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RESEARCH ARTICLE

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Patterns of Riparian and In-stream Large Woody Debris Across a Chronosequence of Southern Appalachian Hardwood Stands

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ABSTRACT: The density and volume of riparian and in-stream large woody debris (LWD) is hypothesized to be a function of forest disturbance and developmental processes. However, these relationships are poorly understood for many forest types, including hardwood forests of the southern Appalachian Highlands. We analyzed patterns of riparian and in-stream LWD in hardwood stands across three establishment classes (pre-1900s, 1930s, and 1950s) on the Cumberland Plateau to elucidate the relationships between forest development and LWD patterns. The stands were dominated by *Fagus grandifolia*, *Quercus alba*, and *Lirodendron tulipifera*. Density and volume of riparian LWD did not differ across the chronosequence. Density of riparian LWD ranged from 367 (1950s) to 407 (1930s) pieces ha^{-1} and volume ranged from 142.0 (pre-1900s) to 187.1 (1930s) m^3 ha^{-1}. Likewise, mean density and volume of in-stream LWD did not differ across the chronosequence. Density of in-stream LWD ranged from 20 pieces 100 m^{-1} (pre-1900s and 1950s) to 28 pieces 100 m^{-1} (1930s) and volume ranged from 4.8 m^3 (1950s) to 8.3 m^3 100 m^{-1} (1930s). We documented significantly greater volume of in-stream LWD in the stabilizing or armoring banks function class in the 1950s establishment class, but no other systematic differences. Based on species composition and size, we speculate that riparian LWD largely originated from trees that grew outside the riparian zone and were transported down slope. In contrast, in-stream LWD inputs were linked directly to the adjacent riparian zones.

Index terms: Appalachian, forest disturbance, forest structure, riparian, streams, woody debris

INTRODUCTION

Large woody debris (LWD), defined as dead standing or downed wood, is structurally and functionally important in riparian and in-stream ecosystems (Harmon et al. 1986; Spies et al. 1988; Bilby and Ward 1991). Riparian LWD provides habitat for a variety of fauna and serves as germination sites for many vascular plants, bryophytes, and fungi (Harmon et al. 1986; Bragg and Kershner 1999; McGee et al. 1999; Webster and Jenkins 2005). In-stream LWD (i.e., dead wood positioned within bankfull margins) may control sediment movement, dissipate stream energy, and serve as substrate for aquatic activity (Hedman et al. 1996; Naiman and Decamps 1997; McGee et al. 1999; Powell et al. 2009; Bendix and Cowell 2010; Jones et al. 2011). As such, density, volume, and composition of LWD can be strong controls of riparian and aquatic habitat quality, nutrient cycling, and geomorphological processes (Harmon et al. 1986; Bilby and Ward 1991; Spetich et al. 1999; Bendix and Cowell 2010).

LWD is created by endogenous and exogenous disturbance events that kill trees or parts of them and deposit wood on the forest floor or in streams. Although the disturbance mechanisms vary, wind is the most common disturbance agent that generates LWD in temperate deciduous forests of the eastern United States (White 1979; Lormier 1980; Runkle 1985; Busing et al. 2009). Density and volume of LWD are hypothesized to be linked to forest developmental processes. When density and volume of LWD have been plotted over the course of long-term forest development (i.e., from stand initiation to complex stages), the frequency distributions have typically been shown to exhibit a parabola (Harmon et al. 1986; Spies et al. 1988; Bormann and Likens 1994; Sturtevant et al. 1997).

The parabola distribution pattern has been explained by forest disturbance and developmental processes. LWD loading at stand initiation (i.e., immediately following a catastrophic disturbance) is high with LWD originating as carryover from the pre-disturbance period combined with debris generated during the stand initiating disturbance event. With time since the catastrophic disturbance, LWD gradually declines in abundance and volume as the material decays and little is added to the system. The rising arm of the parabola corresponds to stand maturation. LWD should increase when stands develop to the point when overstory and midstory tree mortality increases as a result of self-thinning and exogenous disturbance (Harmon et al. 1986; Spies et al. 1988; Sturtevant et al. 1997; Hély et al. 2000; Brassard and Chen 2008). Indeed, LWD is commonly cited as a characteristic of old-growth conditions of temperate deciduous forests (Martin 1992; Tyrrell et al. 1998). However, patterns of abundance and total volume of riparian and in-stream LWD have rarely been analyzed over relatively fine temporal scales (i.e., short periods of stand development). Specifically, riparian and in-stream LWD loadings have not been analyzed across a chronosequence of stands representing the stages of development that characterize general forest conditions of the eastern U.S. Anthropogenic forest clearing in the region peaked in the early-1900s, resulting in large expanses of even-aged secondary stands (Whitney 1994; Dyer 2006). Thus, the region's forests are largely characterized as developing secondary stands that established between ca. 1900 and the 1950s. Furthermore, relatively few riparian and in-stream LWD studies have been conducted in the southern Appalachian Highlands and no such studies have been conducted on the southern Cumberland Plateau. These data are required to improve our understanding of the relationships between forest development and riparian and in-stream LWD in this region. Empirical data on LWD loadings are also important for forest management as LWD is increasingly being considered in forest management plans and LWD enhancement is becoming a common practice in forested stream ecosystems (Hilderbrand et al. 1997; Larson et al. 2001; Benda et al. 2002).

The overarching goals of our study were to characterize patterns of riparian and in-stream LWD across a chronosequence of southern Appalachian hardwood stands. Our specific objectives were to: (1) quantify live tree species composition and stand structure of riparian zones; (2) document the density, volume, composition, and decay class of riparian LWD; and (3) quantify the abundance, volume, size, decay class, position class, and function class of in-stream LWD across the chronosequence to examine these variables in the context of stand development.

METHODS

Study Area

Our study was conducted in the Sipsey Wilderness on the Bankhead National Forest in Alabama (Figure 1). The Sipsey Wilderness was established in 1975 and expanded in 1988 to its current size of 10,085 ha. The Sipsey Wilderness occurs on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman 1938). The geology of this region primarily consists of the Pennsylvanian Pottsville formation characterized by thick-bedded to pebbly quartzose sandstone with variable amounts of interstratified shale, siltstone, and thin discontinuous coal (Szabo et al. 1988). The landscape is dissected to the point that it no longer resembles a true plateau. The topography is characterized by narrow ridges and valleys, extensive hills, and steep slopes (USDA SCS 1959; Smalley 1979). Soils are generally acidic, well drained, and shallow (USDA SCS 1959). The Sipsey Wilderness is drained by the Sipsey Fork of the Black Warrior River.

The climate of the region is classified as humid mesothermal with short, mild winters and long, hot summers (Thornthwaite 1948). Mean annual temperature is 16 °C and the January and July means are 5 °C and 26 °C, respectively. The frost-free period extends from late-March to early-November and is ca. 220 days (Smalley 1979). Precipitation is evenly distributed throughout the year. Mean annual precipitation is 139 cm and monthly mean precipitation for January is 13.5 cm and July is 11.3 cm (PRISM Climate Group 2011). Winter precipitation typically consists of low intensity events that result from frontal lifting. Summer precipitation can be more intense (sometimes accompanied by lightning) and result from extreme low pressure centers and convective lifting (Smalley 1979).

According to Braun's (1950) classification system, the Sipsey Wilderness occurs in a transitional zone between the *Quercus-Pinus* Forest to the south and the Mixed Mesophytic Forest to the north. Species composition on the Cumberland Plateau is largely driven by topographic characteristics and factors related to soil water availability (e.g. stone cover and soil depth; Hinkle 1989). The Cumberland Plateau is noted for high gamma diversity, and forests may contain over 30 tree species with potential to occupy positions in the main forest canopy (Hinkle et al. 1993). In a gradient analysis study, Zhang et al. (1999) documented 14 distinct ecological community types in the Sipsey Wilderness. *Quercus* was the most abundant and widespread genus and it occurred in almost every community type. Environmental gradients in this region are quite steep. Ridges and upper slope positions are often dominated by *Pinus taeda* and *Pinus echinata* Mill. Over a distance of less than 100 m down slope, stands may transition to support a stronger component of hardwood species (Zhang et al. 1999). Middle and lower slope positions may support mesic hardwood stands that include *Fagus grandifolia, Liriodendron tulipifera*, and *Magnolia macrophylla* (Hardin and Lewis 1980; Martin 1992; Zhang et al. 1999; Richards and Hart 2011). Such steep environmental gradients are common on the southern Cumberland Plateau and adjacent Interior Low Plateau. Richards and Hart (2011) analyzed disturbance processes in slope forests of the Sipsey Wilderness and concluded that the disturbance regime was characterized by gap-scale events that modified local environmental conditions.

Pairing Sites

To document differences in composition, density, and volume of LWD across a chronosequence of establishment classes, we paired sites to eliminate factors unrelated to stand age. Previous studies have paired potential research sites in a GIS environment and this method is credited with increasing objectivity, isolating confounding influences, and decreasing error variance (Young et al. 2002; Collier et al. 2007; Roberts et al. 2009). To select our study stands, we first created a map in ArcGIS v. 9 from USDA Forest Service georeferenced, stand-level data that contained information on species composition and establishment age. The map was queried and potential study sites were graphically displayed. We then used a combination of historical and contemporary aerial photographs, personal communication with USDA Forest Service staff, and field reconnaissance to select our study stands. Using this information, we subjectively selected stands (n = 3, one per age class) that: (1) were dominated by *Quercus alba* to ensure similar species composition across treat-

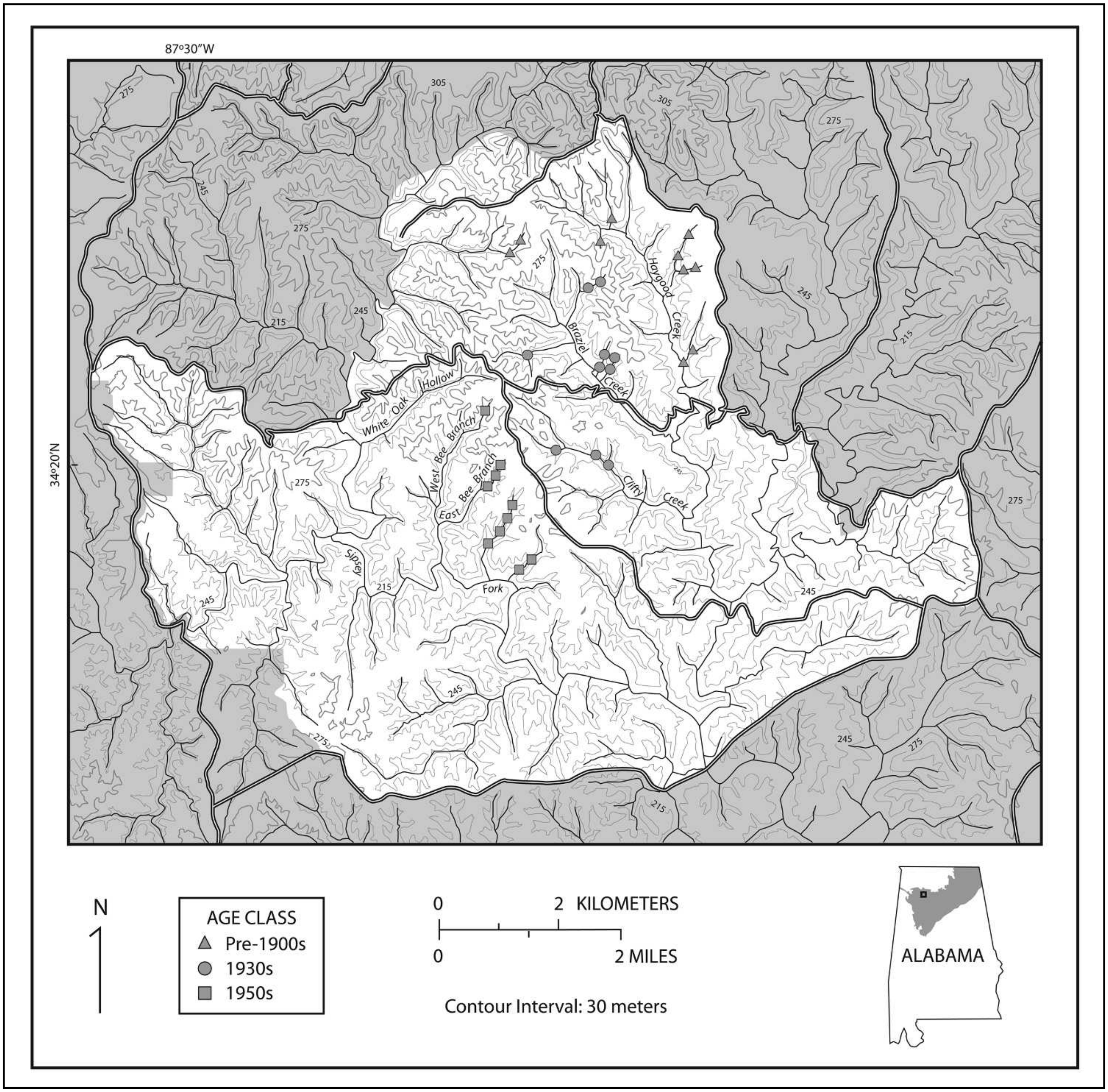

Figure 1. Map of Sipsey Wilderness, Alabama. White area is the Sipsey Wilderness, thin lines are 30 m contour intervals, heavy gray lines are streams, and heavy dark double lines are roads. Shaded portion on Alabama inset map is the Cumberland Plateau physiographic section.

ments and to represent conditions typical of the broader region; (2) represented three distinct establishment classes (pre-1900s, 1930s, and 1950s) to analyze LWD along a chronosequence; (3) were drained by second order streams because streams of that size are most common in the Sipsey Wilderness and the ratio of LWD length to stream width and the recruitment into these size streams was of particular interest; and (4) occurred in watersheds with similar morphometry, in particular similar drainage areas (drainage area of the selected watersheds ranged from 41.3 to 49.6 ha).

Field Methods

Once we determined the stands to be studied, we established 10 sampling sites in each establishment class. Each sampling site contained two 10-m x 30-m riparian plots and a 30-m in-stream reach. At each of the sites, we established two plots on opposite sides of the stream (two riparian plots for each stream reach, 10 reaches for each establishment class for a total of 20 riparian plots age class^{-1}). To capture the interface between the riparian zone and the stream, we established our riparian plots to correspond to the stream channel. We ran a 30-m tape along the stream bank and used survey pins to mark the stream bank shape. We then used a digital hypsometer with transponder to measure 10-m upslope of the 30-m baseline along the stream margin. We used a sighting compass to ensure that the shape of the stream was correctly accounted for in the riparian zone plot making each plot exactly 300 m^2. Riparian zones typically extend 10-m to 20-m from the stream bank (Clinton et al. 2010). Beyond this distance, forests become less coupled to stream ecosystems and, in our study area, may transition to a more upland forest type. By using this sampling technique, we avoided simply establishing rectangular plots that did not correspond to the interface of the terrestrial and aquatic environments.

On each of the 60 riparian plots we measured species, diameter at breast height (dbh), and classified crown class as dominant, co-dominant, intermediate, or overtopped based on the amount and direction of intercepted light (Oliver and Larson 1996) for all living trees ≥ 5 cm dbh. For snags ≥ 5 cm dbh we documented species to the lowest taxonomic level possible, dbh, height, and decay class (Table 1). For all downed logs ≥ 5 cm diameter and ≥ 1 m length, we recorded species to the lowest taxonomic level possible, diameter, length, and decay class. We quantified live trees to characterize composition and structure of the riparian zone for each establishment class and across all age categories to determine general forest-level conditions. The riparian stands were assessed using standard descriptors of density, basal area, and mean tree diameter. Snag characteristics were quantified to examine how stand dynamics influenced LWD patterns because that material would become LWD.

Each piece of LWD was placed into a decay category to test for differences in LWD composition across the chronosequence. For LWD with root plates, we measured dbh and total length to calculate volume using species-specific allometric equations (Honer 1967). For LWD segments without an identifiable root plate, we measured total length and diameter at both ends and used the equation for a conical paraboloid to calculate volume (Fraver et al. 2007). If the segment of LWD was too decayed to accurately measure both ends, we measured

Table 1. Descriptions of position, decay, and function classes used to characterize LWD (adapted from Jones and Daniels 2008).

Parameter	Description
Position Class	
Bridge	Log spans channel, touching both banks and resting on flood plain
Partial Bridge	Spanned log has broken in one or more places within the stream channel
Loose	Log is no longer associated with the floodplain; fully associated with the streambed; log is fully submerged during bank-full
Buried	Log has become incorporated into streambed or the sides of the streambank; sediment stored upstream of the log which is at least partly buried
Decay Class	
I	Wood has >75% bark intact, bark adheres tightly; branches have fine (third order) branchlets; sapwood is sound, and log retains structural integrity
II	Wood has 25%–75% bark intact which, in places, is loosely attached to the bole; first order branches have a solid connection to the bole; wood is solid with evidence of decay on some outer sections of sapwood only
III	Wood has 0–25% bark present, adhering loosely to the sapwood; first order branches and branch nubs are present and sit loosely in the bole; along some parts of the bole, wood shows significant signs of decay to depths of 5–10 cm
IV	Bark is no longer attached; branch nubs only are present; along some parts of the bole, wood is soft, crumbly or fibrous, and decay can penetrate nearly through the sapwood
Function Class	
I	Stabilizing or armoring banks
II	Creating pools and riffles
III	Holding back organic matter
IV	Having no observable influence of function

diameter in the middle and length and calculated volume using Huber's formula (Fraver et al. 2007). After volume was calculated for all riparian LWD, we examined the volume by species and decay class.

We surveyed the in-stream LWD (LWD within bankfull margins) in the 30-m reaches established for the riparian plots as stated above. We measured in-stream LWD with the same size parameters as the riparian zone LWD. For each piece of LWD, we measured length, diameter, decay class, position class, and function class (Table 1). The description of each class was adapted from Jones and Daniels (2008) and each piece of LWD could serve multiple functions. Assigning position and function classes were important to examine the composition and structural importance of in-stream LWD. We collected multiple bankfull width and stream depth measurements of the sampled stream reaches to test for differences in stream width and to standardize the in-stream values for comparative purposes.

Data Analysis

To test for significant differences in the number of trees, mean dbh, density of LWD, volume of LWD, and volume of LWD in the different decay classes across the chronosequence, we used one-way ANOVA. We visually assessed that the data were normally distributed and Levene tests were used to measure variances. A Tukey post-hoc test was used when comparing across the establishment classes ($n = 60$). The same statistical analysis was also completed for the density and volume of in-stream LWD and the volume of in-stream LWD in the different decay, position, and function classes ($n = 30$). Since LWD pieces created a riffle and/or pool (Function II) and held back organic matter (Function III), we combined function classes II and III, henceforth referred to as Function II/III. To test for differences in the volume and length of individual riparian and in-stream LWD pieces across the chronosequence, we used ANOVA with a Scheffe post-hoc test. In addition, we used ANOVA to test for systematic differences in mean bankfull widths across the establishment classes. All statistical tests were performed using SAS v. 9.1 and statistical significance for all tests was set at $P < 0.05$.

RESULTS

Riparian Live Trees

The pre-1900 establishment class was dominated by *F. grandifolia*, *L. tulipifera*, *Acer rubrum*, and *Q. alba* (Table 2). Species richness of stems ≥ 5 cm dbh was 22 and the most abundant species in this establishment class were *F. grandifolia* and *L. tulipifera*. The 1930s establishment class was dominated by *F. grandifolia* and *Q. alba* and notably did not contain any *P. taeda* (Table 3). *Fagus grandifolia* and *Q. alba* were also the most abundant species in this class and species richness was 26. The 1950s establishment class was dominated by *Q. alba*, *Liquidambar styraciflua*, and *Carya alba* (Table 4). The most commonly encountered species in this establishment class were *F. grandifolia*, *M. macrophylla*, *A. rubrum*, and *Q. alba* and species richness was 25. Mean live tree density ha^{-1} ranged from 490 stems for the pre-1900s class to 630 stems for the 1950s class and at the plot-level did not significantly differ across the chronosequence. Mean tree diameter did not differ across the chronosequence. Basal area was 29.55 m^2 ha^{-1} for the pre-1900s class, 17.80 m^2 ha^{-1} for the 1930s class, and 21.55 m^2 ha^{-1} for the 1950s class. Crown class distributions were similar across the three classes (Figure 2). However, the 1950s establishment class had a relatively high number of stems with intermediate crown positions and the ratio of codominant to dominant trees was different compared to the 1930s and pre-1900s establishment classes.

Riparian Snags

We found no significant differences in the mean number of snags per plot (300 m^2). Riparian snag density per plot ranged from a high of 0.95 ± 0.25 SE in the 1950s establishment class to a low of 0.50 ± 0.14 SE in the 1930s establishment class (Table 5). However, the highest mean volume of snags occurred in the pre-1900 establishment class with 0.07 m^3 plot^{-1} ± 0.03 SE (Table 5). The volume of snags was lowest in the 1930s establishment class with 0.02 m^3 plot^{-1} ± 0.01 SE. Across all ages, the mean number of snags was 0.68 ± 0.11 SE and the mean volume of snags was 0.04 m^3 ± 0.01 SE. At the hectare level snag density for the pre-1900s, 1930s, and 1950s establishment classes was 20, 17, and 32 with corresponding total volumes of 2.20 m^3, 1.18 m^3, and 0.79 m^3, respectively.

Riparian LWD

The mean density and volume of LWD across the chronosequence did not differ significantly (Table 5). The mean frequency of LWD across establishment classes ranged from 10.90 ± 1.03 SE (1950s) to 12.20 plot^{-1} ± 1.86 SE (1930s) and mean LWD volume ranged from 4.26 m^3 ± 0.60 SE (1900s) to 5.62 m^3 plot^{-1} ± 1.17 SE (1930s). The frequency of LWD pieces in the pre-1900, 1930s, and 1950s establishment classes was 375, 407, and 367 ha^{-1}, respectively, and LWD volume of these classes was 141.97 m^3 ha^{-1} ± 0.04 SE, 187.05 m^3 ha^{-1} ± 0.04 SE, and 173.77 m^3 ha^{-1} ± 0.05 SE, respectively. When the individual establishment classes were combined to examine forest-scale LWD patterns, the mean number of logs was 382.78 ha^{-1} ± 7.3 SE and the volume of logs was 167.63 m^3 ha^{-1} ± 0.02 SE.

The ratio of live trees to logs was similar across the forest establishment classes. For the pre-1900 establishment class, it was 1.30:1. For the 1930s and 1950s establishment class, it was 1.38:1 and 1.72:1, respectively. The mean volume and mean length of individual logs did not differ significantly across the establishment classes (Table 5). When examining LWD at the log level, the mean volume (m^3) of individual LWD pieces ranged from 0.38 m^3 ± 0.07 SE (pre-1900 establishment class) to 0.47 m^3 ± 0.08 SE (1950s establishment class). The mean length of individual logs ranged from 3.70 m ± 0.19 SE (1900s establishment class) to 4.28 m ± 0.22 SE (1950s establishment class). The mean volume of logs in each decay category did not significantly differ across the establishment classes. At the plot level, the highest mean volume

Table 2. Density and dominance measures for all live stems ≥ 5 cm dbh in riparian zones of a stand that established prior to 1900 on the Sipsey Wilderness, Alabama.

Species	Density (stems ha^{-1})	Relative density	Dominance (m^2 ha^{-1})	Relative dominance
Fagus grandifolia Ehrh.	198	40.2	8.01	27.11
Liriodendron tulipifera L.	60	12.16	4.57	15.46
Acer rubrum L.	25	5.07	4.38	14.83
Quercus alba L.	20	4.05	3.31	11.24
Carya alba (L.) Nutt.	20	4.05	1.87	6.34
Liquidambar styraciflua L.	20	4.05	1.28	4.32
Quercus prinus L.	20	4.05	1	3.39
Quercus rubra L.	5	1.01	0.95	3.23
Pinus taeda L.	2	0.34	0.8	2.69
Nyssa sylvatica Marshall	17	3.38	0.75	2.53
Magnolia macrophylla Michx.	28	5.74	0.7	2.38
Carya ovata (Mill.) K. Koch	7	1.35	0.61	2.07
Oxydendrum arboretum (L.) DC.	12	2.36	0.51	1.72
Carya cordiformis (Wangenh.) K. Koch	5	1.01	0.33	1.1
Ostrya virginiana (Mill.) K. Koch	27	5.41	0.2	0.69
Tilia Americana L.	3	0.68	0.09	0.3
Carya laciniosa (Michx. f.) G. Don	2	0.34	0.04	0.15
Fraxinus Americana L.	3	0.68	0.04	0.15
Carpinus caroliniana Walter	8	1.69	0.04	0.14
Ulmus rubra Muhl.	7	1.35	0.03	0.12
Acer saccharum Marshall	2	0.34	0.01	0.05
Cladrastis kentukea (Dum. Cours.) Rudd	2	0.34	0	0.01
Total	490	99.66	29.55	100

of decay class I and IV was in the 1930s establishment class. The greatest volume of riparian logs was in decay classes II and III. More than half of the LWD pieces for each establishment class could not be taxonomically identified with confidence (Table 6). For each establishment class, *P. taeda* constituted the greatest volume of identified pieces.

In-stream LWD

In-stream LWD density and volume did not differ across the establishment classes at the plot level (i.e., within the bankfull margins of the 30-m transects) (Table 7). The highest mean volume of in-stream LWD occurred in the 1930s establishment class (2.50 m^3 ± 0.72 SE). The pre-1900 stream reaches had a mean LWD density of 6.00 ± 1.24 SE $plot^{-1}$ and a mean LWD volume of 2.24 m^3 ± 0.72 SE. In the 1950s establishment class, mean LWD density was 6.00 ± 0.87 SE and mean volume was 1.45 m^3 $plot^{-1}$ ± 0.45 SE. The mean length of individual in-stream LWD pieces was not significantly different and ranged from 2.79 m ± 0.18 SE (1930s) to 2.20 m ± 0.15 (1950s). The mean volume at the plot level ranged from 0.24 m^3 ± 0.09 (1950s establishment class) to 0.37 m^3 ± 0.15 (pre-1900 establishment class). We found no significant difference in the volume of in-stream LWD across the decay or position classes (Table 8). We documented significantly greater volume of LWD in the function class I in the 1950s establishment class, but no other systematic differences were noted. The mean length of individual in-stream LWD pieces was not significantly different and ranged from 2.79 m ± 0.18 to 2.20 m ± 0.15 (Table 7). For the 30 sampled stream reaches, the mean bankfull width was 3.23 m ± 0.23. The frequency of LWD 100 m^{-1} of stream was highest in the 1930s establishment class with 27.76 LWD pieces ± 4.08 SE. The total volume (m^3 m^{-1}) of in-stream LWD was highest in the 1930s age class with 0.08 m^3 m^{-1} ± 0.02. Although the frequency was the same in the pre-1900 and 1950s establishment classes, the volume was higher in the 1950s class (0.075 m^3 m^{-1} ± 0.02 compared to 0.05 m^3 m^{-1} ± 0.02). The total in-stream

Table 3. Density and dominance measures for all live stems ≥ 5 cm dbh in riparian zones of a stand that established in the 1930s on the Sipsey Wilderness, Alabama.

Species	Density (stems ha^{-1})	Relative density	Dominance (m^2 ha^{-1})	Relative dominance
Fagus grandifolia	118	20.94	3.67	20.61
Quercus alba	58	10.32	3.66	20.56
Quercus prinus	33	5.9	1.72	9.64
Liriodendron tulipifera	10	1.77	1.53	8.61
Carya glabra (Mill.) Sweet	33	5.9	1.41	7.94
Carya alba	22	3.83	1.16	6.53
Liquidambar styraciflua	7	1.18	0.81	4.53
Magnolia macrophylla	55	9.73	0.62	3.49
Acer saccharum	33	5.9	0.59	3.29
Quercus rubra	5	0.88	0.39	2.21
Acer rubrum	33	5.9	0.38	2.14
Carya cordiformis	23	4.13	0.31	1.77
Oxydendrum arboreum	20	3.54	0.31	1.74
Ostrya virginiana	23	4.13	0.31	1.73
Nyssa sylvatica	23	4.13	0.24	1.34
Fraxinus americana	13	2.36	0.24	1.32
Carpinus caroliniana	17	2.95	0.12	0.68
Asimina triloba (L.) Dunal	5	0.88	0.11	0.62
Ulmus Americana L.	7	1.18	0.07	0.37
Cornus florida L.	12	2.06	0.06	0.34
Platanus occidentalis L.	2	0.29	0.04	0.24
Quercus velutina Lam.	3	0.59	0.02	0.1
Tilia americana	2	0.29	0.01	0.08
Sassafras albidum (Nutt.) Nees	3	0.59	0.01	0.05
Cladrastis kentukea	2	0.29	0.01	0.03
Hamamelis virginiana L.	2	0.29	0	0.02
Total	565	100	17.8	100

volume, which takes into account stream width and depth, was highest in the pre-1900 establishment class (0.050 m^3 m^{-2} ± 0.02) and lowest in the 1950s establishment class (0.02 m^3 m^{-2} ± 0.01), but these differences were not systematic across the establishment classes. The highest frequency and volume of in-stream LWD occurred in decay class II/III. The lowest frequency and volume of LWD occurred in the buried position class. We found no systematic differences in the mean length of logs across the chronosequence in the decay, position, or function classes. We were unable to compare in-stream LWD by species because the vast majority of logs were too decayed to be taxonomically identified with confidence.

DISCUSSION

Live Trees and Snags in Riparian Zones

Although basal area contributions and rank orders of species differed across the establishment classes, the same species were common components to all stands. The USDA Forest Service database we used to select stands classified all of them as *Q. alba* dominated. Although *Q. alba* may be considered dominant at the stand-level, this species was only the greatest contributor to riparian zone basal area in the 1950s establishment class. Certainly composition of the riparian zone components of these systems differed from that of the entire stand (Zhang et al. 1999). We are confident that species compositions were sufficiently similar across establishment classes for our purposes and thus, we hypothesize

Table 4. Density and dominance measures for all live stems ≥ 5 cm dbh in riparian zones of a stand that established in the 1950s on the Sipsey Wilderness, Alabama.

Species	Density (stems ha^{-1})	Relative density	Dominance (m^2 ha^{-1})	Relative dominance
Quercus alba	65	10.32	4.59	21.28
Liquidambar styraciflua	37	5.82	3.08	14.29
Carya alba	30	4.76	2.83	13.14
Fagus grandifolia	92	14.55	1.95	9.06
Liriodendron tulipifera	23	3.7	1.81	8.41
Magnolia macrophylla	82	12.96	1.08	4.99
Quercus prinus	8	1.32	1.06	4.91
Acer rubrum	78	12.43	0.89	4.13
Carya glabra	13	2.12	0.84	3.9
Oxydendrum arboreum	35	5.56	0.81	3.74
Quercus rubra	5	0.79	0.55	2.57
Pinus taeda	2	0.26	0.48	2.22
Acer saccharum	20	3.17	0.39	1.83
Nyssa sylvatica	42	6.61	0.36	1.69
Ostrya virginiana	42	6.61	0.23	1.05
Quercus velutina	2	0.26	0.15	0.71
Ulmus rubra	18	2.91	0.1	0.45
Cornus florida	12	1.85	0.07	0.33
Carpinus caroliniana	10	1.59	0.07	0.32
Carya ovata	2	0.26	0.06	0.28
Tilia americana	3	0.53	0.06	0.26
Asimina triloba	3	0.53	0.04	0.19
Carya cordiformis	2	0.26	0.04	0.18
Ulmus americana	3	0.53	0.01	0.04
Hamamelis virginiana	2	0.26	0	0.02
Total	630	100	21.55	100

that composition did not contribute to differences in the amount, or volume, of riparian or in-stream LWD. Although no statistically significant differences were documented, tree density was highest and mean tree diameter was smallest in the 1950s establishment class. In contrast, tree density was lowest and tree diameter was largest for the pre-1900 establishment class. Thus, we found a negative relationship between tree density and stem diameter, which agrees with forest development models (Oliver and Larson 1996).

The highest number of snags occurred in the 1950s establishment class, although the differences were not statistically significant. Several studies on the Cumberland Plateau have found second-growth stands to contain higher snag densities than old-growth remnants (Muller 1982; McComb and Muller 1983; Hart and Grissino-Mayer 2008). Although the 1950s establishment class had the highest density of snags, the overall volume of snags in this class was relatively low. The highest standing dead tree volume occurred in the pre-1900 establishment class. Thus, the youngest stands were characterized by a high density of small snags (i.e., small diameter trees), and the oldest stands were characterized by a lower density of larger standing dead trees. This pattern was not surprising given the differences in tree density and size across the chronosequence. Young secondary stands have a high density of small stems (Oliver and Larson 1996). These stands are characterized by a high frequency of snag formation because competition for growing space is intense and self-thinning is common (Clebsch and Busing 1989; Hart and Grissino-Mayer 2009; Richards and Hart 2011). With maturity, these processes, combined with localized exogenous disturbance, result in

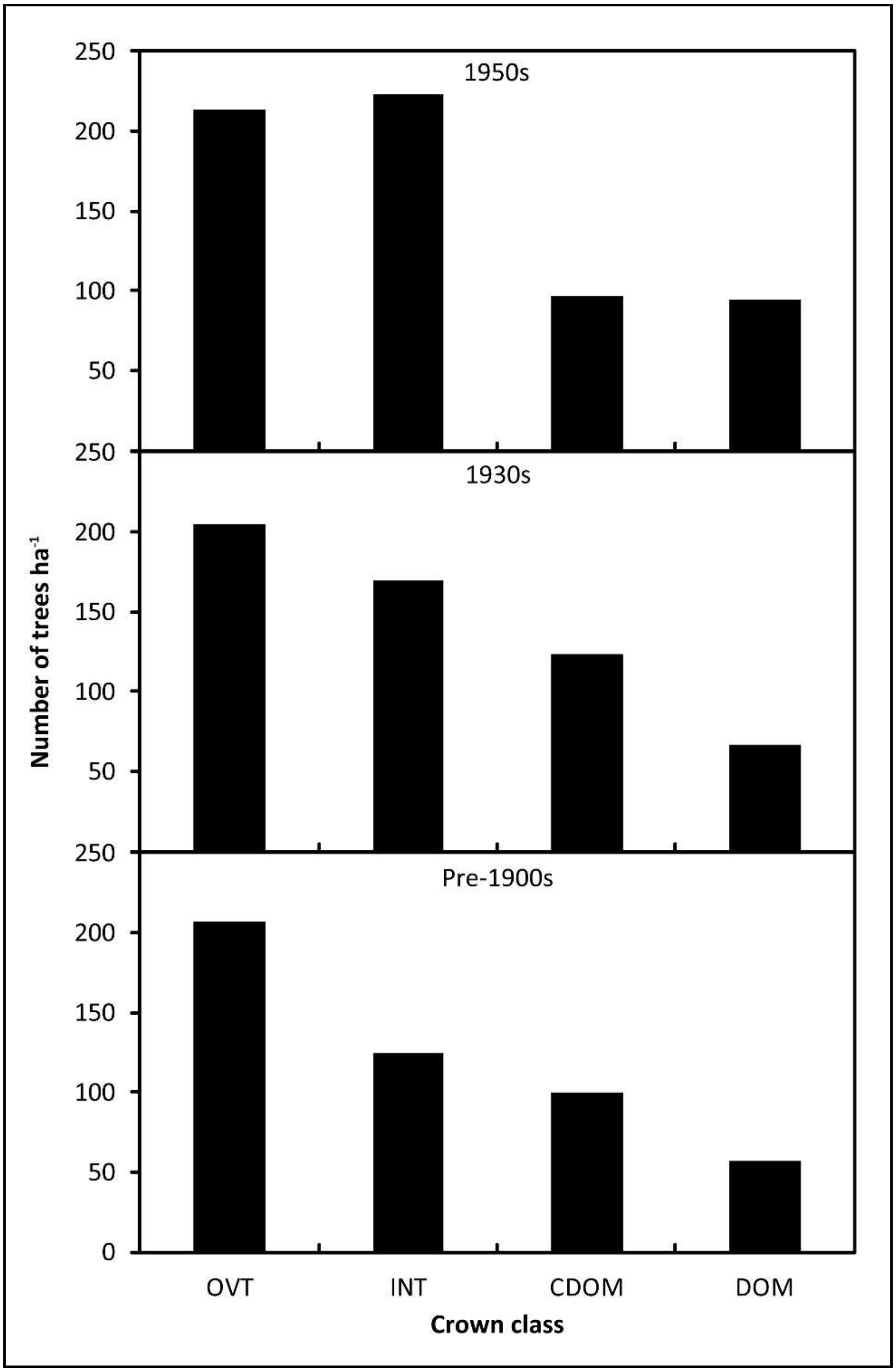

Figure 2. Crown class distributions for trees (≥ 5 cm dbh) per hectare by establishment class in hardwood stands of the Sipsey Wilderness, Alabama. Crown class categories (OVT: overtopped; INT: intermediate; CDOM: codominant; DOM: dominant) were based on the amount and direction of intercepted light (Oliver and Larson, 1996).

stands that contain fewer individuals and thus, reduced competition and mortality rates leading to a lower frequency of tree mortality (Zeide 2005).

Riparian Zone LWD

Based on the species composition of LWD, we speculated that trees outside the riparian zone contributed to riparian LWD loadings. Notably, *P. taeda* logs occurred in riparian zones of all establishment classes, but the species was uncommon as a live tree in these areas. *Pinus taeda* is a common component of upland sites in the Sipsey Wilderness (Zhang et al. 1999), and the region experienced an outbreak of *Dendroctonus frontalis* Zimmerman between 1999 and 2001 that resulted in localized patches of high *Pinus* mortality (Duncan and Linhoss 2005; USDA FS 2004). Although *P. taeda* is largely restricted to upland sites in the Sipsey Wilderness, the environmental gradients are steep and the terrestrial distance between riparian and ridgetop communities is relatively short in this region. Mortality from *D. frontalis* results in snags which later fall and deposit wood pieces that, unlike uprooted trees, have a greater potential to move downslope. Thus, we contend that trees, which occur on middle and upper slope positions, may still have an influence on the abundance and volume of riparian zone LWD on the southern Cumberland Plateau.

We did not find statistically significant differences in the abundance or volume of riparian LWD across our chronosequence. Perhaps the span of development analyzed in our study was not sufficiently long to capture differences in LWD loadings. Prior studies that found LWD abundance and volume to exhibit a parabola distribution across age classes have often been conducted over much longer periods. For example, Sturtevant et al. (1997) found LWD to fit a parabola shape over a 500-year period following a major disturbance in *Abies balsamea* (L.) Mill. and mixed *A. balsamea-Picea mariana* Mill. stands in Newfoundland. Stands of these ages are exceedingly rare in this region. Stand structure and mortality rates certainly differ across the 60-year period of development analyzed in our study, but different stand structures and mortality rates may not result in systematic differences in LWD patterns, at least not at the temporal scale analyzed here.

During early development, stem density is high and competition for resources and growing space is intense (Oliver and Larson

Table 5. Descriptive statistics for riparian zone trees, snags, and LWD by establishment class and cumulatively for our 300 m^2 sampling plots in the Sipsey Wilderness, Alabama. No values were significantly different ($P < 0.05$).

Parameter	Pre-1900s	1930s	1950s	All Ages
Live Trees				
Number	14.65 ± 1.35	16.95 ± 1.69	18.90 ± 1.21	16.83 ± 2.47
DBH (cm)	20.41 ± 0.87	17.88 ± 1.04	16.84 ± 0.88	18.38 ± 0.56
Snags				
Number	0.60 ± 0.18	0.50 ± 0.14	0.95 ± 0.25	0.68 ± 0.11
Volume (m^3)	0.07 ± 0.03	0.02 ± 0.01	0.04 ± 0.01	0.04 ± 0.01
LWD				
Number of pieces	11.25 ± 0.82	12.20 ± 1.86	10.90 ± 1.03	11.48 ± 0.75
Volume (m^3)	4.26 ± 0.60	5.62 ± 1.17	5.09 ± 0.59	5.03 ± 0.48
Volume in decay class I (m^3)	0.13 ± 0.08	0.65 ± 0.28	0.33 ± 0.21	0.37 ± 0.17
Volume in decay class II (m^3)	1.63 ± 0.54	1.15 ± 0.31	1.57 ± 0.38	1.42 ± 0.34
Volume in decay class III (m^3)	1.62 ± 0.33	2.18 ± 0.60	2.13 ± 0.38	1.98 ± 0.37
Volume in decay class IV (m^3)	0.81 ± 0.22	1.63 ± 0.66	1.19 ± 0.36	1.21 ± 0.37
Length of individual LWD	3.70 ± 0.19	3.97 ± 0.17	4.28 ± 0.22	3.98 ± 0.11
Volume of individual LWD	0.38 ± 0.07	0.46 ± 0.06	0.47 ± 0.08	0.44 ± 0.02

1996; Zeide 2005). In hardwood stands of this region, tree mortality increases abruptly after ca. 40 years of development (Hart and Grissino-Mayer 2008; Hart et al. 2011). At this stage, we would expect a high density of small LWD pieces on the forest floor. As stands mature, mean tree size increases, the spacing between canopy trees increases, and the tree mortality rate decreases (Hart and Grissino-Mayer 2009; Richards and Hart 2011). Thus, the size of individual LWD pieces generated in older stands should be larger than those produced in young stands. However, older stands, with decreased mortality, should produce LWD less frequently. The pre-1900s establishment class in our study is transitioning to the complex stage of forest development (Richards and Hart 2011), which is noted for large canopy gaps and high LWD loadings (Tyrrell et al. 1998). However, these LWD producing canopy disturbances are localized and stochastic (Brokaw and Busing 2000). Thus, riparian zones in old-growth stands that are not within a canopy gap environment may not necessarily have higher LWD loadings than young stands with relatively high inputs of small LWD pieces.

Making direct comparisons of LWD loading patterns across different studies is difficult because field sampling and data reporting have not been standardized. Nonetheless, we attempted to place the results of our study in context with other projects in similar forests. Harmon et al. (1986) reported LWD volume of old-growth forests in the Great Smoky Mountains National Park using a minimum size threshold of 7.5 cm diameter. They found volume of LWD was 94 m^3 ha^{-1} in a mixed hardwood-*Quercus* stand, 82 m^3 ha^{-1} in a *Fagus-Betula*-dominated stand,

Table 6. Total volume of riparian LWD by species ha^{-1} across three establishment classes in hardwood stands of the Sipsey Wilderness, Alabama. Bold indicates top 10 rank by volume per establishment class.

Species	Pre-1900	1930s	1950s
Unknown	**73.75**	**53.00**	**61.07**
Pinus taeda	**24.18**	**38.88**	**40.79**
Quercus alba	**3.81**	**26.21**	**18.73**
Carya spp.	**19.25**	**43.57**	**13.38**
Liquidambar styraciflua	**3.99**	N/A	**9.67**
Liriodendron tulipifera	**1.92**	**3.29**	**8.58**
Acer spp.	**2.04**	**6.45**	**4.30**
Magnolia macrophylla	**3.79**	**3.99**	**6.46**
Fagus grandifolia	**5.02**	1.97	**4.07**
Quercus prinus	**1.73**	**2.73**	**1.99**
Platanus occidentalis	N/A	**3.07**	N/A

Table 7. Number and volume of in-stream LWD and the length and volume of individual LWD pieces by establishment class in the Sipsey Wilderness, Alabama. Values are per 30 m in-stream reach. No values were significantly different ($P < 0.05$).

Parameter	Pre-1900s	1930s	1950s
Number of LWD	6.00 ± 1.24	8.30 ± 1.20	6.00 ± 0.87
Volume of LWD (m^3)	2.24 ± 0.72	2.50 ± 0.72	1.45 ± 0.45
Length of individual LWD	2.55 ± 0.18	2.79 ± 0.18	2.20 ± 0.15
Volume of individual LWD	0.37 ± 0.15	0.30 ± 0.10	0.24 ± 0.09

and 132 $m^3 ha^{-1}$ in a *Quercus*-dominated stand. MacMillian (1981) documented a LWD volume of 46 $m^3 ha^{-1}$ in old-growth mixed-Q*uercus* stands in Donaldson's Woods, Indiana, using 5 cm as a minimum diameter limit. In old-growth *Pinus-Quercus* stands of South Carolina, Hardt and Swank (1997) found LWD volume of 66 $m^3 ha^{-1}$ using a 20-cm diameter threshold. In the same study using the same diameter limit, they reported a LWD volume of 86 $m^3 ha^{-1}$ in old-growth mixed mesophytic stands in North Carolina. Additionally, Hardt and Swank (1997) described a wide range of LWD loadings in secondary stands (22-91 $m^3 ha^{-1}$) attributed to unique disturbance histories. Webster and Jenkins (2005) found that in the Great Smoky Mountains National Park, areas of primary forest contained more total LWD than areas with anthropogenic disturbance (134 v. 87 $m^3 ha^{-1}$).

Mean LWD volume (from all sites) was 168 $m^3 ha^{-1}$ and ranged from 142 to 187 $m^3 ha^{-1}$ across our chronosequence. Thus, the volume of riparian zone LWD in secondary stands on the Sipsey Wilderness was within the range reported for old-growth stands in the eastern U.S. and was actually higher than what has been reported for some old-growth stands in the southern Appalachian Highlands. LWD loadings vary by species assemblage, disturbance history, and physical site conditions. The relatively high riparian zone LWD loadings in the Sipsey Wilderness may be a result of the *P. taeda* mortality event and the relatively steep environmental gradients and steep topography of the region, which facilitated the transport of *P. taeda* wood into riparian zones. The influx of *P. taeda* in riparian zones illustrated that LWD loadings are complex and controlled by more variables than simply stand development and associated endogenous mortality. Although LWD loadings in harvested stands may take more than a century to reach values typical of old-growth stands (Webster and Jenkins 2005), intermediate-scale disturbance events, such as those that occurred along ridgetops and upper slope positions in the Sipsey Wilderness, can accelerate the time required for LWD loadings to match the volume that may be expected in late-successional stands.

In-stream LWD

Although upslope positions appeared to be source areas for riparian LWD, based on composition and size distributions, we speculated that riparian zones were likely the source areas for in-stream material. *Pinus taeda* from upslope positions was noted in riparian zones, but was absent from stream channels. We suggest that riparian trees may serve as filters to restrict the movement of upslope generated woody material into stream environments.

Chen et al. (2006, 2008) and Baillie et al. (2008) found that a bankfull channel width of 3 m is a critical threshold for LWD transport processes in small streams. These studies determined that most LWD was suspended above the active channel in streams with bankfull widths below this threshold. We found the mean length of in-stream LWD pieces was longest in the 1930s establishment class, which also had the widest streams 4.08 m ± 0.42 SE. However, the volume of individual pieces was highest in the pre-1900 age class, which only had the second widest streams. Small streams have low streamflow volume and thus, can have a lower capacity

Table 8. In-stream LWD volume by decay, position, and function class across stand establishment class in the Sipsey Wilderness, Alabama. Values are per 30 m in-stream reach. Means with rows followed by the same letter are not significant ($P < 0.05$).

Parameter	Pre-1900s	1930s	1950s
Decay Class (m^3)			
I	0.05 ± 0.05 a	0.39 ± 0.17 a	0.19 ± 0.12 a
II	0.36 ± 0.19 a	0.95 ± 0.49 a	0.40 ± 0.26 a
III	1.30 ± 0.70 a	0.94 ± 0.31 a	0.56 ± 0.18 a
IV	0.54 ± 0.28 a	0.22 ± 0.11 a	0.29 ± 0.16 a
Position Class (m^3)			
Bridge	0.50 ± 0.32 a	0.92 ± 0.26 a	0.50 ± 0.21 a
Partial bridge	0.91 ± 0.46 a	0.91 ± 0.38 a	0.48 ± 0.17 a
Loose	0.55 ± 0.27 a	0.47 ± 0.11 a	0.26 ± 0.13 a
Buried	0.27 ± 0.13 a	0.19 ± 0.09 a	0.21 ± 0.13 a
Function Class (m^3)			
I	0.02 ± 0.02 a	0.37 ± 0.19 a	0.69 ± 0.25 b
II/III	1.97 ± 0.75 a	1.49 ± 0.36 a	0.38 ± 0.08 a
IV	0.24 ± 0.12 a	0.65 ± 0.22 a	0.38 ± 0.25 a

to transport large material such as LWD (Bilby and Ward 1989; Montgomery et al. 1995; Piegay and Gurnell 1997; Chen et al. 2006). Because the streams in this study were small, there was limited LWD transport in all establishment classes. Thus, we contend that LWD transport in these streams is limited and that most woody material remains in the stream reach within which it was deposited.

When in-stream LWD volume was standardized to reflect differences in stream widths, the distribution exhibited a parabola shape with total in-stream volume highest in the 1950s establishment age. Although there were no significant differences in the frequency or volume of in-stream LWD across the age classes, patterns were evident including that the pre-1900s class contained some of the largest pieces of individual in-stream LWD by volume. The pre-1900s establishment class contained the largest riparian zone trees and provided evidence that the in-stream LWD was produced from the adjacent riparian zones and generally not transported by fluvial processes. The frequency distributions of riparian and in-stream LWD volume were similar, which we contend illustrated the coupling between riparian and in-stream ecosystems.

Direct comparison of in-stream LWD loadings are difficult because of the lack of consistent field sampling and reporting protocols. Nonetheless, the volume of LWD 100 m^{-1} of stream in our study (mean of all establishment classes was 6.9 m^3 $100m^{-1}$ ± 1.1 SE) was lower than that reported in other regional studies. Hedman et al. (1996), working in mixed mesophytic systems in the southern Blue Ridge province, reported an average of 13 m^3 100 m^{-1} for streams draining mid-successional (40 – 70 years of age) and late-successional (180 – 221 years of age) secondary stands and 22 m^3 $100m^{-1}$ for streams in old-growth (> 287 years of age) stands. However, they noted that much of the woody material in mid-successional stands was decay resistant material that carried over from the prior stand and they speculated that without this material, LWD loadings in stands of this developmental stage would have been lower (Hedman et al. 1996). Hedman et al. (1996) also noted that in-stream LWD loadings were highly variable, especially in mid-successional stands. On the Alleghany Plateau, Williams and Cook (2010) reported LWD loadings of 4 and 18 m^3 100 m^{-1} for *Tsuga canadensis* (L.) Carr. – *Pinus strobus* L. dominated second-growth and old-growth stream reaches, respectively. The comparatively low in-stream LWD values we documented were interesting because we found higher riparian zone LWD loadings than what has been reported in similarly aged stands in the region. We hypothesize this pattern is a result of the source areas for the documented LWD and the *P. taeda* mortality event. The *P. taeda* inputs originated from upslope areas and were the result of *D. frontalis* mortality, which created snags that eventually fell. In contrast, in-stream LWD typically originated from the adjacent riparian corridors and seemed insensitive to upslope processes.

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LITERATURE CITED

Baillie B.R., L.G. Garrett and A.W. Evanson. 2008. Spatial distribution and influence of large woody debris in an old-growth forest river system, New Zealand. Forest Ecology and Management 256:20-27.

Bendix, J., and C.M. Cowell. 2010. Impacts of wildfire on the composition and structure of riparian forests in Southern California. Ecosystems 13:99-107.

Benda, L.E., P. Bigelow, and T.M. Worsley. 2002. Recruitment of wood to streams in old-growth and second-growth redwood forests, northern California, USA. Canadian Journal of Forest Research 32:1460-1477.

Bilby, R.E., and J.W. Ward. 1989. Changes in the characteristics and function of woody debris with increasing size of stream in western Washington. Transactions of the Fisheries Society 118:368-378.

Bilby, R.E., and J.W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut and second-growth forests in southwestern Washington. Canadian Journal of Fisheries and Aquatic Sciences 48:2499-2508.

Bormann, F.H., and G.E. Likens. 1994. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York.

Bragg, D.C., and J.L. Kershner. 1999. Course woody debris in riparian zones. Journal of Forestry 97:30-35.

Brassard, B.W., and H.Y.H. Chen. 2008. Effects of forest type and disturbance on diversity of coarse woody debris in boreal forest. Ecosystems 11:1078-1090.

Braun, E.L. 1950. Deciduous Forest of Eastern North America. Blakiston, Philadelphia, Pa.

Brokaw, N.V.L., and R.T. Busing. 2000. Niche versus chance and tree diversity in forest gaps. Trends in Ecology and Evolution 15:183-188.

Busing, R.T, R.D. White, M.E. Harmon, and R.S. White. 2009. Hurricane disturbance in a temperate deciduous forest: patch dynamics, tree mortality and course woody detritus. Plant Ecology 201:351-363.

Chen, X., X. Wei, R. Scherer, and D. Hogan. 2008. Effects of large woody debris on surface structure and aquatic habitat in forested streams, southern interior British Columbia, Canada. River Research and Applications 24:862-875.

Chen, Xiaoyong, X. Wei, R. Scherer, C. Luider, and W. Darlington. 2006. A watershed scale assessment of in-stream large woody debris patterns in the southern interior of British Columbia. Forest Ecology and Management 229:50-62.

Clebsch, E.E.C., and R.T. Busing. 1989. Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. Ecology 70:728-735.

Clinton, B.D., J.M. Vose, J.D. Knoepp, K.J. Elliot, B.C. Reynolds and S.J. Zarnoch. 2010. Can structural and functional characteristics be used to identify riparian zone width in southern Appalachian headwater catchments? Canadian Journal of Forest Research 40:235-253.

Collier, K.J., A. Haigh, and J. Kelly. 2007. Coupling GIS and multivariate approaches to reference site selection for wadeable stream monitoring. Environmental Monitoring and Assessment 127:29-45.

Duncan, R.S., and J.E. Linhoss. 2005. Regeneration of Virginia pine (*Pinus virginiana*) following southern pine beetle (*Dendroctonus frontalis*) outbreak in the Sipsey Wilderness, Alabama. Forest Ecology and Management 212:65-74.

Dyer, J.M. 2006. Revisiting the deciduous forests of eastern North America. BioScience 56:341-352.

Fenneman, N.M. 1938. Physiography of Eastern United States. McGraw-Hill, New York.

Fraver, S., A. Ringvall, and B.G. Jonsson. 2007. Refining volume estimates of down woody debris. Canadian Journal of Forest Research 37:627-633.

Hardin, D.E., and K.P. Lewis. 1980. Vegetation analysis of Bee Branch Gorge, a hemlock-beech community of the Warrior River Basin of Alabama. Castanea 45:248-256.

Hardt, R.A., and W.T. Swank. 1997. A comparison of structural and compositional characteristics of southern Appalachian young second-growth, maturing second-growth, and old-growth stands. Natural Areas Journal 17:42-52.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, M.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack, Jr., and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advancement in Ecological Research 15:133-301.

Hart, J.L., A.A.R. Bhuta, and R.M. Schneider. 2011. Canopy disturbance patterns in secondary hardwood stands on the Highland Rim of Alabama. Castanea 76:55-63.

Hart J.L., and H.D. Grissino-Mayer. 2008. Vegetation patterns and dendroecology of a mixed hardwood forest on the Cumberland Plateau: implications for stand development. Forest Ecology and Management 255:1960-1975.

Hart, J.L., and H.D. Grissino-Mayer. 2009. Gap-scale disturbance processes in secondary hardwood stands on the Cumberland Plateau, Tennessee, USA. Plant Ecology 201:131-146.

Hedman, C.W., D.H. Van Lear, and W.T. Swank. 1996. In-stream large woody debris loading and riparian forest seral stage associations in the southern Appalachian Mountains. Canadian Journal of Forest Research 26:1218-1227.

Hély C., Y. Bergeron, and M.D. Flannigan. 2000. Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. Canadian Journal of Forest Research 30:674-687.

Hilderbrand, R.H., A.D. Lemly, C.A. Dolloff, and K.L. Harpster. 1997. Effects of large woody debris placement on stream channels and benthic macroinvertebrates. Canadian Journal of Fisheries and Aquatic Sciences 54:931-939.

Hinkle, C.R. 1989. Forest communities of the Cumberland Plateau of Tennessee. Journal of the Tennessee Academy of Science 64:123-129.

Hinkle, C.R., W.C. McComb, J.M. Safely, Jr., and P.A. Schmatzer. 1993. Mixed mesophytic forests. Pp. 203-253 *in* W.H. Martin, S.G. Boyce, and A.C. Echtemacht, eds., Biodiversity of the Southeastern United States: Upland Terrestrial Communities. John Wiley, New York.

Honer, T.G. 1967. Standard volume tables and merchantable conversion factors for the commercial tree species of central and eastern Canada. Information Report FRM-X-5, Forest Research and Services Institute, Ottawa, Ont.

Jones, T.A., and L.D. Daniels. 2008. Dynamics of large woody debris in small streams disturbed by the 2001 Dogrib fire in the Alberta foothills. Forest Ecology and Management 256:1751-1759.

Jones, T.A., L.D. Daniels, and S.R. Powell. 2011. Abundance and function of large woody debris in small, headwater streams in the Rocky Mountain foothills of Alberta, Canada. River Research and Applications 27:297-311.

Larson, M.G., D.B. Booth, and S.A. Morley. 2001. Effectiveness of large woody debris in stream rehabilitation projects in urban basins. Ecological Engineering 18:211-226.

Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61:1169-1184.

MacMillian, P.C. 1981. Log decomposition in Donaldson's Woods, Spring Mill State Park, Indiana. American Midland Naturalist 106:223-344.

Martin, W.H. 1992. Characteristics of old-growth mixed mesophytic forests. Natural Areas Journal 12:127-135.

McComb, W.C., and R.N. Muller. 1983. Snag densities in old-growth and second growth Appalachian forests. Journal of Wild Management 47:376-382.

McGee, G.G., D.J. Leopold, and R.D. Nyland. 1999. Structural characteristics of old-growth, maturing and partially cut northern hardwood forests. Ecological Applications 9:1316-1329.

Montgomery, D.R., J.M. Buffington, R.D. Smith, K.M. Schmidt, and G. Press. 1995. Pool spacing in forest channels. Water Resources Research 31:1097-1105.

Muller, R.N. 1982. Vegetation pattern in the mixed mesophytic forest of eastern Kentucky. Ecology 63:1901-1917.

Naiman, R.J., and H. DeCamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621-658.

Oliver, C.D., and B.C. Larson. 1996. Forest Stand Dynamics. J. Wiley, New York.

Piégay, H., and A. Gurnell. 1997. Large woody debris and river geomorphological pattern: examples from S.E. France and S. England. Geomorphology 19:99-116.

PRISM Climate Group. 2011. Oregon State University, Corvallis, Ore. Available online <http://www.prism.oregonstate.edu>. Accessed 21 March 2011.

Powell S.R., L.D. Daniels, and T.A. Jones. 2009. Temporal dynamics of large woody debris in small streams of the Alberta foothills, Canada. Canadian Journal of Forest Research 39:1159-1170.

Richards, J.D., and J.L. Hart. 2011. Canopy gap dynamics and development patterns in secondary *Quercus* stands on the Cumberland Plateau, Alabama, USA. Forest Ecology and Management 262:2229-2239.

Roberts, S.W., R. Tankersley, Jr., and K.H. Orvis. 2009. Assessing the potential impacts to riparian ecosystems resulting from hemlock mortality in Great Smoky Mountains National Park. Environmental Management 44:335-345.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. Pp. 17–33 *in* S.T.A. Pickett and P.S. White, eds., The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego, Calif.

Smalley, G.W. 1979. Classification and evaluation for forest sites on the southern Cumberland Plateau. GTR SO-23, U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, La.

Spetich, M.A., S.R. Shiffley, and G.R. Parker. 1999. Regional distribution and dynamics of coarse woody debris in Midwestern old-growth forests. Forest Science 45:302-313.

Spies T.A., J.F. Franklin, and T.B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of Western Oregon and Washington. Ecology 69:1689-1702.

Sturtevant, B.R., J.A. Bissonette, J.N. Long, and D.W. Roberts. 1997. Course woody debris as a function of age, stand structure and disturbance in boreal Newfoundland. Ecological Applications 7:702-712.

Szabo, M.W., E.W. Osborne, C.W. Copeland, Jr., and T.L. Neathery. 1988. Geological map of Alabama. Geoglogical Survey of Alabama Special Map 220, scale 1:250,000. U.S. Department of the Interior, Geological Survey, [Tuscaloosa, Ala.].

Thornthwaite, C.W. 1948. An approach towards a rational classification of climate. Geographical Review 38:55-94.

Tyrrell, L.E., G.J. Nowacki, T.R. Crow, D.S. Buckley, E.A. Nauertz, J.N. Niese, J.L. Rollinger, and J.C. Zasada. 1998. Information about old growth for selected forest type groups in the eastern United States. General Technical Report NC-197, U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, [St. Paul, Minn.].

[USDA SCS] United States Department of Agriculture, Soil Conservation Service. 1959. Soil survey: Lawrence County, AL. Series 1949, No. 10, U.S. Department of Agriculture, Soil Conservation Service, [Auburn, Ala.].

[USDA FS] United States Department of Agriculture, Forest Service. 2004. Revised land and resource management plan: National Forests in Alabama. Management Bulletin R8-MB 112A, U.S. Department of Agriculture, Forest Service, Southern Region, [Asheville, N.C.].

Webster, C.R., and M.A. Jenkins. 2005. Coarse woody debris dynamics in the southern Appalachians as affected by topographic position and anthropogenic disturbance history. Forest Ecology and Management 217:319-330.

White, P.S. 1979. Pattern, process, and natural disturbances in vegetation. Botanical Review 45:229-299.

Whitney, G.G. 1994. From Coastal Wilderness to Fruited Plain: a History of Environmental Change in Temperate North America from 1500 to the Present. Cambridge University Press, Cambridge, U.K.

Williams, C.E., and R.E. Cook. 2010. Forest seral stage and large woody debris in an Allegheny high plateau forest-stream system. Natural Areas Journal 30:20-26.

Young, J.A., D.R. Smith, C.D. Snyder, and D.P. Lemarie. 2002. A terrain-based paired-site sampling design to assess biodiversity losses from eastern hemlock decline. Environmental Monitoring and Assessment 76:167-183.

Zeide, B. 2005. How to measure stand density. Trees 19:1-14.

Zhang, L., B.P. Oswald, and T.H. Green. 1999. Relationships between overstory species and community classification of the Sipsey Wilderness, Alabama. Forest Ecology and Management 114:337-383.