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Woody Plant Dynamics in a Foundation Conifer Woodland of the Appalachian Foothills, Alabama

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Abstract - We documented the structure and composition of a *Pinus palustris* (Longleaf Pine) woodland community in the Appalachian foothills of Alabama using field measurements and investigated the drivers of forest dynamics using dendroecology paired with historical records of disturbance. Longleaf Pine dominated the canopy, exhibiting a reverse-J–shaped diameter distribution not related with age distribution. Longleaf Pines dated as far back as 1669 to as recently as the early 2000s. In contrast to many other forests, the spatial distribution of Longleaf Pine stems in our site trended toward a random distribution when trees were weighted by DBH or age. Based on ring patterns from 322 Longleaf Pine individuals, growth releases from disturbances occurred continuously from the early 1900s through the 1940s and between 1985 and 1995, with Longleaf Pine establishment peaking 3 times: in the 1880s, 1940s, and 1990s. A superposed epoch analysis revealed that release events were not related with recorded large-scale meteorological (e.g., hurricanes) or local human-induced disturbances, suggesting that other factors have influenced the dynamics of this community. This Longleaf Pine community in the Piedmont shared similarities in composition and structure to other Longleaf Pine communities of the southeastern United States. A combination of fire suppression over the last 80 years and high-intensity arson fires over the last decade has caused an increase in density of both live and dead Longleaf Pine and recruitment of fire-sensitive pines and hardwoods into the seedling/sapling classes and canopy. Restoration of the historical fire regime may be needed for Longleaf Pine to maintain its dominance in this community, as fire may have appeared to exert strong control over the dynamics of this community.

Introduction

Foundation tree species, such as *Pinus albicaulis* Englem. (Whitebark Pine), *Tsuga canadensis* (L.) Carrière (Eastern Hemlock), *Rhizophora* spp. (mangroves), and *Pinus palustris* Mill. (Longleaf Pine) are instrumental in defining and regulating ecosystem and community structure and function, but some are in serious decline due to complex natural and human-caused impacts (Ellison 2019, Ellison et al. 2005). Elucidating the connections between the structure, composition, and dynamics of these important species may help with predictions on how their associated ecosystems will adapt to future disturbance regimes. One proven method for disentangling these connections is the use of dendrochronology in reconstructing historical suppressions and releases in annular growth. Patterns in annular growth can often be linked to recorded human and natural disturbance events and can provide insights on how these disturbances have impacted the structure, composition, history, and dynamics of the system

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studied (Abrams and Orwig 1996, Altman 2020, Black and Abrams 2003). Historical recruitment data (inferred from dendrochronology) coupled with information on historical land-management practices and present-day woody stem recruitment can inform future forest management decisions when restoration and ecosystem resiliency are driving factors for such management.

Longleaf Pine is a long-lived foundation tree species integral to the composition, structure, and function of fire-dependent ecosystems occurring throughout the southeastern United States (Outcalt and Sheffield 1996, Peet 2006, Platt et al. 1988). These ecosystems once covered >37 million ha exhibiting high ecological amplitude, complexity, and diversity throughout the plains (Coastal Plain [CP], Southeastern Plains, Middle-Atlantic CP ecoregions) as well as the foothills and mountains (Piedmont, Southwestern Appalachians, and Ridge and Valley (RV) ecoregions) (Omernik 1987, Peet 2006). Compounding human activities, including harvesting and fire suppression, have contributed to the reduction, fragmentation, and degradation of these ecosystems, leaving an estimated 1,736,101 ha remaining in 2009 (McIntyre et al. 2018). Of this estimate, only 607,028 ha were in a condition that supported the fire-adapted and maintained vegetation structure typical for these ecosystems and only 5095 ha were identified as old growth (Frost 2006, McIntyre et al. 2018, Varner and Kush 2004).

The influence of disturbances, human activities, and climate on the structure and dynamics of Longleaf Pine communities in the southeastern plains of the United States have been well studied (Bhuta et al. 2008, Devall et al. 1991, Gilliam and Platt 1999, Gilliam et al. 1993, Henderson and Grissino-Mayer 2009, Kush and Meldahl 2000, Platt et al. 1988, Rutledge et al. 2021). Further study of foothill and mountain Longleaf Pine communities, on the other hand, could provide a clearer picture of how disturbance influences growth across this species' range. One study has inventoried just the Longleaf Pine in a North Carolina Piedmont community (Patterson and Knapp 2016), while 3 others have looked extensively at woody stem structure and dynamics in Longleaf Pine communities: 2 in the Alabama Ridge and Valley (Maceina et al. 2000; Varner et al. 2003a, b) and 1 in the Alabama Piedmont (Kressuk et al. 2020). Unraveling the effects of human and natural disturbances on Longleaf Pine radial growth and forest composition and structure at higher-elevation sites deserves more attention as climate-change models predict future range migration and expansion in these areas (Prasad et al. 2020). The lack of research in the mountain and foothills is likely due to the limited occurrences of second-growth and old-growth Longleaf Pine communities in these settings. Longleaf found in the foothills and mountains are estimated at about 40,000 ha, with only 65 ha of old-growth Longleaf Pine identified (Stokes et al. 2010; Varner et al. 2003a, b).

This research joins only 1 other published study to date (Kressuk et al. 2020) in documenting the structure, composition, and long-term dynamics of a mountain Longleaf Pine community in the Piedmont physiographic province. We used field, geospatial, and dendroecological techniques to examine the role of historical disturbance in shaping the current composition and structure of an old-growth foothills Longleaf Pine community in Alabama. Our objectives included (1) relating composition, structure, and site characteristics (e.g., physiographic location, aspect, slope) to other old-growth Longleaf Pine communities in foothills and mountains; (2) predicting future trends in forest composition and structure based on both the dendroecology and conifer and hardwood recruitment; (3) investigating links between large-scale (tornadoes and hurricanes in this case) and local-scale (e.g., fire, thinning, tornadoes, and small-scale clearance) disturbances and canopy recruitment; and (4) determining the spatial arrangement of Longleaf Pine on the landscape by diameter at breast height (DBH) or age.

Methods

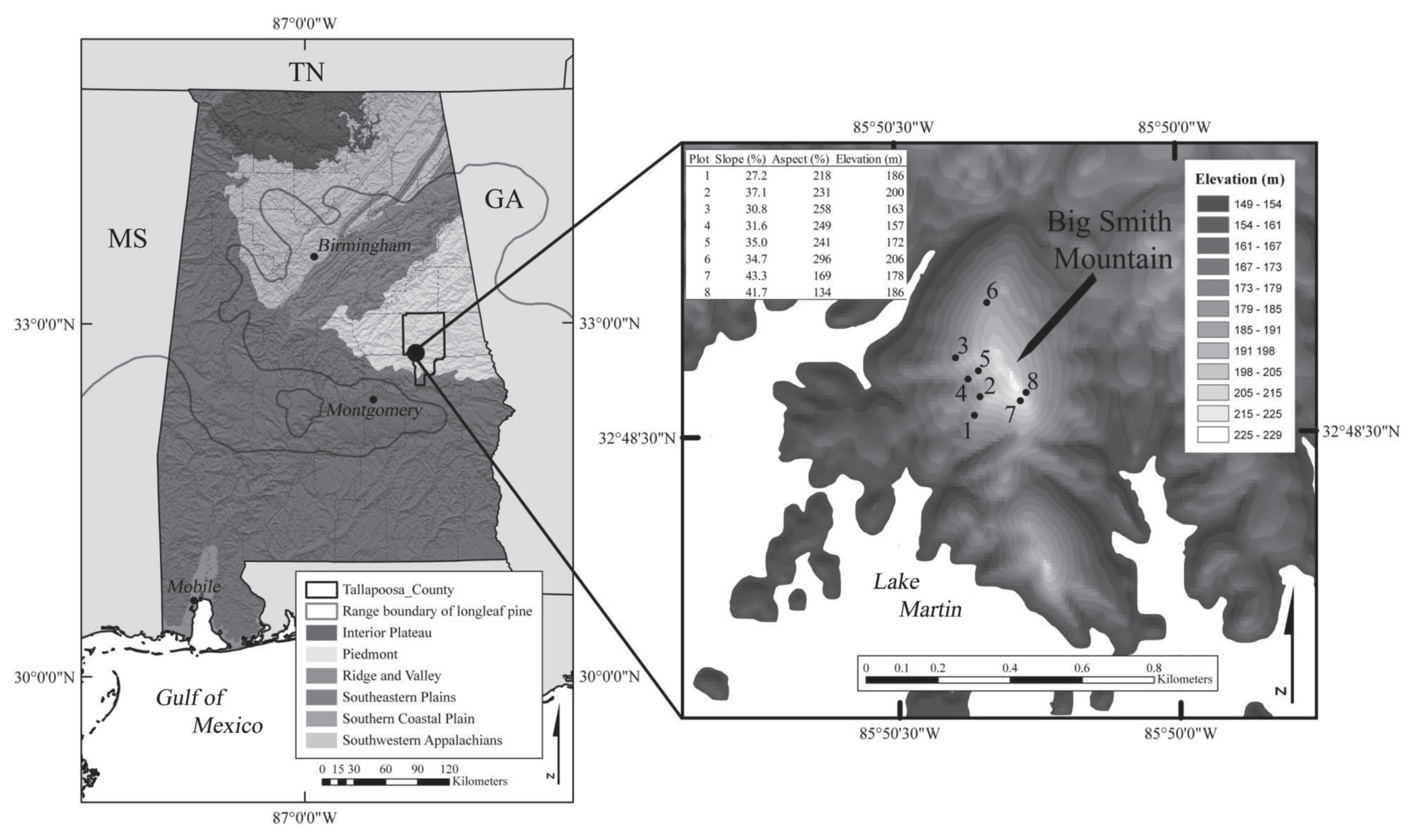
Study area and land-use history

Our study site, Big Smith Mountain (BSM), is a part of Smith Mountain Forest (SMF; 295.1 ha) on the Piedmont Ridge, which is wedged between the Ashland and Opelika plateaus of the Southern-Inner Piedmont section of the Piedmont, or foothills, in Tallapoosa County, AL (Fig. 1; Griffith et al. 2001). Phyllite, quartzite, and sericite schist bedrock of Precambrian and Paleozoic origins contribute to the parent material of the moderately eroded Tallapoosa–Fruithurst soil complex which consists of gravelly loam Typic Hapludults (McGhee 2007). This soil complex is found on 15–40% slopes from 122 to 335 m in elevation with depth to the high-water table being >1.83 m. Soils are low in fertility, moderate in permeability, and low in available water capacity, with a surface layer high in organic matter (McGhee 2007). The climate of this portion of the Southern-inner Piedmont area is humid subtropical with mean annual precipitation of 132–152 cm, mean annual air temperature varying from 5 to 26 °C, and frost-free periods of 185–220 days (Griffith et al. 2001). The fire-return interval in this region before European settlement has been estimated to be 4–6 years (Frost 2006).

The SMF is owned and managed by the Alabama Power Company (APC), a subsidiary of the Southern Company, a publicly owned electric utility company. The forest straddles both BSM (maximum elevation 238 msl), and Little Smith Mountain (LSM; maximum elevation of 213 msl), and borders Lake Martin (16,187 ha), a reservoir created by the Martin Dam, which generates hydroelectric power for the APC. According to personal communications with APC foresters and historians and Alabama Forestry Commission Foresters, there are 60 ha of old growth forest (never harvested) within the SMF. The only known records of land use on or near BSM include a fire tower built in 1939 near the summit, development of a road to the fire tower, and a timber sale (1959) surrounding BSM (W.A. Tharpe, APC historian, Birmingham, AL, pers., comm.). Steep slopes prevented commercial harvesting of forests on BSM and LSM, and there were no records of harvests prior to APC's acquisition of the land between 1914 and 1926.

Field methods

We chose 8 random compass bearings that served as transects emanating from the summit and ending at the base of BSM. We avoided the eastern aspect of BSM due to the absence of a live tree canopy and the presence of an herbaceous layer



Plot	Slope (%)	Aspect (%)	Elevation (m)
1	27.2	218	186
2	37.1	231	200
3	30.8	258	163
4	31.6	249	157
5	35.0	241	172
6	34.7	296	206
7	43.3	169	178
8	41.7	134	186

Figure 1. The location of the study plots on Big Smith Mountain in relation to the Piedmont ecoregions in Alabama. Numbers on the inset map indicate plot locations. Table inset provides the slope, aspect, and elevation of each plot.

of grasses and shrubs that developed after an intense 2007 arson fire (M. Tuggle, former APC forester, Alexander City, AL, pers. comm.), which rendered the tree community unsuitable for sampling. The northern to southeastern aspects of BSM were also affected by the 2007 fire, but the density of live trees on these slopes allowed for sampling. Along each transect, 1 randomly selected elevation served as plot center for a 20 m x 50 m (0.1 ha) permanent plot (8 plots total) established parallel to the slope's contour. If topography prevented establishing a parallel plot along the contour line, we laid plots out perpendicular to the contour, as tree community composition remained the same.

We tagged, identified, measured for height and DBH, and georeferenced with a GPS unit all trees and snags ≥5.0 cm DBH. We measured canopy cover by recording the presence or absence of the vertical projection of the most dominant tree species' crown in the canopy to the forest floor via a vertical densitometer (Stumpf 1993). We made observations ~1.8 m above ground level at 5-m intervals along the 50-m length of the plot on 5 equally distanced transects (5 m apart) within the plot. Data recorded for canopy cover was binary, with the absence of tree canopy recorded as no canopy cover and the presence of a tree's canopy recorded with the species providing the canopy cover.

We tallied seedlings and saplings by species in a nested 20 m by 20 m subplot between the 20-m and 40-m section of the plot. Saplings were <5.0 cm DBH but >1 m in height, while seedlings were <1 m in height. We used increment borers to core all trees and snags ≥5.0 cm DBH within the subplot and ≥15.0 cm DBH outside of the subplot but within the plot. We cored trees at 30 cm above the ground, parallel to the contour, and perpendicular to the slope to account for compression (pines) or tension (hardwood) wood on both sides of the tree. We also cored Longleaf Pine ≥20.0 cm DBH adjacent to plots to increase the sample size of older trees that would be useful for dendroecological analysis. We did not quantify shrubs but noted their species to compare forest composition at BSM to Longleaf Pine communities in other physiographic settings.

Dendroecological analysis

We processed all tree-core samples by air drying and affixing them to mounts with cells vertically aligned and then sanding with progressively finer abrasives using standard techniques (Speer 2010). We crossdated tree rings using the list-year method (Yamaguchi 1991) and measured them at a resolution of 0.001 mm using a stereo-zoom microscope (Nikon SMZ800; Nikon Instruments, Inc., Tokyo, Japan) and a tree-ring measuring system (Velmex Tree Ring Measuring System; Velmex, Inc., Bloomfield, NY) coupled with Measure J2X software (Version 5.0; Voortech Consulting, Holderness, NH). We statistically verified crossdating for quality assurance and control using COFECHA (Holmes 1983). Tree age was based on the date of the individual's pith, if present, or innermost tree ring. We did not use pith estimators. Sample sizes from other woody plants (e.g., *Acer rubrum* L. [Red Maple], *Nyssa sylvatica* Marshall [Blackgum], and *Pinus taeda* L. [Loblolly Pine]) were too small for our release-pattern analysis.

We used raw ring widths to determine minor (>20% but <50%) and major (>50%) species-specific releases based on the development of a site-specific modified boundary-line criterion of growth following Black and Abrams (2003) but modified using median radial-growth change. Use of the median, instead of the mean, in calculating growth change allows for greater statistical robustness in determining release patterns since tree-ring data could be non-normally distributed (Rubino and McCarthy 2004). We chose this method of detecting growth releases and the use of the median because we successfully used this approach on a smaller population of Longleaf Pine in a previous study (Bhuta et al. 2008) and because this method is applicable (e.g., autoecology and growth patterns, sensitivity, and responses; Altman 2020) and conservative in detecting releases (Black and Abrams 2003). We calculated median percent growth change (MPGC) for all years for all Longleaf Pine in the chronology by taking the 10-year median growth change before (MGCB) and after (MGCA) that year, subtracting MGCB from MGCA, and dividing the difference by MGCB (MPGC = [MGCA - MGCB] / MGCB). To calculate the boundary line, we plotted MGCB against MPGC, placed MGCB into 0.5-mm segment classes, selected the 10 highest MPGC values in each MGCB class, and averaged the 10 highest MPGC values. The averaged segment classes with positive values were graphed and fitted to exponential, logarithmic, linear, and power trend lines. The exponential trend line had the best fit and the highest r^2 value. We used its equation, generated from the trend line, to create a boundary line for species-specific growth.

We developed a minor (20%) and major (50%) release chronology for Longleaf Pine based on mean yearly MPGC and used superposed epoch analyses (SEA; EVENT software 6.02P; Holmes and Swetnam 1994) to statistically determine whether historically recorded disturbance events influenced release events at BSM. These included the 1939 construction of the fire tower, the 1959 logging event, tornadoes, and hurricanes. Historical tornado data for the area showed only a single tornado with an intensity of greater than enhanced fujita (EF) scale 3, which crossed the Lake Martin area in 1996. We chose Saffir-Simpson hurricane wind-scale category 2 and higher (before landfall) hurricanes (through 2000) for analysis if their tracks passed within Tallapoosa or adjacent counties. We overlaid historical hurricane tracks across the counties in a GIS: 5 unnamed hurricanes (in 1881 [category 2], 1887 [category 2], 1893 [category 4], 1902 [category 2], and 1915 [category 2]) and 3 named hurricanes (in 1950 [Hurricane Easy, category 3], 1975 [Hurricane Eloise, category 3], and 1995 [Hurricane Opal, category 4]). Hurricane intensities are recorded before landfall, so their strength would have weakened by the time they reached the study area. We should point out that there are several other unknown hurricane variables, which include size, duration, and exact wind direction, that we cannot account for in this analysis; however, our primary goal was to only identify and examine hurricane events as a possible large-scale disturbance to our site. We tested for the effects of all events, the effects of hurricanes only, and the effects of human disturbances only, on release patterns for the 20% and 50% release chronologies. We left out the 1996 tornado event because it occurred after the time span of our dendroecological analysis. We performed 2 SEAs per event within a 12-year window, spanning 1 year prior through to 10 years after the event. The first SEA had no segments, while the second SEA was processed by 50-year segments with 25-year overlaps.

Geospatial analysis

We analyzed plot metrics and the spatial distribution of trees using ArcGIS 9.3.1 (ESRI, Redlands, CA). We derived slope (%), aspect (%), and elevation (m) for the study area from a 1/3 arc-second digital elevation model (United States Geological Survey 2011). We used georeferenced trees and the spatial statistics toolbox in ArcGIS to determine Ripley's K-function (Ripley 1981). Ripley's K-function is a point-pattern cluster analysis that identifies the dispersion or clustering of individual points over multiple distances from each other through comparison with Monte Carlo simulations. The result indicates whether the observed dataset significantly deviates from expected values along a gradient of distance. If the observed K exceeds the higher confidence interval produced from the Monte Carlo simulation, then the trees at BSM are clustered, but if the observed K exceeds the lower confidence interval, then the trees at BSM are dispersed. The trees mapped at the plot level were weighted by DBH and age and ran against 999 simulations with 100 distance bands using Ripley's edge-correction formula, a correction method appropriate for square and rectangular study areas. We created an output in ArcGIS with an expected and observed dataset and upper and lower confidence intervals to determine if the spatial relationship was significantly clustered or dispersed along a gradient of distance.

Results

Forest composition and structure

Our study plots varied in elevation from 157 to 206 m, with slopes from 27.2% to 41.7%, and southeasterly aspects (134°) to almost north-northwestern aspects (296°) (see table inset in Fig. 1). We collected data on 436 Longleaf Pine stems inside our plots. Longleaf Pine dominated BSM, accounting for 97.5% of live trees and 96.4% of snags, followed by a combination of Loblolly Pine (1.2% of live trees and 0.7% of snags), and Blackgum (0.9% of live trees and 2.5% of snags) (Table 1). Longleaf Pine also had the highest importance values for both live trees (76.5%) and snags (82.7%) . *Sassafras albidum* (Nutt.) Nees (Sassafras) dominated live seedlings, and Blackgum and *Prunus serotina* Ehrh. (Black Cherry) dominated live saplings (Table 2). Longleaf Pine seedlings (<10%) and saplings (<20%) were present at relatively low frequencies. The following species were observed in the shrub layer: *Symplocos tinctoria* (L.) L'Hér. (Horse Sugar), *Kalmia latifolia* L. (Mountain Laurel), *Rhus copallinum* var. *latifolia* Engl. (Winged Sumac), *Vaccinium arboreum* Marsh (Farkleberry), and *Rhododendron minus* Michx. (Carolina Rhododendron).

Diameter distribution for all trees at BSM showed a reverse-j shaped curve with 415 Longleaf Pine stems across all size classes varying from 5.0 to 50.0 cm. All

Loblolly Pine stems fit into the 5.0–15.0 cm diameter classes, while nearly all hardwood species fit the 5.0 and 10.0 cm classes (Fig. 2). Canopy cover was dominated by Longleaf Pine (53.6%) or open canopy (45.0%), with Loblolly Pine and Blackgum rarely contributing to cover (1.2% and 0.2%, respectively) (Fig. 3).

Based on DBH, the spatial point-pattern analysis for trees at BSM showed that plot #8 had trees that were significantly dispersed along the first 3-quarters of the generated distance bands, while all other plots tended toward dispersed values but were not significant (Fig. 4**)**. Point-pattern analysis, weighted by age, showed that plot #1 was significantly clustered throughout the entire distance of the plot, while plot #7 was significantly clustered at greater distances. The 4 other plots show variation between clustering and dispersion, but with no significance results (Fig. 5**)**. Two plots were excluded from the geospatial analyses due to field errors that could not be corrected with GPS software.

Age distributions, recruitment, and disturbance patterns inferred from annual rings

The Longleaf Pine tree-ring chronology consisted of 362 cores. The series intercorrelation was 0.500, the mean age series length was 82.5 years, with a mean sensitivity of 0.477. Tree age was based on the pith or innermost year: 302 individuals from live Longleaf Pine (203 without pith, 78 with pith, and 21 from outside of the plots); 8 Longleaf Pine snags; 2 fallen Longleaf Pine snags; 8 live Loblolly Pine; 1 live Blackgum; and 1 live Red Maple. Nine live and 3 standing dead Longleaf Pine were not dated due to damaged cores. The oldest individual cored, which was fallen when sampled, established in 1669, while the youngest established in 2003; both were Longleaf Pine. Most Longleaf Pine dated back to the 1860s, with

Table 1. Raw density, relative density, dominance, relative dominance, and importance values for woody stems (live and snags) on Big Smith Mountain, AL.

Species	Frequency	Relative frequency (%)	Density (stems ha^{-1})	Relative density (%)	Dominance (m^2 ha^{-1})	Relative dominance (%)	Importance value
Live							
Longleaf Pine	1.0	38.1	427.5	94.0	17.0	97.5	76.5
Loblolly Pine	0.6	23.8	12.5	2.7	0.2	1.2	9.2
Blackgum	0.5	19.0	8.8	1.9	0.2	0.9	7.3
Common Persimmon	0.3	9.5	2.5	0.5	0.0	0.1	3.4
Red Maple	0.1	4.8	2.5	0.5	0.0	0.3	1.9
Blackjack Oak	0.1	4.8	1.3	0.3	0.0	0.0	1.7
Total	2.6	100.0	455.0	100.0	17.4	100.0	100.0
Snags							
Longleaf Pine	0.9	63.6	55.0	88.0	1.7	96.4	82.7
Blackgum	0.3	18.2	5.0	8.0	0.0	2.5	9.6
Loblolly Pine	0.1	9.1	1.3	2.0	0.0	0.7	3.9
Common Persimmon	0.1	9.1	1.3	2.0	0.0	0.3	3.8
Total	1.4	100.0	62.5	100.0	1.8	100.0	100.0

5 individuals dating prior to that decade. All Loblolly Pine dated to 1987–2000, the Blackgum dated to 1995, and the Red Maple dated to 1962.

To understand the age/size relationship, we compared cores with pith years or the innermost ring dates of live Longleaf Pines to their respective DBHs and heights. Longleaf Pine approached a maximum DBH of 50.0 cm and a maximum height of 25.0 m (Fig. 2). The largest Longleaf Pine was 48.2 cm DBH and had an innermost date of 1908; the oldest live individual, however, was 38.0 cm DBH and dated back to 1802. Some Longleaf Pine below 15.0 cm DBH dated 50 years or older, appearing to be heavily suppressed in the mid- or understory. One stunted individual that was 6.2 m in height and 12.2 cm DBH dated back to 1891.

It is important to note that capturing the true age of Longleaf Pine at any site is elusive since this species can persist as a seedling (the grass stage) for up to 20 years after germination (Bruce 1959) with no annual rings produced and no height growth observed (Boyer 1990, Pessin 1934). Thus, we are reporting the ages for

Table 2. Frequency, relative frequency, density, and relative density for seedlings, saplings, and dead saplings at Big Smith Mountain, AL.

Species	Frequency (occurrence plots^{-1})	Relative frequency (%)	Density (seedlings ha^{-1})	Relative density (%)
Seedlings				
Sassafras	0.6	16.1	213	35.6
Blackgum	0.8	19.4	172	28.8
Common Persimmon	0.8	19.4	75	12.6
Blackjack Oak	0.8	19.4	72	12.0
Quercus falcata Michx. (Southern Red Oak)	0.3	6.5	25	4.2
Longleaf Pine	0.4	9.7	22	3.7
Black Cherry	0.3	6.5	16	2.6
Quercus alba L. (White Oak)	0.1	3.2	3	0.5
Total	3.9	100.0	597	100.0
Live saplings				
Blackgum	0.8	22.2	316	47.2
Black Cherry	0.1	3.7	150	22.4
Common Persimmon	0.8	22.2	69	10.3
Longleaf Pine	0.6	18.5	63	9.3
Sassafras	0.4	11.1	53	7.9
Southern Red Oak	0.3	7.4	6	0.9
Blackjack Oak	0.3	7.4	6	0.9
Red Maple	0.1	3.7	3	0.5
Loblolly Pine	0.1	3.7	3	0.5
Total	3.4	100.0	669	100.0
Dead saplings				
Longleaf Pine	0.4	60.0	34	64.7
Blackgum	0.1	20.0	16	29.4
Red Maple	0.1	20.0	3	5.9
Total	0.6	100.0	53	100.0

Longleaf Pine as the age at coring height, validated by crossdating, and with the understanding that we are underestimating the true age. Age-class distributions showed 3 noticeable recruitment peaks in the 1880s (11 trees ha^{-1}), 1940s (33 trees ha^{-1}), and 1990s (30 trees ha^{-1}) (Fig. 6).

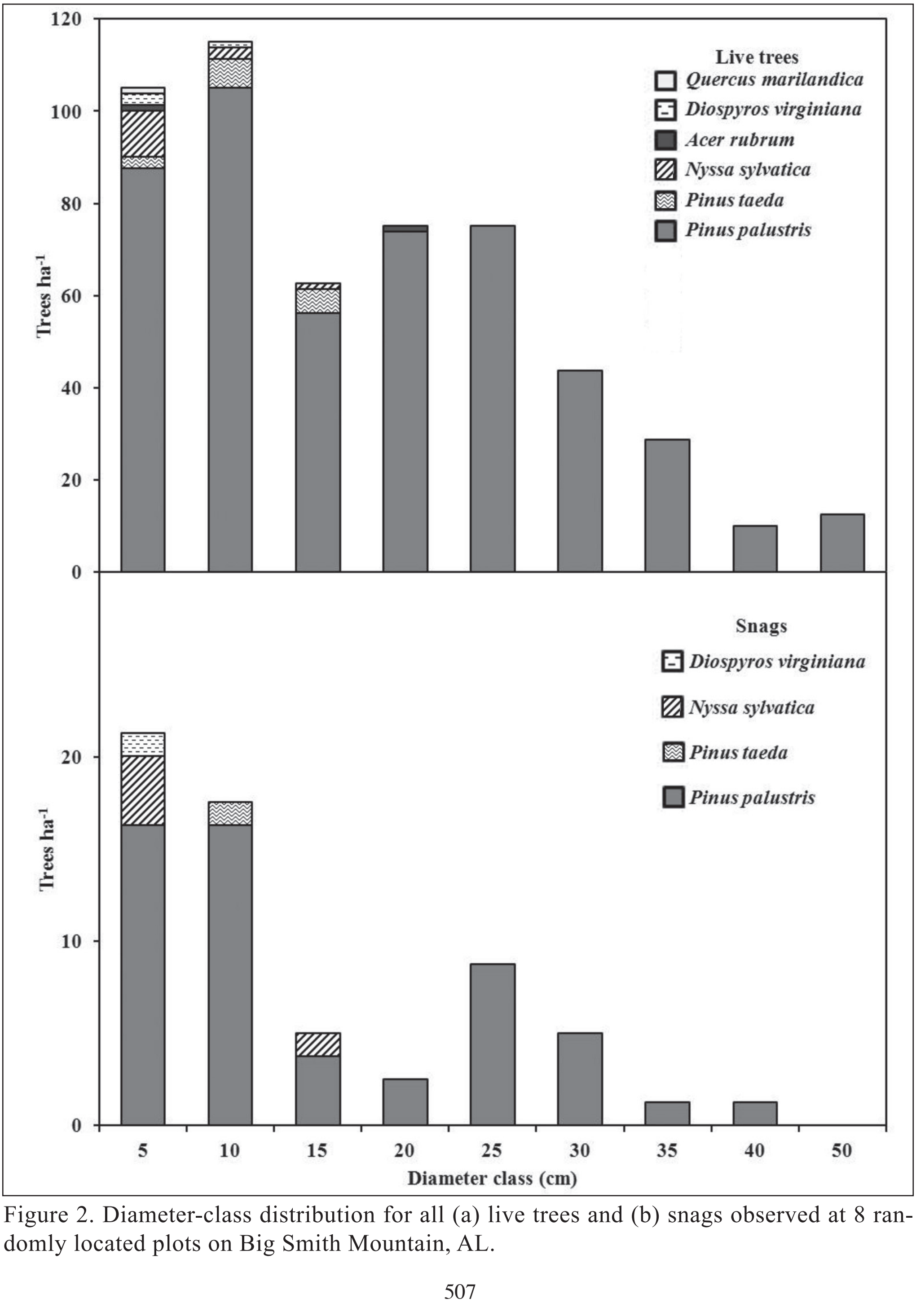


Figure 2. Diameter-class distribution for all (a) live trees and (b) snags observed at 8 randomly located plots on Big Smith Mountain, AL.

Release patterns for Longleaf Pine were identified by analysis of 286 cores from 261 individuals (dating from 1670 to 2008); 76 cores from young Longleaf Pine (dating from 1984 to 2008) were excluded because release patterns could not be developed from their cores due to the methodology in developing release patterns. Of the 23,606 annual rings measured, a total of 18,174 rings were used to calculate MPGC and MGCB and to develop a site-specific boundary line for BSM. No releases were observed for 17,286 rings (118 individuals), 782 annual rings (122 individuals) released 20–50%, and 107 annual rings (21 individuals) released greater than 50%. Releases (greater than 50%) occured over the history of the site, with most releases occurring from 1985 to 1995, a small blip from 1965 to 1970, and other releases spread between 1900 and 1945 (Fig. 7). The SEA that was performed on both the 20% and 50% disturbance chronologies revealed no statistical significance for natural and human-caused disturbance events that occurred in proximity to the study plots (Fig. 8).

Discussion

Forest composition and structure in a regional and local context

At the regional scale, Peet (2006) described 2 Longleaf Pine communities relegated to clayey and rocky uplands like BSM. These 2 communities provide some context for interpreting our results: one community described in the Fall-line

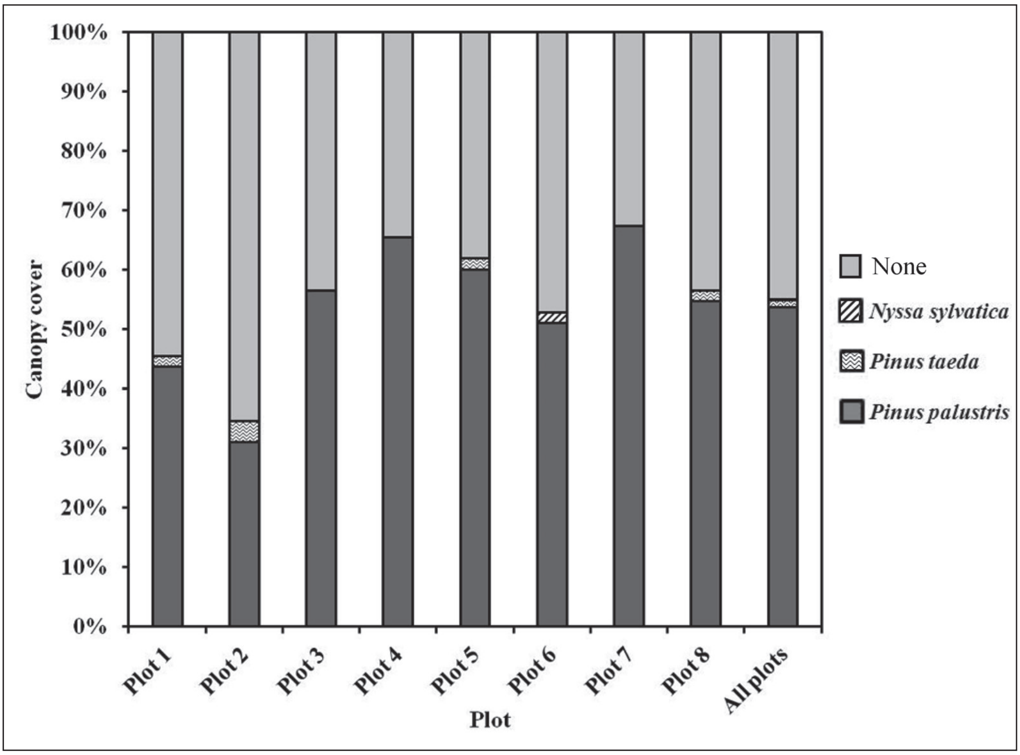


Figure 3. Canopy cover for all trees observed in 8 random plots determined via a densitometer at Big Smith Mountain, AL.

Sandhills of the Atlantic CP of North and South Carolina and another in the interior of the Alabama and Georgia Eastern CP, based on descriptions by Mohr (1901) and Harper (1943). The Atlantic CP community was dominated by Longleaf Pine canopy, a dense shrub layer of *Kalmia latifolia* L. (Mountain Laurel) and other Piedmont shrubs and lacked an herbaceous layer. The Eastern CP community was also dominated in the canopy by Longleaf Pine but was mixed with xeric oaks (*Quercus marilandica* Münchh. [Blackjack Oak] and *Quercus laevis* Walter [Turkey Oak]), the shrub layer consisted of Mountain Laurel, and the herbaceous layer was sparse. One contrast between BSM and these 2 other communities is the absence of Turkey Oak, *Aristida stricta* Michx. (Wiregrass), and *Vaccinium crassifolium* Andrews

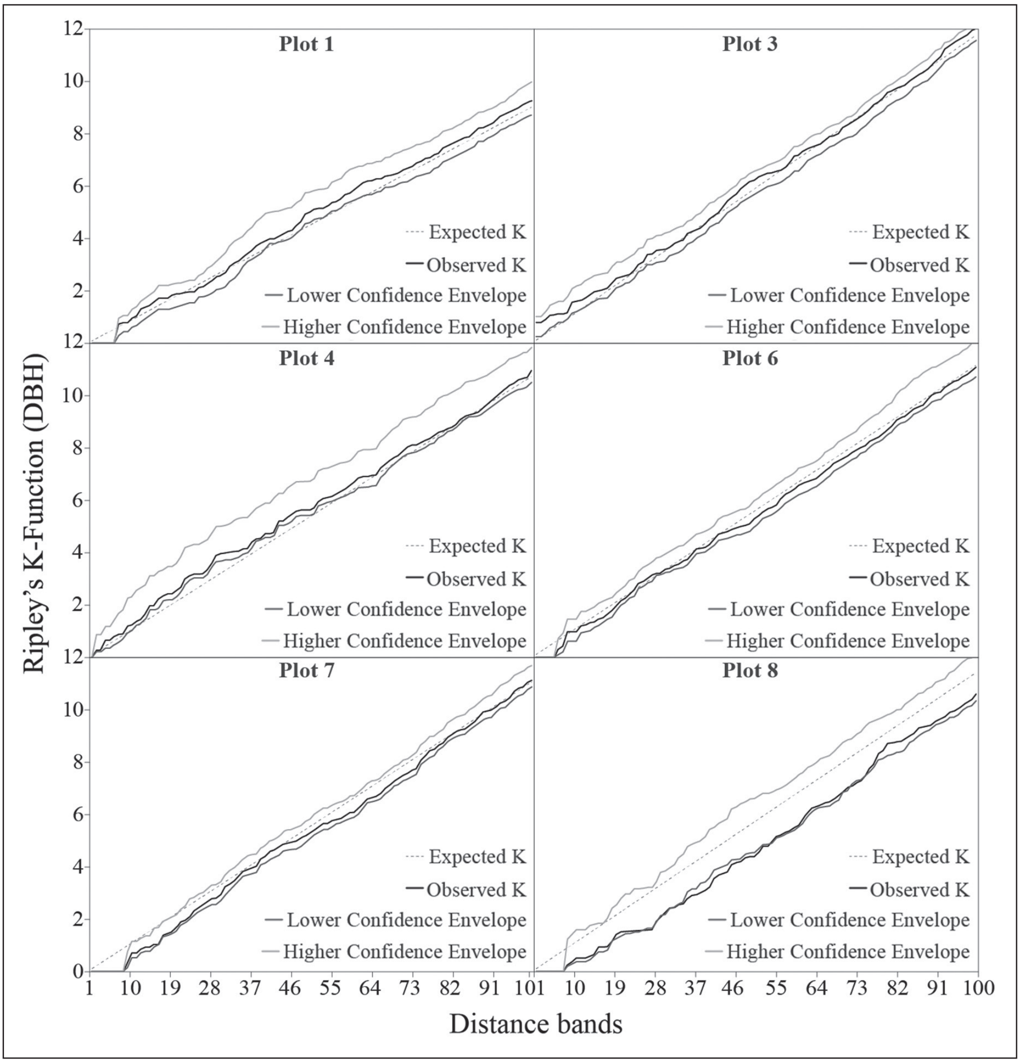


Figure 4. Ripley's K function point-pattern analysis for all trees weighted by diameter at breast height in plots 1, 3, 6, 7, and 8 at Big Smith Mountain, southern-inner Piedmont, AL. Plots 2 and 5 were not included in this analysis due to GPS collection errors encountered in the field that could not be corrected in laboratory.

(Creeping Blueberry) at BSM because it is outside of these species' ranges (Peet 2006). BSM is, however, similar to these 2 other communities in that all (1) share similar edaphic patterns, (2) are dominated by Longleaf Pine in the overstory, and (3) have a shrub layer of mountain laurel and a herbaceous layer that is lacking. These similarities thereby provide some guidance in understanding how the patterns at our site fit within the context of restoration at other known or unknown degraded Longleaf Pine stands sharing similar vegetation and edaphic patterns ranging from the CP through the Fall-line Sandhills and into the Piedmont.

In a study focused on determining lower Alabama Piedmont forest community types, Golden (1979) found that out of 53 plots across 83,290 ha, 6 plots were

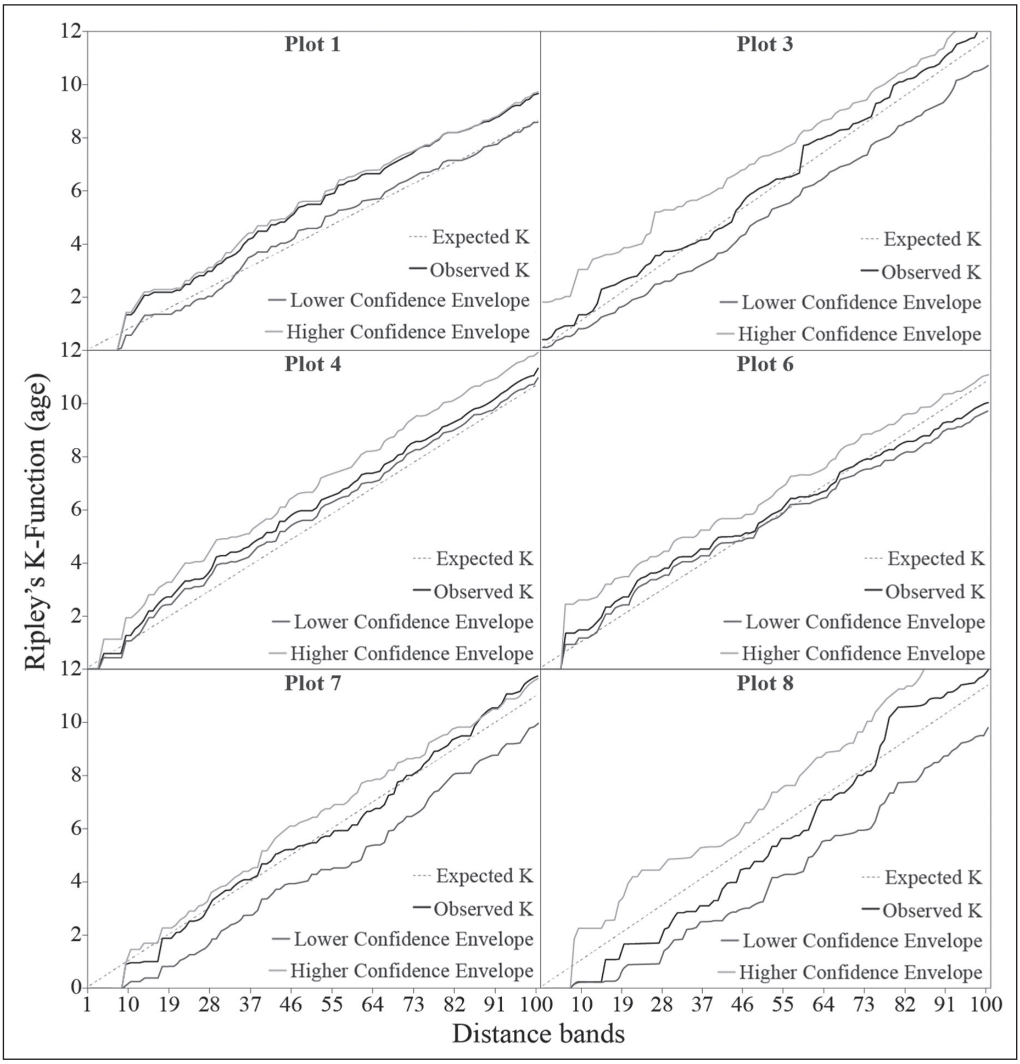


Figure 5. Ripley's K function point-pattern analysis for all trees weighted by age in plots 1, 3, 6, 7, and 8 at Big Smith Mountain, southern-inner Piedmont, AL. Plots 2 and 5 were not included in this analysis due to GPS collection errors encountered in the field and which could not be corrected in laboratory.

dominated by Longleaf Pine, with an average relative canopy dominance of 86%; the remaining canopy was shared amongst *Pinus echinata* Mill. (Shortleaf Pine), Loblolly Pine, and 17 other hardwood species. The plots dominated by Longleaf Pine were not mentioned as old growth, and ages were never ascertained as the goal of the study was to determine forest community types within this area of the Piedmont. At BSM, the relative dominance for Longleaf Pine was 11.5% higher than the mean of Golden's (1979) 6 sites, with similar hardwood species in the canopy. At BSM, hardwoods provided little to no canopy cover; rather, the canopy was open or nearly completely dominated by Longleaf Pine. Red Maple was present at BSM but did not occur in any of Golden's (1979) Longleaf Pine-dominated plots.

At the local scale, most historical accounts and recent studies suggest that foothill/mountain Longleaf Pine ecosystems are located on exposed ridges, upper portions of slopes, and south-facing aspects (Kressuk et al. 2020; Mohr 1901; Peet 2006; Womack and Carter 2011; Varner et al. 2003a, b). Longleaf Pine at BSM were also located on steep southwestern- to southeastern-facing aspects and slopes (>25.0%) on 7 of the 8 plots. One of our plots located on a northwestern-facing (291°) aspect was also dominated by Longleaf Pine (94.1% dominance). Similarly, we observed Longleaf Pine as the dominant tree on other non-south-facing aspects in and around the SMF, although none of our transects fell within these areas. Our data and observations, in agreement with prior research by Reed (1905), show that

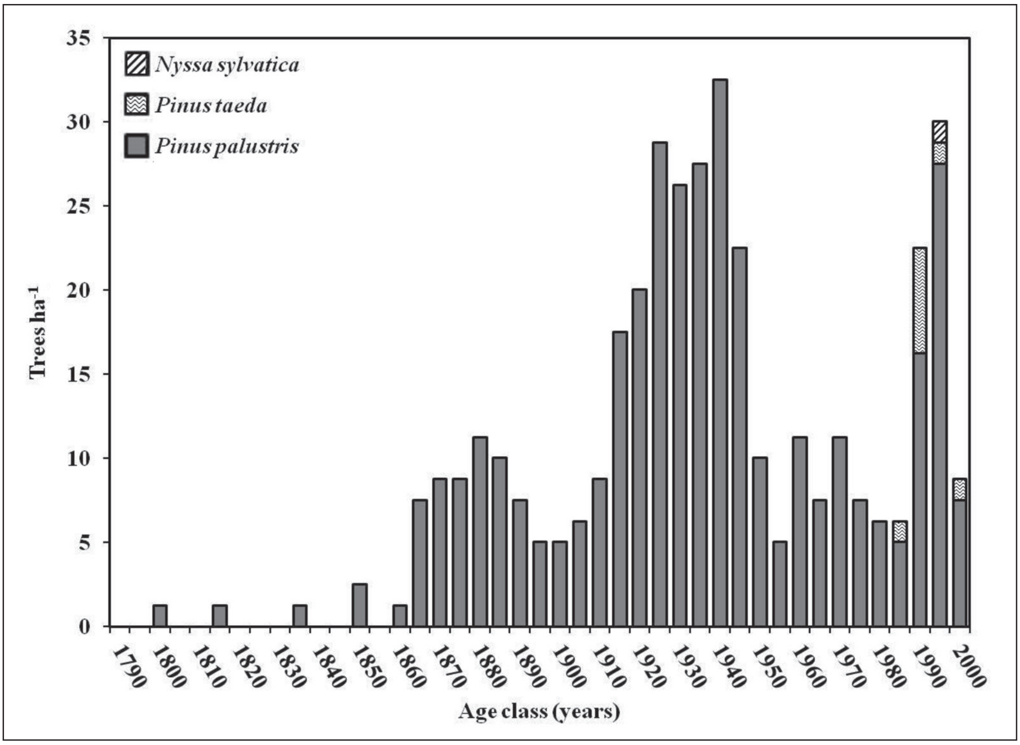


Figure 6. Age-class distribution in 5-year increments for all living canopy trees observed at 8 random plots on Big Smith Mountain, AL.

western- to northeastern-facing aspects can support Longleaf Pine systems in the Alabama foothills, due to the rolling topography, which allows for fire to flow freely across this terrain until it hits a major fire break (Frost 2006). Research and mapping of old-growth Piedmont Longleaf Pine ecosystems in adjacent Coosa County more than a century ago showed Longleaf Pine dominating western, northern, and eastern aspects (Reed 1905).

Longleaf Pine historically dominated the tree canopy on all slopes and aspects across 14,562 ha of old-growth Piedmont forests in adjacent Coosa County, west of Tallapoosa County (Reed 1905). Reed (1905) surveyed, inventoried, and mapped these forests, determining that Longleaf Pine dominated 11,252 ha of the landscape, while Loblolly Pine and other hardwoods dominated 1605 ha along rivers and creeks. A recent study (Kressuk et al. 2020) provided perspective on changes in an old-growth Longleaf Pine stand situated across a southeast-facing slope at Weogufka State Forest that was formerly surveyed by Reed (1905). Kressuk et al. (2020) found that Longleaf Pine was still the canopy dominant even after 115 years; however, fire exclusion since the 1920s and intensive harvesting of Longleaf Pine in the 1930s have led to an increase in species that are less fire-tolerant including hardwoods and Loblolly Pine. The consistent findings of hardwood recruitment at our site and in nearby areas (Golden 1979, Kressuk et al. 2020) suggests that a lack of fire throughout this portion of the foothills has caused recruitment of fire-

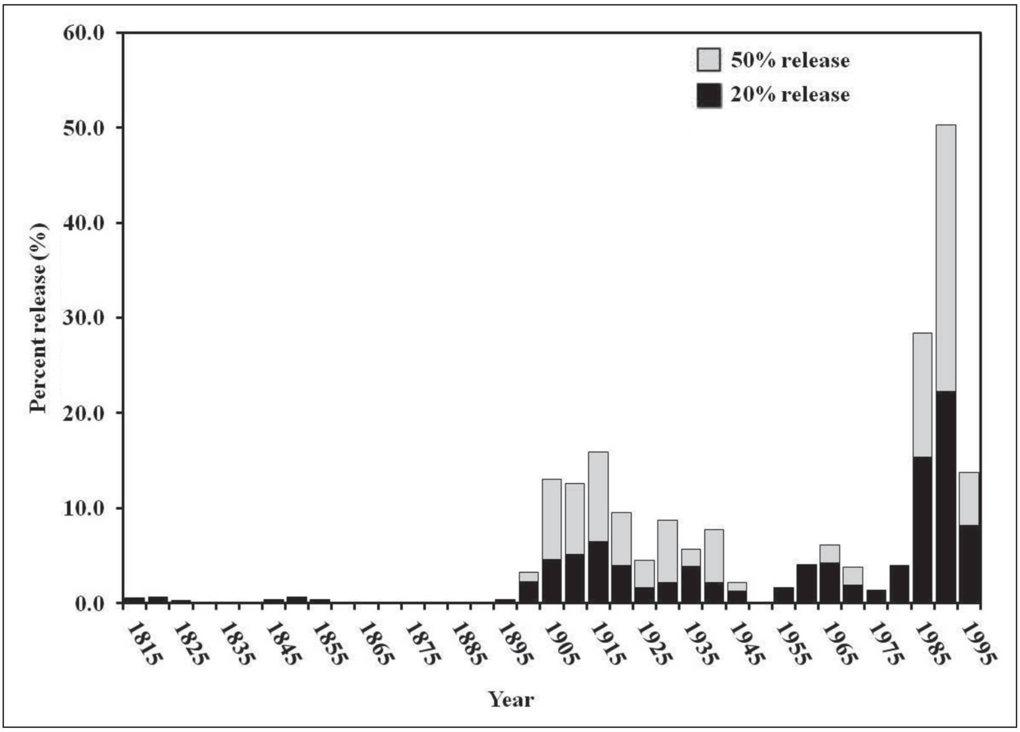


Figure 7. Release events (20% and 50%) at Big Smith Mountain, AL, derived from 18,174 *Pinus palustris* (Longleaf Pine) annual rings using boundary-line criteria (Black and Abrams 2003).

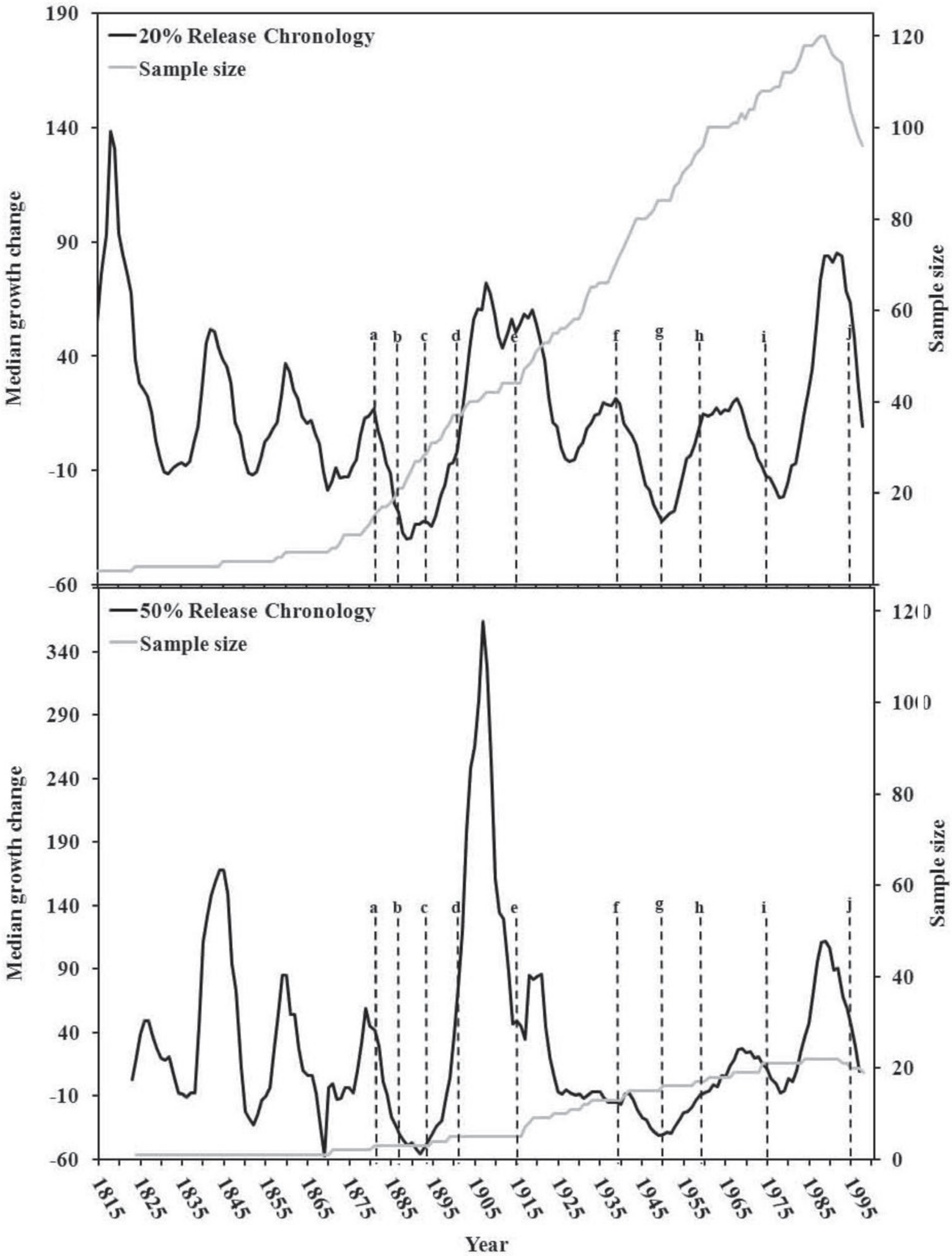


Figure 8. Release event chronologies (20% and 50%) derived for Big Smith Mountain, AL. Left-hand vertical axis = median growth change, the right-hand vertical axis = sample size, and dashed lines = event years used in the superposed epoch analysis. Letters above lines refer to the following events: (a) 1881 unnamed hurricane category 2; (b) 1887 unnamed hurricane, category 2; (c) 1893 unnamed hurricane, category 4; (d) 1902 unnamed hurricane, category 2; (e) 1915 unnamed hurricane category 2; (f) 1939 construction of fire tower; (g) 1950 Hurricane Easy, category 3; (h) 1959 timber harvest; (i) 1975 Hurricane Eloise, category 3; and (j) 1995 Hurricane Opal, category 4.

intolerant species into stands that were once dominated by Longleaf Pine*,* Shortleaf Pine*,* and fire-tolerant hardwoods.

Longleaf Pine density was higher (428 stems ha^{-1}) at BSM than in all other Longleaf Pine old-growth sites in the RV (298 and 283 stems ha^{-1}; Varner et al. 2003b), the CP (36–395 stems ha^{-1}; Meldahl et al. 1999, Platt et al. 1988, Schwarz 1907), and the Piedmont (131–205 stems ha^{-1}; Reed 1905). Kressuk et al. (2020) showed a 63% increase in stem density (214 stems ha^{-1}) of the modern forest compared to Reed's survey from 1905. BSM snag density (55 stems ha^{-1}) was also substantially higher than those reported for another montane site in Alabama (<20.0 stems ha^{-1}; Varner et al. 2003b). The high density of Longleaf Pine stems at BSM could be attributed to periods of intense fires, associated with unreported arson fires after longer periods of fire suppression, which could also explain the high mortality of Longleaf Pine observed from the 2007 arson fire. This high density also contributes to the reverse J-shaped diameter-class distribution at BSM, which is consistent with reports for old-growth Longleaf Pine at the Wade Tract in the Eastern CP (Platt et al. 1988), Caffey Hill and Red-tail Ridge in the RV (Varner et al. 2003b), and Weogufka State Forest (Kressuk et al. 2020).

Longleaf Pine at BSM approached a 50-cm DBH limit, regardless of age, which is noticeably smaller when compared to other old-growth and second-growth sites. Even the fallen Longleaf Pine dating to 1669 at BSM had a DBH of only 46.3 cm. Reduced diameter size at BSM may be related to the high density of Longleaf Pine and limited soil nutrients in the clays at the site. Gilliam et al. (1993) and Peet (2006) have suggested that geographical variation in vegetation for Longleaf Pine ecosystems can be attributed to soil texture and soil moisture in the CP and soil clay and incident solar radiation in the Piedmont and Montane Uplands. When comparing BSM to other sites, Longleaf Pines at Red-tail Ridge and Caffey Hill in the Alabama RV (Varner et al. 2003b) approached limits of ≤55 cm DBH, while those at the Wade Tract in the Georgia CP (Noel et al. 1998, Platt et al. 1988), the Boyd Tract in the Sandhills of North Carolina (Gilliam and Platt 1999), and Weogukfa State Forest in the Piedmont (Kressuk et al. 2020) approached a DBH limit of ≤65 cm, and 1 site in in the North Carolina Piedmont approached a limit of 75 cm DBH (Patterson and Knapp 2016). Longleaf Pine from other locations in the general area of the Devil's Backbone of the Piedmont were in size classes ≥30 cm DBH, but their maximum sizes were not reported (Golden 1979). Interactions of soil characteristics including nutrients, recruitment of fire-intolerant trees, and the disruption of fire regimes may have likely contributed to limited Longleaf Pine basal area at BSM when compared to other sites across this species' range. However, further testing of the differences of soil nutrients, density, and fire history need to be examined across these sites to determine if these variables significantly influence basal area.

Recruitment dynamics, disturbance, and spatial patterns

When comparing releases to the RV Longleaf Pine communities, BSM exhibited similar release patterns, but in the case of those RV communities, heartwood decay caused by the fungus *Phellinus pini,* along with ice and wind storms, may have contributed to recruitment and release patterns there (Varner et al. 2003b). Heartwood decay is a common feature for older Longleaf Pine throughout its range, but we only noted 1 incidence, in an individual that was dead, on the ground, and dated to 1669. This individual also showed evidence of 3 former cavities created by locally extinct populations of the endangered *Leuconotopicus borealis* (Vieillot) (Red-cockaded Woodpecker). Any other evidence of individuals with heartwood rot may have been removed from the canopy or the herbaceous layer (fallen individuals) due to prior high-intensity fires. The drivers of recruitment patterns of Longleaf Pine in the Piedmont require further study and testing but may be related to a combination of unrecorded wind events, ice storms, and fires. We interpret the high density of both living and dead Longleaf Pine, intense arson fires, and the encroachment of fire-sensitive pines and hardwoods over the last 20 years as evidence of the disruption of the historical fire regime at BSM.

The SEA did not determine a significant relationship between the recorded large-scale natural or human-caused disturbances and release patterns; thus we speculate that the causes may have been localized, unrecorded meteorological events (e.g., ice storms, tornadoes or other high wind events) and human disturbances (e.g., selective timber harvesting, high-intensity arson fires). One other possibility is that climate could have contributed to the release patterns at BSM. In a site on the CP of southern Georgia, Longleaf Pine release patterns were significantly correlated with increased temperature and reduced precipitation (Pederson et al. 2008). Such conditions would increase drought stress, reduce vigor, and increase the probability of fires of greater intensity, thereby increasing fire mortality, which could lead to growth pulses in the understory, midstory, and overstory of Longleaf Pines and other species at BSM. As yet, studies of climatic influences on Longleaf Pine radial growth and disturbance patterns in interior sites (like BSM) are lacking and needed to fully understand differences in tree behaviors and forest dynamics across the Longleaf Pine's range and how climate could potentially influence release patterns.

The lack of wide-scale disturbance as exhibited from the SEA might explain why spatial patterns of trees weighted by DBH or age are not significantly clustered. Usually Longleaf Pine is clustered at younger ages or smaller DBH due to the establishment of seedlings in canopy gaps (Palik et al. 1997). Clustering by size was not evident in our spatial analysis at BSM. Instead, almost all plots weighted by DBH trended towards random or dispersed distributions. Unrecorded disturbances, such as harvesting or windthrows, could be affecting the distribution. Alternatively, the lack of Longleaf Pine clustering (by DBH) could be related to the scale of the unit of analysis; that is, the study plots (0.1 ha) may not be large enough to capture the spatial patterns adequately. Future research using differently sized units of analysis would shed light on the spatial scales related to recruitment patterns for Longleaf Pine and allow them to be compared to those in CP and RV populations.

The Longleaf Pine population at BSM has developed an uneven-aged recruitment pattern over the last 2 centuries. Continuous recruitment of 5-year age classes has occurred since 1860, but with 3 high-recruitment periods: 1860–1890, 1930–1940, 1960–1970, and 1990–2000 (Fig. 6). The latter 3 recruitment periods match the release pattern we see with our documented 20% and 50% release events (Fig. 7). As a result, the reverse-J–shaped diameter-class distribution is not translatable to a reverse-J–shaped age-class distribution as would be expected (Oliver and Larson 1996, Platt et al. 1988). Although Longleaf Pine recruitment has occurred consistently over the last 2 centuries, the last 3 decades have witnessed increased recruitment of Loblolly Pine and Blackgum, with some as large as 20 cm DBH, as well as other hardwoods. At the time of our study, Longleaf Pine occurred in the understory, but was only barely recruiting in the seedling and sapling layer, indicating a recent decline in recruitment. The density of dead Longleaf Pine saplings was the highest compared to the other saplings, but those were at heights most susceptible to fire (0.6– 0.9 m; Boyer 1990). Beyond this height and in the grass stage, Longleaf Pine is fire resistant (Boyer 1990). The apical meristem of these saplings must have been subjected to the arson fire which was intense enough to kill them.

Conclusions

This in-depth study of canopy trees in an old-growth Piedmont Longleaf Pine forest community has provided insight into this tree species' ecology. At BSM, we found that neither hurricanes nor localized human-induced disturbances (e.g., thinning stands or the construction of a fire tower) had observable effects on tree community. The fire tower was unlikely to have an effect on much of BSM as its impacts were limited to an immediate area in proximity to the access road and the tower itself. Age classes in our study site did not correlate well with diameter classes, and spatial patterns showed that all trees across DBH values trended towards being dispersed. Taken together, these patterns suggest that undocumented human-caused or natural disturbances, possibly a combination of climate variation or events, unrecorded fires, and heartwood decay, may be driving the dynamics of this community.

Some characteristics at BSM, such as the Longleaf Pine-dominated canopy, the ericaceous shrub layer, and the poorly defined herbaceous layer, were much like communities examined by Golden (1979) and Kressuk et al. (2020) at the local scale and Peet (2006) at the regional scale. However, Longleaf Pines at BSM were smaller in basal area when compared to those at other studied Longleaf Pine sites, which might be attributed to localized biophysical characteristics associated with BSM. Further work investigating this variability at a variety of different sites situated across the range of Longleaf Pine could help to provide a more holistic understanding of how these biophysical characteristics play an influence on basal area. A quantitative analysis of the BSM shrub and herbaceous layer could offer a fuller comparison of BSM to other sites and show how those layers contribute to fully defining the Longleaf Pine community across multiple scales in the Piedmont.

The historical fire regime at BSM cannot be fully documented mainly due to the absence of fire-scarred trees. However Frost (2006) suggested that this part of the Longleaf Pine's range should be burned every 4–6 years to reduce hardwood competition and promote Longleaf Pine regeneration. Restoration of regular fire at BSM will decrease fuel loads and thus avoid canopy fires like the 2007 incident, which likely contributed to the mortality of Longleaf Pine in all diameter classes. Another arson fire was reported in 2010 (J. Lanier, Cherokee Ridge Alpine Trail Association, Eclectic, AL, pers. comm.) after our field study was completed. The combined effects of this fire and the intense fire of 2007 have probably temporarily reduced recruitment by Loblolly Pine and hardwoods. If not managed with fire, BSM may follow the trend of CP Fall-Line Sandhills Longleaf Pine communities, albeit at a possibly slower pace, which have been replaced, due to the disruption of pre-European settlement fire regimes, by hardwoods that are more shade tolerant (Gilliam and Platt 1999), even though BSM has had continuous Longleaf Pine recruitment over the past 2 centuries. This study highlights the need for developing more sophisticated knowledge of the ecology of mountain Longleaf Pine communities as they are understudied relative to the other, more common Longleaf Pine systems. A more precise understanding of the patterns and dynamics of these communities can inform conservation strategies under changing climate and disturbance patterns.

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