)	1.35 ± 0.57 (12.78)	3.73 ± 3.70 (33.28)	2.82 ± 2.73 (27.49)	1.40 ± 0.72 (4.79)	0.04 ± 0.03 (1.61)
5	0.07 ± 0.05 (5.06)	0 ± 0 (0)	0.15 ± 0.07 (1.42)	0.13 ± 0.13 (1.13)	0 ± 0 (0.01)	2.01 ± 1.92 (6.92)	0 ± 0 (0)
6	0.97 ± 0.62 (69.52)	0.66 ± 0.22 (88.23)	7.01 ± 2.10 (66.2)	1.49 ± 0.46 (13.31)	4.605 ± 2.82 (44.75)	5.87 ± 2.18 (20.18)	1.36 ± 0.63 (54.23)
7	0.07 ± 0.07 (5.28)	0 ± 0 (0)	1.29 ± 0.39 (12.16)	0 ± 0 (0)	0 ± 0 (0)	0.06 ± 0.06 (0.21)	0 ± 0 (0)
Total	1.39 ± 0.69	0.75 ± 0.20	10.59 ± 2.50	11.20 ± 5.92	10.28 ± 5.25	29.10 ± 14.55	2.51 ± 0.79

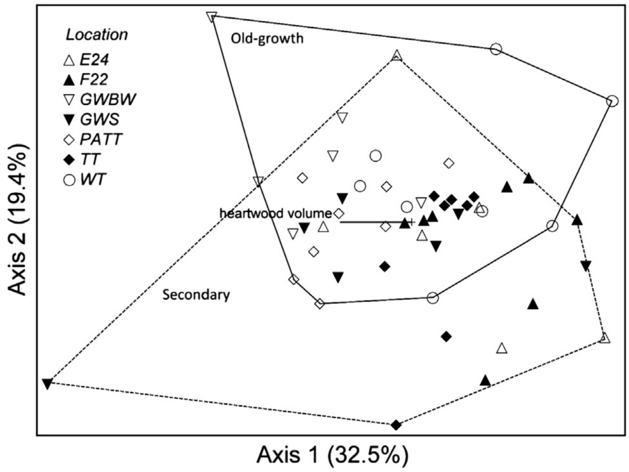

Fig. 3. NMS ordination showing differences in downed woody debris composition among plots. Solid and dashed lines denote areas occupied by old-growth and secondary sites, respectively. Abbreviations for locations are as follows: PATT = Patterson Natural Area; TT = Tall Timbers; GWS = Greenwood Secondary; GWBW = Greenwood Big Woods and WT = Wade Tract. Vector shows relationship between the axes and total heartwood volume.

forests (Lachat and Müller, 2018), ranging from 2.51 ± 0.79 to 29.10 ± 14.55 m^3 per ha. To our knowledge, the only previous study in old-growth forests to yield similar values was that of Robertson and Bowser (1999) who reported volumes of < 20 m^3 per ha from frequently burned conifer forests in the western United States. The low volumes reported in this study can be attributed in part to the low basal areas characteristic of longleaf pine forests and the high variability observed among plots reflects the fine scale at which this material is added to the ecosystem via individual tree mortality events (Palik and Pederson, 1996). Several additional factors also likely contributed to these patterns, however.

First, the high frequency at which forests in our study area are burned (i.e., every 1.5–2.5 years) likely contributed to both the low wood volumes and highly variable distribution of CWD observed in this study. Pine forests growing on the coastal plain of the southeastern US historically experienced some of the most frequent burns in North America, occurring about every 1–3 years (Guyette et al., 2012; Stambaugh et al., 2017). Although casual observations suggest that some wood is completely consumed by these fires, including even recently fallen trees, this question has not received much attention in the region. In one of the only studies to experimentally test this in longleaf pine, Hanula et al (2012) reported no differences in coarse woody debris volume among stands subjected to different burn frequencies (burned every 1, 2 or 4 years or left unburned) in Florida. The low intensity of these frequent burns may explain this lack of effect. Studies from other forest types have reported large reductions in woody fuels following prescribed fire, however, especially in xeric regions that experience more intense fires (Sackett, 1980; Randall-Parker and Miller, 2002; Fulé and Covington, 2006). Nonetheless, the xeric Patterson Natural Area old-growth location (Eglin AFB) had higher accumulations of CWD than paired secondary locations, suggesting fire is not simply a coarse filter for volumes (Agee, 2002) but that the quality of CWD substrate (i.e., the presence of fire-resistant heartwood remnants) in old-growth locations interacts with fire.

Termites may also contribute to the low wood volumes present in longleaf pine forests of the southeastern United States. Research from Mississippi found that termites consume about 20% of wood volume (Ulyshen et al., 2014) and significantly accelerate wood decay rates (Ulyshen, 2014; Stoklosa et al., 2016). During the course of data collection, termites or signs of their activity were consistently observed in all logs that still possessed sapwood. Termite activity was also commonly observed on heartwood although this appeared to be largely limited to the soil-wood interface. Carpenter ants (*Camponotus* spp.) were also commonly observed under pieces of heartwood and apparently contribute to the comminution of this material.

The subtropical climate of our study area may have also contributed to the relatively low wood volumes measured in this study by favoring the activities of wood-decomposing microbes, including fungi. The sandy soil of Eglin AFB is likely to result in more xeric conditions compared to other soil conditions in the southeastern U.S., however (Craul et al., 2005). This could in part explain why Patterson Natural Area, the old-growth Eglin AFB location, had accumulated larger volumes of heartwood than the old-growth Red Hills locations despite the fact that the Eglin AFB locations generally had less wood overall. There are also large differences in the density of vegetation growing on the Eglin AFB vs. Red Hills locations, with a much sparser coverage characterizing the Eglin AFB locations sampled in this study (Means, 1996). The thicker layer of vegetation in the Red Hills may maintain a microclimate of more humid conditions around and under downed woody debris, thus promoting the decomposition of this material.

The differences in wood volume among old-growth longleaf pine forests measured in this study are extreme. The Greenwood Big Woods had over eleven times more wood than the Wade Tract, for example, despite the fact that these two old-growth locations are separated by just a few kilometers and have similar site histories. This variability probably reflects the patchiness of disturbance, with recent wind disturbance contributing to the much higher values reported at Greenwood. The Wade Tract also has been managed with more fires during the seasonally dry months of May-June, which could have led to more CWD consumption by fire. Despite having a recent fire regime similar to that of the Wade Tract, however, Patterson Natural Area had consistently higher volumes. This suggests that seasonality of fire may have little influence on wood qualities although it should be noted that a high percentage of wood volume at Patterson Natural Area consisted of heartwood which resists ignition. In addition to the large differences in wood volume among locations, we also detected a high degree of variability among plots at each location (Fig. 2) and this is consistent with observations in other forest types (Muller and Liu, 1991).

All nine of the downed wood categories that were significant indicators of old-growth conditions in this study belonged to advanced decay classes, with five of them consisting of heartwood (decay classes 6 or 7). These findings suggest that of all the deadwood characteristics examined in this study, heartwood in the CWD pool is most indicative of old-growth conditions. In addition to entire logs and associated branches (Fig. 1e), much of this heartwood material consisted of small fire-hardened pieces that appear to be extremely persistent. Because heartwood, once charred, appears to be largely resistant to ignition as well as to termites, the major mechanism by which this material is lost from these ecosystems remains uncertain. Although the age of these persistent heartwood remnants is not known, Rother et al. (2018) found heartwood stump material in longleaf pine forests to be exceptionally recalcitrant, persisting for nearly a century. Heartwood with visible signs of decomposition, assigned decay class 7, was absent from four of the locations (three of which were secondary) and rare at the other three. Heart rot occurs in the centers of even living trees, however, and was likely present within much of the heartwood occurring within our sampling plots (Varner and Kush, 2004). Despite being an indicator of old-growth forests, heartwood made up a substantial fraction of the downed woody debris volume at all of our locations. It is important to note that the secondary forests sampled in this study all exceeded a century in age, however. With the exception of legacy heartwood from previous stands, young longleaf pine forests can be expected to lack heartwood until mature trees begin to die.

5. Conclusions and future directions

It is widely recognized that deadwood accumulates as forests age and large amounts of downed and standing wood are old-growth attributes in many forest types. While our results from Eglin AFB are generally consistent with these patterns, those from the Red Hills are less so. The volume of wood measured on the Wade Tract, one of the best remaining examples of undisturbed old-growth longleaf pine in North America, was only a fraction of the volumes measured at the Greenwood Big Woods location and the two secondary forests. It is clear from these findings that forest age is just one of many factors contributing to the amount and variety of deadwood in longleaf forests. A suite of other factors, including soil conditions, fire history and recent wind damage interact to create highly variable and dynamic CWD pools. While our findings suggest that total wood volume may not be as reliable an indicator of old-growth conditions as it is in other forest types, the volume of heartwood does appear to characterize old-growth conditions with an accumulation of this material over time. Future studies conducted at other locations and involving more sampling plots per location (to reduce inter-site variation) would help clarify these patterns.

Studies addressing the biodiversity associated with woody debris in longleaf pine forests would also be of great interest. Work from other forest types suggests that roughly 20–30% of insect diversity is dependent on dying or deadwood, for example, and some species are known to be strongly associated with old-growth forests. To our knowledge, no effort has been made to explore this question in longleaf pine forests (but see Folkerts et al. (1993) for an overview of arthropods associated with this ecosystem). Forests with a history of frequent fires are also known to support a number of pyrophilic species and this too may be the case in the longleaf pine ecosystem.

Acknowledgments

We thank the Wade family for permission to sample at the Wade Tract and Greenwood Plantation and Jim Cox and Paul Massey for facilitating access to these properties. We are also grateful to Brett Williams and David Grimm for facilitating our work at Eglin Air Force Base and to two anonymous reviewers for commenting on an early draft of the manuscript. This project was funded by the USDA Forest Service, Southern Research Station.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.07.017.

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