

# Vegetation patterns and dendroecology of a mixed hardwood forest on the Cumberland Plateau: Implications for stand development

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## Abstract

Forest disturbance history reconstructions provide information on the processes that influenced forest composition and structural characteristics during stand development. In this study, we quantified species composition, stand structure, a composite *Quercus* tree-ring chronology, and radial growth patterns of individual *Quercus* trees to document the processes that shaped a mixed hardwood forest on the Cumberland Plateau in Tennessee. The forest was dominated by *Carya ovata*, *Quercus rubra*, *Quercus alba*, and *Quercus montana*. The sapling layer was sparse and dominated by *Acer saccharum*. *Acer saccharum* and *Acer rubrum* represented almost 69% of all seedlings. The majority of the canopy trees established in 1920s after the last anthropogenic clearing of the forest. The diameter structure of the stand revealed a reverse J-shaped distribution. Statistically significant relationships were documented between radial tree growth and precipitation during late summer and early fall of the previous year. However, both relationships were weak, indicating the forest was not responsive to regional-scale climate conditions. A total of 63 *Quercus* tree-ring series were analyzed for release events. In these series, 88 release events were detected from 53 individuals. With the exception of one stand-wide release episode in the early 1980s, the disturbance regime of the forest was characterized by asynchronous events that occurred at variable spatial and temporal scales. Small-scale disturbance events became abundant after *ca.* 40 years of forest development. Under the current disturbance regime, the successional trajectory of the forest is projected to shift from a *Quercus*–*Carya* dominated system to one with a much stronger *Acer*–*Fagus* component, especially *A. saccharum*. Stand structure is also projected to shift from a high density of small trees to a lower density of larger trees at wider spacings.

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## 1. Introduction

The forests of the Cumberland Plateau are among the most diverse of the world's temperate-zone forests (Hinkle et al., 1993). The Cumberland Plateau is an extremely varied landscape that consists of mountains, deeply incised stream valleys, broad floodplains, steep to rolling hills, and a tableland surface with minimal relief. Each of these land types is inhabited by different forest communities as variability is largely influenced by topographic and edaphic conditions, such that fine-scale community composition and structure are highly complex (Hinkle et al., 1993; Muller, 1982). A great variety of microenvironmental conditions have resulted in high diversity at the community level and have allowed the region to support

taxa that generally dominate forests of higher and lower latitudes (Braun, 1942, 1950; Muller, 1982; Hinkle, 1989).

Most forests on the Cumberland Plateau are far from pristine, however, and reflect a long history of anthropogenic land use. Human artifacts on the Cumberland Plateau have been dated to 15,000 BP, indicating that forests of the region have likely been disturbed by anthropogenic activities for millennia (Delcourt and Delcourt, 2000). With the arrival of European settlers, the spatial extent and intensity of human impacts on forest communities increased throughout the eastern U.S. (Cronon, 1983; Whitney, 1994; Motzkin et al., 1999; Foster et al., 2003), and the Cumberland Plateau was no exception. Widespread European settlement on the Cumberland Plateau did not occur until the mid-1800s (Fullerton et al., 1977) as the eastern escarpment and rugged terrain made travel difficult and the unfertile soils made the region less attractive to settlers (Luther, 1977; Manning, 1993). During the Civil War, large tracts of forested land on the Cumberland Plateau were cleared

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largely for wood products and fuel. As a result, forest vegetation was removed from large contiguous areas. The rate of forest exploitation in the region increased with the arrival of the rail lines (Manning, 1993). By 1910, approximately 227 saw mills were operating on the Cumberland Plateau (Hall, 1910), but logging activity did not peak until 1920 (Hinkle et al., 1993). Large land tracts now support forest vegetation, the composition and structure of which is dependent upon a suite of conditions including physical site characteristics, land-use history, and natural and anthropogenic disturbance events during stand development (Raup, 1966; Cronon, 1983; Christensen, 1989; Whitney, 1994; Cowell, 1998; Foster, 2002; Frelich, 2002; Foster et al., 2003).

Because the majority of the forests in the region consist of secondary stands (i.e., not old growth) that developed after widespread timber removal that during the 19th and early 20th centuries, the documentation of successional patterns is important to our understanding of pattern and process in contemporary forest communities. Following a stand-initiating disturbance event (such as anthropogenic clearing, a large wildfire, or an insect outbreak), forest development may follow predictable patterns in accordance with biotic and abiotic site characteristics (Bormann and Likens, 1979). Oliver and Larson (1996) established a theoretical model of forest growth and development following the removal of overstory vegetation. Forest development is divided into four distinct phases, including stand initiation, stem exclusion, understory reinitiation, and complex stages of development. Each stage is accompanied by changes in species composition and stand structure, as these characteristics are influenced by a number of variables including the accumulation of biomass, the vertical stratification of tree crowns, tree longevity, and growth potential.

Reconstructions of stand development patterns are useful to our understanding of successional processes that influence forest communities (Lorimer, 1980; Nowacki and Abrams, 1994; Foster et al., 1996; Goebel and Hix, 1996; McCarthy and Bailey, 1996; Oliver and Larson, 1996; Goebel and Hix, 1997). By analyzing characteristics of live and dead stems and through the interpretation of radial growth patterns of individual trees and composite stand chronologies, we can quantify the processes that have helped shape current forests (Lorimer and Frelich, 1989; Fritts and Swetnam, 1989; Whitney, 1994; Abrams et al., 1995; Frelich, 2002; Black and Abrams, 2005). The specific objectives of this study were to: (1) quantitatively describe species composition and stand structural attributes, (2) create a *Quercus* tree-ring chronology to determine relationships between radial tree growth and climate, (3) reconstruct the disturbance history of the stand using composition and structural measures in conjunction with tree-ring data to determine the spatial extent, magnitude, and frequency of disturbance events, and (4) compare the findings of this study with findings for other forests in the region to elucidate forest growth and development patterns. Data collected and analyzed may also be used as a baseline to which results from future studies can be compared to analyze future changes in forest composition, structure, and disturbance events.

## 2. Study area and methods

### 2.1. Study site

The study was conducted in the Pogue Creek Natural Area (PCNA) located in Fentress County, Tennessee in the north-central portion of the state (Fig. 1). The 1505 ha that comprise the PCNA were acquired by The Nature Conservancy in 2004. In 2006, ownership and management of the property were turned over to the State of Tennessee, Department of Environment and Conservation, Division of Natural Areas. The reserve is adjacent to the Big South Fork National River and Recreation Area and the Pickett State Park and Pickett State Forest Complex.

The study site is located within the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman, 1938). The underlying geology consists largely of Pennsylvanian sandstone, conglomerate, siltstone, shale, and coal of the Crab Orchard and Crooked Forked Groups (Smalley, 1986). The area has irregular topography (Fenneman, 1938) characterized by long, narrow to moderately broad ridges and narrow to moderately broad valleys (Smalley, 1986). The stream networks are deeply incised and are capped with sandstone cliffs. The PCNA contains a number of unique geologic features including arches, caves, large boulders, and rock outcrops that are scattered along the slopes. Soils of the region are highly variable but are generally acidic, highly leached, and low in fertility (Francis and Loftus, 1977; Smalley, 1982). The cobbly loam soils of the PCNA are of the Grimsley–Jefferson–Bouldin association (USDA, 1995). They are acidic and relatively low in organic matter. Depth to bedrock varies

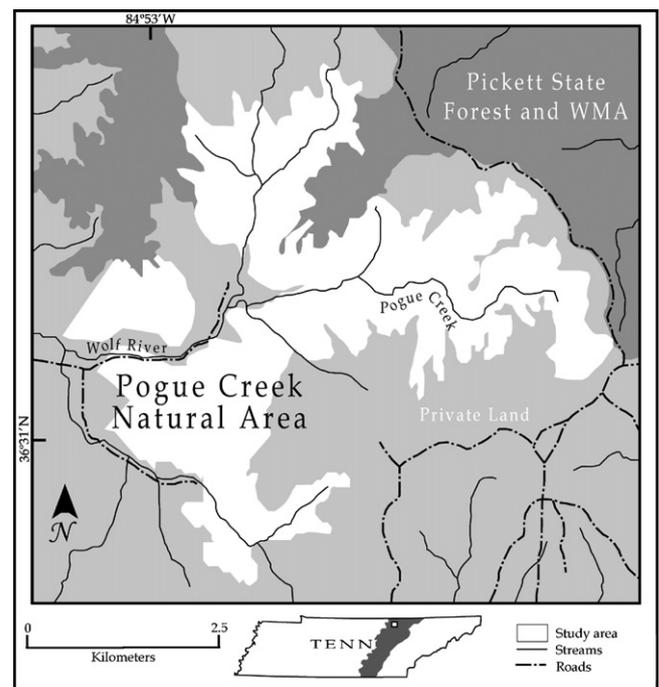


Fig. 1. Map of the Pogue Creek Natural Area, Fentress County, Tennessee. Shaded portion of the Tennessee inset map is the Cumberland Plateau physiographic section.

from 1 to 1.8 m and slope gradients range from 15% to 60%. The elevation of the study plots range from 265 to 460 m.

The climate is classified as humid mesothermal (Thornthwaite, 1948), with moderately hot summers and short-mild to moderately cold winters, although local topography strongly influences microclimatic conditions. The average frost-free period is 160 days (from early-May to late-October) and the mean annual temperature is 13 °C. The July average is 23 °C and the January average is 2 °C (USDA, 1995). The area receives steady precipitation during the year with no distinct dry season. Mean annual precipitation is 137 cm and mean annual snowfall is 50 cm (USDA, 1995). Late spring and summer are characterized by heavy rains that are often accompanied by moderate to severe thunderstorms (ca. 55 days with thunderstorms annually) and strong winds (Smalley, 1982).

Braun (1950) classified the area as part of the Cliff Section of the Mixed Mesophytic Forest Region, but local topography influences forest composition and true mesophytic species only dominate on protected sites. Slope forests of the region are generally dominated by mixed *Quercus* species with *Q. alba* being the most abundant followed by *Q. coccinea* and *Q. velutina* (Hinkle, 1978, 1989). Many forest stands on this section of the Cumberland Plateau are dominated by mixed *Quercus* and *Carya* species. Regionally, the vegetation is intermediate between mixed mesophytic and *Quercus*–*Carya* forest types. On upland sites of the Cumberland Plateau, species composition is largely controlled by topographic characteristics and factors related to soil water availability (Hinkle, 1978). The forests of the Cumberland Plateau are characterized by high biodiversity at the community level and contain over 30 canopy species (Hinkle et al., 1993). Although small old growth remnants do exist, the vast majority of forest stands in the region are second growth at various stages of succession.

The forests of the PCNA established in the late 1920s after the cessation of local logging operations. From field observations and investigation of 17 tree cross sections from a previous study, no signs of fire or other large-scale disturbance events were evident since the anthropogenic disturbances of 1920s (Hart, 2007). *Castanea dentata* was a component of the forests prior to the arrival of *Cryphonectria parasitica* (Murrill) M.E. Barr (chestnut blight). The blight reached the Cumberland Plateau in 1920s and by the end of 1930s most *C. dentata* in the region were dead. Only one *C. dentata* shrub was documented while working in the reserve and loss of the species roughly coincided with stand initiation. A number of cut stumps exist throughout the forest that indicate selective logging. The stumps were in an advanced state of decay and could not be used for dendroecological investigation. The property has been owned by several different timber companies during the development of the current stand and management records indicate minimal anthropogenic activity. Some logging roads have been maintained throughout the reserve, while others have been abandoned. To minimize anthropogenic influences in this study, care was taken to ensure no cut stumps or abandoned logging roads were in close proximity to the study plots.

## 2.2. Field methods

We quantified forest composition and stand structure using 20 0.04 ha fixed-radius ( $r = 11.29$  m) plots established along randomly placed transects throughout the PCNA. All study plots were located at mid-slope positions because the mid-slope forests of the reserve are indicative of slope forests of the greater Cumberland Plateau region. In each plot, we recorded species, crown class, and diameter at breast height (dbh, ca. 1.4 m above the surface) of all stems  $\geq 5$  cm dbh to quantify species composition and the vertical and diameter structure of the stand. Crown class categories (dominant, codominant, intermediate, and overtopped) were based on the amount and direction of intercepted light (Oliver and Larson, 1996). We collected core samples from all trees  $\geq 5$  cm dbh using an increment borer to determine stand age and recruitment pulses, and to evaluate radial growth patterns. The number of snags in each plot was also recorded to document structural features, disturbance history, and decay dynamics.

To characterize the understory, each plot contained nested sapling (9 m<sup>2</sup>) and seedling (5 m<sup>2</sup>) circular plots. All individuals  $\geq 1$  m in height and less than 5.0 cm dbh were considered saplings and all individuals  $< 1$  m in height were considered seedlings. At each plot, we recorded slope gradient, slope position, aspect, and other information useful to infer past disturbance history, such as fire-scarred trees. To document the horizontal structure of the forest, including the locations of live trees, snags, logs, and large boulders, we mapped all stems  $\geq 5$  cm dbh, snags  $\geq 10$  cm dbh, downed logs  $\geq 25$  cm diameter, and boulders in six (30%) of the 20 0.04 ha plots. From plot center, an azimuth was shot to all mapped features and distances were measured with a ground tape. Stems were divided into three groups (*Quercus*–*Carya*, *Acer*–*Fagus*, and others) and are shown graphically by color and size using 15 cm dbh quartiles (size is to scale of the maximum value). The vegetation measures were analyzed by standard descriptors of stem density, basal area (dominance), species richness, the Shannon diversity index ( $H'$ ), and evenness ( $J$ ) (Cottam and Curtis, 1956; Ludwig and Reynolds, 1988).

## 2.3. Laboratory methods

In the laboratory, tree core samples were prepared and processed for dating using the methods outlined in Stokes and Smiley (1996). The cores were air-dried, glued to wooden mounts, and sanded to reveal the cellular structure of the wood (Orvis and Grissino-Mayer, 2002) before dating the tree rings on all cores with the aid of a stereo zoom microscope. Forest disturbance history was analyzed using *Quercus* individuals because they have clear ring boundaries, do not commonly exhibit locally absent or false rings, were dominant canopy species, and have been used successfully in other studies to document disturbance history in the eastern U.S. (McCarthy and Bailey, 1996; Nowacki and Abrams, 1997; Rubino and McCarthy, 2004). Tree rings were measured to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software for all *Quercus* series ( $n = 66$ ). The

measurement series were visually compared and statistically analyzed to ensure each growth ring was assigned with the exact year of formation using the computer software COFECHA (Holmes, 1983; Grissino-Mayer, 2001a). The COFECHA program uses segmented time series correlation analyses to determine the strength of association between 50-year segments lagged 25 years from each individual series against a master chronology created from the remaining series. Segments that fell below the predetermined significance threshold ( $r = 0.32$ ,  $P > 0.01$ ) were flagged by the program and all flagged segments were re-inspected for dating errors. The program ARSTAN (Cook, 1985) was used to standardize the raw-ring measurements. The raw measurement files were detrended using the default 30-year smoothing spline. The standard chronology was developed by dividing the actual tree-ring measurements by the predicted values generated by the deterministic linear growth models fit to each individual series. The standard chronology was used to document periods of above and below average growth at the stand level and to compare radial growth to climate variables.

Correlation analysis was used to investigate the relationships between climate and radial tree growth. We used divisional climate data available online from the National Climatic Data Center (NCDC, 2006) rather than single station data because regionally averaged values generally have stronger relationships to tree growth (Blasing et al., 1981). Single station data are influenced by unique microclimate conditions and recording histories, thus contain more noise than divisional data (Cook et al., 1995). The climatic variables analyzed included monthly average temperature, monthly total precipitation, the Palmer Drought Severity Index (PDSI), and the Palmer Hydrological Drought Index (PHDI). PDSI and PHDI are used by the National Weather Service to monitor drought and wetness conditions and are commonly used in dendroclimatological studies in the eastern U.S. because they are good measures of moisture conditions during the growing season (Cook et al., 1988, 1995; Cleaveland et al., 1992; Grissino-Mayer and Butler, 1993; Dai and Trenberth, 1998; Stahle et al., 1998). We calculated Pearson correlation coefficients between the standardized tree-ring chronology and the climate variables for a 16-month period (previous July–current October). The prior growing season was included in the analysis because previous and current conditions influence the amount of carbon fixed and subsequently used for secondary growth during the subsequent growing season (Kozłowski, 1979; Grissino-Mayer and Butler, 1993; Kozłowski and Pallardy, 1997; Foster and Brooks, 2001; Fritts, 2001).

Dendroecological techniques were used to quantify the magnitude and frequency of forest disturbance events. The identification of release episodes in radial growth patterns is one of the fundamental dendroecological techniques used to reconstruct the disturbance history of a forest stand (Fritts and Swetnam, 1989; Lorimer and Frelich, 1989; Abrams and Nowacki, 1992; Nowacki and Abrams, 1994; Frelich, 2002; Rubino and McCarthy, 2004; Black and Abrams, 2005). Release episodes are defined as changes in radial growth relative to a predetermined criterion and can be documented

using a percent growth change equation (Nowacki and Abrams, 1997; Rubino and McCarthy, 2004). We analyzed changes in raw-ring widths with respect to the running median of the previous and subsequent 10 years. Release events were identified as periods in which raw-ring width was  $\geq 25\%$  (minor) or  $\geq 50\%$  (major) of the 10-year preceding and superseding median, sustained for a minimum of 3 years (Rubino and McCarthy, 2004). Understory *Quercus* individuals were not included in release investigation. Release data were analyzed using FHX2 software to graphically display spatial and temporal patterns of release episodes (Grissino-Mayer, 1995, 2001b). The FHX2 software displays release events by individual trees and as a composite sample, which allows for the investigation of disturbance events at the stand level.

### 3. Results

#### 3.1. Forest composition

The four most dominant species in the forest based on relative dominance were *Carya ovata*, *Quercus rubra*, *Q. alba*, and *Q. montana* (Table 1). Basal area ( $\text{m}^2/\text{ha}$ ) for these species ranged from  $5.30 \text{ m}^2/\text{ha}$  for *C. ovata* to  $2.51 \text{ m}^2/\text{ha}$  for *Q. montana*. A distinct second tier of species with high relative dominance values included *Fagus grandifolia*, *Carya tomentosa*, *Acer saccharum*, *Carya glabra*, *Fraxinus americana*, and *Acer rubrum*. These species had basal area values ranging from  $2.28 \text{ m}^2/\text{ha}$  for *Q. montana* to  $1.2 \text{ m}^2/\text{ha}$  for *A. rubrum* (Table 1).

The most abundant species in the tree layer (individuals  $\geq 5 \text{ cm dbh}$ ) based on relative density were *A. saccharum*, *C. ovata*, and *A. rubrum* (Table 1). A clear second tier of species with high densities was evident and included *Q. montana*, *F. grandifolia*, and *C. tomentosa*. Total basal area of overstory trees was  $29.43 \text{ m}^2/\text{ha}$  and stem density of trees  $\geq 5 \text{ cm dbh}$  was  $630 \text{ stems}/\text{ha}$  (Table 2). Species richness of stems  $\geq 5 \text{ cm dbh}$  was 30, diversity ( $H'$ ) was 2.57, and evenness ( $J$ ) was 0.75 (Table 2).

Only five species were documented in the sapling layer: *A. saccharum*, *Asimina triloba*, *Q. montana*, *F. grandifolia*, and *Nyssa sylvatica* (Table 3). The sapling layer was rather sparse with a sapling density of  $2695 \text{ stems}/\text{ha}$ . Of these sapling individuals, over 61% were *A. saccharum*. Diversity of the sapling layer was 0.99 and evenness was 0.62 (Table 2).

The seedling layer contained  $27,300 \text{ individuals}/\text{ha}$  (Table 2). Species richness was 12, diversity was 1.77, and evenness was 0.71. The most abundant species were *A. rubrum* and *A. saccharum*, with relative densities of 39.56% and 27.11% respectively. These abundance values far exceeded those of other species in the seedling layer. All *Carya* species were placed into one category because seedlings could not be identified with confidence in the field. The *Carya* species ranked third based on relative density. Only one species, *N. sylvatica*, occurred in the sapling layer but not in the seedling layer. Of the 30 tree species that occurred in the study plots, only one alien species was documented (*Ailanthus altissima*).

Table 1  
Density and dominance measures for all stems  $\geq 5$  cm dbh at the Pogue Creek Natural Area, Fentress County, Tennessee

Species	Density (stems/ha)	Relative density	Dominance (m <sup>2</sup> /ha)	Relative dominance
<i>Carya ovata</i> (P. Mill.) K. Koch	90.00	14.29	5.30	17.99
<i>Quercus rubra</i> L.	20.00	3.17	3.19	10.83
<i>Quercus alba</i> L.	21.25	3.37	2.93	9.94
<i>Quercus montana</i> Willd.	33.75	5.36	2.51	8.51
<i>Fagus grandifolia</i> Ehrh.	33.75	5.36	2.28	7.76
<i>Carya tomentosa</i> (Poiret) Nutt.	36.25	5.75	2.09	7.11
<i>Acer saccharum</i> Marsh.	178.75	28.37	2.00	6.80
<i>Carya glabra</i> (P. Mill.) Sweet	17.50	2.78	1.98	6.74
<i>Fraxinus americana</i> L.	21.25	3.37	1.71	5.81
<i>Acer rubrum</i> L.	61.25	9.72	1.20	4.06
<i>Quercus velutina</i> Lam.	6.25	0.99	0.84	2.85
<i>Tilia heterophylla</i> Vent.	18.75	2.98	0.75	2.56
<i>Liriodendron tulipifera</i> L.	15.00	2.38	0.69	2.34
<i>Quercus coccinea</i> Muenchh.	2.50	0.40	0.46	1.55
<i>Magnolia acuminata</i> (L.) L.	11.25	1.79	0.41	1.39
<i>Oxydendrum arboreum</i> (L.) DC.	7.50	1.19	0.28	0.96
<i>Carya cordiformis</i> (Wangenh.) K. Koch	10.00	1.59	0.27	0.92
<i>Nyssa sylvatica</i> Marsh.	13.75	2.18	0.25	0.84
<i>Ostrya virginiana</i> (P. Mill.) K. Koch	3.75	0.60	0.06	0.21
<i>Ulmus rubra</i> Muhl.	3.75	0.60	0.05	0.18
<i>Prunus serotina</i> Ehrh.	1.25	0.20	0.03	0.12
<i>Diospyros virginiana</i> L.	2.50	0.40	0.03	0.12
<i>Cornus florida</i> L.	5.00	0.79	0.03	0.10
<i>Asimina triloba</i> (L.) Dunal	6.25	0.99	0.03	0.09
<i>Aesculus flava</i> Ait.	1.25	0.20	0.02	0.06
<i>Sassafras albidum</i> (Nutt.) Nees	1.25	0.20	0.02	0.06
<i>Ailanthus altissima</i> (Mill.) Swingle	2.50	0.40	0.02	0.05
<i>Cercis canadensis</i> L.	1.25	0.20	0.00	0.02
<i>Betula lenta</i> L.	1.25	0.20	0.00	0.01
<i>Carpinus caroliniana</i> Walt.	1.25	0.20	0.00	0.01
Total	630	100	29.43	100

In the 20 study plots, we documented 68 individuals with dominant positions in the canopy representing 14 species. Of all canopy dominants, 49% were *Quercus* species (Fig. 2). *C. ovata* and *Q. montana* were the most common species with dominant positions in the canopy, representing 21% and 19% of canopy dominants respectively. A total of 79 individuals representing 14 species occurred in canopy codominant positions. The most common canopy codominant was *C. ovata* (representing 25% of codominant individuals), followed by *F. americana* (13%), *C. tomentosa* (10%), *Q. alba* (9%), and *Q. rubra* (9%). A total of 231 individuals occurred in overtopped positions with *A. saccharum* (45%) and *A. rubrum* (13%) being the most abundant.

Table 2  
Composition and structural measures for tree, sapling, and seedling layers at the Pogue Creek Natural Area, Fentress County, Tennessee

Parameter	Layer		
	Tree	Sapling	Seedling
Density (stems/ha)	630	2695	27300
Basal area (m <sup>2</sup> /ha)	29.43	–	–
Species richness	30	5	12
Diversity ( $H'$ )	2.57	0.99	1.77
Evenness ( $J$ )	0.75	0.62	0.71

Trees:  $\geq 5$  cm dbh; saplings:  $< 5$  cm dbh,  $\geq 1$  m ht; seedlings:  $< 1$  m ht.

Species were grouped and values were standardized at the hectare level to reveal canopy class distribution patterns. *Quercus* species were most abundant in dominant canopy positions and the number of individuals decreased with decreased height and position (Fig. 3). In contrast to the *Quercus* distribution, *Acer* species, *F. grandifolia*, and species grouped as “other” had the majority of individuals in overtopped positions followed by intermediate positions. The *Carya* species exhibited a bell-shaped canopy class distribution with the majority of individuals in intermediate canopy positions.

### 3.2. Stand structure

The diameter distribution of all stems was indicative of a mature, regenerating forest as the number of individuals was greatest in the smallest size class and density decreased with increased diameter (Fig. 4). Individuals occurred in every size class ( $n = 13$  classes). Species were grouped and standardized at the hectare level to reveal patterns of regeneration and recruitment. All groups (*Quercus*, *Carya*, *Acer-Fagus*, and others) contained individuals in the smallest size class. *Quercus* species were sparse in the small size classes, but occurred in all categories with the exception of the largest class. *Carya* species had a bell-shaped curve that peaked in the 15–25 cm dbh range and individuals occurred in all but the 60–65 cm dbh class.

Table 3  
Density and relative density for seedlings and saplings at the Pogue creek Natural Area in Tennessee

Species	Seedlings/hectare	Relative density	Saplings/hectare	Relative density
<i>Acer rubrum</i>	10800	39.56	–	–
<i>Acer saccharum</i>	7400	27.11	1650	61.22
<i>Carya</i> spp.	2400	8.79	–	–
<i>Quercus montana</i>	1500	5.49	110	4.08
<i>Fagus grandifolia</i>	1400	5.13	110	4.08
<i>Quercus rubra</i>	1100	4.03	–	–
<i>Asimina triloba</i>	700	2.56	770	28.57
<i>Cercis canadensis</i>	500	1.83	–	–
<i>Quercus alba</i>	500	1.83	–	–
<i>Fraxinus americana</i>	400	1.47	–	–
<i>Magnolia acuminata</i>	400	1.47	–	–
<i>Sassafras albidum</i>	200	0.73	–	–
<i>Nyssa sylvatica</i>	–	–	55	2.04
Total	27300	100	2695	100

Seedlings:<1 m ht; saplings:<5 cm dbh, ≥1 m ht.

*Acer* species and *F. grandifolia* had a reverse J-shaped diameter distribution. These species were by far most abundant in the smallest size class (170 stems 5–10 cm dbh/ha), and individuals were present in all but two categories (37.5 and 47.5 cm dbh classes). Species listed as “other” also showed a reverse J-shaped diameter structure and were only absent from the three largest size classes. Although the size of individual snags was not recorded, we documented 26 snags ≥10 cm dbh/ha.

The largest documented individual in the study plots was a *C. glabra* at 69.5 cm dbh followed by an *A. saccharum* at 67.25 cm, a *F. grandifolia* at 65 cm, a *Q. alba* at 64.5 cm, and a *Q. rubra* at 61.5 cm. A total of seven trees ≥60 cm in diameter were documented. The largest *C. ovata* was 53.5 cm, the largest *C. tomentosa* was 54 cm, the largest *Q. velutina* was 54 cm and the largest *Q. montana* was 51 cm in diameter. Of note, when walking a transect through the forest, we came across a *F. americana* with a dbh of 125 cm. This large individual was an anomaly relative to other trees in the forest, as the largest *F. americana* documented in a study plot was only 53.25 cm in diameter.

The oldest tree in a study plot was a *C. glabra* with an inner date of 1753. A period of 85 years lapsed before the next tree

established, a *C. tomentosa* with an inner date of 1837. The next tree that established was a *Q. alba* with an inner date of 1872 (Fig. 5). Only 11 trees in the study plots established before 1900 and they were all of the *Quercus* and *Carya* genera with the exception of one *A. saccharum* (inner date 1850) and one *F. americana* (inner date 1898). Two trees established at the turn of the century, a *Q. rubra* with an inner date of 1900 and a *F. grandifolia* with an inner date of 1901. When grouped by species, establishment pulses were evident (Fig. 5). Although older trees representing several species established before 1920s, during this decade there was an establishment pulse of *Carya*. Establishment pulses for *Quercus* and *Acer–Fagus* began in 1930s and 1940s, respectively. There was a lack of *Carya* establishment after 1950 and a lack of *Quercus* establishment after 1960. Establishment of *Acer–Fagus* and species listed as “other” was continuous.

Age-structure graphs were created for the eight most important species based on relative importance values (Fig. 6). *C. ovata* and *C. tomentosa* exhibited bell-shaped curves with peaks in 1930s and 1940s, respectively, and neither of these species has established since 1970s. *Quercus rubra* and *Q. alba* had similar age structures with the majority of individuals establishing between 1930 and 1950. *Quercus montana* was offset from the other two *Quercus* species by a decade as establishment was highest between 1940 and 1960. Establishment of *A. rubrum* peaked in 1940s and gradually declined while *A. saccharum* began in 1950s and peaked in 1970s. *Fagus grandifolia* had a rather uniform age distribution as individuals established in all but the three most recent decades. Like *A. saccharum*, *F. grandifolia* establishment peaked in 1970s.

Stem maps help illustrate the horizontal structure of the forest by showing the distribution of live stems, snags, logs, and boulders (Fig. 7). The majority of all stems were in the smallest size class (5–15 cm dbh) and all mapped plots contained stems in the largest size class (>45 cm dbh). All plots contained trees in all four size categories except plots 11 and 18. Downed logs occurred in all plots, four plots contained snags, and three plots contained large boulders. Plot 11 had the steepest slope gradient

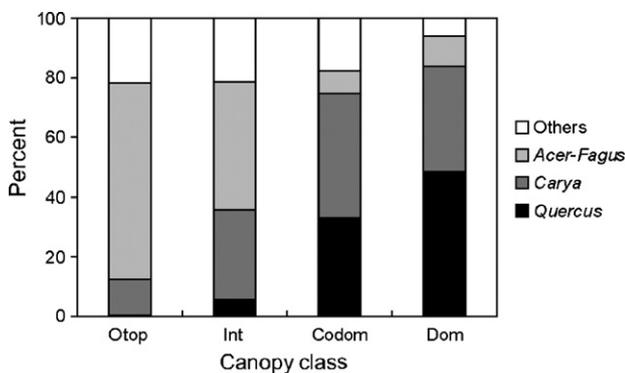


Fig. 2. Canopy class percentages by group. Canopy class categories are based on the amount and direction of intercepted light (Oliver and Larson, 1996). Dom: dominant, Codom: codominant, Int: intermediate, Otop: overtopped.

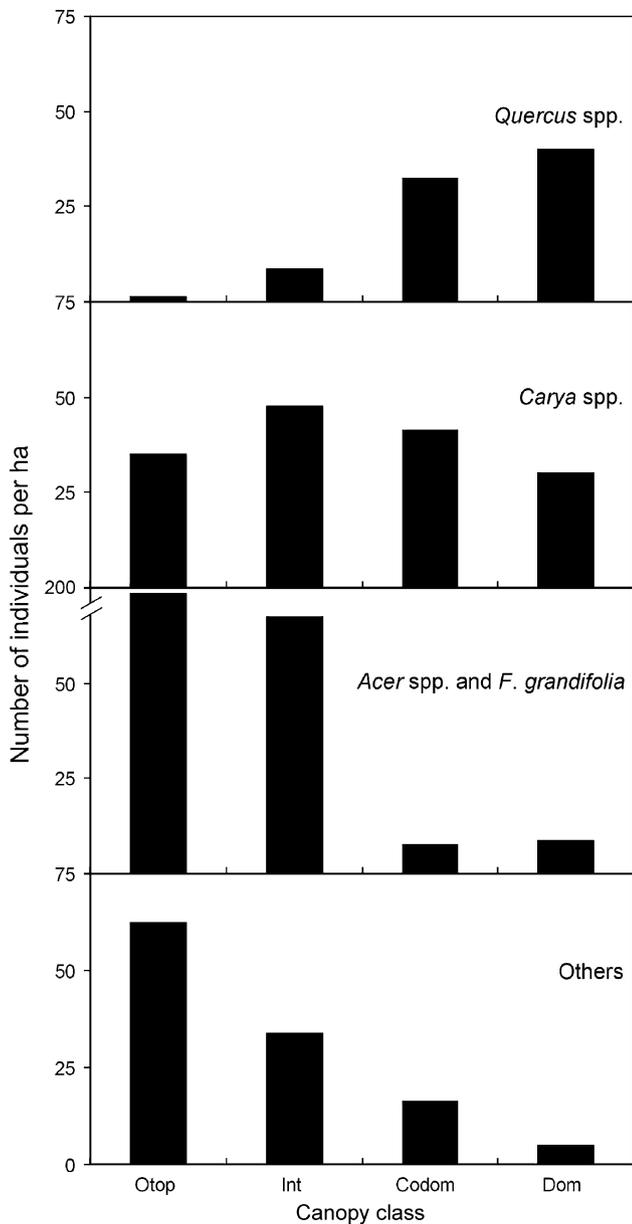


Fig. 3. Canopy class distributions per hectare by group. Canopy class categories are based on the amount and direction of intercepted light (Oliver and Larson, 1996). Dom: dominant, Codom: codominant, Int: intermediate, Otop: overtopped. Note broken scale for *Acer* species and *F. grandifolia* for overtopped individuals.

(55%) and also contained the fewest number of live stems ( $n = 14$ ). Although tree crowns were not mapped, all plots had closed canopies and lacked light gaps on the forest floor.

### 3.3. Dendroecology

All *Quercus* individuals were crossdated with confidence. The interseries correlation of the 66 *Quercus* series (from 64 individuals) was significant at 0.44. The interseries correlation is the average of all Pearson correlation coefficients calculated for each series compared to all other series in the tree-ring record and is used as an index of the signal-to-noise ratio in the chronology (Foster and Brooks, 2001). A total of 177 50-year

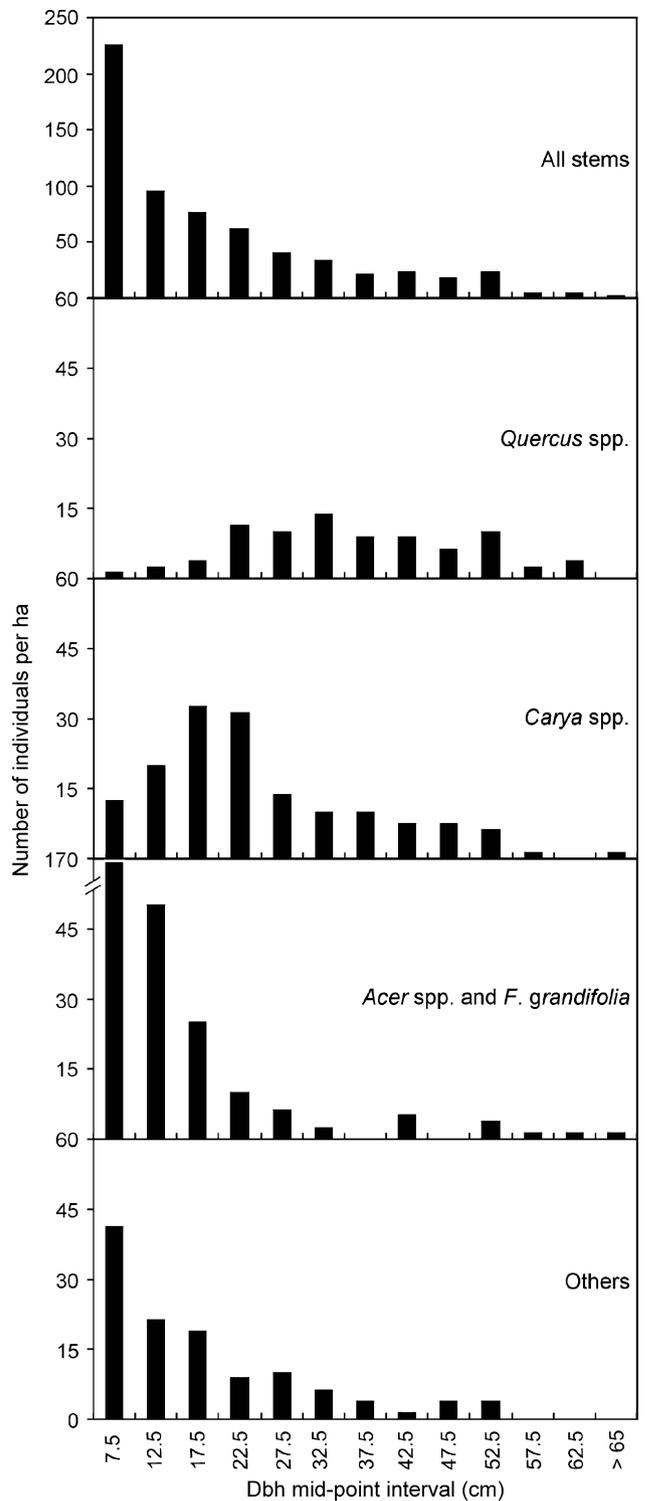


Fig. 4. Number of trees ( $\geq 5$  cm dbh) per hectare for all species, divided into four groups at the Pogue Creek Natural Area, Fentress County, Tennessee. Each dbh interval includes stems  $\pm 2.5$  cm of the stated value with the exception of the  $>65$  cm class.

segments were analyzed by the COFECHA program. Of these 177 segments, 47 (26.5%) were flagged (indicating they were not statistically significant with contemporary segments). Although the percentage of flagged segments was higher than we would like to accept, none of the problems indicated

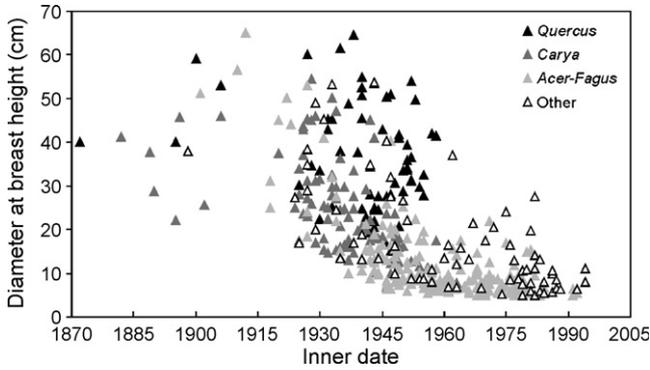


Fig. 5. Diameter–age relationships for all cored trees that could be accurately dated and that established after 1870 in the Pogue Creek Natural Area in Tennessee.

incorrect dating. Average mean sensitivity was 0.22 which is typical for *Quercus* in the southeastern U.S. (DeWitt and Ames, 1978). Mean sensitivity is a measure of the relative difference in ring width of adjacent rings and is an indicator of climate sensitivity in the tree-ring record (Fritts, 2001).

The tree-ring record extended 138 years from 1868 to 2005. A composite radial-growth chronology was created where mean annual growth was standardized to equal 1.0. The composite chronology extends from 1902 to 2005. The first 35 years of the record were truncated so the start of the chronology

(1902) had a sample depth of three series (Fig. 8). Sample depth increased to four series in 1906. From the standardized chronology, below average radial growth was apparent until 1920s, followed by a period of above average radial growth from the early 1920s through the late 1930s. There was another notable period of above average growth from the late 1950s through the late 1960s and a period of below average radial growth from 1990 through the end of the chronology.

No significant relationships were found between the standardized chronology and monthly mean temperature, PDSI, or PHDI for the previous and current years (Fig. 9). Significant positive relationships occurred between total monthly precipitation of the previous August ( $r = 0.30$ ,  $P < 0.05$ ) and previous October ( $r = 0.27$ ,  $P < 0.05$ ) and the standardized chronology. We found no clear patterns for monthly mean temperature. Patterns were evident for PDSI and PHDI. PDSI and PHDI had the strongest negative relationships to the chronology in spring and both relationships were weak in January and June.

Of the 63 *Quercus* individuals analyzed using the 10-year running median method, 53 (84%) exhibited release events. A total of 88 release events were detected from the 53 individuals with some trees experiencing multiple releases during their life (Fig. 10). All detected release episodes were visually checked to ensure accurate dating. Of the 88 detected release events, 54 (61%) were minor and 34 (39%) were major. One individual (a *Q. rubra*) experienced five separate release episodes during its

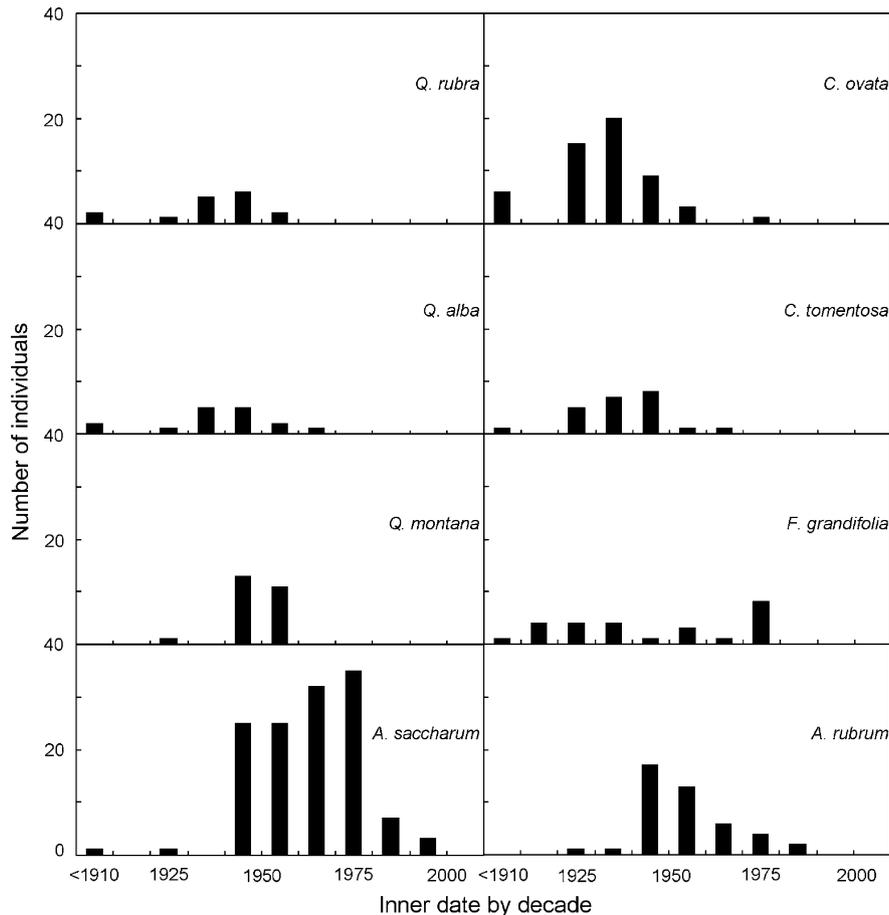


Fig. 6. Age structure of the eight most important species (based on relative importance values) at the Pogue Creek Natural Area, Fentress County, Tennessee.

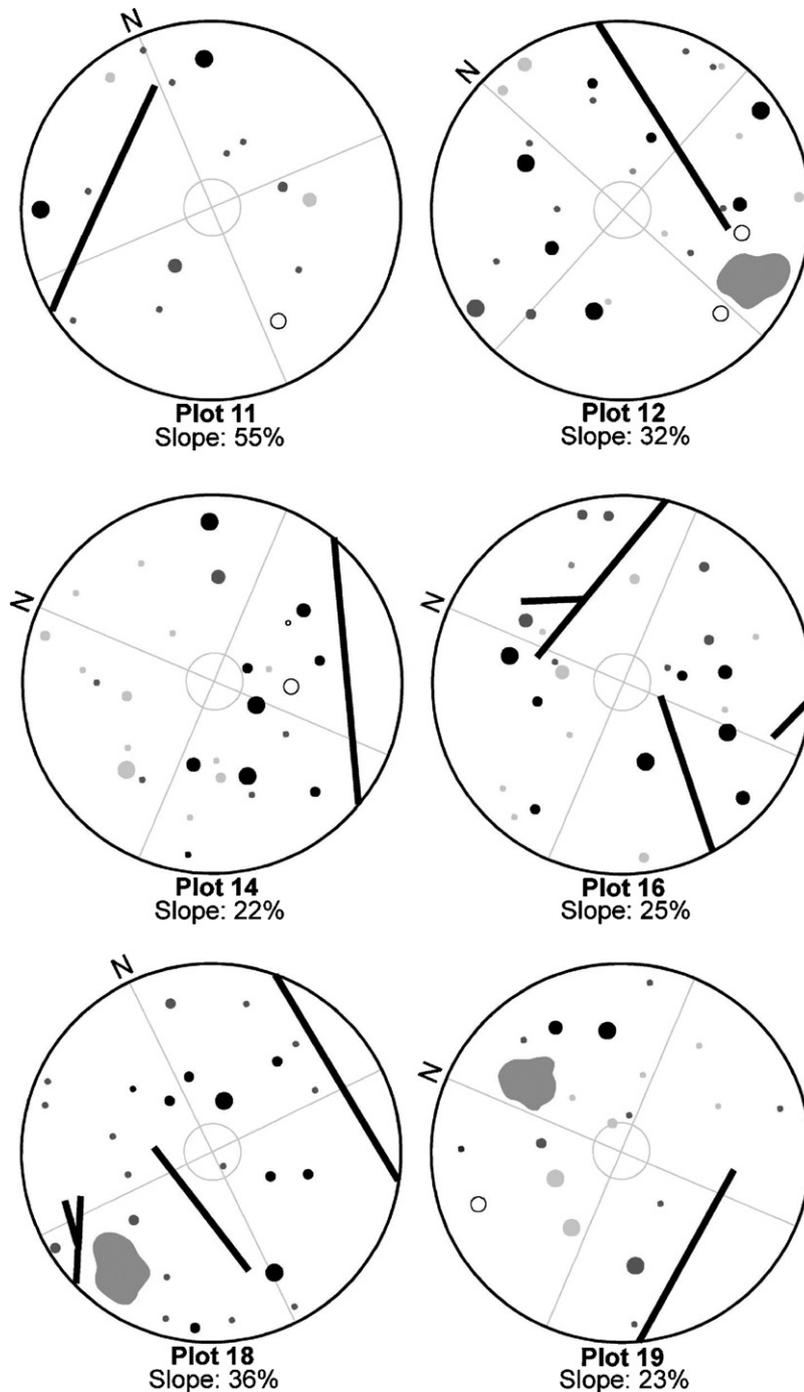


Fig. 7. Maps of all stems ( $\geq 5$  cm dbh), snags ( $\geq 10$  cm dbh), downed logs, and boulders in six 0.04 ha plots at the Pogue Creek Natural Area. North arrows are oriented to slope aspect. Filled circles indicate live stems (black: *Quercus* and *Carya*; dark gray: *Acer* and *F. grandifolia*; light gray: other) and hollow circles indicate snags. Circle sizes are classed into quartiles at 15 cm dbh intervals. Irregular shapes with medium gray fill represent boulders while dark lines represent downed logs.

life (1900–2005, Fig. 11a), while two individuals (a *Q. alba* and a *Q. velutina*) experienced four separate release events during their lives (1868–2005 and 1929–2005, respectively). A *Q. rubra* experienced the greatest percent growth change of 380% over the 10-year running median (Fig. 11b). Six individuals sustained increased radial growth of over 100% for 3 years. The longest sustained release was 9 years observed in a *Q. montana* from 1982 to 1990 (Fig. 11c). The mean release duration was 4.2 years  $\pm$  1.4 (S.D.). The longest period between release

events (after 1920s) was 11 years (occurring from 1947 to 1958) and the shortest was 1 year. Releases occurred in consecutive years in many instances (e.g., 1979–1982) (Fig. 10 composite). The mean release return interval was 2.4 years  $\pm$  3.2 (S.D.).

We analyzed the temporal and spatial patterns of release episodes to determine if disturbance events were stand-wide or local in spatial scale. Stand-wide disturbances are typically defined as release episodes where a minimum of 25% of

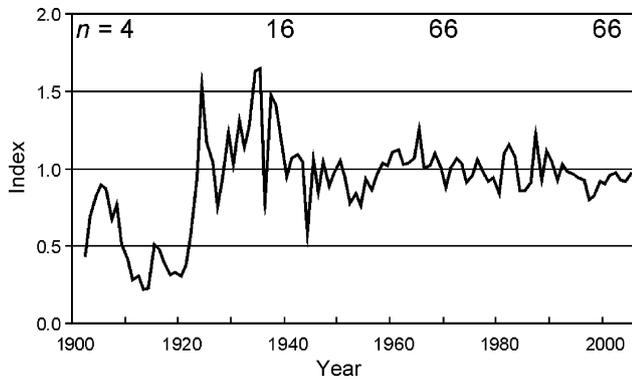


Fig. 8. Composite ring-width index generated from all *Quercus* series sampled at the Pogue Creek Natural Area with mean growth standardized to 1.0 ( $n$  = number of series in that year).

individuals release simultaneously (Nowacki and Abrams, 1997; Rubino and McCarthy, 2004). In this study, we consider a stand-wide disturbance event an episode where there was a simultaneous release experienced by a minimum of one tree in 25% ( $n = 5$ ) of the study plots. By evaluating release events across plots, we eliminate the possibility of labeling a local event that causes all individuals in one plot to release a stand-wide phenomenon. At this level, stand-wide release events indicate exogenous disturbances that removed overstory vegetation at a larger spatial scale than local events. Possible disturbance agents include insect attacks, tornado events, and ice storms. Only one stand-wide release was documented and it was initiated in 1981. During this stand-wide event, individuals in seven (35%) of the 20 plots experienced a release in radial growth. In two of these individuals, the radial growth release lasted until 1987 with releases in other trees ending in 1983 and 1984. Archives of *Monthly Weather Review* from 1980 to 1982 were studied to determine if a notable extreme weather event may have caused the stand-wide release. No extreme events were recorded in the journal, but this does not mean a local storm that may have killed trees throughout the reserve did not occur.

With the exception of this one stand-wide episode, release events were asynchronous throughout the forest. Release events occurred over variable temporal and spatial scales. The spatio-temporal patterns of release events indicated a disturbance regime characterized by localized disturbance events that influence only neighboring trees such as small canopy gaps (Lorimer, 1980; Orwig and Abrams, 1994; Black, 2003). The majority of the forest trees established in 1920s and there was a pulse of release events in 1960s (Fig. 12), indicating that small-scale canopy disturbance events became important mechanisms of forest change after *ca.* 40 years of development.

## 4. Discussion

### 4.1. Composition, structure, and dendroecology

Species diversity was highest for the tree layer and lowest in the sapling layer. A similar pattern was evident for species evenness. Individuals were more evenly distributed among the

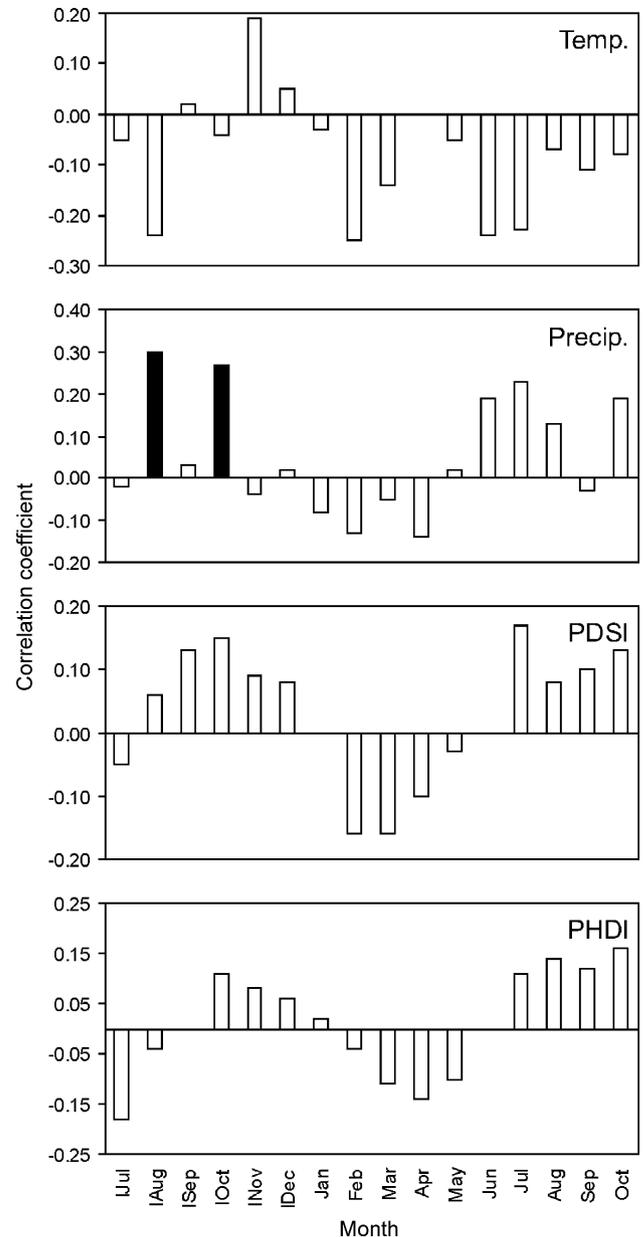


Fig. 9. Correlation analysis between the standardized tree-ring chronology and regional climate variables. Temp: monthly mean; Precip: monthly total; PDSI: Palmer Drought Severity Index; PHDI: Palmer Hydrological Drought Index. Month abbreviations preceded with an "I" indicate the previous year. Solid bars indicate significant values ( $P < 0.05$ ). Note that y-scale varies.

represented species in the tree layer. The relatively low evenness value for the sapling layer was the result of the majority of saplings (61%) being of one species (*A. saccharum*). Although species abundance in the seedling layer was more evenly distributed, *Acer* species represented 67% of all seedlings. Species richness was lowest in the sapling layer. Species richness could not be directly compared between forest layers because true richness was used rather than a richness index. However, the seedling plots which represented a smaller area compared to sapling plots contained more species. The sapling layer was sparse and only five species were represented (note *Carya* species were grouped for seedling and sapling layers).

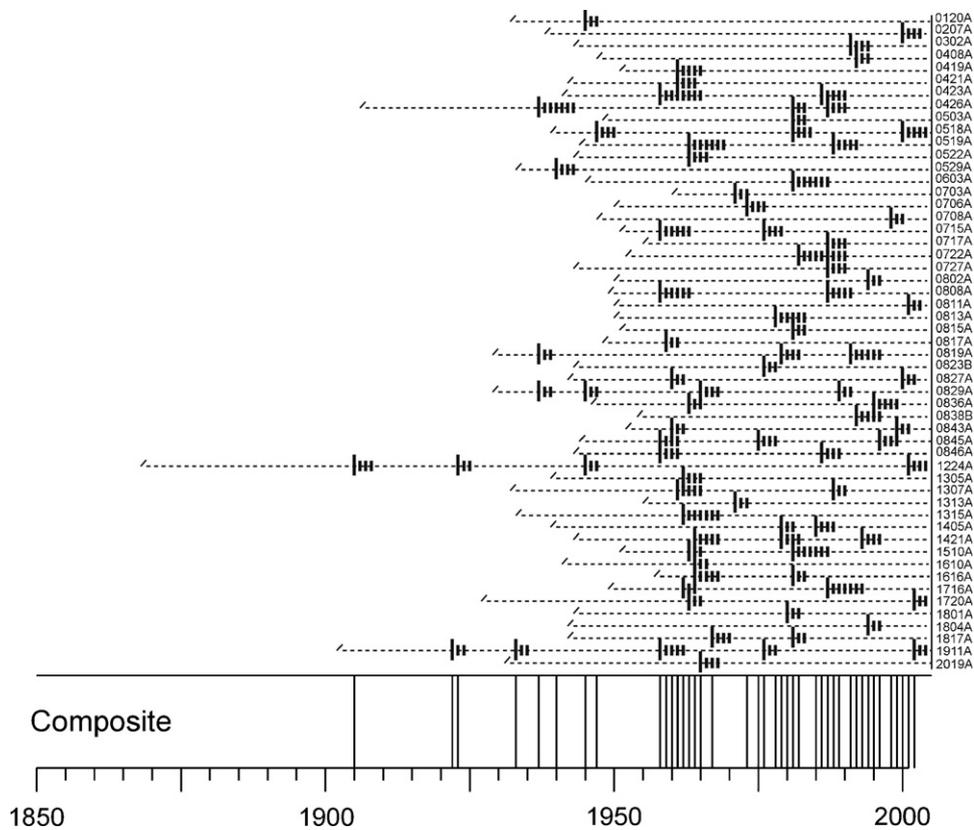


Fig. 10. Detected release events using the 10-year running median method for 63 *Quercus* individuals sampled at the Pogue Creek Natural Area, Fentress County, Tennessee. Each horizontal line represents the record from one individual tree, long vertical bars indicate release events, and short vertical bars indicate release duration. A composite of release events for the study site is shown across the bottom.

Only the tree layer contained a woody alien species. *Ailanthus altissima* is shade-intolerant (Miller, 2003) and its clustered distribution (both spatially and temporally) indicated it established in a small canopy gap. It is believed that gaps serve as sites for the diffusion of alien plants into forest interiors (Goldblum and Beatty, 1999). The likely establishment of *A. altissima* in a small gap indicates that canopy gaps have enabled this species to extend into the forest interior. *Ailanthus altissima* has been shown to successfully invade old growth forests by colonizing canopy gaps (Knapp and Canham, 2000). The species has a rapid growth rate and the potential to outcompete native trees in large gaps.

The stand exhibited a reverse J-shaped diameter distribution. The number of individuals was greatest in the smallest size class and density declined with increased size. This diameter structure indicates a regenerating forest (Smith et al., 1996). In the absence of a large-scale disturbance event, composition of the forest is projected to shift. The forest canopy was dominated by *Quercus* and *Carya* species. However, the most abundant individuals in the understory were *Acer* species and *F. grandifolia*. *Acer rubrum* and *A. saccharum* were also the most abundant species in seedling plots. In the absence of a large-scale disturbance event, *Acer* species will likely increase in dominance as understory individuals are recruited to larger size classes and to codominant and dominant positions in the forest canopy. Both *A. saccharum* and *A. rubrum* are shade-tolerant species that may remain suppressed in the understory

until the occurrence of small-scale disturbance events allows them to recruit. *Acer saccharum* has been shown to respond quickly and substantially to canopy disturbances (Tryon et al., 1992). As *Acer* individuals in understory and intermediate canopy positions reach dominant and codominant positions in the canopy, the forest will change from a *Quercus*–*Carya* dominated system to one with a much more important *Acer* component. This pattern of *Acer* regeneration (coupled with a lack of regeneration of other species, especially *Quercus*) has been documented throughout the eastern U.S. (Lorimer, 1984; Crow, 1988; Fralish et al., 1991; Abrams, 1992; Loftis and McGee, 1993; Mikan et al., 1994; Goebel and Hix, 1997; Signell et al., 2005; Albrecht and McCarthy, 2006; McEwan and Muller, 2006; Pierce et al., 2006).

The interseries correlation for the 66 *Quercus* series was significant, but low by dendrochronological standards. The interseries correlation was lowered by 12 segments that fell below the significance threshold of 0.33. We sampled relatively young trees from a closed-canopy forest at mid-slope positions from a number of different aspects. The sampling scheme was not designed to analyze regional-scale patterns, but rather local microsite conditions within the forested environment. The sampling resulted in an average mean sensitivity of 0.22 which is low (meaning the tree-ring series were rather complacent as opposed to sensitive), but typical for forest interior trees in the eastern U.S. Also, the *Quercus* series measured and statistically analyzed represented five different species and species specific

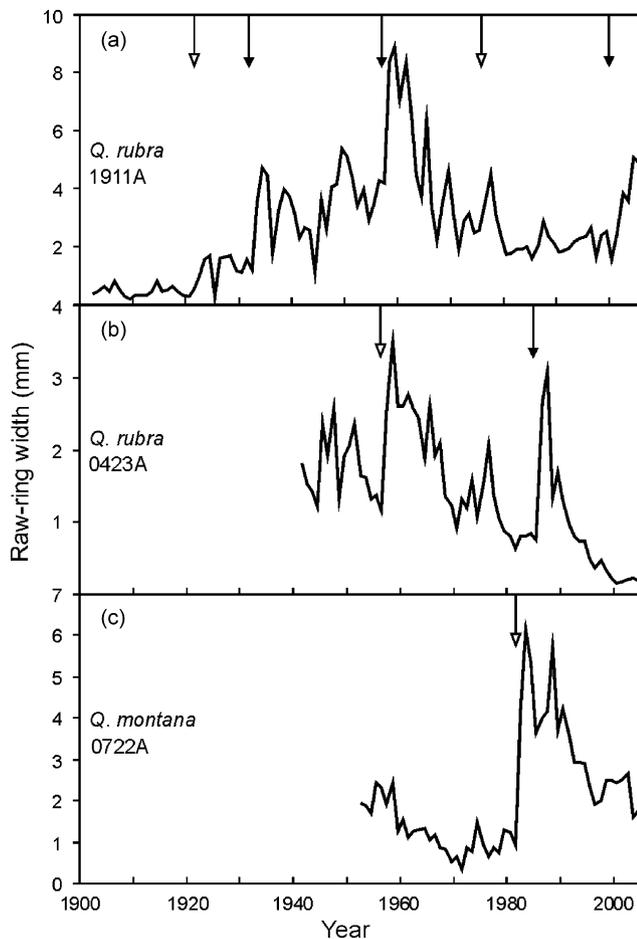


Fig. 11. Raw-ring width measurements for individuals sampled at the Pogue Creek Natural Area. Open arrows indicate minor release and filled arrows indicate major release episodes. (a) *Q. rubra* with five release events, (b) *Q. rubra* with a growth change of 380%, (c) *Q. montana* with a minor release sustained for 9 years.

responses to environmental conditions may have contributed to the rather low interseries correlation.

The standardized chronology showed below average radial growth from the start of the chronology in 1902 until 1920s. This increase in radial growth is likely related to the disturbance history of the site. The forest was last cleared in 1920s and all economically mature *Quercus* individuals would have been

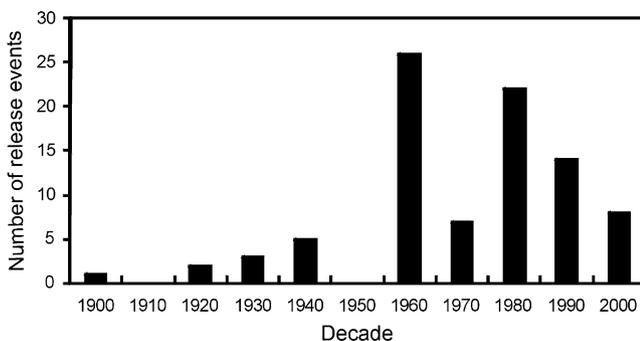


Fig. 12. Number of release events per decade at the Pogue Creek Natural Area, Fentress County, Tennessee. Release events were detected using the 10-year running median method.

removed. The *Quercus* individuals that were spared likely exhibited poor form or were of a small size. We speculate the clearing of the forest reduced competition and the remnant individuals were allowed to increase growth and become dominant trees in the next stand.

Although significant relationships were found between the standardized tree-ring chronology and late summer and early fall precipitation of the previous year, both relationships were weak, indicating that the forest was not responsive to broad-scale climate conditions. The tree-ring chronology was developed to ensure accurate dating of release events and thus no series (even those that fell below the significance threshold) were removed from the chronology, which is a common practice in dendroclimatological studies. Variations in radial growth patterns have likely been influenced by forest stand dynamics. The sampled trees were growing in a closed-canopy forest, where the effects of climate were likely overshadowed by competition (Fritts, 2001). In mesic closed-canopy forests, such as the PCNA, light is generally the factor limiting tree growth. Thus, variations in radial growth likely result from increased light caused by canopy disturbances rather than broad-scale climatic conditions. The weak relationship between the chronology and the climate variables emphasizes the influence of canopy disturbance events on forest productivity.

Only one stand-wide release event was detected in the tree-ring record from the PCNA. This stand-wide release episode occurred in the early 1980s. A stand-wide release indicates overstory vegetation was removed from the forest at a large spatial scale, as trees experienced simultaneous releases in 25% of the study plots. A stand-wide release would be the result of an exogenous disturbance event that influenced large areas of the reserve. At the PCNA, such exogenous disturbance events may have included strong winds associated with tornadic storms, ice storms, or snow loading, among other factors.

With the exception of this one stand-wide release episode, forest disturbance events were asynchronous. They occurred at variable spatial and temporal scales. Interestingly, other studies in mixed *Quercus* forests of the eastern U.S., using similar release detection methods, have documented the return interval of stand-wide release events to be 20–30 years (Nowacki and Abrams, 1997; Rubino and McCarthy, 2004). For the PCNA, only one stand-wide release event was detected in the 130+ years of record indicating the return interval for stand-wide disturbances is longer at the PCNA than has been reported elsewhere in the eastern U.S. The return interval of these events may be related to biotic or abiotic site characteristics, atmospheric events, or the stage of forest development as other studies were conducted in different physiographic sections, at higher latitudes, and in older forests. Based on the occurrence of only one stand-wide release episode and the high number ( $n = 88$ ) of release events detected in the 63 individuals sampled, we conclude that gap-phase dynamics are the primary forest disturbance events at the PCNA. The majority of release episodes were detected in only one or a few individuals, indicating increased radial growth during release episodes likely resulted from small, localized canopy disturbances that involved the partial or total death of one or a

small group of canopy individuals (Runkle, 1982; Nowacki and Abrams, 1997; Rubino and McCarthy, 2004; Black and Abrams, 2005). These small-scale events would have only influenced neighboring individuals, and that is the pattern revealed from the disturbance reconstruction.

The magnitude of the disturbance may be inferred from the release duration. The duration of increased radial growth varied by event, but in general was 4 years. Because the 10-year running median method takes into account the 10-year preceding and superseding each growth ring, release events indicate a period of above average growth relative to the previous and subsequent decades. Thus, release events indicate periods when trees were responding to increased available resources (largely light) due to the removal of an adjacent individual. We interpret the mean release duration to indicate that the voids from canopy disturbance events closed in approximately four years. This is not enough time to allow individuals in the understory to recruit to the canopy. These gaps closed by lateral branch growth and release events coincide with lateral crown expansion (Rubino and McCarthy, 2004). In these small gaps, it is possible for understory trees to be released and then become suppressed again as the gap closes (Oliver and Larson, 1996). For example, multiple gap events may be required for understory *Quercus* individuals to reach canopy positions (Rentch et al., 2003). Some canopy disturbances lasted longer than the 4-year average and may have allowed individuals in the understory to reach canopy positions before becoming suppressed.

#### 4.2. Forest growth and development

The forest is currently in a stage of understory reinitiation (Oliver and Larson, 1996). As individuals die and are removed from the canopy, canopy individuals are expanding their crowns and understory trees are being recruited to larger size classes. Although some trees pre-date 1900s, the majority of canopy individuals established in 1920s. To investigate forest development patterns, we compared composition and structural attributes of the secondary forest of the PCNA to those of an old growth remnant on the Cumberland Plateau (Table 4). Martin (1975, 1992) summarized forest composition and structural measures of Lilley Cornett Woods (LCW), an old growth forest in Kentucky approximately 130 km northeast of the PCNA. Both forests are located on the Cumberland Plateau, but the PCNA is near the western boundary and LCW is near the eastern boundary of the province. A moisture gradient across the plateau does exist and may influence species composition of the region. Old growth remnants are often used to predict the development of maturing stands. Although this technique is not without problems (Sprugel, 1991; Drury and Runkle, 2006) it does provide a model of forest development and a baseline for which to compare developing stands.

Species richness was similar for the PCNA and old growth mixed *Quercus* stands at LCW as the old growth remnant contained only one species more than the secondary forest. However, tree species diversity was lower for the secondary forest relative to old growth mixed mesophytic stands at LCW.

Table 4

Comparisons of composition and structural measures of second growth stands at the Pogue Creek Natural Area (PCNA) with old growth stands at Lilley Cornett Woods (LCW)

Parameter	PCNA	LCW <sup>a</sup>
Species richness	25	26 <sup>b</sup>
Diversity ( $H'$ )	2.57	3 <sup>c</sup>
Canopy species	16	20 <sup>c</sup>
Basal area (m <sup>2</sup> /ha)	28.6	25–35 <sup>c</sup>
Trees $\geq$ 75 cm dbh/ha	0	7 <sup>c</sup>
Trees $\geq$ 10 cm dbh/ha	413	250 <sup>c</sup>
Snags $\geq$ 10 cm dbh/ha	26	10 <sup>c</sup>

<sup>a</sup> Data from Martin (1992).

<sup>b</sup> Data from mixed *Quercus* stands at LCW.

<sup>c</sup> Data from mixed mesophytic stands at LCW.

Mixed mesophytic forests are known for their high diversity (Muller, 1982; Martin, 1992; Hinkle et al., 1993; Runkle, 1996; McEwan et al., 2005) and the PCNA, while within the Mixed Mesophytic Forest Region (Braun, 1950), is dominated by *Quercus* and *Carya* species. Perhaps the difference in species diversity is more a function of forest type over forest age. Old growth mixed mesophytic stands at LCW contained 20 canopy species while the PCNA had only 16 species with dominant or codominant positions in the canopy. As the secondary forest matures, it is possible the number of canopy species will increase because some species that existed only in the understory have the potential to reach canopy positions, such as *Nyssa sylvatica*.

Basal areas between the PCNA and LCW were similar, or at least the basal area of the PCNA is within the range expected for old growth mixed mesophytic forests (Held and Winstead, 1975; Muller, 1982). However, the arrangement of the biomass was very different. LCW contained about 250 trees  $\geq$  10 cm dbh/ha while the PCNA contained over 400 trees of this size (60% increase). Further, while LCW contained at least seven trees  $\geq$  75 cm dbh/ha, no tree of this size occurred in any of the study plots at the PCNA (although one *F. americana* in this size category was documented while walking a transect). Tree biomass between the sites was similar, but the arrangement of that biomass was represented in vastly different ways. LCW contained large trees at a relatively low density, while the PCNA contained small trees at a much higher density. Based on the abundance of snags and the high number of release events at the PCNA, we propose that the frequency of canopy gap events is higher in secondary forests relative to old growth remnants, but the magnitude of the disturbances is less (i.e., a higher frequency of small gaps in secondary forests compared to old growth stands).

Based on these comparisons, we hypothesize the biomass of the PCNA will remain at a dynamic equilibrium, but the spatial arrangement of the biomass will change as the forest matures. At the PCNA, it is apparent that trees are dying and being removed from the canopy. In fact, the number of snags  $\geq$  10 cm dbh/ha was higher for the PCNA than at LCW. This finding supports other studies that have found second growth stands to have higher snag densities than old growth remnants (Muller, 1982; McComb and Muller, 1983). Localized small-scale canopy gaps are occurring at the PCNA based on the

disturbance history of the stand. The duration of radial growth release events was much shorter than what has been reported in older forests, indicating that canopy disturbances at the PCNA are relatively small compared to similar disturbances in other forests. These small canopy gaps are likely being filled via lateral branch growth. Thus, as individuals are removed from the canopy (the losers), neighboring trees (the winners) increase radial growth and overall diameter. The lost basal area from the dead tree is recovered by the increased growth of residual individuals. Over time, this process will cause the diameter structure of the PCNA to more closely resemble that of an old growth stand. The biomass will be distributed among a lower number of larger individuals as opposed to a high number of small individuals.

The last stand-initiating disturbance that occurred at the PCNA was in 1920s. That event was anthropogenic, caused by timber removal. The return interval of natural stand-initiating disturbances is not known for the region. Stand-initiating events in the region are likely highly variable depending on a suite of biotic and abiotic characteristics including species composition, slope aspect, and elevation and are thus unpredictable. Possible stand-initiating events at the PCNA include high winds associated with tornadoes, severe ice or snow loading from polar outbreaks, and large wildfires. In the absence of a stand-initiating disturbance, species composition is predicted to change as *Acer* and to a lesser degree *Fagus* individuals in sub-canopy positions are recruited to larger size classes. The structure of the stand will also shift to larger, but fewer trees at wider spacings. We predict the number of canopy disturbances will decrease, but that the magnitude of each individual disturbance will increase. If a stand-initiating event does occur, the development of the next stand would likely follow the successional pattern documented in this study. However, some variables that will exist during the development of the next stand will be inherently different. Biotic and abiotic characteristics of the site have changed during the growth of the current stand and disturbance events themselves often have long lasting influences. It is also possible new factors, such as *Lymantria dispar* L. (gypsy moth), may alter development of future stands.

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