



## **Disturbance, Succession, and Structural Development of an Upland Hardwood Forest on the Interior Low Plateau, Tennessee**

Authors: Hart, Justin L., Cowden, Merrit M., Torreano, Scott J., and R. Vestal, J. Patrick

Source: Natural Areas Journal, 36(1) : 557-573

Published By: Natural Areas Association

URL: <https://doi.org/10.3375/043.036.0102>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

•

# Disturbance, Succession, and Structural Development of an Upland Hardwood Forest on the Interior Low Plateau, Tennessee

Justin L. Hart<sup>1,3</sup>

<sup>1</sup>Department of Geography  
University of Alabama  
Tuscaloosa, AL 35487 USA

Merrit M. Cowden<sup>1</sup>  
Scott J. Torreano<sup>2</sup>  
J. Patrick R. Vestal<sup>2</sup>

<sup>2</sup>Department of Forestry and Geology  
University of the South  
Sewanee, TN 37383 USA

•

<sup>3</sup> Corresponding author: hart013@ua.edu;  
+1 205 348 1673; fax: +1 205 348 2278

*Natural Areas Journal* 35:557–999

**ABSTRACT:** An appreciation for the importance of structural complexity, combined with the acknowledgment that stands with complex structures are uncommon compared to pre-European settlement estimates, has led to a growing interest in restoring late-successional forests. The success of these projects is dependent upon our understanding of the variability of late-successional structure and the disturbance events that produced this structure. We quantified woody species composition, stand structure, canopy disturbance history, and *Quercus* establishment and canopy accession patterns to document processes that resulted in the structural conditions of an upland hardwood forest in Tennessee. The forest established in the mid-1800s and exhibited structural characteristics that were within the range of what has been reported from other late-successional forests in the region. The forest overstory was dominated by *Quercus prinus*, but *Acer saccharum* was the most abundant species. *Quercus* recruitment was continuous from stand initiation through the 1950s. The vast majority of *Quercus* trees that established prior to 1880 established in closed canopy conditions, whereas most *Quercus* trees that established after 1880 established in high light environments. *Quercus* establishment in canopy gaps resulted in multi-aged *Quercus* populations in the forest. We documented three forest-wide disturbances during development (1922, 1945, and 1973). The 1922 forest-wide disturbance coincided with an establishment pulse of largely understory taxa, and the broad-scale event of 1945 corresponded with an establishment pulse of *A. saccharum*. Our results provide benchmarks for a region that lacks other reference conditions and can be used to inform structure and process based restoration approaches.

*Index terms:* disturbance, *Quercus*, stand development, structure, succession

## INTRODUCTION

Late-successional hardwood stands throughout the temperate zone are noted for their unique structural characteristics, which are often described as complex (Oliver and Larson 1996; Hale et al. 1999; Johnson 2004). Ironically, we know little about the disturbance processes that occurred during development to create the structures that characterize these late-successional stands. Furthermore, late-successional stands vary considerably in their structural attributes (Parker 1989; Boyce 1995; Tyrrell et al. 1998), and it is unknown to what extent that variability is controlled by a stand's unique disturbance history (Burrascano et al. 2013).

When combined with forest inventory data, forest reconstructions allow us to analyze stand development and succession and to examine the relationships between these processes and disturbance events (Henry and Swan 1974; Oliver and Stephens 1977; Lorimer 1985; Lorimer and Frelich 1989). Reconstructions of disturbance and development in late-successional stands provide quantitative information on these processes over long periods. These data improve our ability to develop silvicultural prescriptions designed to manage stands according to historical disturbance regimes (i.e., the historical range of variation) or to enhance elements of late-successional

structure in young stands (Seymour et al. 2002; Hart, Clark et al. 2012).

Late-successional hardwood stands with complex structure are rare in the eastern United States (Parker 1989; Dyer 2006). Most stands in the region established following timber harvesting. This activity peaked in the early 1900s, and thus, forests over vast expanses of the eastern United States are characterized as even-aged, less than 100 years old, and in the stem exclusion or understory reinitiation stages of development (Whitney 1994; Lorimer 2001). Therefore, forests that exhibit the structural complexity that epitomizes late-successional stands are underrepresented on the landscape (Keeton 2005). Late-successional structural characteristics of temperate hardwood stands include live large trees, multiple age classes, a range of canopy tree size classes, multilayered canopies, snags, and logs on the forest floor (Oliver 1981; Martin 1992; Hale et al. 1999). These structural features serve as critical habitats for the maintenance of native forest biodiversity and provide important ecosystem functions such as carbon storage (Begon et al. 1986; Hunter 1990; Kenefic and Nyland 2000). The importance of late-successional forest structure and function for the maintenance of biodiversity and ecosystem services, combined with the acknowledgment that such structures are uncommon compared to pre-Euro-

pean settlement estimates (Whitney 1994; Lorimer 2001), has led to a growing interest in restoring late-successional forests, especially on public lands. Recommendations have been provided for structure- (e.g., Keeton 2005, 2006) and disturbance- (e.g., Seymour et al. 2002) based restoration approaches. The success of either of these approaches to forest management designed to restore late-successional forests is dependent upon our understanding of the variability of late-successional structure and the long-term disturbance histories that produced this structure. Stand structures and disturbance regimes vary across space. Indeed, estimates on simple forest measures such as trees ha<sup>-1</sup> and basal area ha<sup>-1</sup> vary widely within a single forest type (Tyrrell et al. 1998; Burrascano et al. 2013). Thus, quantitative silvicultural guidelines for restoration should be place-based and developed from sites in similar biophysical settings.

The overarching goal of our study was to document long-term patterns of forest development and disturbance in a late-successional *Quercus*-dominated forest on the southern Interior Low Plateau in Tennessee, United States. Our specific objectives were to: (1) quantify species composition and structural elements, (2) reconstruct the frequency, magnitude, and spatial extent of canopy disturbance events during forest development, and (3) elucidate relationships between disturbance processes and forest development. We hypothesized that the conditions of the study site were representative of forests throughout the broader area such that the data reported here may be used as reference conditions for restoration planning.

## STUDY AREA AND METHODS

### Study Site

Our study was conducted on the Hill Forest State Natural Area (HFNA) located 20 km southwest of Nashville, Tennessee. The 91-ha reserve is managed as a state natural area by the Tennessee Department of Environment and Conservation. The HFNA is a component of the Warner Parks system of metropolitan Nashville. The

land constituting HFNA and a surrounding (buffering) area were formally established as forest reserves when the property was transferred to the State of Tennessee in 2010. Our study was specifically focused within an approximately 60-ha portion within the core section of the 91-ha reserve. Permanent European settlement of the area did not begin until 1785 when settlers first built homesteads near Nashville. By 1810, several farms were established within 6 km of the study site, but land clearing was limited to stream bottoms and relatively level areas. We do not know the exact extent to which the study area within the HFNA was affected by land-use activities by early settlers, but we assume that the area was not immune to some level of grazing and timber harvesting. Within the core of the study area, we noted no cut stumps or old logging roads; however, the outer portions, lower in elevation and slope gradient, likely experienced some direct human disturbance including logging, fire, and grazing prior to 1924. Since 1924, fencing around the perimeter of the area we studied has been well maintained, effectively preventing livestock grazing on the core portion of the reserve. Grazing and fire have been excluded from the forest since that time.

The HFNA is located in the outer portion of the Central (Nashville) Basin of the Interior Low Plateau (Fenneman 1938; Edwards et al. 1974). Braun (1950) classified the study area as the Nashville Basin section of the Western Mesophytic (*Quercus-Carya*) Forest Region. True mixed mesophytic communities occur here only in riparian areas and in shaded hollows (Smalley 1983). The Central Basin features rolling to steep topography. The higher elevations are capped by cherty limestone of the Fort Payne Formation. These are posterosional remnants of the Highland Rim Physiographic Province. Soils on the side slopes developed in the Chattanooga Shale, which represents the contact between the Highland Rim and the Nashville Basin. The soil series encountered included Bodine silty loams, 5–20% slopes on the highest elevations, the Bodine-Sulphura Complex, 20–50% slopes, and Dellrose cherty silt loams, 12–20%, forming a natural moisture and

fertility gradient that generally increases with decreasing elevation (North 1981). The elevation of the study plots ranged from approximately 217 to 279 m.

The climate is classified as humid mesothermal (Thorntwaite 1948) with long, moderately hot summers and short, mild winters. The average frost-free period is approximately 209 days and the mean annual temperature is 15 °C. The July average temperature is 26 °C and the January average temperature is 3 °C (PRISM Climate Group 2013). 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 121 cm (PRISM Climate Group 2013). Thunderstorms accompanied by intense rainfall and sometimes hail occur over 55 days annually and are most common in late spring and summer. Snowfall is minimal and generally melts within a few days (North 1981).

### Field Methods

To quantify forest composition and structure, we established 27 0.04-ha fixed-radius ( $r = 11.29$  m) plots throughout the inner core of the HFNA. Prior to field data collection, plot locations were selected using ArcGIS v. 9. Plots were arranged in a systematic grid pattern at 188-m (E-W) x 135-m (N-S) spacing and coordinate pairs were downloaded as waypoints into GPS receivers so the plots could be located in the field. In each plot, we recorded species, crown class, and diameter at breast height (dbh, approximately 1.4 m above the surface) of all stems  $\geq 5$  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 and recruitment pulses and to reconstruct canopy disturbance history, we used increment borers to extract tree core samples from all trees  $\geq 20$  cm dbh and the four trees  $\geq 5$  cm and  $< 20$  cm dbh nearest to plot center on each plot. To increase our sample size of trees to reconstruct disturbance history, we opportunistically

collected increment cores from *Quercus* canopy trees immediately adjacent to our inventory plots that exhibited characteristics of being old (Pederson 2010). These samples were labeled accordingly and in our analyses were grouped to the plot to which they were adjacent. These samples were only used to reconstruct canopy disturbance history and to quantify canopy accession strategies of *Quercus*. We identified all snags (standing dead trees  $\geq 5$  cm dbh with crowns mostly intact) on each plot to the lowest taxonomic level possible and recorded snag diameter and decay class using criteria adapted from Spetich et al. (1999) to quantify structural features, disturbance history, and woody debris decay patterns. The regeneration layer was quantified using nested 0.004-ha circular plots located 7.2 m due north of overstory plot center. In the 27 regeneration plots, we tallied all woody stems  $\geq 0.7$  m in height and  $< 5$  cm in dbh. We defined seedlings as stems  $> 0.7$  m and  $< 1.4$  m tall; saplings were stems  $> 1.4$  m tall and  $< 5$  cm in dbh. Multistemmed woody plants in the regeneration plots were considered separate individuals if the stems separated below ground (i.e., were not visible) and as one individual if the stems separated above ground.

### Laboratory and Analytical Methods

Tree, seedling, and sapling layers were analyzed using standard descriptors. For trees we calculated density (number of stems  $\text{ha}^{-1}$ ), relative density (contribution to total trees), dominance (basal area,  $\text{m}^2 \text{ha}^{-1}$ ), relative dominance (contribution to total basal area), and relative importance (sum of relative density and relative dominance) for each species. For seedlings and saplings 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 a series of progressively finer abrasives to reveal the cellular structure of the wood surface

(Orvis and Grissino-Mayer 2002). Once processed, tree rings on all core samples were dated to the calendar year of formation. Inner dates were estimated using pith estimators for series that included substantial ring curvature but lacked pith. Forest disturbance history was reconstructed using the *Quercus* individuals  $\geq 20$  cm dbh from our collection because the genus typically produces rings with clear boundaries and does not commonly contain locally absent rings or produce false rings. *Quercus* were also the oldest trees documented on the site and were dominant and codominant canopy species, had high relative frequency, and have been used successfully in other studies to document canopy disturbance history (e.g., Nowacki and Abrams 1997; Rubino and McCarthy 2004; Hart and Grissino-Mayer 2008; Buchanan and Hart 2012). 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 overstory *Quercus* series ( $n = 56$ ). The measurement series were visually compared and statistically analyzed using segmented time series correlation analysis in the COFECHA program to ensure each growth ring was assigned to the proper calendar year of formation (Holmes 1983; Grissino-Mayer 2001a). 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 possible dating errors. Dating was adjusted if deemed necessary.

Once we were confident all tree rings on all canopy *Quercus* series 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 (i.e., pulses of increased growth) in radial growth patterns of canopy trees is the primary technique in dendroecology to reconstruct canopy disturbance events (Lorimer 1980, 1985; Abrams and Nowacki 1992; Nowacki and Abrams 1997; Frelich 2002; Fraver and White 2005). Release episodes are often 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 three years (Hart and Grissino-Mayer 2008; Hart et al. 2008; Hart, Clark et al. 2012). We classified forest-wide canopy disturbance events as episodes when there was a synchronous release experienced by a minimum of one tree at least 10 years of age on 25% of the study plots (Nowacki and Abrams 1997; Rubino and McCarthy 2004; Hart and Grissino-Mayer 2008). This spatially explicit method prevented us from mislabeling a localized event that may have resulted in the release of  $\geq 25\%$  of trees from a small portion of the forest as true forest-wide episodes. We used the FHX2 software to graphically display spatio-temporal patterns of release events (Grissino-Mayer 2001b; Hart and Grissino-Mayer 2008; Hart et al. 2008). To account for variability in sample size through forest history, we used a relativized descriptor of release frequency (Rubino and McCarthy 2004; Buchanan and Hart 2012).

To examine canopy disturbance patterns and *Quercus* recruitment strategies, all *Quercus* trees  $\geq 20$  cm dbh were classified into two groups (gap or understory origin) based on early radial growth rates (Rentch et al. 2003). Trees with mean radial growth rates of  $\geq 2.00 \text{ mm yr}^{-1}$  for the first 10 years were considered to be of gap origin (Ruffner and Abrams 1998; Hart and Grissino-Mayer 2008; McEwan and McCarthy 2008). Trees with mean radial growth rates of  $< 2.00 \text{ mm yr}^{-1}$  for the first 10 years were classed as understory origin. We subsequently determined if and when the trees experienced growth releases identified by the 10-year running mean method. To corroborate these quantitative classifications, we graphically analyzed the radial growth patterns of each of these *Quercus* series. We combined the recruitment strategy classes with the detection of

subsequent release event(s) to assign all *Quercus* trees  $\geq 20$  cm dbh to an establishment and canopy accession strategy class as defined by Rentch et al. (2003): gap origin-no release, gap origin-gap release, or understory origin-gap release.

## RESULTS

### Forest Composition

Species richness of the tree layer (stems  $\geq 5$  cm dbh) was 29, diversity ( $H'$ ) was 2.61, and evenness ( $J$ ) was 0.78. Basal area of the

tree layer was  $24.0 \text{ m}^2 \text{ ha}^{-1}$  and tree density was  $426 \text{ ha}^{-1}$  (Table 1). The most important species (based on relative importance) were *Acer saccharum* (relative importance value (RIV): 38) and *Quercus prinus* (RIV: 34, Table 1). These were the only species with importance values greater than 19. At the

**Table 1.** Density, dominance, and importance (sum of relative density and relative dominance) measures for all live woody stems  $\geq 5$  cm dbh in the Hill Forest State Natural Area, Tennessee.

Species	Density (stems $\text{ha}^{-1}$ )	Relative density	Dominance ( $\text{m}^2 \text{ ha}^{-1}$ )	Relative dominance	Relative importance
<i>Acer saccharum</i> Marsh.	119	27.9	2.4	10.2	38.2
<i>Quercus prinus</i> L.	31	7.2	6.3	26.3	33.5
<i>Sassafras albidum</i> (Nutt.) Nees	62	14.6	1.1	4.4	19.0
<i>Fagus grandifolia</i> Ehrh.	35	8.1	0.9	3.8	11.9
<i>Quercus rubra</i> L.	8	1.8	2.2	9.3	11.1
<i>Quercus alba</i> L.	9	2.0	1.9	8.0	10.1
<i>Quercus velutina</i> Lam.	9	2.0	1.8	7.3	9.3
<i>Nyssa sylvatica</i> Marsh.	27	6.3	0.4	1.5	7.8
<i>Diospyros virginiana</i> L.	17	4.1	0.7	2.9	6.9
<i>Carya alba</i> (L.) Nutt.	10	2.3	1.0	4.1	6.4
<i>Ulmus rubra</i> Muhl.	14	3.4	0.6	2.6	5.9
<i>Cornus florida</i> L.	20	4.7	0.1	0.5	5.3
<i>Carya pallida</i> (Ashe) Engl. and Graebn.	10	2.3	0.6	2.4	4.7
<i>Liriodendron tulipifera</i> L.	2	0.5	1.0	4.2	4.6
<i>Fraxinus americana</i> L.	7	1.6	0.7	2.8	4.4
<i>Carya glabra</i> (Mill.) Sweet	12	2.7	0.4	1.7	4.4
<i>Carya ovata</i> (Mill.) K. Koch	6	1.4	0.6	2.7	4.0
<i>Juglans nigra</i> L.	5	1.1	0.4	1.6	2.7
<i>Celtis occidentalis</i> L.	6	1.4	0.2	1.0	2.3
<i>Quercus coccinea</i> Münchh.	1	0.2	0.3	1.1	1.3
<i>Oxydendrum arboreum</i> (L.) DC.	3	0.7	0.1	0.5	1.2
<i>Tilia americana</i> L.	3	0.7	0.1	0.3	1.0
<i>Asimina triloba</i> (L.) Dunal	4	0.9	0.0	0.0	0.9
<i>Ostrya virginiana</i> (Mill.) K. Koch	3	0.7	0.0	0.1	0.7
<i>Ulmus serotina</i> Sarg.	2	0.5	0.0	0.1	0.6
<i>Cercis canadensis</i> L.	2	0.5	0.0	0.1	0.5
<i>Robinia pseudoacacia</i> L.	1	0.2	0.1	0.3	0.5
<i>Celtis laevigata</i> Willd.	1	0.2	0.1	0.2	0.4
<i>Carya cordiformis</i> (Wangenh.) K. Koch	1	0.2	0.0	0.0	0.2
<b>Total</b>	<b>426</b>	<b>100.0</b>	<b>24.0</b>	<b>100.0</b>	<b>200.0</b>

genus level, *Quercus* was clearly the most important contributor to the tree layer, comprising over 65% relative importance. The most dominant species in the forest based on basal area was *Quercus prinus*, with a basal area of 6.3 m<sup>2</sup> ha<sup>-1</sup> (Table 1). The next most dominant species were *Acer saccharum*, *Quercus rubra*, *Quercus alba*, and *Quercus velutina*. Collectively, these five species represented more than 61% of the tree layer basal area. No other species contributed to more than 5% of the forest basal area and 11 species each represented less than 1% of the basal area total.

The most abundant species in the tree layer was *Acer saccharum* with 119 stems ha<sup>-1</sup> (Table 1). This species represented almost 28% of all stems  $\geq 5$  cm dbh in the forest. The second most abundant species was *Sassafras albidum* with 62 stems ha<sup>-1</sup>. These species were followed by *Fagus grandifolia*, *Quercus prinus*, and *Nyssa sylvatica*. Combined, these five species made up over 64% of all trees in the forest. *Cornus florida* was the only other species with at least 20 trees ha<sup>-1</sup>. Of the 29 species in the tree layer, four species were represented by only one tree ha<sup>-1</sup>.

Seedling layer species richness, diversity, and evenness were 19, 2.19, and 0.74, respectively. We documented 4320 stems ha<sup>-1</sup> in the seedling layer (Table 2). The most abundant species in the seedling layer was *Sassafras albidum*. The second most abundant species was *A. saccharum*, but density of this species was 44% lower than that of *S. albidum*. Sapling layer species richness was 7, diversity was 1.73, and evenness was 0.89. Sapling density was 182 ha<sup>-1</sup>. The most abundant sapling species were *Lindera benzoin* and *Ulmus serotina*, which collectively represented 53% of all individuals in the sapling layer. We did not document any *Quercus* in the sapling layer. *Cladrastis kentukea* was the only species present in the sapling layer, but not the seedling layer. *Acer rubrum* was the only species with canopy potential in the seedling layer that was absent from the sapling and tree layers. Notably, we documented only one woody alien species in our forest plots, *Lonicera maackii*. This alien shrub represented over 7% of seedling layer stems.

When species were taxonomically grouped and their relative contributions by crown position were analyzed, a clear pattern emerged where *Quercus* and *Carya* species collectively represented 82% of canopy dominants, but only 7% of overtopped stems. In contrast, *A. saccharum* and *F. grandifolia* represented 46% of overtopped stems, but did not occur as canopy dominants. We documented 11 individuals ha<sup>-1</sup> with canopy dominant positions and 108 trees ha<sup>-1</sup> with codominant positions in the canopy (Figure 1). Eight species were represented in canopy dominant positions with *Q. alba* being the most common (represented 27% of canopy dominants). *Liriodendron tulipifera* was the only species other than those from the *Quercus* or *Carya* genera to occupy dominant positions in the forest canopy. A total of 20 species occurred in canopy codominant positions. The species with the highest frequency in the codominant position was *Q. prinus* ( $n = 27$  ha<sup>-1</sup>) followed by *A. saccharum* (16 ha<sup>-1</sup>). A total of 56 trees ha<sup>-1</sup> were classed as intermediate. The most common species with intermediate positions were *A. saccharum* and *S. albidum*, which represented 31% and 22% of all intermediate trees respectively. The overtopped category had the highest number of trees, with 252 individuals ha<sup>-1</sup>. Of the 29 species in the tree layer, 22 (76%) occurred in overtopped positions. The most common overtopped trees were *A. saccharum* (84 stems ha<sup>-1</sup>), *S. albidum* (45 ha<sup>-1</sup>), and *F. grandifolia* (33 ha<sup>-1</sup>). Together these three species represented 64% of all overtopped trees. Of the *Quercus* genus, only *Q. alba* (1 stem ha<sup>-1</sup>) and *Q. prinus* (2 ha<sup>-1</sup>) occurred in overtopped positions. All five *Carya* species that occurred in the tree layer were documented in overtopped positions, but collectively they represented only 17 of the 252 overtopped stems ha<sup>-1</sup>.

The crown class distribution for the stand was bimodal, with peaks in the overtopped and codominant positions (Figure 1). *Quercus* trees were most common in codominant canopy positions (45 ha<sup>-1</sup>) and least common in overtopped (3 ha<sup>-1</sup>) and intermediate (3 ha<sup>-1</sup>) positions. Although *Carya* represented 27% of canopy dominant trees and only 6% of overtopped trees, the genus was most abundant in

overtopped positions (16 ha<sup>-1</sup>). *Acer saccharum* and *F. grandifolia* did not occur as canopy dominants. These species did occur in canopy codominant positions (17 *A. saccharum* ha<sup>-1</sup> and 1 *F. grandifolia* ha<sup>-1</sup>). These species were most abundant in overtopped positions, as we documented 84 overtopped *A. saccharum* ha<sup>-1</sup> and 33 overtopped *F. grandifolia* ha<sup>-1</sup>. The most abundant codominant species from the “others” group was *Diospyros virginiana*, with eight such trees ha<sup>-1</sup>. *Sassafras albidum* was the most abundant tree from this group in the intermediate position, with a frequency of 12 ha<sup>-1</sup>. *Sassafras albidum*, *Nyssa sylvatica*, and *Cornus florida* were the most abundant species from the “other” group in overtopped positions, with densities of 45, 23, and 20 ha<sup>-1</sup>, respectively.

## Forest Diameter and Age Structure

The diameter structure of all trees in the forest revealed an inverse J-shape from small size classes to large size classes (Figure 2). The mean q-factor was 1.38 with a maximum of 2.60 between the 55–60 cm and 60–65 cm size classes and a minimum of 0.75 between the 35–40 cm and 40–45 cm classes. *Quercus* exhibited a uniform distribution and was present in all but the 25–30 cm size class, with an apex in the 55–60 cm size class ( $n = 11$ ). *Carya* was most abundant in the 10–15 cm size class and was present in all but four of the larger size classes. The *Acer–Fagus* and “others” groups exhibited declines in stem density with increased size, indicative of a reverse J-shaped distribution. We documented 64 *A. saccharum* and 27 *F. grandifolia* ha<sup>-1</sup> in the 5–10 cm class. Collectively, these two species represented 53% of all stems in this size class. In contrast, we noted just seven stems ha<sup>-1</sup>  $\geq 40$  cm dbh from the *Acer–Fagus* group. The most abundant species in the smallest size class from the “others” group were *S. albidum* (29 trees ha<sup>-1</sup>) and *N. sylvatica* (19 ha<sup>-1</sup>). Combined, these two species represented 62% of all stems in the smallest size class in the “others” category. Only four trees ha<sup>-1</sup> from this taxonomic group occurred in the forest (two *L. tulipifera* and two *F. americana*).

**Table 2** Density measures for all live woody stems  $\geq 0.7$  m height,  $< 1.4$  m height (seedlings) and stems  $\geq 1.4$  m height,  $< 5$  cm dbh (saplings) in the Hill Forest State Natural Area, Tennessee.

Species	Seedlings		Saplings	
	Density ha <sup>-1</sup>	Relative density	Density ha <sup>-1</sup>	Relative density
<i>Acer rubrum</i> L.	19	0.4	0	0.0
<i>Acer saccharum</i>	691	16.0	10	5.3
<i>Asimina triloba</i>	490	11.3	10	5.3
<i>Carya glabra</i>	38	0.9	0	0.0
<i>Carya ovata</i>	10	0.2	0	0.0
<i>Cercis canadensis</i>	48	1.1	0	0.0
<i>Celtis occidentalis</i>	451	10.4	0	0.0
<i>Cladrastis kentukea</i> (Dum. Cours.) Rudd	0	0.0	10	5.3
<i>Fagus grandifolia</i>	38	0.9	38	21.1
<i>Fraxinus americana</i>	67	1.6	0	0.0
<i>Lindera benzoin</i> (L.) Blume	451	10.4	48	26.3
<i>Lonicera maackii</i> (Rupr.) Herder	307	7.1	0	0.0
<i>Nyssa sylvatica</i>	96	2.2	19	10.5
<i>Ostrya virginiana</i>	19	0.4	0	0.0
<i>Quercus alba</i>	10	0.2	0	0.0
<i>Quercus prinus</i>	19	0.4	0	0.0
<i>Quercus rubra</i>	10	0.2	0	0.0
<i>Quercus velutina</i>	77	1.8	0	0.0
<i>Sassafras albidum</i>	1229	28.4	0	0.0
<i>Ulmus serotina</i>	250	5.8	48	26.3
<b>Total</b>	<b>4320</b>	<b>100.0</b>	<b>182</b>	<b>100.0</b>

We documented 20 trees ha<sup>-1</sup>  $\geq 60$  cm dbh and eight trees ha<sup>-1</sup>  $\geq 70$  cm dbh. Of these 20 trees, 14 were *Quercus*, two were *Carya*, two were *L. tulipifera*, and two were *F. grandifolia*. The largest trees in our dataset were a *Q. alba* and a *Q. prinus*, both at 90 cm dbh. The third largest tree was a *L. tulipifera* at 86 cm dbh. Trees  $\geq 70$  cm dbh represented only 2% of all trees ha<sup>-1</sup>, but individuals of this size comprised 18% of total basal area ha<sup>-1</sup>. The quadratic mean diameter of the forest was 29 cm and the mean dbh of canopy trees was 43 cm  $\pm$  2 (SE). The mean dbh of *A. saccharum* was 13 cm and the maximum dbh was 57 cm. The mean and maximum dbh of *F. grandifolia* was 11 cm and 72 cm, respectively. *Sassafras albidum* mean dbh was 13 cm and the largest tree of this species was 35 cm dbh. In contrast, the most dominant

species in the forest, *Q. prinus*, had a mean dbh of 48 cm.

The oldest tree we documented was a *Q. prinus* with an inner date at breast height of 1841 and a dbh of 66 cm (Figure 3). Only one other tree, a *Q. prinus* with a dbh of 58 cm and an inner date of 1847, established prior to 1850. In total we documented 25 *Quercus* trees that established prior to 1900. Of these trees, 18 were *Q. prinus*, four were *Q. alba*, two were *Q. velutina*, and one was a *Q. coccinea*. In total, we had *Quercus* trees that predated 1900 on 11 (41%) of our 27 inventory plots. The youngest *Quercus* in our dataset was a *Q. alba* with an inner date of 1980 and a dbh of 8 cm. *Quercus* establishment was continuous from the mid-1800s through the 1950s. However, establishment was

greatest from the 1890s to the 1910s, as 45% of all *Quercus* trees in our sample established during this 30-year period. In contrast, only 32% of the *Quercus* stems we documented established after 1918. The oldest *Carya* in our collection was a *C. pallida* with an inner date of 1849 and a dbh of 45 cm. *Carya* recruitment in the forest was low, but continuous from that point through the 1960s. The oldest *A. saccharum* we documented had an inner date of 1932 and was 22 cm dbh. This was the only *A. saccharum* in our dataset that established in the 1930s, but seven *A. saccharum* trees had inner dates in the 1940s and eight in the 1950s. Establishment of this species was continuous from the 1940s through the 1970s, with the highest frequencies in the 1960s (30% of the *A. saccharum* samples) and 1970s (25% of the samples).

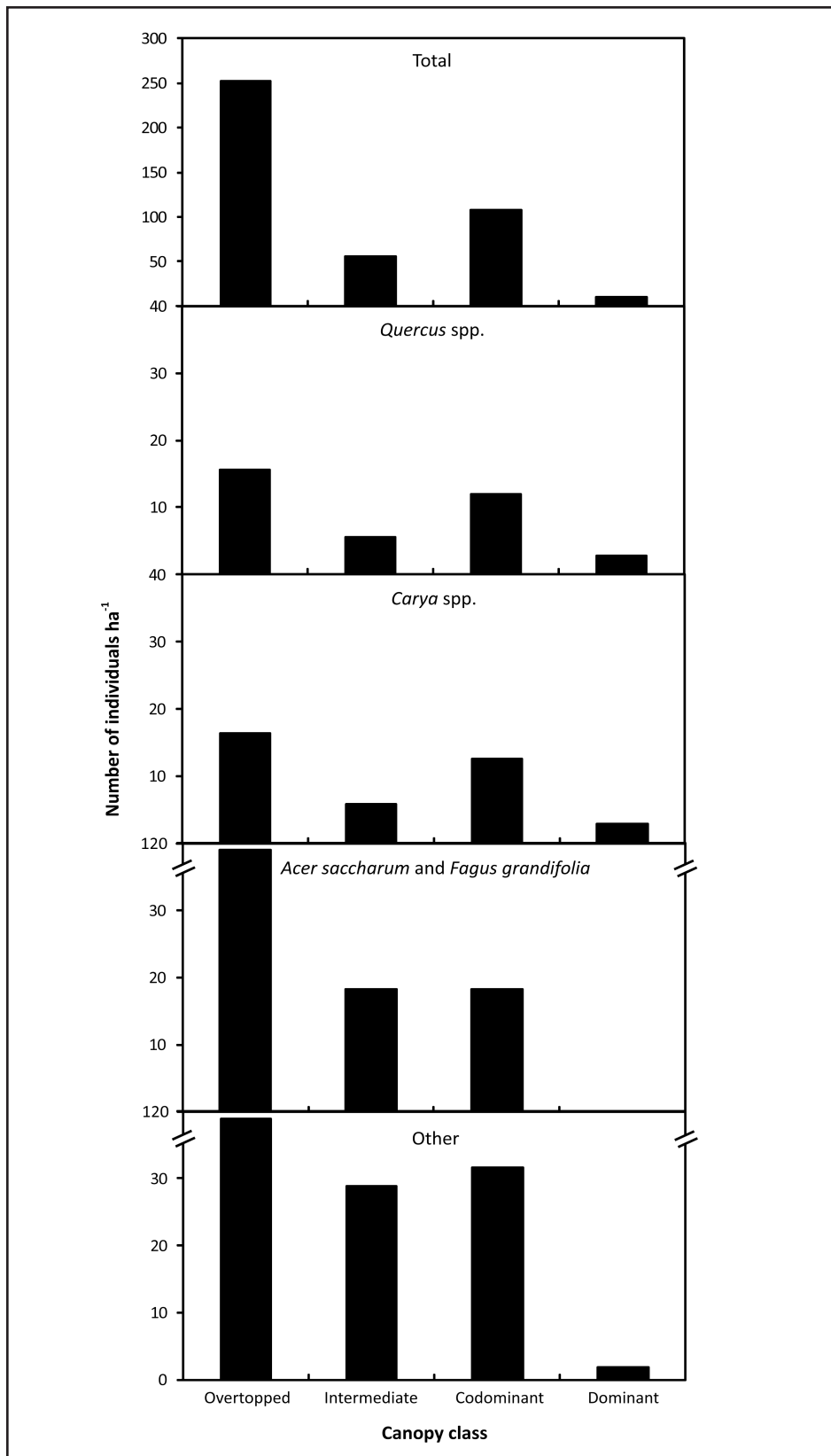


Figure 1. Crown class distributions per hectare by group. Crown class categories are based on the amount and direction of intercepted light (Oliver and Larson, 1996). Note broken scale for *A. saccharum* and *F. grandifolia* and “other” groups. For a list of species included in the “others” group see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

The oldest *F. grandifolia* in our dataset had an inner date at breast height of 1950 and was 23 cm dbh. Within the “others” group, recruitment began in the 1920s with the oldest tree being a *S. albidum* with an inner date at breast height of 1923 and a dbh of 32 cm. From this taxonomic group, two other trees established prior to the 1930s; a *D. virginiana* with an inner date of 1925 and a dbh of 38 cm and a *F. americana* with an inner date of 1926 and a dbh of 57 cm. Recruitment from this group was greatest during the 1950s and 1960s as 22% and 33% of the samples in this category established in those decades, respectively. No species-specific establishment patterns with the “others” category were evident.

### Snag Characteristics

We documented 61 snags  $\geq 5$  cm dbh  $\text{ha}^{-1}$  and five snags  $\geq 40$  cm dbh  $\text{ha}^{-1}$  across the study site (Table 3). Mean snag dbh was  $15 \text{ cm} \pm 2$  (SE) with a maximum of 69 cm for a *S. albidum* individual. The basal area of snags was  $1.8 \text{ m}^2 \text{ ha}^{-1}$ . Snag frequency was highest in the smallest dbh class and abundance generally decreased with increased size, indicative of a reverse J-shaped distribution (Figure 4). We were able to identify 81% of all snags to species with confidence. Of the snags that were taxonomically identified, we documented 11 different species. The majority (58%) of snags were *S. albidum*. *Sassafras albidum* represented 50% of snag basal area. The mean dbh of *S. albidum* snags was  $13 \text{ cm} \pm 2$  (SE). We documented six *S. albidum* snags  $\geq 20$  cm dbh and two such trees  $\geq 40$  cm dbh. With the exception of *S. albidum*, the only other snag identified to species that was over 40 cm dbh was a *L. tulipifera* with a dbh of 47 cm. The largest snag identified as *Quercus* was a *Q. velutina* with a dbh of 13 cm.

### Canopy Disturbance History and Structural Development

We analyzed 56 overstory *Quercus* trees using the 10-year running mean method and 46 (82%) of these individuals exhibited at least one release event. In total, 101 release events were detected from



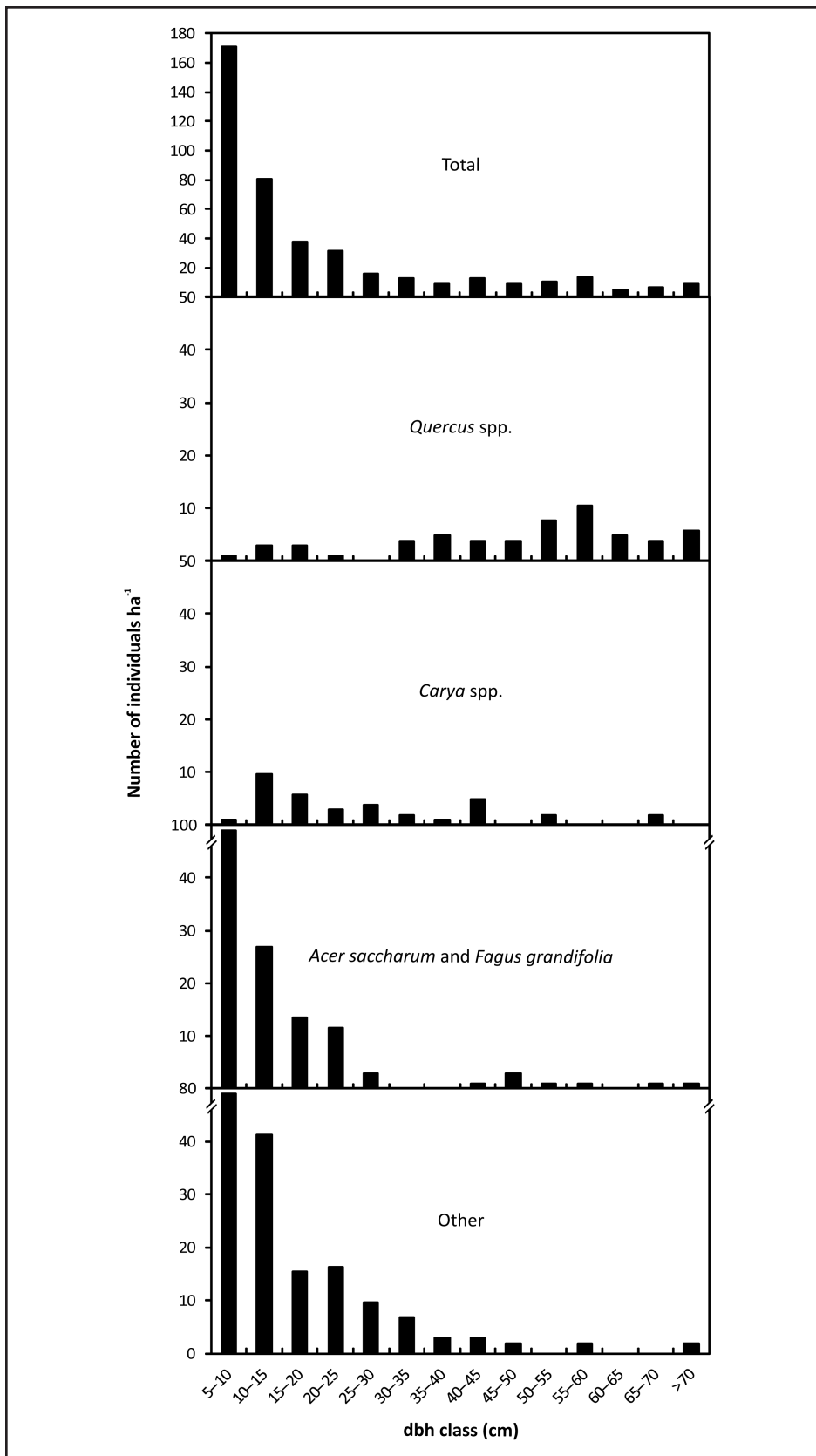


Figure 2. Number of trees ( $\geq 5$  cm dbh) per hectare for all species, divided into four groups in the Hill Forest State Natural Area, Tennessee. Note broken scale for *A. saccharum* and *F. grandifolia* and “other” groups. For a list of species in the “other” group see Table 1.

these individuals with 33 trees (59% of samples analyzed) experiencing multiple releases, including 15 trees (27%) with three or more releases in their lifespans. In fact, one tree, a *Q. rubra*, exhibited six release events from 1904 to 2011. Of the 101 detected release events, 90 (89%) were minor and 11 (11%) were major. The mean release duration was  $4.6 \text{ years} \pm 0.2$  (SE). The longest sustained release was 11 years, observed in a *Q. alba* from 1910 to 1920. The longest period between release initiation events after 1900 was 10 years (occurring from 1924 to 1934). Release initiations often occurred in consecutive years; the longest periods of consecutive initiations were from 1968 to 1975 and 1942 to 1947. The single year with the highest frequency of release initiations was 1945 ( $n = 14$  release initiations). The mean release initiation return interval was  $2.8 \text{ years} \pm 0.3$  (SE).

We documented three forest-wide disturbances during stand development. These episodes were initiated in 1922 (a simultaneous release from trees at least 10 years of age on 31% of our plots), 1945 (53% of plots), and 1973 (25% of plots; Figure 5). The highest decadal release to sample size ratio value occurred in the 1940s when 40% of the trees at least 10 years of age exhibited a growth release (Figure 6). The second highest value was 29% and occurred in the 1970s. From the late-1800s to the end of the record, decadal release to sample size percentages exhibited an oscillating pattern, with peaks occurring approximately every three decades. Peaks in release to sample size ratio values occurred in the 1910s, 1940s, 1970s, and 1990s. The mean percent of trees that experienced releases during these four peaks was 29%.

Radial growth patterns varied between understory origin and gap origin trees (Figure 7). Of the 56 overstory *Quercus* trees analyzed, 31 (55%) established in a canopy gap and 25 (45%) established under a closed forest canopy (Figure 8). Mean radial growth rate for understory origin *Quercus* trees was  $1.79 \text{ mm yr}^{-1}$  and for gap origin trees was  $2.07 \text{ mm yr}^{-1}$ . Early in stand development, most *Quercus* trees established in closed canopy environments. Prior to 1880, only two *Quercus* trees es-

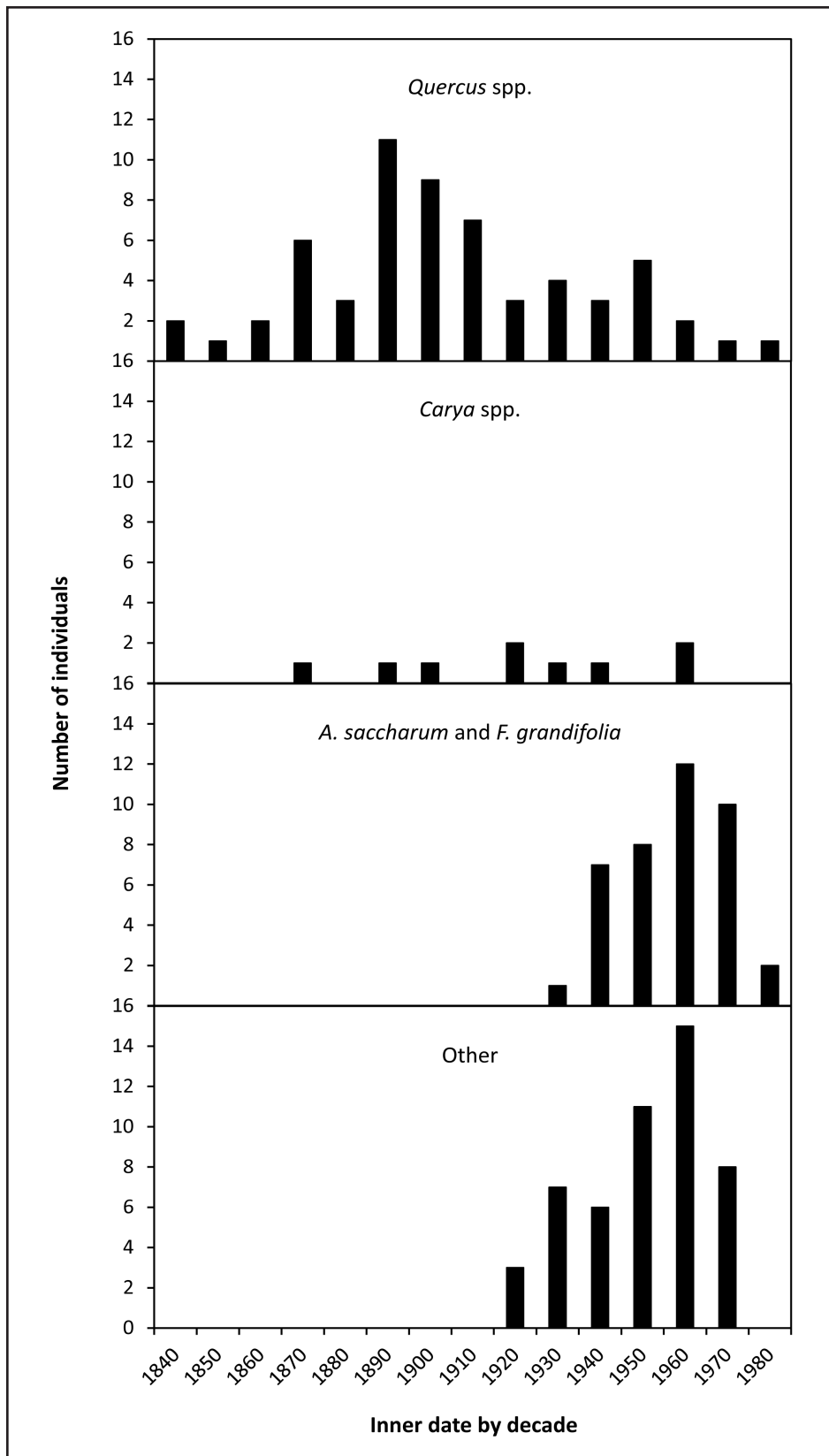


Figure 3. Age structure by taxonomic group for the Hill Forest State Natural Area, Tennessee. For a list of species in the “other” group see Table 1.

established in high light (e.g., open canopy) environments. In contrast, nine *Quercus* trees established in low light (e.g., closed canopy) environments prior to 1880. Establishment of gap origin trees peaked from the 1890s to the 1910s, as 58% of gap origin trees established during this 30-year period. From the 56 *Quercus* trees in our dataset, eight individuals established in a high light environment and reached the canopy without a subsequent release (i.e., reached a canopy position before canopy closure). The 23 remaining gap origin *Quercus* trees (41% of the *Quercus* samples) established in a gap and subsequently released following additional canopy disturbance. Of the 25 *Quercus* individuals that established in the understory of a closed canopy, the mean period of suppression was 27.4 years  $\pm$  2.9 (SE). The longest residence time in the understory prior to overstory release was 62 years observed and was observed in a *Q. alba*.

## DISCUSSION

### Forest Composition

Species richness and diversity were highest for the tree layer. In fact, species richness and diversity of the tree layer were comparatively high for the region (e.g., Hart et al. 2008,  $S$ : 30,  $H'$ : 2.97; Hart and Grissino-Mayer 2008,  $S$ : 30,  $H'$ : 2.57; Schweitzer and Dey 2011,  $S$ : 20,  $H'$ : 3.00; Hart, Clark et al. 2012,  $S$ : 30,  $H'$ : 2.25). We documented trees on our plots that commonly occur on xeric (e.g., *Quercus coccinea*) and mesic (e.g., *Tilia americana*) sites. Species richness of the tree layer has the potential to increase as we noted four species in seedling and sapling layers that were absent as trees, but have the potential to reach dbh of 5 cm (the lower size limit of trees as defined in this study). The sapling layer exhibited the lowest species diversity, but the highest species evenness value. The sapling layer was relatively sparse, but these individuals were rather evenly distributed across the seven species present. The seedling layer had the lowest evenness value. We attributed this to the abundance of *S. albidum*; the species represented 28% of all seedlings. The next most abundant seedling species was *A. saccharum*, but it

**Table 3** Cumulative density (stems ha<sup>-1</sup> and percent (%) of total stems ha<sup>-1</sup>) and basal area (m<sup>2</sup> ha<sup>-1</sup> and percent (%) of total basal area ha<sup>-1</sup>) of snags by diameter at breast height (cm) class in the Hill Forest State Natural Area, Tennessee.

DBH (cm)	Density		Basal area	
	Stems ha <sup>-1</sup>	Percent of total	Basal area ha <sup>-1</sup>	Percent of total
≥5	61	100	1.82	100
≥10	30	49	1.69	93
≥20	12	20	1.42	78
≥30	7	11	1.16	64
≥40	5	8	1.02	56
≥50	2	3	0.55	30

was 44% less common than *S. albidum*. Although *S. albidum* is a common component in old field stands in this region, we are uncertain why it was so abundant in this reserve. *Acer rubrum* and *Lonicera maackii* were the only species unique to the seedling layer and *Cladrastis kentukea* was the only species unique to the sapling layer. The only other species present in the regeneration plots but absent from our tree plots was *Lindera benzoin*. We speculate that *A. rubrum* seedlings will recruit to larger size classes following canopy disturbance events. The species is able to sustain slow growth in light-limited conditions for decades and then respond rapidly to increases in understory insolation (Hart, Buchanan et al. 2012). Furthermore, we hypothesize that the absence of this species in larger size classes was attributed to the timing of its establishment on the site.

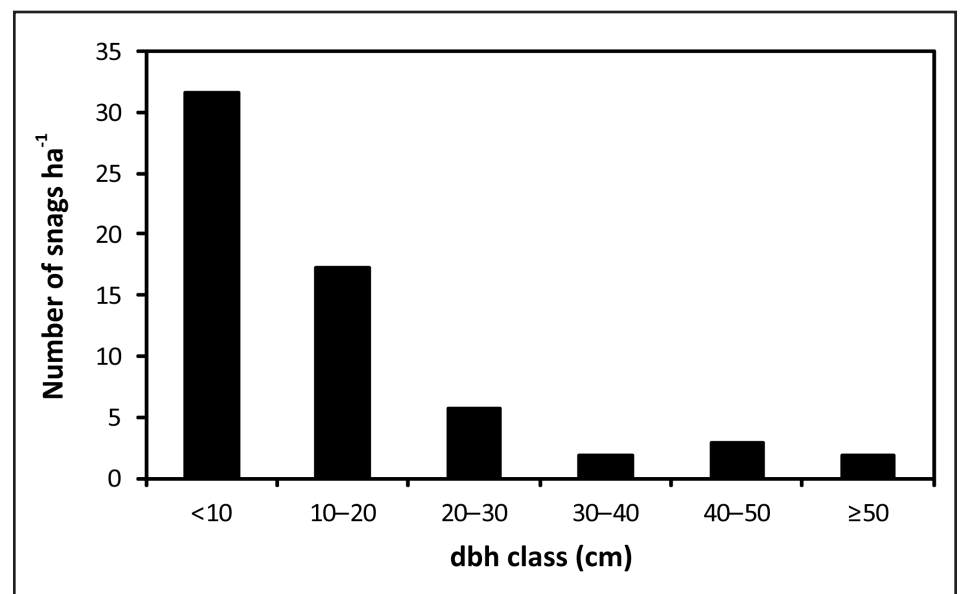
The only woody alien species documented in our study was *L. maackii*. *Lonicera maackii* has invaded forests throughout the eastern United States. This species has seeds that are dispersed widely by birds, do not require a period of dormancy, and can germinate throughout the year (Luken and Goessling 1995; Luken and Thieret 1996). *Lonicera maackii* also has been documented to have a longer growing season than most co-occurring native plants (McEwan et al. 2009) and may benefit from allelopathy (McEwan et al. 2010). *Lonicera maackii* typically occurs in edge habitats and in forests with some canopy disturbance (Hutchinson and Vankat 1997).

We did not collect and analyze age data for *L. maackii*, but it is possible establishment of this species in the HFNA was related to canopy disturbance events. This species represented 7% of woody stems in the seedling layer and occurred on 11% of our plots. This species has been documented to negatively impact native plant growth, survivorship, and reproduction (Collier et al. 2002; Gorchoff and Trisel 2003). Wilson et al. (2013) found that *Quercus* forests, especially mature stands, were more resistant to invasion by this alien species compared to other forest types. The HFNA occurs within metropolitan Nashville, Tennessee, and we speculate that propagule

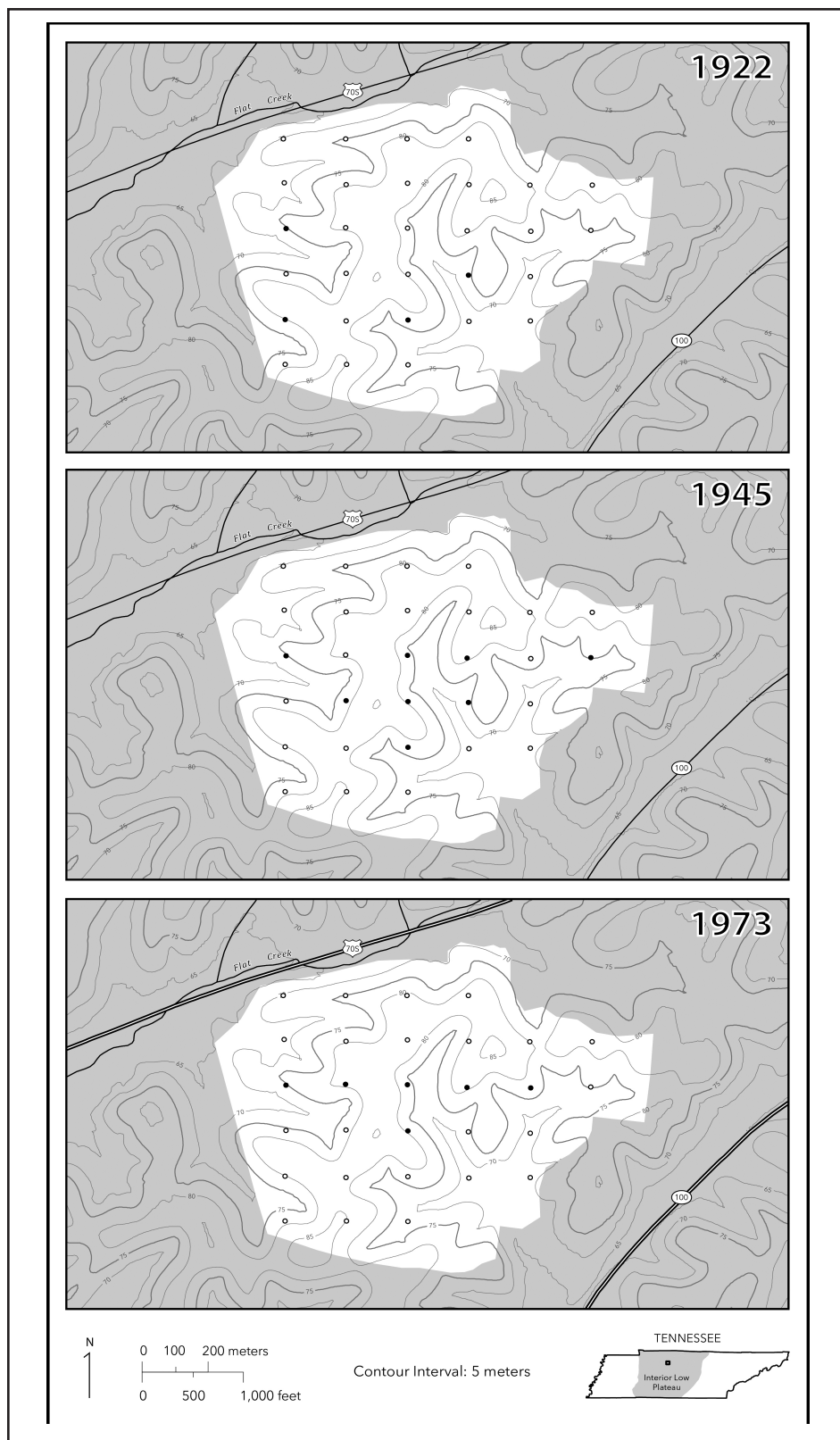
pressure was high. Distance to urban areas has been shown to be positively correlated with *L. maackii* presence in woodlots (Bartuszevige et al. 2006). We hypothesize that this alien species may present a problem for reserve managers.

### Forest Structure

The HFNA exhibited some structural characteristics that typify late-successional forests. For example, basal area of stems ≥10 cm dbh was 23 m<sup>2</sup> ha<sup>-1</sup> and 25 m<sup>2</sup> ha<sup>-1</sup> for live stems ≥5 cm dbh. These values approximate the 25–35 m<sup>2</sup> ha<sup>-1</sup> that has been reported from other late-successional stands in the region (Parker 1989; Martin 1992; Hart, Clark et al. 2012). Martin (1992) suggested that 25 m<sup>2</sup> ha<sup>-1</sup> was the minimum basal area for stems ≥10 cm dbh in late-successional mixed mesophytic forests of the region. Held and Winstead (1975) suggested that 30 m<sup>2</sup> ha<sup>-1</sup> was the average value for late-successional mesic forests. Also, the number of live trees was within the range of what has been reported from late-successional stands elsewhere. We documented 252 live stems ≥10 cm dbh ha<sup>-1</sup> for the HFNA. Stem densities reported from late-successional hardwood forests of the eastern United States vary widely (Tyrell et al. 1998). Parker (1989) reported a range of 161–427 trees ha<sup>-1</sup> in late-suc-



**Figure 4.** Number of snags (≥5 cm dbh) per hectare by diameter class interval in the Hill Forest State Natural Area, Tennessee.

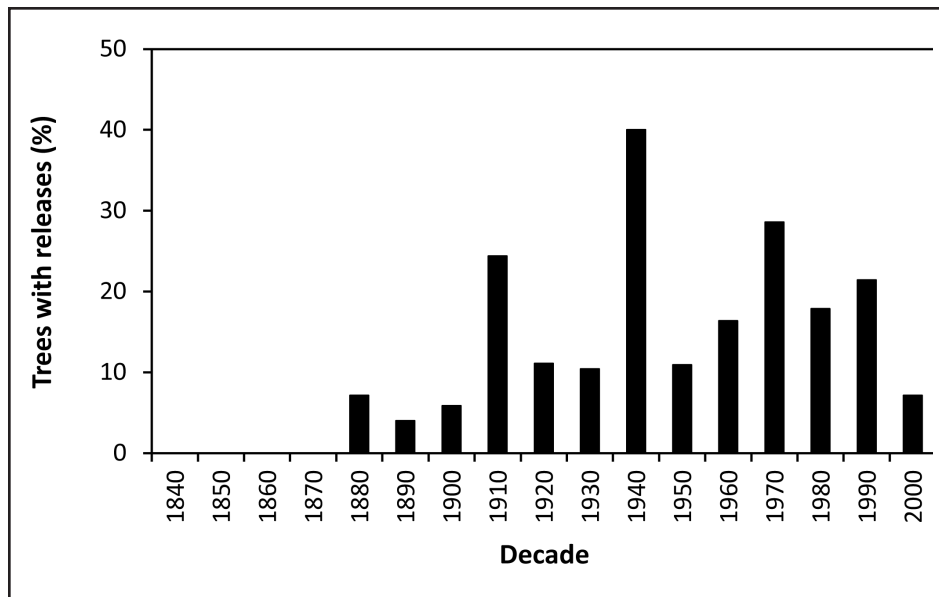


**Figure 5.** Maps of the Hill Forest Natural Area (white) on the Interior Low Plateau in central Tennessee. Hollow circles represent the location of vegetation plots and filled circles represent plots on which a *Quercus* stem exhibited a radial growth release during the forest-wide canopy disturbance events (see text for criteria). On the 1973 map, one filled circle was included because it contained a tree that released in 1974. This plot is depicted here simply to illustrate the spatial extent of the canopy disturbance.

cessional stands of the Central Hardwood Forest, Kupfer and Kirsch (1998) documented a density of 363 trees  $\text{ha}^{-1}$  for a late-successional hardwood stand on the Chickasaw Bluffs of west Tennessee, and Martin (1992) reported a live stem density of 250  $\text{ha}^{-1}$  in a late-successional forest on the Cumberland Plateau in Kentucky. An important structural feature in late-successional forests is the abundance of large trees (Burrascano et al. 2013). The density of live stems  $\geq 70$  cm dbh reported from late-successional stands in the Central Hardwood Forest varies from 0–27  $\text{ha}^{-1}$  (Tyrrell et al. 1998). Parker (1989) suggested that late-successional mesophytic stands should contain a minimum of seven trees  $\geq 75$  cm dbh  $\text{ha}^{-1}$ . On the HFNA we documented eight stems  $\geq 70$  cm dbh  $\text{ha}^{-1}$  and six stems  $\geq 75$  cm dbh  $\text{ha}^{-1}$ . Of note, we documented 20 trees  $\text{ha}^{-1}$  over 60 cm dbh.

Quadratic mean diameters reported from late-successional *Quercus* stands in the Central Hardwood Region range from 32 to 42 cm (Parker et al. 1985; McCarthy et al. 1987; Goebel and Hix 1996; Abrams et al. 1997; Kupfer and Kirsch 1998; McCarthy et al. 2001). Quadratic mean diameter on the HFNA was 29 cm and mean canopy tree dbh was 43 cm. The relatively low quadratic mean diameter of the HFNA may be attributed to forest age, site conditions, and/or disturbance history. For example, larger trees are often disproportionately killed during strong wind events (Peterson 2007; Cowden et al. 2014), such as those that likely resulted in the forest-wide disturbances documented in our study, and the removal of the largest trees would lower quadratic mean diameter. Site factors influence species composition and species-specific growth rates could lead to variability in tree sizes. Regardless of species composition, quadratic mean diameter is influenced by site productivity as productivity affects the rate at which volume accumulates (Nyland 2002). The mean q-factor for the HFNA was 1.4 using 5 cm dbh classes. The inverse J-shaped distribution of the HFNA was within the range of what has been reported from other late-successional *Quercus* stands (Loewenstein 1996; Rentch 2001).

Coarse woody debris, including snags, is



**Figure 6.** 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.

often considered to epitomize late-successional forest structure (Martin 1992; Tyrrell et al. 1998). McComb and Muller (1983) documented 43 snags  $\geq 10$  cm dbh  $ha^{-1}$  in an old-growth forest and Martin (1992) suggested that old-growth forests typically have approximately 10 snags  $\geq 30$  cm dbh  $ha^{-1}$ . We documented 61 total snags of at least 5 cm dbh, 30 snags  $\geq 10$  cm dbh, and seven snags  $\geq 30$  cm dbh  $ha^{-1}$ . Thus, large snag densities on the HFNA were slightly below the values reported in the literature for other late-successional stands in the region. However, we did document two snags  $\geq 50$  cm dbh, with the largest being 69 cm dbh. Most snags were relatively small (mean dbh = 15 cm) and, depending on species-specific decay rates, would be short-lived. We attribute the snag dominance of *S. albidum* to rot resistance and its sensitivity to air pollution, especially ozone (Hacker and Renfro 1992). *Sassafras albidum* heartwood is resistant to decay so *S. albidum* woody debris has a relatively long residence time. Thus, the abundance of *S. albidum* snags may not indicate an unusually high mortality rate for the species, but rather its abundance may be attributed to its decay resistance (Graves et al. 2000). Snag density alone may not be a useful indicator of late-successional structure as a wide range of densities have been reported in the literature and some

studies have found no differences in snag density across stand ages (e.g., Parker and Hart 2014).

### Canopy Disturbance History and Structural Development

From our results, we deduce that the disturbance regime during development of the forest was characterized by broad-scale canopy disturbance events at approximately 30 year intervals. Between these punctuated events, the disturbance regime was characterized by more localized disturbances caused by the death of single trees or small clusters of trees—events which typify most disturbances in deciduous forests of eastern North America (Lorimer 1980; Runkle 1981, 1985, 2000).

Although most canopy disturbances we documented were localized and influenced only microenvironments, the three forest-wide events that occurred over the past century were clearly important drivers of stand development. These events were initiated in 1922, 1945, and 1973. Synchronous release initiations across broad areas indicate exogenous disturbances such as high wind events, ice storms, or selective timber harvesting that would remove canopy trees throughout much of the forest. Although trees may have been

removed individually or in small groups, these disturbances may be considered intermediate-stand scale events (as opposed to gap- or stand-scale) because trees were removed from throughout the forest at a rate well above that of background mortality (Oliver and Larson 1996). Interestingly, the oldest trees in the HFNA established in the 1840s and the first forest-wide disturbance event did not occur until the 1920s. Hart and Grissino-Mayer (2008) documented only one broad-scale canopy disturbance in a hardwood stand 80 years of age on the adjacent Cumberland Plateau in Tennessee. Likewise, Hart et al. (2011) did not document any such disturbances in a hardwood stand 70 years of age on the Highland Rim of Alabama. The absence of forest-wide canopy disturbances during the first 80 years of development may be related to stand age. Although stand age has no bearing on the occurrence of exogenous disturbance events (such as tornadoes), the resulting impacts of these disturbances and responses of residual trees are strongly influenced by stand age. During the stem exclusion and understory reinitiation stages, stands are characterized by high densities of relatively small individuals (Oliver and Larson 1996). The crowns of these trees occupy only small portions of the forest canopy and the loss of such trees via exogenous disturbance results in relatively small canopy voids (Clebsch and Busing 1989; Yamamoto and Nishimura 1999; Hart and Grissino-Mayer 2008; Hart et al. 2011). The resultant void space is rapidly filled by lateral branch growth of adjacent canopy individuals, which are young and grow vigorously (Dahir and Lorimer 1996; Richards and Hart 2011). The mean return interval of forest-wide canopy disturbances from the 1920s through the 1970s was 26 years. Our tree-ring record ended in 2012, which was 39 years since the last forest-wide disturbance event.

We noted relationships between forest-wide canopy disturbance events and tree establishment in the HFNA. The earliest forest-wide disturbance coincided with an establishment pulse of trees in the “others” category. Trees from this taxonomic group that established in the 1920s and 1930s included *S. albidum*, *F. americana*,

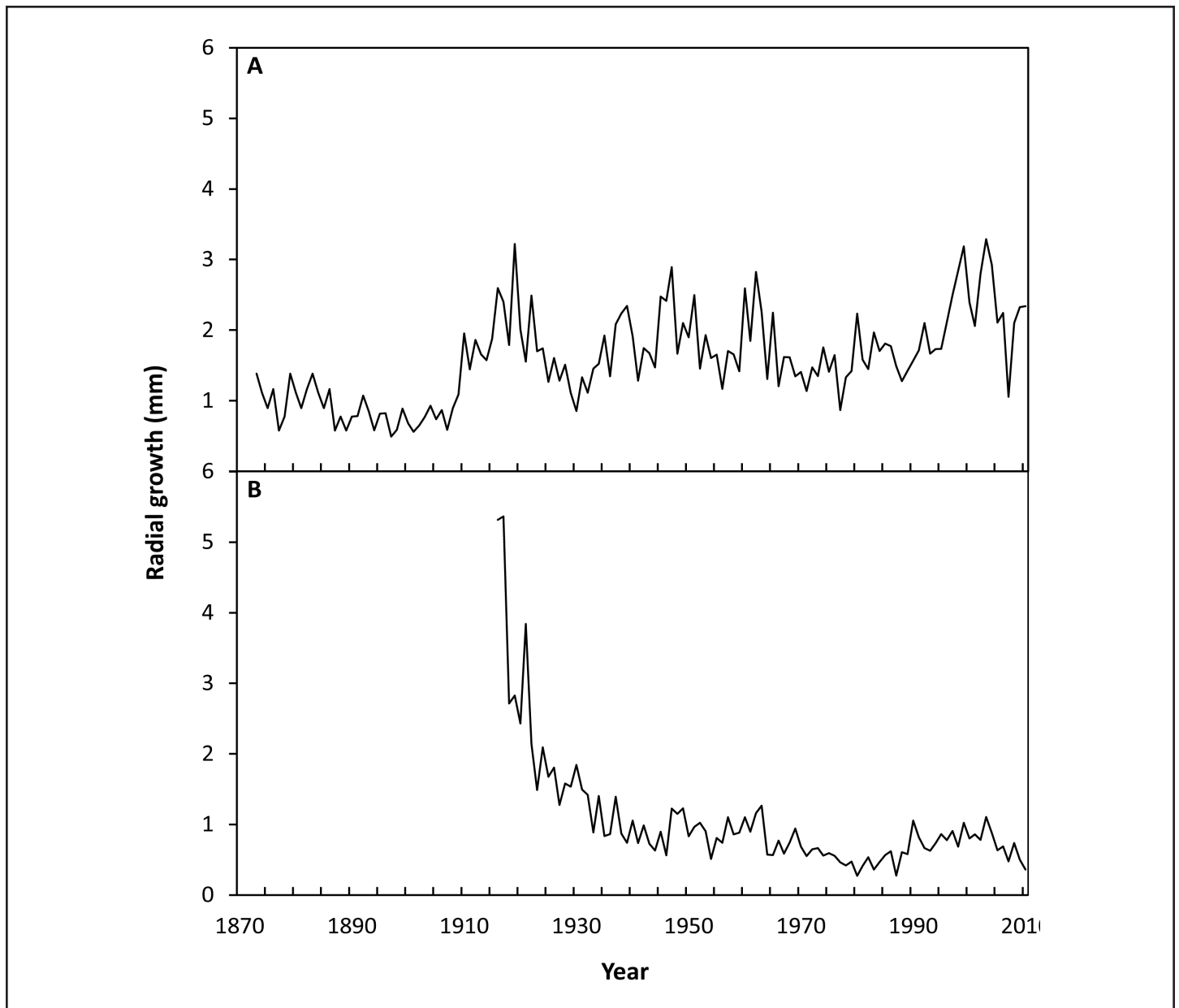


Figure 7. Raw-ring width measurements for (A) an understory origin *Quercus velutina* and (B) a gap origin *Quercus prinus*, from the same overstory vegetation plot in the Hill Forest Natural Area, Tennessee. A forest-wide canopy disturbance event was initiated in 1910.

*D. virginiana*, *U. rubra*, *O. arboretum*, and *C. occidentalis*. It is likely that the enhanced recruitment of *Quercus* and the aforementioned taxa came about after the loss of *Castanea dentata* (Marsh.) Borkh., following the introduction of *Cryphonectria parasitica* Murrill M.E. Barr. Additionally, grazing in the forest stopped with the construction of a fence in the 1920s and an establishment pulse in the 1930s and 1940s could have been a post-grazing release. The forest-wide event of the 1940s coincided with an establishment pulse

of *A. saccharum*. *Carya* species did not exhibit a relationship to these broad-scale disturbance events. In contrast, Cowden et al. (2014) found that establishment and recruitment of *Carya glabra*, *C. ovata*, and *C. alba* were responsive to canopy disturbance events in upland hardwood stands on the Cumberland Plateau in Tennessee. *Quercus* individuals exhibited small and lagged responses. In the decades immediately following the forest-wide events of the 1920s and 1940s, establishment of *Quercus* increased slightly in what was

otherwise a trend toward diminishing establishment. Similar patterns of establishment have been noted in old *Quercus* stands elsewhere in the Central Hardwood Forest Region (e.g., Shumway et al. 2001; Hart et al. 2008; Goins et al. 2013), where a change in disturbance regime coincided with a change in the species composition of the stems which established.

The majority (55%) of *Quercus* trees in our dataset established in open canopy conditions. However, temporal trends in

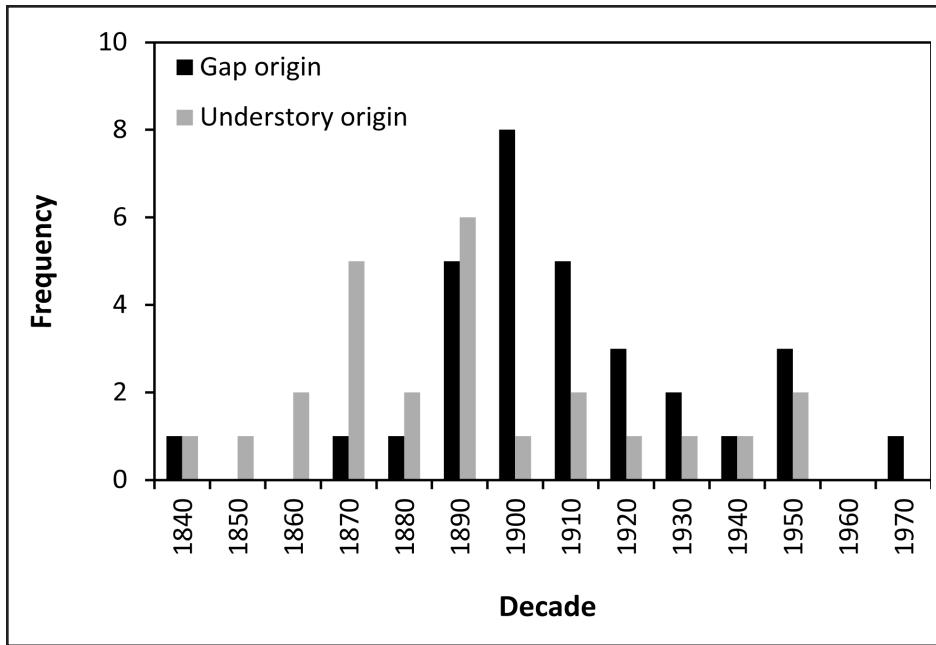


Figure 8. Frequency of establishment dates by decade of *Quercus* trees that established in open (gap) v. closed (understory) canopy conditions.

establishment mode were apparent. Of the 25 *Quercus* trees that established prior to 1900, 68% established in closed canopy conditions, and of the 31 trees that established after 1900, 74% established in open canopy conditions. Thus, canopy establishment mode changed during the development of the forest. Early in forest development, most trees established in the understory of a closed canopy forest. As the forest aged, most *Quercus* trees established in high light environments associated with disturbance. The mean suppression period for understory origin trees was 27 years, with a maximum understory residence of 62 years. These times are within the range reported by Rentch et al. (2003) and Hart, Clark et al. (2012). Our findings support the hypothesis of Abrams (1996), that in the absence of competition from shade-tolerant taxa in the sub-canopy, *Quercus* trees are relatively tolerant of understory conditions. Without competition from mesophytes, *Quercus* have the physiological capability for long-term survival beneath a *Quercus* canopy and may be considered a gap-phase genus (Orwig and Abrams 1995; Abrams 1996) as these trees are able to persist in low light conditions and maintain the ability to respond to increased resources associated with canopy disturbance in their vicinity. The abundance of understory

origin trees prior to 1900 indicates that the site had forest cover at the time the oldest trees in our dataset established during the mid-1800s. Thus, we hypothesize the stand was not completely cleared in the 1800s and may not have been cleared since Euro-American settlement.

### Management Implications

Restoration of late-successional structure is becoming an increasingly prevalent objective of forest management throughout the eastern United States and this is especially true for public lands. To our knowledge, the HFNA is the only documented late-successional forest on the southern Interior Low Plateau. Although many structural characteristics of the HFNA are within the range of those reported from late-successional *Quercus*-dominated forests throughout the eastern United States, estimates on simple structural attributes such as trees  $\text{ha}^{-1}$  and basal area  $\text{ha}^{-1}$  vary greatly within a single forest type (Tyrrell et al. 1998; Burrascano et al. 2013). Therefore, the HFNA may provide a reference for stands situated in comparable biophysical settings and provides another datum for meta-analyses of forest disturbance and structural conditions.

Restoration of late-successional structure in *Quercus*-dominated forests is complicated if managers wish to maintain a strong *Quercus* component. *Quercus* are only moderately tolerant of shade and most species are typically classed as mid-successional. Indeed, a widespread regeneration failure has been documented in *Quercus* stands throughout the Central Hardwood Forest of the eastern United States (Nowacki and Abrams 2008; McEwan et al. 2011). These stands contain abundant shade-tolerant mesophytes, especially *A. saccharum*, *A. rubrum*, and *F. grandifolia*, in the understory. Without active management, large expanses of this region are expected to experience major shifts in canopy species composition. Regeneration of *Quercus* in *Quercus*-dominated systems is largely dependent upon canopy disturbance and associated changes in the understory light regime (Gottschalk 1983; Dey 2002). Indeed, spatial and temporal variability in understory light should be considered when planning silvicultural entries (Grayson et al. 2012). Group selection and shelterwood systems, treatments that are in accord with the historical disturbance regime of the HFNA, may modify sub-canopy light to favor *Quercus* and other shade-intolerant and moderately tolerant taxa (Schweitzer and Dey 2011; Grayson et al. 2012). In stands with abundant shade-tolerant mesophytes in the understory, these regeneration harvests should be timed in conjunction with competition reduction measures such as fire or herbicide application (Schweitzer and Dey 2011; Hutchinson et al. 2012; Brose et al. 2013). Such competition reduction measures may not have been elements of the historical disturbance regime, but may now be needed to maintain *Quercus* and other mid-successional taxa.

### ACKNOWLEDGMENTS

Funding for this research was provided by the University of the South through the Raoul Conservation and Environmental Studies Fund and the Department of Forestry and Geology. We thank the staff of Percy Warner Parks, Nashville, Tennessee, and the Friends of Warner Parks for facilitating our research and for access to the study area. We also thank the Tennessee

Department of Environment and Conservation for access to the Hill Forest Natural Area. Additional thanks are extended to the H.G. Hill Company for access to land records and for consultation.

*Justin Hart is an Associate Professor in the Department of Geography and Director of the Environmental Science Program at the University of Alabama. His research interests are in forest developmental patterns and processes and forest disturbance ecology.*

*Merrit Cowden earned an MS with a focus in Forest Science and Management from the University of Alabama. She is currently an Environmental Analyst with Kimley-Horn, Inc.*

*Scott Torreano is a Professor of Forestry in the Department of Forestry and Geology, The University of the South, Sewanee, TN. His research interests include forest soils and ecology.*

*Patrick Vestal earned a BS in Natural Resources and the Environment from The University of the South, Sewanee, TN. He currently works as a Staff Scientist with Environmental Resources Management.*

## LITERATURE CITED

- Abrams, M.D. 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. *Annales des Sciences Forestieres* 53:487-512.
- Abrams, M.D., and G.J. Nowacki. 1992. Historical variation in fire, oak recruitment, and post-logging accelerates succession in central Pennsylvania. *Journal of the Torrey Botanical Society* 119:19-28.
- Abrams, M.D., D.A. Orwig, and M.J. Dockry. 1997. Dendroecology and successional status of two contrasting old-growth oak forests in the Blue Ridge Mountains, USA. *Canadian Journal of Forest Research* 27:994-1002.
- Bartuszevige, A., D. Gorchoff, and L. Raab. 2006. The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape. *Ecography* 29:213-222.
- Begon, M., J.L. Harper, and C.R. Townshend. 1986. *Ecology: Individuals, Populations, and Communities*. Sinauer Associates, Sunderland, MD.
- Boyce, S.G. 1995. *Landscape Forestry*. John Wiley and Sons, New York.
- Braun, E.L. 1950. *Eastern Deciduous Forests of North America*. Blakiston Publishing, Philadelphia, PA.
- Brose, P.H., D.C. Dey, R.J. Phillips, and T.A. Waldrop. 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America? *Forest Science* 59:322-334.
- Buchanan, M.L., and J.L. Hart. 2012. Canopy disturbance history of old-growth *Quercus alba* sites in the eastern United States: examination of long-term trends and broad-scale patterns. *Forest Ecology and Management* 267:28-39.
- Burrascano, S., W.S. Keeton, F.M. Sabatini, and C. Blasi. 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: a global review. *Forest Ecology and Management* 291:458-479.
- Clebsch, E.E.C., and R.T. Busing. 1989. Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. *Ecology* 70:728-735.
- Collier, M.H., J.L. Vankat, and M.R. Hughes. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *American Midland Naturalist* 147:60-71.
- Cowden, M.C., J.L. Hart, and M.L. Buchanan. 2014. Canopy accession strategies and climate responses for three *Carya* species common in the Eastern Deciduous Forest. *Trees* 28:223-235.
- Cowden, M.C., J.L. Hart, C.J. Schweitzer, and D.C. Dey. 2014. Effects of intermediate-scale wind disturbance on composition, structure, and succession in *Quercus* stands: implications for natural disturbance-based silviculture. *Forest Ecology and Management* 330:240-251.
- Dahir, S.E., and C.G. Lorimer. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. *Canadian Journal of Forest Research* 26:1875-1892.
- Dey, D.C. 2002. Ecological basis for oak silviculture in eastern North America. Pp. 60-79 in W.J. McShea and W.M. Healey, eds., *Oak Forest Ecosystems: Ecology and Management for Wildlife*. Johns Hopkins University Press, Baltimore, MD.
- Dyer, J.M. 2006. Revisiting the deciduous forests of eastern North America. *BioScience* 56:341-352.
- Edwards, M.J., J.A. Elder, and M.E. Springer. 1974. The soils of the Nashville Basin. *Bulletin* 499, University of Tennessee Agricultural Experimental Station, US Department of Agriculture, Soil Conservation Service, [Washington, D.C.].
- Fenneman, N.M. 1938. *Physiography of Eastern United States*. McGraw-Hill Book Company, New York.
- Fraver, S., and A.S. White. 2005. Identifying growth releases in dendrochronological studies of forest disturbance. *Canadian Journal of Forest Research* 35:1648-1656.
- Frellich, L.E. 2002. *Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-deciduous Forests*. Cambridge University Press, Cambridge, UK.
- Goebel, P.C., and D.M. Hix. 1996. Development of mixed-oak forests in southeastern Ohio: a comparison of second-growth and old-growth forests. *Forest Ecology and Management* 84:1-21.
- Goins, S.M., J.I. Chapman, and R.W. McEwan. 2013. Composition shifts, disturbance, and canopy-accession strategy in an old-growth forest of southwestern Ohio, USA. *Natural Areas Journal* 33:384-394.
- Gorchoff, D.L., and D.E. Trisel. 2003. Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. *Plant Ecology* 166:13-24.
- Gottshalk, K.W. 1983. Management strategies for successful regeneration: oak-hickory. Pp. 190-213 in *Proceedings of 1983 Pennsylvania State Forestry Issues Conference—Regenerating Hardwood Stands*. Pennsylvania State University, University Park.
- Graves, A.T., M.A. Fajvan, and W.G. Miller. 2000. The effects of thinning intensity on snag and cavity tree abundance in an Appalachian hardwood stand. *Canadian Journal of Forest Research* 30:1214-1220.
- Grayson, S.F., D.S. Buckley, J.G. Henning, C.J. Schweitzer, K.W. Gottshalk, and D.L. Loftis. 2012. Understory light regimes following silvicultural treatments in central hardwood forests in Kentucky, USA. *Forest Ecology and Management* 279:66-76.
- Grissino-Mayer, H.D. 2001a. Evaluating cross-dating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57:205-221.
- Grissino-Mayer, H.D. 2001b. FHX2—Software for analyzing temporal and spatial patterns of fire regimes from tree rings. *Tree-Ring Research* 57:115-124.
- Hacker, D., and J. Renfro. 1992. Great Smoky Mountain plants studied for ozone sensitivity. *Park Science* 12:6-7.
- Hale, C.M., J. Pastor, and K.A. Rusterholz. 1999. Comparison of structural and com-



- positional characteristics in old-growth and mature, managed hardwood forests of Minnesota, U.S.A. *Canadian Journal of Forest Research* 29:1479-1489.
- Hart, J.L., A.A.R. Bhuta, and R.M. Schneider. 2011. Canopy disturbance patterns in secondary hardwood stands on the Highland Rim of Alabama. *Castanea* 76:55-63.
- Hart, J.L., M.L. Buchanan, S.L. Clark, and S.J. Torreano. 2012. Canopy accession strategies and climate-growth relationships in *Acer rubrum*. *Forest Ecology and Management* 282:124-132.
- Hart, J.L., S.L. Clark, S.J. Torreano, and M.L. Buchanan. 2012. Composition, structure, and dendroecology of an old-growth *Quercus* forest on the tablelands of the Cumberland Plateau, USA. *Forest Ecology and Management* 266:11-24.
- Hart, J.L., and H.D. Grissino-Mayer. 2008. Vegetation patterns and dendroecology of a mixed hardwood forest on the Cumberland Plateau: implications for stand development. *Forest Ecology and Management* 255:1960-1975.
- Hart, J.L., S.L. van de Gevel, and H.D. Grissino-Mayer. 2008. Forest dynamics in a natural area of the southern Ridge and Valley, Tennessee. *Natural Areas Journal* 28:275-289.
- Held, M.E., and J.E. Winstead. 1975. Basal area and climax status in mesic forest systems. *Annals of Botany* 39:1147-1148.
- Henry, J.D., and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material: an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55:772-783.
- Holmes, R.L. 1983. Computer assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43:69-78.
- Hunter, M.L., Jr. 1990. *Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity*. Prentice-Hall, Englewood Cliffs, New Jersey.
- Hutchinson, T.F., R.E.J. Boerner, S. Sutherland, E.K. Sutherland, M. Ortt, and L.R. Iverson. 2012. Prescribed fire effects on the herbaceous layer of mixed-oak forests. *Canadian Journal of Forest Research* 35:877-890.
- Hutchinson, T.F., and J.L. Vankat. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. *Conservation Biology* 11:1117-1124.
- Johnson, P.S. 2004. Thinking about oak forests as responsive ecosystems. Pp. 13-18 in M.A. Spetich, ed., *Upland Oak Ecology Symposium: History, Current Conditions, Sustainability*. GTR-SRS-73, USDA Forest Service, Asheville, NC.
- Keeton, W.S. 2005. Managing for old-growth structure in northern hardwood forests. Pp. 107-117 in C.E. Peterson and D.A. Maguire, eds., *Balancing Ecosystem Values: Innovative Experiments for Sustainable Forestry*. GTR-PNW-635, USDA Forest Service, Portland, OR.
- Keeton, W.S. 2006. Managing for late successional/old-growth characteristics in northern hardwood-conifer forests. *Forest Ecology and Management* 235:129-142.
- Kenefic, L.S., and R.D. Nyland. 2000. *Habitat Diversity in Uneven-aged Northern Hardwood Stands: A Case Study*. GTR-NRS-714, USDA Forest Service, Newtown Square, PA.
- Kupfer, J.A., and S.W. Kirsch. 1998. Heterogeneity of forest characteristics in primary and secondary forest stands on the Third Chickasaw Loess Bluff, Tennessee. *Physical Geography* 19:35-54.
- Loewenstein, E.F. 1996. *An Analysis of the Size- and Age-structure of a Managed Uneven-aged Oak Forest*. PhD dissertation, University of Missouri, Columbia.
- Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 61:1169-1184.
- Lorimer, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. *Canadian Journal of Forest Research* 15:200-213.
- Lorimer, C.G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. *Wildlife Society Bulletin* 29:425-439.
- Lorimer, C.G., and L.E. Frelich. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* 19:651-663.
- Ludwig, J.A., and J.F. Reynolds. 1988. *Statistical Ecology: A Primer on Methods and Computing*. John Wiley and Sons, New York.
- Luken, J.O., and N. Goessling. 1995. Seedling distribution and potential persistence of the exotic shrub *Lonicera maaackii* in fragmented forests. *American Midland Naturalist* 13:124-130.
- Luken, J.O., and J.W. Thieret. 1996. Amur honeysuckle, its fall from grace. *BioScience* 46:18-24.
- Martin, W.H. 1992. Characteristics of old-growth mixed mesophytic forests. *Natural Areas Journal* 12:127-135.
- McCarthy, B.C., C.A. Hammer, G.L. Kauffman, and P.D. Cantino. 1987. Vegetation patterns and structure of an old-growth forest of southeastern Ohio. *Bulletin of the Torrey Botanical Club* 114:33-45.
- McCarthy, B.C., C.J. Small, and D.L. Rubino. 2001. Composition, structure, and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. *Forest Ecology and Management* 140:193-213.
- McComb, W.C., and R.N. Muller. 1983. Snag densities in old-growth and second-growth Appalachian forests. *Journal of Wildlife Management* 47:376-382.
- McEwan, R.W., M.K. Birchfield, A. Schoerendorfer, and M.A. Arthur. 2009. Leaf phenology and freeze tolerance of the invasive shrub Amur honeysuckle and potential native competitors. *Journal of the Torrey Botanical Society* 136:212-220.
- McEwan, R.W., L.G. Arthur-Paratley, L.K. Rieske, and M.A. Arthur. 2010. A multi-assay comparison of seed germination inhibition by *Lonicera maaackii* and co-occurring native shrubs. *Flora* 205:475-483.
- McEwan, R.W., J.M. Dyer, and N. Pederson. 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography* 34:234-256.
- McEwan, R.W., and B.C. McCarthy. 2008. Anthropogenic disturbance and the formation of oak savanna in central Kentucky, USA. *Journal of Biogeography* 35:965-975.
- North, O.L. 1981. *Soil Survey of Davidson County, Tennessee*. USDA Soil Conservation Service, Nashville, TN.
- Nowacki, G.J., and M.D. Abrams. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67:225-249.
- Nowacki, G.J., and M.D. Abrams. 2008. The demise of fire and "mesophication" of forests in the eastern United States. *BioScience* 58:123-138.
- Nyland, R.D. 2002. *Silviculture: Concepts and Applications*. McGraw-Hill, New York.
- Oliver, C.D. 1981. Forest development in North America following major disturbances. *Forest Ecology and Management* 3:153-168.
- Oliver, C.D., and B.C. Larson. 1996. *Forest Stand Dynamics*. McGraw-Hill, New York.
- Oliver, C.D., and E.P. Stephens. 1977. Reconstruction of a mixed-species forest in central New England. *Ecology* 58:562-572.
- Orvis, K.H., and H.D. Grissino-Mayer. 2002. Standardizing the reporting of abrasive papers used to surface tree-ring samples. *Tree-Ring Research* 58:47-50.
- Orwig, D.A., and M.D. Abrams. 1995. Dendroecological and ecophysiological analysis of gap environments in mixed-oak understories of northern Virginia. *Functional Ecology* 9:799-806.

- Parker, G.R. 1989. Old-growth forests of the central hardwood region. *Natural Areas Journal* 9:5-11.
- Parker, R.P. and J.L. Hart. 2014. Patterns of riparian and in-stream large woody debris across a chronosequence of southern Appalachian hardwood stands. *Natural Areas Journal* 34:65-78.
- Parker, G.R., D.J. Leopold, and J.K. Eichenberger. 1985. Tree dynamics in an old-growth, deciduous forest. *Forest Ecology and Management* 11:31-57.
- Pederson, N. 2010. External characteristics of old trees in the eastern deciduous forest. *Natural Areas Journal* 30:396-407.
- Peterson, C.J. 2007. Consistent influence of tree diameter and species on damage in nine eastern North America tornado blow-downs. *Forest Ecology and Management* 250:96-108.
- PRISM Climate Group. 2013. PRISM Climate Data [online]. Accessed 3 June 2013 <<http://www.prism.oregonstate.edu/>>.
- Rentch, J.S. 2001. Stand Dynamics and Disturbance History of Five Oak-dominated Old-growth Stands in the Unglaciaded Appalachian Plateau. PhD dissertation, West Virginia University, Morgantown.
- Rentch, J.S., M.A. Fajvan, and R.R. Hicks, Jr. 2003. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region. *Forest Ecology and Management* 184:285-297.
- Rentch, J.S., D. Fekedulegn, and G.W. Miller. 2002. Climate, canopy disturbance, and radial growth averaging in a second-growth mixed-oak forest in West Virginia, USA. *Canadian Journal of Forest Research* 32:915-927.
- Richards, J.D., and J.L. Hart. 2011. Canopy gap dynamics and development patterns in secondary *Quercus* stands on the Cumberland Plateau, Alabama, USA. *Forest Ecology and Management* 262:2229-2239.
- Rubino, D.L., and B.C. McCarthy. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia* 21:97-115.
- Ruffner, C.M., and M.D. Abrams. 1998. Relating land-use history and climate to the dendroecology of a 326-year old *Quercus prinus* talus slope forest. *Canadian Journal of Forest Research* 28:347-358.
- Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62:1041-1051.
- Runkle, J.R. 1985. Disturbance regimes in temperate forests. Pp. 17-33 in S.T.A. Pickett and P.S. White, eds., *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Runkle, J.R. 2000. Canopy tree turnover in old growth mesic forests of eastern North America. *Ecology* 81:554-567.
- Schweitzer, C.J., and D.C. Dey. 2011. Forest structure, composition, and tree diversity response to a gradient of regeneration harvests in the mid-Cumberland Plateau escarpment region, USA. *Forest Ecology and Management* 262:1729-1741.
- Seymour, R.S., A.S. White, and P.G. DeMaynard. 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management* 155:357-367.
- Shumway, D.L., M.D. Abrams, and C.M. Ruffner. 2001. A 400-year history of fire in an old-growth oak forest in western Maryland, USA. *Canadian Journal of Forest Research* 31:1437-1443.
- Smalley, G.W. 1983. Classification and Evaluation of Forest Sites on the Mid-Cumberland Plateau. GTR-SRS-38, USDA Forest Service, New Orleans, LA.
- Spetich, M.A., S.R. Shifley, and G.R. Parker. 1999. Regional distribution and dynamics of coarse woody debris in Midwestern old-growth forests. *Forest Science* 45:302-313.
- Stokes, M.A., and T.C. Smiley. 1996. *An Introduction to Tree-Ring Dating*. University of Arizona Press, Tucson.
- Thornthwaite, C.W. 1948. An approach towards rational classification of climate. *Geographical Review* 38:55-94.
- Tyrrell, L.E., G.J. Nowacki, T.R. Crow, D.S. Buckley, E.A. Nauertz, J.N. Niese, J.L. Rollinger, and J.C. Zasada. 1998. Information about Old-growth for Selected Forest Type Groups in the Eastern United States. GTR-NC-197, USDA Forest Service, St. Paul, MN.
- Whitney, G. 1994. *From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America from 1500 to the Present*. Cambridge University Press, Cambridge, UK.
- Wilson, H.N., M.A. Arthur, A. Schorgendorfer, R.D. Paratley, B.D. Lee, and R.W. McEwan. 2013. Site characteristics as predictors of *Lonicera maackii* in second-growth forests of central Kentucky, USA. *Natural Areas Journal* 33:189-198.
- Yamamoto, S., and N. Nishimura. 1999. Canopy gap formation and replacement pattern of major tree species among development stages of beech (*Fagus crenata*) stands. *Japanese Plant Ecology* 140:167-176.