



Composition, structure, and dendroecology of an old-growth *Quercus* forest on the tablelands of the Cumberland Plateau, USA

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ABSTRACT

Forest reconstructions provide information on the processes that influence forest development and successional patterns. In this study, we quantified woody species composition, stand structure, and radial growth patterns of individual *Quercus* trees to document the processes that shaped a forest on the Cumberland Plateau in Tennessee over the past three centuries. The oldest trees on the site established in the late-1600s. The forest was dominated by *Quercus alba*, but *Acer rubrum* and *Oxydendrum arboreum* were the most abundant species in small size and young age classes. *Quercus* recruitment was continuous over the past three centuries whereas *Pinus* established in the late-1800s and early-1900s and *Acer* established in the 1940s. Most overstory *Quercus* recruited via gap-phase regeneration and ca. one-third established under a closed canopy and were suppressed for up to 80 years prior to overstory release. *Pinus* recruitment corresponded to stand-wide canopy disturbance while *Acer* recruitment had no relationship to overstory removal. Over the last three centuries, we contend *Quercus* has been the dominant genus with *Pinus* restricted to patches that corresponded to canopy disturbances. The recent profusion of *Acer* in the understory will likely inhibit regeneration of *Pinus* and *Quercus*. Indeed, the composition of the overstory and understory were dissimilar and under the current disturbance regime, the *A. rubrum* component should increase. Gap-scale disturbance frequency has remained relatively stable since the mid-1700s. However, the frequency of stand-wide canopy disturbance events has decreased since the mid-1800s and the last initiated in 1903.

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1. Introduction

Forest reconstructions, coupled with forest inventory data, provide insight into patterns of stand development and succession and strengthen our understanding of the processes that influence forest communities (Henry and Swan, 1974; Lorimer, 1985; Lorimer and Frelich, 1989; Oliver and Stephens, 1977). In addition, the results of forest reconstructions can be used by land managers to establish a site's historic range of variability and to implement silvicultural treatments that mimic historical disturbance characteristics and ecological processes (Coates and Burton, 1997; Swetnam et al., 1999; Webster and Lorimer, 2005). A majority of the Eastern Deciduous Forest of North America consists of secondary stands at various stages of development. These forests provide information on development and succession only since the last stand initiating disturbance event, which in many systems was anthropogenic clearing in the late 19th or early 20th centuries (Parker, 1989; Whitney, 1994). Therefore, reconstructions in old-growth forests

(defined here as forests with an abundance of relatively old trees for the species and in the complex stage of development (Oliver and Larson, 1996)) are particularly valuable as long-term developmental processes and successional trends can be ascertained. Many stands in the Eastern Deciduous Forest are not returning to their pre-European settlement conditions as vegetation–environment relationships have been modified by land-use practices (Cowell, 1998; Foster et al., 1998; Motzkin et al., 1999) and exotic pests and pathogens (Paillet, 2002). Thus, retrospective studies in old-growth stands provide insight on forest characteristics prior to alteration of these relationships (Foster et al., 1996; McCarthy and Bailey, 1996; Nowacki and Abrams, 1994; Ruffner and Abrams, 1998).

The Cumberland Plateau supports forests that are among the most diverse in the temperate zone (Hinkle et al., 1993). The Cumberland Plateau is topographically complex and since forest community composition and structure are largely functions of topographic and edaphic conditions, these measures are highly variable across the region (Clatterbuck et al., 2006; Hinkle, 1989). This landscape heterogeneity has resulted in a wide variety of microenvironmental conditions inhabited by different species

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assemblages and thus the region has high gamma diversity. Although the Cumberland Plateau is noted for its high biodiversity, the vegetation of the region can be broadly classed into two categories: that of the flat to rolling plateau tablelands with minimal topographic relief and that of the highly dissected plateau sections consisting of coves and gorges (Hinkle, 1989). Although the vast majority of the Cumberland Plateau is composed of the tableland surface, the overwhelming majority of scientific research and conservation efforts in the region have been focused specifically on cove and gorge communities which comprise a relatively small percentage of the Cumberland Plateau landscape.

In general, the undissected Cumberland Plateau tableland surface has lower species diversity and is lower in quality for commercial hardwood timber production compared to the highly dissected areas of the plateau (Braun, 1950; Smalley, 1982, 1986). The tableland surface of the Cumberland Plateau has a high potential and value for surface mining, conversion to intensively managed *Pinus* plantations, agricultural fields, and urban development (McGee, 1982; Smalley, 1982, 1986). Additionally, the plateau tablelands are most likely to support naturally occurring *Pinus*-dominated forests or *Pinus-Quercus* forests, forest types that are decreasing in spatial extent hypothesized to be attributed to a lack of forest management and/or natural disturbances that maintained them (Oswalt and King, 2010; Schweitzer, 2000). The Cumberland Plateau tablelands are predominately owned by non-industrial private landowners (Oswalt and King, 2010; Schweitzer, 2000), and are generally unprotected from non-forest conversion or poor harvesting practices. Plateau tablelands, therefore, represent at-risk communities because of the potential for forest conversion and the lack of existing management recommendations that can restore ecologically important processes.

Although tracts of old-growth forests have been identified in plateau gorges (e.g. Clark et al., 2007; Martin, 1975; Quarterman et al., 1972; Schmalzer et al., 1978), only one large expanse of old-growth forest has been discovered on the tableland surface of the Cumberland Plateau (Haney and Lydic, 1999). This forest has not been previously studied for forest history reconstruction or dendrochronological purposes and represents a unique opportunity to quantify long-term patterns of stand development, canopy disturbance, and forest succession.

The specific objectives of this study were to: (1) quantify species composition and stand structural attributes, (2) reconstruct the frequency, magnitude, and spatial extent of past canopy disturbance events, and (3) elucidate forest growth and development patterns over the last three centuries with particular emphasis on strategies of *Quercus* recruitment and canopy ascension. Data reported here may be used as reference conditions for similarly situated forests on the Cumberland Plateau that are being managed for old-growth characteristics (i.e. complex age, diameter, and vertical structures). Forest communities of the tableland surface of the Cumberland Plateau would have resembled the conditions of the old-growth stand quantified here in the absence of direct and intense Euro-American disturbances.

2. Study area and methods

2.1. Study site

This study was conducted on the Savage Gulf Natural Area (SGNA) located in southeastern Tennessee (Fig. 1). The reserve consists of 6309 ha and is managed as a Class II Natural Area by the Tennessee Department of Environment and Conservation. The SGNA is a component of the South Cumberland Recreation Area which contains 10 distinct state-managed reserves. The SGNA is listed as a National Natural Landmark by the US Department of

the Interior because of its biodiversity and unique geologic features (DeSelm and Clark, 1975). The nature reserve was formally established when the property was transferred to the State of Tennessee in 1973. Since that time use of the reserve has been restricted to recreation and research. Our study was specifically focused within a ca. 600 ha *Quercus* forest on the tablelands in the northeastern section of the reserve. While most of the 600 ha study area appeared to be old-growth (e.g. abundance of old trees, complex diameter and vertical structures), portions likely experienced some level of human disturbance that would include logging prior to creation of the SGNA. Although road construction and coal extraction in Grundy County, Tennessee began in the 1850s, permanent settlement of the area did not begin until 1870 when Swiss colonists, primarily focused on dairy and agriculture crops, established communities. During the 1870s rail lines were constructed and the number of saw mills increased (Manning, 1993). Old railroad beds exist within the SGNA, but records that would help determine the extent of logging in the study area do not exist. We excluded areas from our study with obvious signs of past Euro-American disturbances (e.g. those near cut stumps or old logging roads).

The SGNA is located on the mid-Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman, 1938; Smalley, 1982). The Cumberland Plateau is the westernmost physiographic province of the Appalachian Highland realm. It is bordered by the Ridge and Valley to the east and the Interior Low Plateau to the west. Our study plots were located on the weakly dissected plateau landtype association of the true plateau subregion as defined by Smalley (1982). The true plateau has an undulating surface submaturely dissected by young valleys (Fenneman, 1938; Smalley, 1982). These tablelands are extensive through the mid-Cumberland Plateau and have led some authors to consider them a distinct unit called the Central Uplands (DeSelm and Clark, 1975). Several incised bedrock streams flow across the study site into Savage Creek and disrupt the tableland surface. The underlying geology consists largely of Pennsylvanian sandstone, conglomerate, siltstone, shale, and coal of the Crab Orchard and Crooked Forked Groups (Miller, 1974; Smalley, 1982). Regionally, soils are acidic, highly leached, and low in fertility (Francis and Loftus, 1977; Springer and Elder, 1980). The elevation of the study plots ranged from ca. 500–575 m amsl.

The climate is classified as humid mesothermal (Thorntwaite, 1948) with long, moderately hot summers and short, mild winters. Regionally, the complex topography is a strong control on fine-scale climate conditions. The average frost-free period is ca. 200 days and the mean annual temperature is 14 °C. The July average temperature is 24 °C and the January average temperature is 3 °C (PRISM Climate Group, 2011). The area typically receives steady precipitation during the year with no distinct dry season; however, short periods of water surplus or deficit are common. Mean annual precipitation is 145 cm (PRISM Climate Group, 2011). Thunderstorms accompanied by intense rainfall and sometimes hail occur over 50 days annually and are most common in late spring and summer. Snowfall is minimal and generally melts within a few days (Smalley, 1982).

Braun (1950) classified the study area as part of the Cliff Section of the Mixed Mesophytic Forest Region. However, true mixed mesophytic communities occur only in riparian areas and coves. The most spatially comprehensive study on Cumberland Plateau forests was conducted by Hinkle (1978) and summarized in Hinkle (1989). Across the Cumberland Plateau, vegetation is intermediate between mixed mesophytic, mixed hardwood, and mixed *Pinus*-hardwood forest types (Hinkle, 1978, 1989; Smalley, 1982). The flat to rolling plateau uplands supported 12 community types that ranged from stands dominated by *Acer rubrum*, *Betula nigra* L., and *Ilex opaca* on floodplain terraces, stands dominated by *A. rubrum*, *Quercus alba*, and *Nyssa sylvatica* on poorly drained swales, and

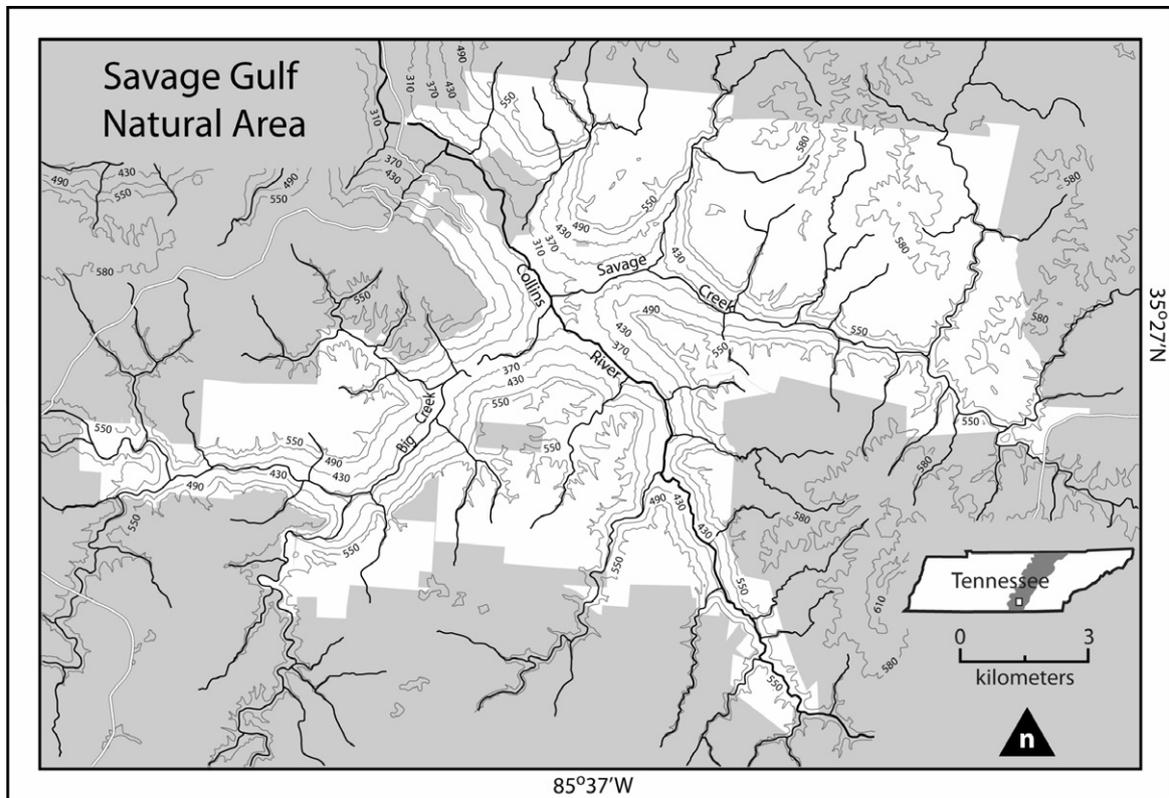


Fig. 1. Map of Savage Gulf Natural Area, Tennessee. Shaded portion on Tennessee inset map is the Cumberland Plateau physiographic section.

stands dominated by *Quercus marilandica* Munchh. and *Pinus virginiana* on xeric ridge tops (Hinkle, 1978, 1989). On upland sites of the Cumberland Plateau, species composition is largely controlled by topographic characteristics, factors related to soil water availability, and disturbance history (Hinkle, 1978; Smalley, 1982).

2.2. Field methods

To quantify biophysical conditions, we established 87 fixed-radius plots of 0.04 ha size throughout the 600 ha old-growth remnant on the Cumberland Plateau uplands of the SGNA. Prior to field data collection, plot locations were selected systematically using ArcGIS v. 9 in the old-growth stand. Plots were arranged in a grid pattern at 240 × 240 m spacing and coordinate pairs were downloaded as waypoints into GPS receivers so the plots could be located in the field. Plots that occurred within trails or streams were moved at least 25 m in one direction. The center of every plot was marked with a pre-numbered brass tag and stake and the base of the canopy tree nearest due north was blazed so the plots could be relocated for subsequent investigation. In each plot, we recorded species, crown class, and diameter at breast height (dbh, ca. 1.4 m above the root collar) of all stems ≥ 5 cm dbh to quantify species composition and stand structural characteristics. Crown class categories (dominant, codominant, intermediate, and overtopped) were based on the amount and direction of intercepted light following Oliver and Larson (1996). To document stand age, recruitment pulses, and canopy disturbance history we used increment borers to extract tree core samples from all trees ≥ 20 cm dbh and the four trees ≥ 5 cm, < 20 cm dbh nearest to plot center. We identified all snags to the lowest taxonomic level possible and recorded snag diameter and decay class using criteria adapted from Spetch et al. (1999) to quantify structural features, disturbance history, and woody debris decay patterns.

All live and dead stems ≥ 5 cm dbh, hereafter referred to as the overstory, in every plot were mapped to document the horizontal structure of the forest and to establish baseline data for repeat sampling. A sighting compass was used to determine the azimuth from plot center to each tree. We documented the distance from plot center to the tree using a digital hypsometer with 360° transponder. The regeneration layer was quantified using nested 0.004 ha circular plots located 7.2 m due north of plot center. In the 87 regeneration plots, we tallied all trees ≥ 1.4 m height, < 5 cm dbh, hereafter referred to as the understory, by species (with the exception of *Carya* and *Vaccinium* stems which were only classed to genus).

2.3. Quantitative and laboratory methods

Overstory and understory strata were analyzed using standard descriptors. For the overstory we calculated density (number of stems ha^{-1}), relative density (contribution to total trees), dominance (basal area (m^2) ha^{-1}), relative dominance (contribution to total basal area), and relative importance (average of relative density and relative dominance) of each species. For the understory we calculated density and relative density. For both layers we quantified species richness, species diversity (H'), and species evenness (J ; Ludwig and Reynolds, 1988).

In the laboratory, all 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 with cells vertically aligned, and sanded with progressively finer abrasives to reveal the cellular structure of the wood (Orvis and Grissino-Mayer, 2002). Once processed, tree rings on all cores were dated 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, had high relative frequency, and have been used successfully in other studies to document disturbance history in the eastern US (Hart and Grissino-Mayer, 2008; McCarthy and Bailey, 1996; Nowacki and Abrams, 1997; Rubino and McCarthy, 2004). Once all rings were visually dated, we measured raw-ring width to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software for all canopy *Quercus* series ($n = 200$). The measurement series were visually compared and statistically analyzed to ensure each growth ring was assigned to the proper calendar year of formation using the computer program COFECHA (Grissino-Mayer, 2001a; Holmes, 1983). Segments that fell below the predetermined significance threshold ($r = 0.32$, $P > 0.01$) were flagged by the program. All flagged segments were re-inspected for possible dating errors and dating was adjusted if necessary.

Once we were confident all canopy *Quercus* tree rings were dated to their exact calendar year of formation, we used dendroecological techniques to quantify the magnitude, frequency, and spatial extent of canopy disturbance events. The identification of release episodes in radial growth patterns of canopy trees is the primary technique in dendroecology to reconstruct canopy disturbance events (Abrams and Nowacki, 1992; Frelich, 2002; Fraver and White, 2005; Lorimer, 1980, 1985; Nowacki and Abrams, 1997). Commonly, release events are defined as changes in radial growth relative to a predetermined criterion and are identified using a percent growth change equation (Nowacki and Abrams, 1997; Rentch et al., 2002; Rubino and McCarthy, 2004). We analyzed changes in raw-ring widths with respect to the running mean 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 mean (Nowacki and Abrams, 1997), sustained for a minimum of 3 years (Hart and Grissino-Mayer, 2008; Hart et al., 2008). The duration criterion results in a relatively conservative estimate of canopy disturbance, but this technique has been widely used to quantify canopy disturbance history in the eastern US (e.g. Buchanan and Hart, 2011; Hart and Grissino-Mayer, 2008; Hart et al., 2008, 2010, 2011). This technique provides quantification of canopy disturbances that would be on the landscape for longer periods and thus be theoretically larger in size. We considered stand-wide disturbances as release episodes where a minimum of 25% of the individuals at least 10 years of age at that time experienced a contemporary release (Hart and Grissino-Mayer, 2008; Nowacki and Abrams, 1997; Rubino and McCarthy, 2004). The program FH2 was used to graphically display spatial and temporal patterns of release episodes (Grissino-Mayer, 1995, 2001b; Hart and Grissino-Mayer, 2008; Hart et al., 2008). The FH2 software displays release events at individual tree and forest levels, which allows for the investigation of disturbance events at multiple spatial scales.

To infer long-term canopy coverage patterns and to provide quantitative information on *Quercus* recruitment strategies, all *Quercus* trees with radial growth records beginning prior to 1850 were classified into two groups, gap or understory origin, according to early radial growth patterns (Rentch et al., 2003). Mean radial growth of years 1 through 20 was compared to mean radial growth of years 21 through 40 (McCarthy and Bailey, 1996). If the mean of the first 20 years exceeded the mean of the second 20-year window the tree was classed as establishing in a forest canopy gap. If mean growth of the first 20 years was below that of the second 20-year period the tree was classified as being of understory origin (Lorimer et al., 1988; McCarthy and Bailey, 1996). To confirm these quantitative classifications, we graphically analyzed the radial growth trends of each of these series. We then determined if and when the trees experienced growth releases identified by the 10-year running mean method. We combined the recruitment strategy classes with the detection of subsequent

release event(s) to assign all *Quercus* trees dating prior to 1850 to one of three establishment and accession strategy classes as established by Rentch et al. (2003): gap origin-no release, gap origin-gap release, or understory origin-gap release.

3. Results

3.1. Forest composition

The basal area of stems ≥ 5 cm dbh was $28.58 \text{ m}^2 \text{ ha}^{-1}$ and total density was $1168 \text{ trees ha}^{-1}$ (Table 1). Species richness of the overstory layer was 30, diversity (H') was 2.25, and evenness (J) was 0.66. The most important species (based on relative importance) were *A. rubrum*, *Oxydendrum arboreum*, and *Q. alba* (Table 1). These three species had similar relative importance values and represented a clear break from all other species. A distinct second tier of species importance included *Pinus echinata*, *Quercus coccinea*, and *Quercus velutina*. At the genus level, *Quercus* was the most important contributor to the tree community, with 67% relative importance.

The most dominant overstory layer species (based on basal area) was *Q. alba* with a basal area of $6.49 \text{ m}^2 \text{ ha}^{-1}$. *A. rubrum*, *P. echinata*, *O. arboreum*, *Q. coccinea*, and *Q. velutina* were the next most dominant species with basal areas ranging from $4.48 \text{ m}^2 \text{ ha}^{-1}$ for *A. rubrum* to $2.57 \text{ m}^2 \text{ ha}^{-1}$ for *Q. velutina*. Over 75% of tree biomass was represented in the five most dominant species alone. The mean dbh of *P. echinata* was 23 cm, of *Q. alba* was 16 cm, of *O. arboreum* was 12 cm, and of *A. rubrum* was 11 cm.

Acer rubrum and *O. arboreum* had the highest tree densities ($>305 \text{ trees ha}^{-1}$) and were nearly twice as abundant as any other species. These species were followed by *Q. alba* ($158 \text{ trees ha}^{-1}$) and *P. echinata* (71 trees ha^{-1}). Together these four species represented greater than 72% of all overstory layer trees. These species were followed by *N. sylvatica* and *Q. velutina* with over 51 and 39 individuals ha^{-1} , respectively. No other species had 30 trees ha^{-1} or represented over 3% of total stem density.

The understory layer contained $1514 \text{ stems ha}^{-1}$ (Table 2). Species richness was 21, nine lower than the overstory layer. Diversity was 2.37, similar to the value for the overstory, and evenness was 0.78, 0.12 higher than the overstory layer. The most abundant species in the understory stratum was *A. rubrum*, representing 33% of all stems. *Quercus alba* had 147 understory layer stems ha^{-1} or 10% of this stratum. *Quercus* species as a group comprised 15% of the understory layer and *Carya* species comprised 7%. We did not find any *Pinus* in the understory. We documented only one arboreal species in the regeneration layer that was absent from the overstory layer; *Magnolia accuminata*, representing less than three stems ha^{-1} . No woody alien species were documented in our overstory or understory plots.

When the relative contribution of species were grouped and analyzed by crown position a clear pattern emerged where *Quercus* and *Pinus* species were most abundant in canopy positions and *Acer* and "other" species were most abundant in subcanopy positions (Fig. 2). We documented 11 individuals ha^{-1} with canopy dominant positions and 185 trees ha^{-1} with codominant positions in the canopy. Seven species were represented in canopy dominant positions with *P. echinata* being the most common (represented 26% of all canopy dominants). At the genus-level, 54% of all canopy dominants were *Quercus*. No canopy dominant individuals were recorded outside of the genera *Pinus*, *Quercus*, and *Acer*. A total of 15 species occurred in canopy codominant positions. At the genus level, *Quercus* had the highest relative density of codominant trees followed by *Pinus*. The *Quercus* and *Pinus* genera combined represented 92% and 70% of all canopy dominants and codominants, respectively. A total of 103 trees ha^{-1} were classed as intermediate. The most common

Table 1

Density, dominance, and importance (average of relative density and relative dominance) measures for all live stems ≥ 5 cm dbh in an old-growth *Quercus* forest at Savage Gulf Natural Area, Tennessee.

| Species | Density (stems ha ⁻¹) | Relative density | Dominance (m ² ha ⁻¹) | Relative dominance | Relative importance |
|---|-----------------------------------|------------------|--|--------------------|---------------------|
| <i>Acer rubrum</i> L. | 306 | 26.22 | 4.48 | 15.67 | 41.90 |
| <i>Oxydendrum arboreum</i> (L.) DC. | 306 | 26.17 | 3.77 | 13.18 | 39.35 |
| <i>Quercus alba</i> L. | 158 | 13.55 | 6.49 | 22.71 | 36.26 |
| <i>Pinus echinata</i> Mill. | 71 | 6.10 | 3.89 | 13.59 | 19.69 |
| <i>Quercus coccinea</i> Muenchh. | 28 | 2.44 | 2.96 | 10.34 | 12.78 |
| <i>Quercus velutina</i> Lam. | 39 | 3.35 | 2.57 | 8.99 | 12.33 |
| <i>Nyssa sylvatica</i> Marsh. | 51 | 4.40 | 0.55 | 1.92 | 6.32 |
| <i>Pinus virginiana</i> Mill. | 24 | 2.02 | 0.90 | 3.14 | 5.15 |
| <i>Quercus prinus</i> L. | 18 | 1.50 | 1.02 | 3.58 | 5.08 |
| <i>Carya alba</i> (L.) Nutt. | 28 | 2.41 | 0.60 | 2.09 | 4.50 |
| <i>Cornus florida</i> L. | 29 | 2.51 | 0.14 | 0.48 | 2.99 |
| <i>Sassafras albidum</i> (Nutt.) Nees | 24 | 2.09 | 0.22 | 0.76 | 2.86 |
| <i>Carya glabra</i> (P. Mill.) Sweet | 8 | 0.69 | 0.32 | 1.13 | 1.81 |
| <i>Hamamelis virginiana</i> L. | 16 | 1.40 | 0.05 | 0.19 | 1.59 |
| <i>Kalmia latifolia</i> L. | 14 | 1.23 | 0.04 | 0.14 | 1.37 |
| <i>Quercus stellata</i> Wangenh. | 3 | 0.30 | 0.22 | 0.75 | 1.05 |
| <i>Crataegus phaenopyrum</i> (L. f.) Medik. | 10 | 0.84 | 0.06 | 0.20 | 1.04 |
| <i>Ilex opaca</i> Aiton | 10 | 0.84 | 0.05 | 0.18 | 1.02 |
| <i>Liquidambar styraciflua</i> L. | 7 | 0.62 | 0.05 | 0.18 | 0.80 |
| <i>Tsuga canadensis</i> (L.) Carr. | 5 | 0.44 | 0.06 | 0.21 | 0.65 |
| <i>Liriodendron tulipifera</i> L. | 2 | 0.15 | 0.11 | 0.40 | 0.55 |
| <i>Ostrya virginiana</i> (P. Mill.) K. Koch | 4 | 0.34 | 0.01 | 0.05 | 0.39 |
| <i>Quercus falcata</i> Michx. | 1 | 0.10 | 0.01 | 0.04 | 0.14 |
| <i>Fagus grandifolia</i> Ehrh. | 1 | 0.07 | 0.01 | 0.03 | 0.10 |
| <i>Castanea dentata</i> (Marsh.) Borkh. | 1 | 0.05 | 0.00 | 0.01 | 0.06 |
| <i>Rhododendron maximum</i> L. | 1 | 0.05 | 0.00 | 0.01 | 0.06 |
| <i>Alnus serrulata</i> (Aiton) Willd. | 1 | 0.05 | 0.00 | 0.01 | 0.05 |
| <i>Prunus serotina</i> Ehrh. | 0 | 0.02 | 0.00 | 0.00 | 0.03 |
| <i>Ulmus rubra</i> Muhl. | 0 | 0.02 | 0.00 | 0.00 | 0.03 |
| <i>Amelanchier arborea</i> (Michx. f.) F. | 0 | 0.02 | 0.00 | 0.00 | 0.03 |
| Total | 1168 | 100.00 | 28.58 | 100.00 | 200 |

Table 2

Density measures for all live stems ≥ 1.4 m height, < 5 cm dbh in an old-growth *Quercus* forest at Savage Gulf Natural Area, Tennessee.

| Species | Density (stems ha ⁻¹) | Relative density (%) |
|-----------------------------------|-----------------------------------|----------------------|
| <i>Acer rubrum</i> | 497 | 32.83 |
| <i>Quercus alba</i> | 147 | 9.68 |
| <i>Vaccinium</i> spp. | 118 | 7.78 |
| <i>Ilex opaca</i> | 112 | 7.40 |
| <i>Carya</i> spp. | 101 | 6.64 |
| <i>Cornus florida</i> | 98 | 6.45 |
| <i>Kalmia latifolia</i> | 78 | 5.12 |
| <i>Oxydendrum arboreum</i> | 78 | 5.12 |
| <i>Quercus velutina</i> | 75 | 4.93 |
| <i>Liquidambar styraciflua</i> | 57 | 3.80 |
| <i>Hamamelis virginiana</i> | 34 | 2.28 |
| <i>Nyssa sylvatica</i> | 29 | 1.90 |
| <i>Fagus grandifolia</i> | 20 | 1.33 |
| <i>Rhododendron maximum</i> | 20 | 1.33 |
| <i>Amelanchier arborea</i> | 14 | 0.95 |
| <i>Crataegus phaenopyrum</i> | 9 | 0.57 |
| <i>Ostrya virginiana</i> | 9 | 0.57 |
| <i>Quercus coccinea</i> | 6 | 0.38 |
| <i>Quercus prinus</i> | 6 | 0.38 |
| <i>Sassafras albidum</i> | 6 | 0.38 |
| <i>Magnolia acuminata</i> (L.) L. | 3 | 0.19 |
| Total | 1514 | 100.00 |

species with intermediate positions were *O. arboreum* and *A. rubrum*, which represented 36% and 32% of all intermediate trees respectively. The largest category was the overtopped classification with 869 individuals ha⁻¹. All 30 tree species documented in the old-growth remnant occurred in overtopped positions with *O. arboreum* (29%) and *A. rubrum* (27%) being the most common. The *Quercus* and *Pinus* genera combined represented 20% and 25% of overtopped and intermediate trees, respectively.

The crown class distribution for *Pinus* species revealed that the majority of these individuals had codominant positions in the main forest canopy ($n = 57$ ha⁻¹). The second highest value for *Pinus* was recorded for the overtopped classification and only five *Pinus* trees ha⁻¹ had intermediate crown positions. The crown distribution for *Quercus* species was bimodal as well, with 149 trees ha⁻¹ in overtopped positions and 72 trees ha⁻¹ in codominant positions. In total, we documented 80 canopy *Quercus* stems ha⁻¹ which was the highest value of any group. The majority of *A. rubrum* individuals were overtopped. Approximately the same number of *A. rubrum* stems occurred in intermediate and codominant positions (33 and 36 ha⁻¹, respectively). *Acer rubrum* had one canopy dominant individual ha⁻¹. The “others” group revealed an inverse J-shape distribution with 454 individuals ha⁻¹ in overtopped positions.

3.2. Diameter and age structure

The diameter structure of all trees in the forest revealed a reverse J-shaped distribution from small size classes to large size classes (Fig. 3). When species were grouped into four categories (*Pinus*, *Quercus*, *A. rubrum*, and others) recruitment and regeneration patterns were apparent. Individuals from each species group were present in the smallest size class. *Pinus* was the only group that had a unimodal distribution, with an apex in the 15–20 cm dbh class. *Pinus* was represented in all but three of the largest size classes. The *Quercus*, *A. rubrum*, and “others” groups all exhibited steady declines in stem density with increased size, indicative of a reverse J-shaped distribution. Notably, *Quercus* had a uniform distribution from the 25–30 cm to the ≥ 65 cm dbh classes. *Acer rubrum* was sparse in the medium to large size classes and was totally absent from the largest size categories. Species listed as “other” were the most abundant in the smallest size classes and were only absent from the largest category.

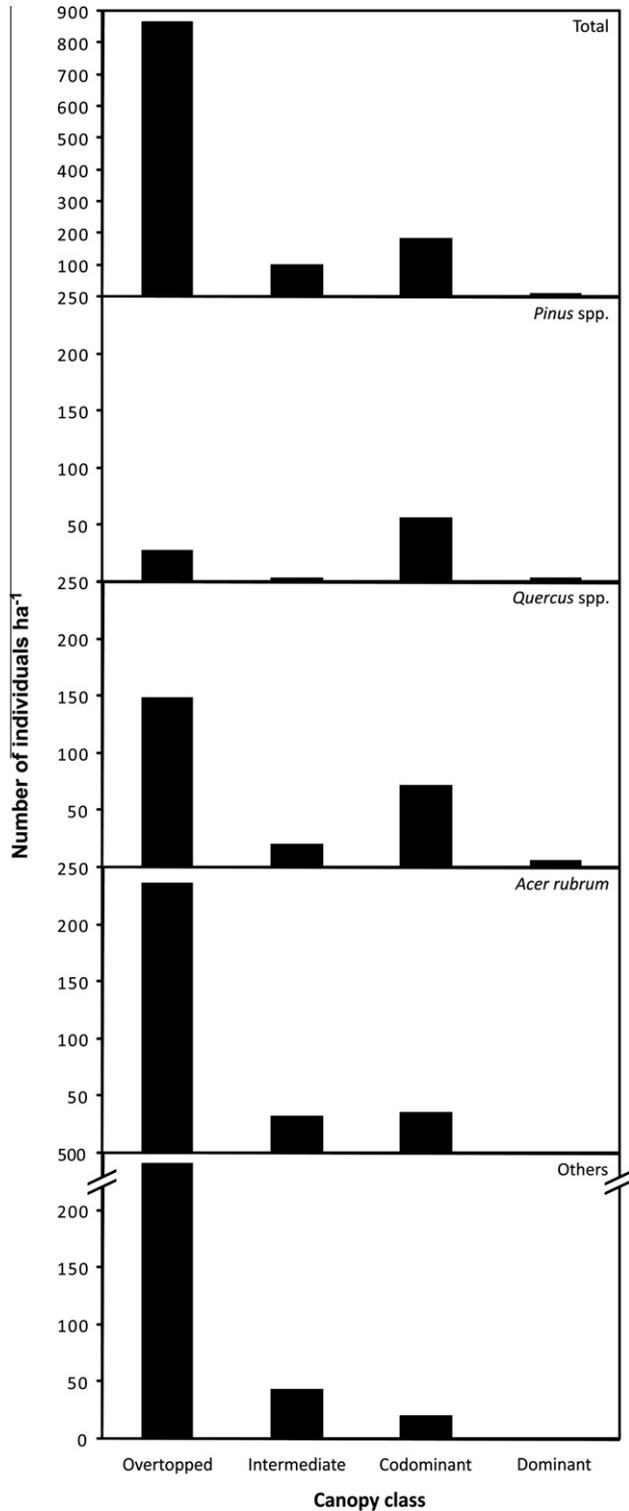


Fig. 2. Crown class distributions per hectare by group. Crown class categories are based on the amount and direction of intercepted light (Oliver and Larson, 1996). Note broken scale for “others” group. For a list of species included in the “others” group see Table 1.

The age-diameter distributions revealed that size was a relatively poor predictor of age (Fig. 4). We documented a total of 16 trees ≥ 65 cm dbh on our study plots (5 ha^{-1}), all of which were *Quercus* (Table 3). The largest individual documented was a *Q. prinus* at 81 cm dbh and it was 269 years old. The 18 largest trees were *Quercus* individuals and they ranged from 269 to

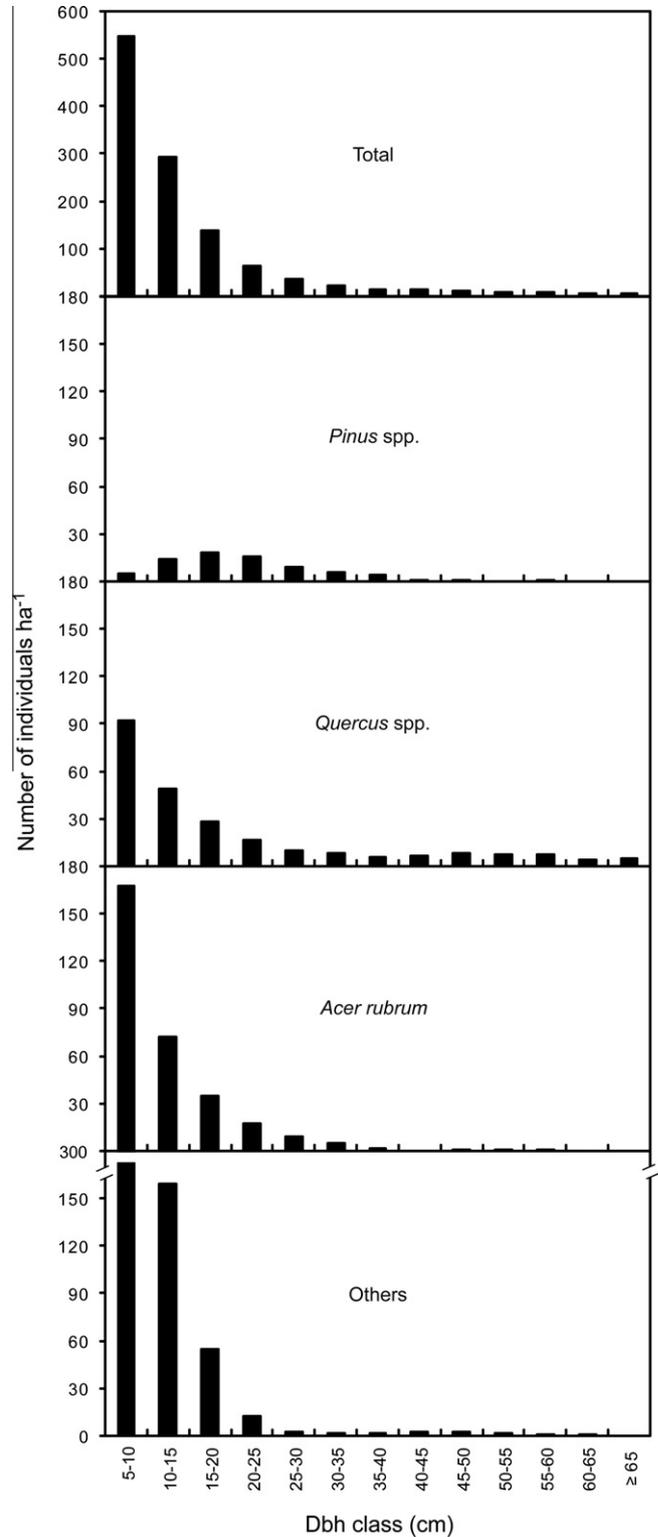


Fig. 3. Number of trees (≥ 5 cm dbh) per hectare for all species, divided into four groups in an old-growth *Quercus* forest at Savage Gulf Natural Area, Tennessee. For a list of species in the “others” group see Table 1.

50 years of age. In fact, 31 of the 34 trees ≥ 60 cm dbh we documented were *Quercus*. The largest non-*Quercus* was a *P. echinata* at 64 cm dbh and 286 years old. The largest *A. rubrum* was 56 cm dbh and 130 years old. Although trees ≥ 65 cm dbh represented less than 1% of all trees ha^{-1} , individuals of this size comprised 7% of total basal area ha^{-1} (Table 3).

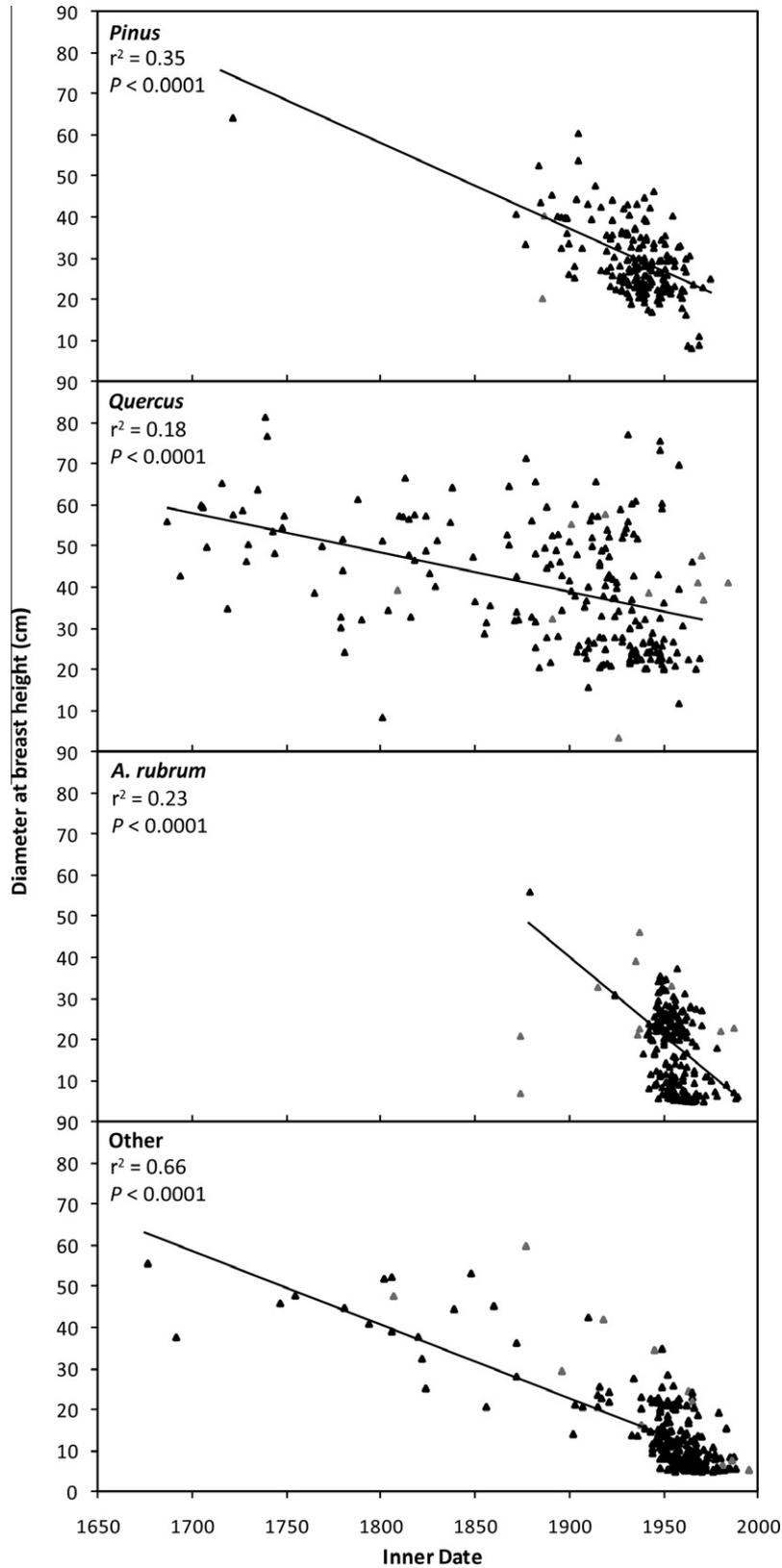


Fig. 4. Diameter–age relationships for all cored trees in our sample plots at Savage Gulf Natural Area, Tennessee. Gray triangles are minimum dates only as the trees contained rot and rings near the pith could not be dated. These series were not included in statistical analyses.

The oldest tree we documented was a *N. sylvatica* with an inner date at breast height of 1677 and a dbh of 56 cm (Fig. 4). Two other *N. sylvatica* established in the mid-1700s and these represented the third and fourth oldest trees documented from the “others”

category. The second oldest tree that established was a *Q. alba* with an inner date of 1687 and a dbh of 56 cm. Prior to 1700 we also recorded a *Carya alba* and a *Q. alba*. *Quercus* recruitment was continuous from 1700 through the 1950s. A total of 27 *Quercus*

Table 3

Density (stems ha^{-1} and percent (%) of total stems ha^{-1}) and basal area ($\text{m}^2 \text{ha}^{-1}$ and percent (%) of total basal area ha^{-1}) by diameter at breast height (cm) class in an old-growth *Quercus* forest at Savage Gulf Natural Area, Tennessee.

| DBH (cm) | Density | | Basal area | |
|-----------|------------------------|------------------|-----------------------------|------------------|
| | Stems ha^{-1} | Percent of total | Basal area ha^{-1} | Percent of total |
| ≥ 5 | 1168 | 100 | 28.6 | 100 |
| ≥ 10 | 620 | 53 | 26.0 | 91 |
| ≥ 20 | 189 | 16 | 19.4 | 68 |
| ≥ 65 | 5 | <1 | 1.9 | 7 |

established prior to 1800. Of these, 89% were *Q. alba*. A pulse of *Quercus* recruitment occurred from 1910 to 1940. Composition of this younger *Quercus* age class was not dominated by a single *Quercus* species. The oldest *Pinus* individual was a *P. echinata* with

Table 4

Density (stems ha^{-1}), relative density (%), basal area ($\text{m}^2 \text{ha}^{-1}$), and relative basal area (%) to the lowest taxonomic level identified for snags in an old-growth *Quercus* forest at Savage Gulf Natural Area, Tennessee.

| Species | Density (stems ha^{-1}) | Relative density | Basal area ($\text{m}^2 \text{ha}^{-1}$) | Relative basal area |
|--------------------------------|-----------------------------------|------------------|--|---------------------|
| <i>Acer rubrum</i> | 10 | 7.74 | 0.08 | 3.23 |
| <i>Carya unidentifed</i> | 1 | 0.44 | 0.00 | 0.08 |
| <i>Carya glabra</i> | 0 | 0.22 | 0.01 | 0.24 |
| <i>Carya alba</i> | 0 | 0.22 | 0.00 | 0.03 |
| <i>Cornus florida</i> | 10 | 7.52 | 0.05 | 1.92 |
| <i>Crataegus phaenopyrum</i> | 1 | 0.66 | 0.00 | 0.13 |
| <i>Hamamelis virginiana</i> | 0 | 0.22 | 0.00 | 0.09 |
| <i>Liriodendron tulipifera</i> | 0 | 0.22 | 0.08 | 3.15 |
| <i>Nyssa sylvatica</i> | 3 | 2.43 | 0.08 | 3.29 |
| <i>Ostrya virginiana</i> | 0 | 0.22 | 0.00 | 0.03 |
| <i>Oxydendrum arboreum</i> | 22 | 17.26 | 0.22 | 9.14 |
| <i>Pinus unidentifed</i> | 2 | 1.33 | 0.04 | 1.62 |
| <i>Pinus echinata</i> | 16 | 11.95 | 0.41 | 16.74 |
| <i>Pinus virginiana</i> | 5 | 3.54 | 0.07 | 2.76 |
| <i>Quercus unidentifed</i> | 9 | 6.64 | 0.55 | 22.63 |
| <i>Quercus alba</i> | 26 | 19.91 | 0.33 | 13.47 |
| <i>Quercus coccinea</i> | 5 | 3.98 | 0.24 | 9.67 |
| <i>Quercus prinus</i> | 2 | 1.55 | 0.02 | 0.69 |
| <i>Quercus velutina</i> | 4 | 3.10 | 0.17 | 6.79 |
| <i>Sassafras albidum</i> | 1 | 0.88 | 0.00 | 0.12 |
| <i>Tsuga canadensis</i> | 0 | 0.22 | 0.00 | 0.06 |
| Unidentifed | 13 | 9.73 | 0.10 | 4.12 |
| Total | 130 | 100.00 | 2.44 | 100.00 |

an inner date at breast height of 1722. No *Pinus* individuals were documented with inner dates between 1722 and 1872. After this period, moderate *Pinus* recruitment occurred from the 1870s until a major recruitment pulse began in the 1910s that lasted through the 1940s. The oldest *A. rubrum* had an inner date at breast height of 1878 (with a dbh of 56 cm) and two other *A. rubrum* established prior to 1900 but decay prevented us from establishing a pith date. *Acer rubrum* exhibited a prominent recruitment pulse from the 1940s until the 1960s. Within the “others” group, recruitment from the late-1700s through the late-1800s was dominated by *Carya* species (92% of such trees). A recruitment pulse within this category began in the 1940s and was largely comprised of *O. arboreum*. In fact, 88% of trees in the “other” class that established from 1940 to 1960 were *O. arboreum*.

3.3. Snag characteristics

We recorded 130 snags ≥ 5 cm dbh ha^{-1} across the study site. These snags represented 18 different species (Table 4). In total, we were able to identify 81% of all snags to the species level and 90% to the genus level. The majority (73%) of snags only identified to the genus were *Quercus*. *Q. alba*, *O. arboreum*, and *P. echinata* had the highest relative snag densities (Table 4). Combined these species represented 49% of all snags. At the species level, *P. echinata* and *Q. alba* represented the most snag basal area, and *Quercus* comprised over 46% of snag basal area. Mean snag dbh was $12 \text{ cm} \pm 0.5$ (SE) with a maximum of 74 cm for a *Quercus* individual. The basal area of snags was $2.44 \text{ m}^2 \text{ha}^{-1}$. Snags were most abundant in the smallest dbh class and frequency generally decreased with increased size, indicative of a reverse J-shaped distribution (Fig. 5). Decay class 4 had the highest density of snags and decay class 1 had the lowest snag density (Fig. 6). A similar pattern was found for the basal area of snags across decay classes, with class 4 having the greatest value and class 1 having the lowest. The advanced decay classes had a higher number of snags and more biomass relative to the less decayed classes.

3.4. Dendroecology

From the 200 overstory *Quercus* individuals analyzed using the 10-year running mean method, 146 (73%) exhibited at least one release event. A total of 295 release events were detected from the 146 individuals with 74 (51%) trees experiencing multiple releases (Fig. 7). Of the 295 detected release events, 237 (80%) were minor and 58 (20%) were major. The longest sustained release was

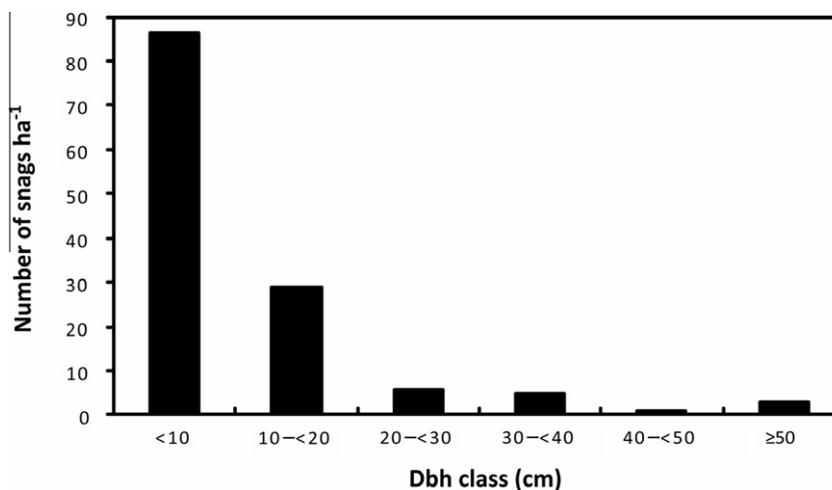


Fig. 5. Number of snags (≥ 5 cm dbh) per hectare by diameter class interval in an old-growth *Quercus* forest at Savage Gulf Natural Area, Tennessee.

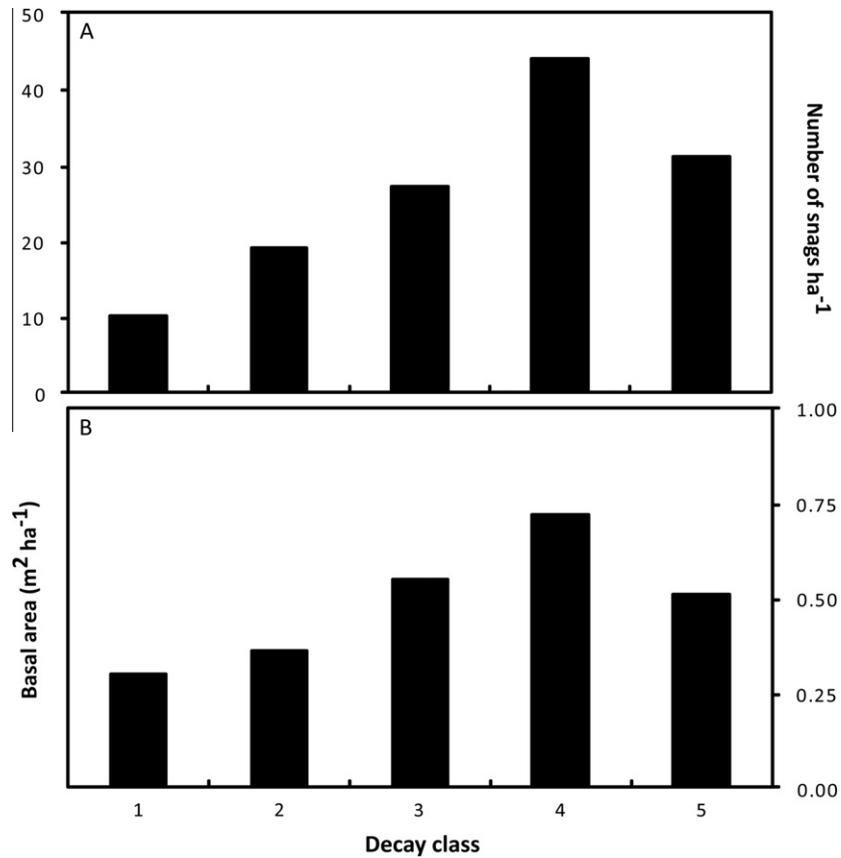


Fig. 6. (A) Number of snags ha⁻¹ by decay class and (B) basal area (m² ha⁻¹) of snags by decay class in an old-growth *Quercus* forest at Savage Gulf Natural Area, Tennessee. Decay class 1 is the least decayed and 5 is the most decayed.

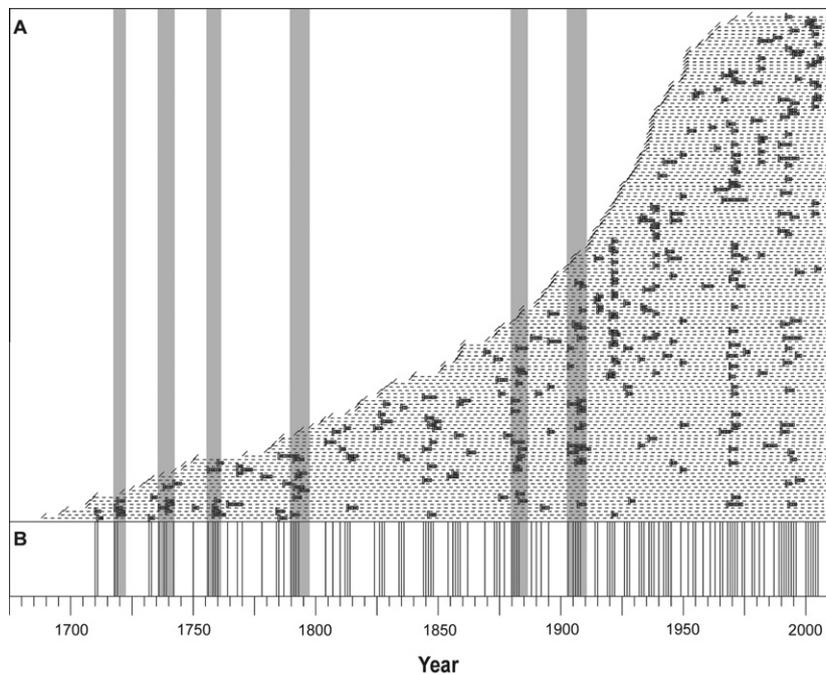


Fig. 7. Detected release events using the 10-year running mean method for 146 overstory *Quercus* individuals sampled at Savage Gulf Natural Area, Tennessee. Each dashed horizontal line represents the record from one individual tree, vertical bars indicate release events, and solid horizontal lines indicate release duration. A composite of release events for the study site is shown across the bottom.

11 years observed in a *Q. coccinea* from 1966 to 1976. Notably, this event was classified as a major release. The mean release duration

was 4.0 years ± 0.1. The longest period between release initiation events was 13 years (occurring from 1719 to 1732). In many

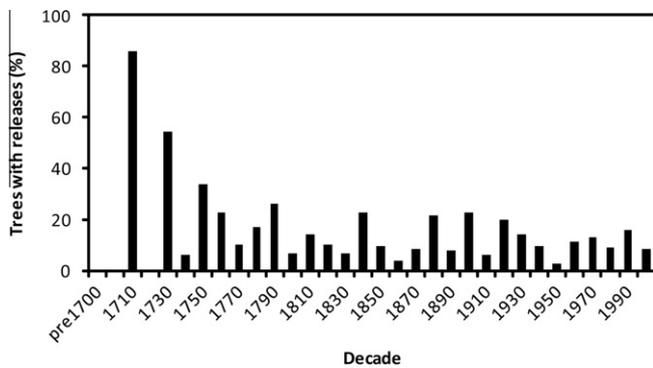


Fig. 8. Release to sample depth ratio (%) by decade. Releases were identified using the 10-year running mean method and sample depth is the number of trees at least 10 years of age at that time.

instances release initiations occurred in consecutive years; the longest period of consecutive initiations was 8 years from 1968 to 1975. The mean release initiation return interval was 2.4 years \pm 1.4.

We documented six stand-wide disturbances during the ca. three centuries of record (Fig. 7). These episodes occurred from 1718 to 1722 (67% of all living trees at least 10 years of age), 1736 to 1742 (56%), 1756 to 1763 (38%), 1790 to 1797 (35%), 1880 to 1886 (25%), and 1903 to 1912 (27%). Additionally, three episodes fell just below the 25% threshold: 1844–1851 (23%), 1919–1924 (22%), and 1968–1975 (17%). The stand-wide disturbance return interval was 50 years. However, the last stand-wide disturbance occurred in 1903 and the return interval prior to this last disturbance was ca. 33 years.

For all overstory *Quercus* that established prior to 1850 ($n = 46$), one individual established in a gap and reached the canopy without a subsequent release (i.e. reached a canopy position before the gap closed). Twenty-nine individuals (63%) established in a gap and subsequently released following additional canopy disturbance. Sixteen individuals (35%) established under a closed canopy, were suppressed for a period, and were eventually released from overstory competition. Of the 16 *Quercus* individuals that established in the understory of a closed canopy, the mean period of suppression was 31.6 years \pm 4.8. The longest understory residence time prior to overstory release was 80 years observed in a *Q. velutina*.

The highest decadal release to sample size ratio value occurred in the 1710s when 86% of the trees at least 10 years of age exhibited a growth release (Fig. 8). The second highest value was 54% and occurred in the 1730s. From the late-1700s to the end of the record, decadal release to sample size percentages exhibited an oscillating pattern with peak values lower than those in the earliest portion of the record. The six notable peaks in these values occurred in the 1790s, 1840s, 1880s, 1900s, 1920s and 1990s had a mean 21%. The average value of releases to sample size post European settlement (ca. 1870) was 12% compared to the pre-settlement value of 19%.

4. Discussion

4.1. Species composition and stand structure

The tablelands of the Cumberland Plateau have traditionally been viewed as low quality sites with low biodiversity. However, species richness on the tablelands of the SGNA was relatively high, even when compared to productive, high quality sites in the southern Appalachian Highlands (e.g. Hart and Grissino-Mayer, 2008: $S = 30$, $H' = 2.57$; Hart et al., 2008: $S = 30$, $H' = 2.97$).

Microenvironmental conditions, especially those created by streams flowing across the surface, likely increased heterogeneity and thus biodiversity on this site. We also postulate that the topographic character and elevation of the study area allow the site to support species that typically occur at higher and lower latitudes. We documented the crowns of *Tsuga canadensis* individuals occurring immediately adjacent to the crowns of *P. echinata* individuals. Almost pure stands of *T. canadensis* are known to occur within the gorge of the SGNA but we noted a high density of the species in riparian zones on the tableland surface of the Cumberland Plateau on what were otherwise xeric sites. Additionally, species such as *Kalmia latifolia* and *Rhododendron maximum* occurred in these tableland riparian zones. Species diversity and evenness were lowered by the overwhelming abundance of *A. rubrum* and *O. arborescens*. We speculate the absence of alien species in overstory and understory strata was a function of reserve isolation from human settlements.

The forest on the tablelands of the SGNA was dense, diverse in structure and species composition, and dominated by old (>200 years) *Quercus* trees. The SGNA had some characteristics typical of old-growth forests (e.g. abundance of old trees and snags), but also had some parameters characteristic of younger stands (e.g. relatively high stem density). Although the basal area documented on the SGNA ($26 \text{ m}^2 \text{ ha}^{-1}$) was within the range of what has been reported for other old-growth remnants in the region, stem density was much higher ($620 \text{ stems} \geq 10 \text{ cm dbh ha}^{-1}$). In dry or xeric *Quercus* forests throughout the eastern United States, density of stems $\geq 10 \text{ cm dbh}$ in old-growth stands typically ranges from 280 to 443 ha^{-1} (Tyrrell et al., 1998). Thus, the old-growth remnant at SGNA supported a high number of relatively small stems compared to other old-growth stands in the region. In fact, the mean diameter of canopy trees was only 33 cm at breast height. Hart and Grissino-Mayer (2009) found mean canopy tree diameter to be 39 cm in an 80-year old *Quercus* stand on the Cumberland Plateau. Furthermore, Martin (1992) reported that old-growth stands on the Cumberland Plateau typically have seven trees greater than 75 cm dbh ha^{-1} . At the SGNA the density of stems $\geq 75 \text{ cm dbh ha}^{-1}$ was one. We speculate the low frequency of large trees and the high density of smaller stems was attributed to relatively lower site quality in this stand compared to other published reports of old-growth forests on higher quality sites in the region.

Indeed, old-growth stands on xeric sites often have fewer large trees and higher stem densities compared to old-growth stands on mesic sites (Fralish et al., 1991; Martin, 1992). Sites on the Cumberland Plateau tablelands are often described as xeric attributed to low availability of soil water (Smalley, 1982) because of coarse soil texture, shallow depth to bedrock, and surface stone cover. These characteristics have a strong influence on forest composition, growth, and development (Hart and Kupfer, 2011; Hinkle, 1989). Furthermore, canopy trees on the tablelands of the Cumberland Plateau are more susceptible to windthrow relative to protected, mesic sites where the majority of old-growth stands in the region exist (Martin, 1992; Smalley, 1982). Thus, the few large trees present on these sites may have a higher probability of being removed by strong wind events compared to large individuals in cove sites.

Old-growth stands are often characterized by an abundance of coarse woody debris including snags (Martin, 1992; Tyrrell et al., 1998). McComb and Muller (1983) documented 43 snags $\geq 10 \text{ cm dbh ha}^{-1}$ in an old-growth forest and Martin (1992) suggested that old-growth forests typically have ca. 10 snags $\geq 30 \text{ cm dbh ha}^{-1}$. We documented similar snag densities with 43 ha^{-1} for trees $\geq 10 \text{ cm dbh}$ and 9 ha^{-1} for trees $\geq 30 \text{ cm dbh}$. We found it interesting that snag density was not higher because: (1) stem density at the SGNA was higher than other sites and (2) drier sites

like the SGNA typically have a higher abundance of snags relative to more mesic sites (McComb and Muller, 1983). We contend this pattern was attributed to the exposed nature of the tablelands (i.e. trees and snags were more exposed to high wind events). It is possible that snag formation was more frequent on the exposed site but snags did not remain on the landscape for a long period before becoming downed debris that we did not measure. Most snags were relatively small (mean dbh = 12 cm) and would be short-lived. *Quercus* was the most dominant snag genus, likely attributed to rot resistance of *Quercus* and because the genus had the highest importance values. *Quercus* mortality was within the typical range of variability and can be attributed to natural senescence. *Pinus echinata* had a higher snag density than expected given its relative density in the overstory. We speculate that most of these individuals were killed by *Dendroctonus frontalis* Zimmermann during an outbreak from 1999 to 2001.

Old-growth forests may be more likely to have stronger age–diameter relationships compared to younger stands (Lorimer, 1980; Morey, 1936; Tyrrell and Crow, 1994). As a stand reaches the old-growth stage (c.f. Oliver and Larson, 1996), the dominant species should have multiple age classes because of disturbances that create gaps and allow irregular and continuous recruitment of even-aged cohorts of similar sizes into the canopy (Tyrrell and Crow, 1994). *Quercus* may have a relatively weak age–diameter relationship, as we found, because of the inability to tolerate shade and recruit trees to intermediate classes. The age–size relationship for *Quercus* on this site may have also been weakened by selective harvesting that likely occurred over the past 140 years. Selective logging in this region was targeted towards larger trees and likely left smaller trees of a similar age. Additionally, our sampling over a large area with much fine-scale heterogeneity may have influenced the age–diameter relationship. Productive microsites within the study area would support relatively large trees, while lower productivity microsites would support relatively small trees of similar age. Our results show that across a relatively large study area with some selective harvesting, the use of diameter distributions to infer population structure of species that are not shade tolerant may be misleading (Lorimer, 1985; Morey, 1936).

4.2. Dendroecology

Of all radial growth release events ($n = 295$), 81% were localized (i.e. not stand-wide events). The majority of release events were not detected in 25% or more of the trees living at that time, indicating releases resulted from gap-scale canopy disturbances that involved the death of a single or small cluster of canopy trees and only influenced microenvironmental conditions (Black and Abrams, 2005; Nowacki and Abrams, 1997; Rubino and McCarthy, 2004; Runkle, 1982). Recent studies have shown that the analysis of a single tree-ring series per individual, as done in this study, may result in an underrepresentation of radial growth release events (Buchanan and Hart, 2011; Copenheaver et al., 2009). To ascertain a more accurate frequency of disturbance events, we applied the release frequency factor of 1.72 (Buchanan and Hart, 2011) to the documented release frequency and determined that we would have identified ca. 572 release events if two increment cores had been extracted and analyzed from each canopy *Quercus* individual.

We documented six stand-wide disturbance events during the last three centuries. These episodes occurred in the 1710s, 1730s, 1750s, 1790s, 1880s, and 1900s. Such synchronous release events indicate exogenous disturbances such as high wind events, ice storms, or selective timber harvesting that would remove canopy trees over a large area. Although we can only speculate as to the drivers of these stand-wide disturbance episodes, it is clear that the frequency of such events has decreased over the last two centuries. Indeed, it has been more than 100 years since the last

stand-wide release episode (although some events during the 20th century did approach the 25% threshold used to identify such disturbances). A decline in stand-wide disturbances after European settlement has been documented in other dendroecological studies of old-growth *Quercus* stands (Nowacki and Abrams, 1997). The pre-European interval (prior to 1870) documented here (ca. 42 years) was similar to what has been reported elsewhere. However, the post-European settlement return interval of stand-wide disturbances far exceeded the intervals documented in other studies (e.g. Nowacki and Abrams, 1997: return interval = 31 years; Ruffner and Abrams, 1998: return interval = 31 years). Interestingly, other dendroecological studies of forest disturbance history in this region have noted a paucity or lack of stand-wide episodes during the 20th century. For example, Hart and Grissino-Mayer (2008) and Hart et al. (2008) documented a single stand-wide disturbance event during the 20th century in *Quercus* stands on the Cumberland Plateau and adjacent Ridge and Valley, respectively. In addition, Hart et al. (2011) found no such disturbances in *Quercus* stands on the adjacent Interior Low Plateau. Therefore, we speculate this pattern may represent a regional phenomenon related to physical and cultural dynamics (e.g. changes in climate, land use, and wildlife populations).

The majority (63%) of all *Quercus* that dated prior to 1850 established in gap environments and subsequently released following canopy disturbance. Thus, most *Quercus* recruited via gap-phase regeneration. We note that some releases coincided with single or small multi-tree fall gaps, but others certainly corresponded with stand-wide disturbance events illustrating that all canopy disturbances, whether they are associated with localized canopy gaps or broader scale canopy removal are important in stand development. Approximately one-third of *Quercus* trees that dated prior to 1850 established in the understory of a closed canopy and were suppressed for a period prior to overstory release. Notable was the suppression periods for these trees. The mean suppression period for trees that established in the understory of a closed canopy was 32 years and one *Q. velutina* individual was suppressed for 80 years prior to release. The understory residence times reported here were within the range of those documented by Rentch et al. (2003) and illustrate the understory tolerance of *Quercus* in the absence of competition from more shade-tolerant taxa. Notably, the understory residence times of *Quercus* reported here were shorter than those documented by Orwig and Abrams (1994) for the more shade-tolerant *N. sylvatica* (suppression periods ranging from 43 to 66 years) and longer than those for the shade-intolerant *Liriodendron tulipifera* (2–11 years). Also of note, the second oldest *Quercus* in our dataset (inner date at breast height of 1694) established in the understory of a closed canopy indicating at least portions of the site have had continuous forest cover since at least the late 17th century.

The decadal analysis of the percentage of trees that exhibited a release highlighted the disturbance events of the 1710s and 1730s when 67% and 56% of all *Quercus* trees at least 10 years of age at that time exhibited radial growth releases, respectively. Based on the extent of these early release events, we suggest they may have resulted from incomplete stand-scale disturbances whereas the other stand-wide release events were likely the result of high frequency, stochastic gap-scale disturbances.

4.3. Development and succession

The oldest trees we documented on the SGNA old-growth remnant established in the late-1600s. The site had at least some canopy cover at this time based on the radial growth patterns of older *Quercus* individuals (i.e. establishment in the understory of a closed canopy). Canopy disturbance history analyses revealed two potential incomplete stand-scale disturbance events in the

early 1700s. *Quercus* recruitment was continuous on the site since the late-1600s. Most *Quercus* individuals that established prior to 1850 recruited via gap-phase regeneration, but ca. one-third of such trees established in the understory of a closed canopy and were suppressed for a period prior to overstory release.

Only one *Pinus* individual on our study plots established prior to 1850, in 1722 coincident with a stand-wide release. The increase of *Pinus* recruitment in the late-1800s that lasted through the 1940s largely coincided with stand-wide canopy disturbance events. Although few old *Pinus* trees were recorded on our study plots, *P. echinata* was capable of attaining more than 280 years of age on the site. A narrow-gauge rail system was established through portions of the SGNA in the early 1900s for the main purpose of logging for large *Pinus* trees (B. Werner, personal communication). Selective logging at the turn of the century, particularly for railroad ties, likely contributed to the demise of the older age classes of this species except in remote areas of the SGNA.

The major onset of *Acer* establishment began in the 1940s. Only three *Acer* individuals established prior to 1900. Unlike the *Pinus* establishment pulses, *Acer* establishment did not correspond to stand-wide disturbance events. Although some of these *Acer* trees certainly established in canopy gaps, many established under a closed canopy. *Acer* is shade-tolerant and can withstand long periods of suppression before overstory release (Canham, 1985).

We speculate that over the last three centuries the stand has been dominated by *Quercus* with patches of *Pinus* that established in canopy gaps. Over the last 70 years *Acer* became abundant in the understory. Age and diameter structure indicate a shift in species composition away from *Quercus* and towards an *A. rubrum* dominated stand. This same species shift has been widely reported throughout the Central Hardwood Forest of North America (Abrams, 1998; McEwan et al., 2011; Nowacki and Abrams, 2008). Canopy trees greater than 120 years of age were almost completely comprised of *Quercus* and *Pinus* species whereas younger trees and the regeneration layer received small contributions from these genera and large contributions from *A. rubrum* and the “other” class (e.g. *O. arboreum*, *N. sylvatica*, *Cornus florida*, *Sassafras albidum*). We contend the lack of older cohorts of *A. rubrum* and some of the species in the “other” class (e.g. *N. sylvatica*) is not attributed to short longevity of these species. In fact, *N. sylvatica* is capable of attaining old ages (300–600 years) as seen in this study and others (Abrams, 2007; Abrams and Orwig, 1996). Although the maximum age of *A. rubrum* has typically been reported to be less than 150 years in eastern old-growth stands (Abrams and Downs, 1990; Abrams and Orwig, 1996; Lorimer, 1980), the species has been shown to reach 300 years of age (Pederson et al., 2007).

A major question in the development of this stand is what factor or factors changed over the last century that allowed for the profusion of *A. rubrum*. The most often cited explanation for the *Quercus* to *Acer* transition has been changes in fire regimes, specifically active fire suppression that began in the early 20th century. *Quercus* are considered tolerant of fire as they typically have thick bark, the ability to stump sprout, and resist rot after scarring (Abrams, 1992; Smith and Sutherland, 1999). In contrast, *Acer* are thin barked and shallow rooted and thus sensitive to fire. It is widely hypothesized that historic surface fire maintained *Quercus* dominance on many sites throughout the Central Hardwood Forest by removing shade-tolerant and fire-sensitive competition from the understory (Abrams, 1992; Lorimer, 2001; Nowacki and Abrams, 2008). In the absence of intense competition, *Quercus* can withstand prolonged periods of understory suppression as documented in this study and others (e.g. Rentch et al., 2003). In the absence of frequent fire, *A. rubrum* can become dense in the understory and inhibit *Quercus* recruitment thereby altering stand development and forest succession (i.e. mesophication; Lorimer et al., 1994; Nowacki and Abrams, 2008). Although alternative hypotheses have been

proposed to explain the *Quercus* to *Acer* phenomenon (e.g. growing season climate change, alterations in land use, facilitative processes, extirpation of species such as *Castanea dentata* (Marsh.) Borkh., and changes in wildlife population densities (Lorimer, 1993; Hart et al., 2008; McEwan et al., 2011)), the fire hypothesis is unquestionably the dominant paradigm. Although we do not know the history of fire on the site, we know the frequency of stand-wide canopy disturbance events across the old-growth remnant has changed in the past three centuries. Stand-wide canopy disturbances preceded and succeeded European settlement, but none have occurred since 1903. Although we do not understand the process or processes responsible for this pattern, we speculate that the disturbance agents that created stand-scale release events have been absent for over 100 years. Alteration of the disturbance regime has likely influenced forest structure and function and may be related to the documented shift in species composition.

5. Management implications

If the documented successional pattern is not driven by anthropogenic means, then managers of the natural area need not be concerned about the future trajectory of this old-growth stand. However, if the *Quercus* to *Acer* pattern is anthropogenic as many authors have proposed (e.g. Abrams and Nowacki, 2008; Fei and Steiner, 2009; McEwan et al., 2011; Nowacki and Abrams, 2008), resource managers should actively manage the stand to return the site composition and structure to within its historic range of variability. Silvicultural treatments through timber harvesting are not allowed in a Tennessee State Natural Area. Without forest management, this designated natural area (along with many others in the Central Hardwood Forest) may become less “natural” with the continued invasion of *Acer* and inhibition of *Quercus* and *Pinus*.

To maintain the *Quercus* and *Pinus* components in this system, resource managers would likely need to: (1) create canopy gaps and (2) remove shade-tolerant competition from the understory. Because harvesting is not a management option, prescribed fire in conjunction with the timing of natural disturbances that create canopy gaps may be a viable means to restore forest conditions to those prior to the onset of the *Acer* invasion in the mid-1900s (Abrams, 2005). Low intensity, surface fires may not have been the mechanisms that historically prevented *Acer* establishment on the site (McEwan et al., 2011); however, given the constraints of management guidelines and the drastic changes in other potential drivers, this management option may now be the most viable.

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