Investigating the composition and structure of old-growth forests provides information about the spatial and temporal variability of processes responsible for stand development, succession, and biogeographic patterns of forests. This study quantifies stand structure in the Marshall Forest Preserve, an old-growth forest remnant located in northwest Georgia. We established forest inventory plots to quantify species composition, stand structure, and successional dynamics. We also analyzed the radial growth patterns of trees to document stand age, recruitment, and the frequency of canopy disturbance within the preserve. The forest was dominated by shortleaf pine (Pinus echinata Mill.) and chestnut oak (Quercus montana Willd.), while red maple (Acer rubrum L.) and mockernut hickory (Carya tomentosa Nutt.) were abundant in the understory. Shortleaf pine was the oldest tree species in the preserve, with the oldest individuals exceeding 220 years in age. A clear successional pattern developed over the 20th century with the establishment of hickory and maple after pine and oak. The major agent of 20th century canopy disturbance was ice storms, which generally resulted in suppression of radial growth in pines and increased radial growth in oaks. Additionally, pulses of understory establishment coincided with major ice storms. The lack of understory disturbance such as fire may be allowing the establishment of shade tolerant understory species while limiting the establishment of pine and oak. Canopy disturbance from ice storms may be accelerating the pace of this compositional shift. Under the current disturbance regime, composition of the preserve is likely to change, leading to an increase in red maple and mockernut hickory and a decline in pine and oak species.

Investigando la composición y estructura de los bosques de viejo crecimiento proporciona información acerca de la variabilidad espacial y temporal de los procesos responsables de desarrollo del rosal, la sucesión y los patrones biogeográficos de los bosques. Este estudio cuantifica la estructura rosal en la reserva de bosque Marshall, un remanente de bosque de viejo crecimiento situada en el noroeste de Georgia. Establecimos
parcelas de inventario forestal para cuantificar la composición de especies, la estructura rodal y la dinámica sucesional. También analizamos los patrones de crecimiento radial de los árboles para documentar la edad del rodal, el reclutamiento y la frecuencia de perturbación del dosel dentro de la reserva. El bosque era dominado por el pino de hoja corta (Pinus echinata Mill.) y el castaño de roble (Quercus montana Willd.), mientras que el arce rojo (Acer rubrum L.) y la nuez dura de mockernut (Carya tomentosa Nutt.) eran abundantes en el sotobosque. Pino de hoja corta fue la especie de árbol más antiguo en la reserva, con los más viejos excediendo 220 años de edad. Un patrón sucesional claro desarrolló sobre del siglo 20 con el establecimiento de la nuez dura y arce después de pino y roble. El agente principal de perturbación del dosel en el siglo 20 fue tormentas de hielo, que en general resultaron en la supresión del crecimiento radial de los pinos y el aumento en el crecimiento radial de los robles. Además, los pulsos de establecimiento sotobosque coincidieron con grandes tormentas de hielo. La falta de perturbación del sotobosque como el fuego puede estar permitiendo el establecimiento de especies tolerantes a la sombra de sotobosque mientras limitan el establecimiento de pino y roble. La perturbación del dosel por causa de las tormentas de hielo puede estar acelerando el ritmo de este cambio composicional. Bajo el régimen de perturbación actual, la composición de la reserva es probable que cambie, lo que lleva a un aumento de arce rojo y nuez dura de mockernut y una disminución de las especies de pino y roble.

**PALABRAS CLAVE:** dendroecología, sucesión ecológica, reserva de bosque Marshall, bosque caducifolio oriental

**INTRODUCTION**

North American old-growth forests are important for understanding both forest conditions prior to the influence of European settlers, as well as biogeographic patterns such as long-term variability in stand structure, composition, and disturbance regimes. Rare, remnant patches of old-growth forests permit the reconstruction of forest conditions prior to landscape-scale, anthropogenic alteration of ecosystems. Reconstruction of long-term variability in forest composition, structure, and disturbances also provide understanding of the ecological processes influencing stand development and community dynamics (Lorimer 1985; Hart et al. 2012).

Disturbance events such as fire (Abrams 1992), wind throw (Brewer and Merritt 1978), and ice storms (Lafon and Speer 2002; Knight 2003) can alter forest structure and affect stand development by creating canopy gaps of various sizes, which allows tree colonization within gaps and results in a landscape mosaic of uneven-aged patches (Lorimer 1980; Barden 1981; Runkle 1982). Additionally, reconstructions can provide valuable reference conditions for land management efforts aimed at maintaining or restoring the historic patterns of ecological processes in forests (Swetnam et al. 1999). For example, silvicultural treatments intended to create canopy gaps have been refined to mimic the size and spatial arrangement of historic disturbances at landscape scales based on reconstructions conducted in old-growth stands (Coates and Burton 1997; Seymour et al. 2002; Hanson and Lorimer 2007).

**PALABRAS CLAVE:** dendroecología, sucesión ecológica, reserva de bosque Marshall, bosque caducifolio oriental
Old-growth forest remnants—stands with trees that are old for their species and a high degree of structural complexity (Oliver and Larson 1996)—are rare in the eastern United States (Davis 1996). Most of the deciduous forests of eastern North America were subject to widespread land clearing for agriculture and timber harvest during the period of European settlement in the 18th and 19th centuries (Cowell 1998). Thus, most contemporary stands of Eastern Deciduous Forest consist of second-growth stands in recent stages of stand development (Cowell 1998; Motzkin et al. 1999; Hart and Shankman 2005; Hart et al. 2010). Due to the scarcity of old-growth forests, the amount of empirical data on the contemporary and historical conditions of eastern old-growth forests is limited. Therefore, the remaining patches of old-growth forest provide an important opportunity to examine past and present compositional and structural patterns, as well as the successional trajectory of stands (Abrams and Copenheaver 1999).

Following the severe disturbances during the period of European settlement, many stands in the Eastern Deciduous Forest are thought to be undergoing structural and compositional shifts instead of returning to their pre-settlement conditions (Cowell 1998). Oaks (Quercus spp.) are dominant in the overstory of many eastern deciduous forests, but a scarcity of oak regeneration along with abundant regeneration of shade-tolerant species, such as red maple (Acer rubrum L.), in the understory has been documented in locations across eastern North America (Lorimer 1984; Goebel and Hix 1996; Hutchinson et al. 2005; McEwan and Muller 2006). The compositional transition from oak-dominated to maple-dominated stands is often attributed to a change in disturbance regimes. Specifically, a decrease in fire frequency is generally recognized as the cause of this compositional shift (Abrams 1992; Brose and Waldrop 2006). However, several other factors coinciding with the shift in species dominance have been proposed as drivers of compositional dynamics including, climate change, land-use change, loss of foundation species, and herbivore population dynamics (McEwan et al. 2011).

A similar decline of pine (Pinus spp.) regeneration in mixed oak-pine stands in the Eastern Deciduous Forest is also attributed to an alteration of disturbance regimes (Brose and Waldrop 2006, 2010). Oak-pine forest communities in the southern Appalachian Mountains form distinct stands that contrast sharply with surrounding forest dominated solely by deciduous tree species (Braun 1950). These forest communities are valued for wildlife habitat, watershed protection, timber resources, and are recognized for the contribution they make to the compositional and structural diversity of landscapes of the Eastern Deciduous Forest et al. 2010). Dendrochronological reconstructions of tree establishment in Appalachian pine-oak stands have revealed that continuous or episodic establishment of pine and oak species was related to stand-replacing fires and canopy disturbances such as ice storms and wind throw (Brose and Waldrop 2010). Furthermore, the second half of the 20th century was characterized by fewer disturbances and limited pine and oak regeneration (Brose and Waldrop 2006).

In the Eastern Deciduous Forest biome of the United States, the few stands of old-growth forest that remain are dominated
In this study, we investigate the composition, structure, and disturbance history of Marshall Forest Preserve (MFP), a small natural area containing old-growth pine-oak forest in northwest Georgia (Figure 1). Situated in the city of Rome, Georgia, the site is one of the only remaining parcels of old-growth forest located entirely within the city limits of any city in eastern North America (DeSelm 1984). In addition to its importance as a remnant old-growth pine-oak stand, MFP contains approximately 23 individuals of montane longleaf pine (Pinus palustris Mill.), a critically endangered ecotype of longleaf pine (Noss et al. 1995). In this paper, we used dendroecological methods to investigate the structure and dynamics of Marshall by oak and pine species with an understory of red maple and other shade-tolerant, fire-intolerant species. Previous research in eastern deciduous forests demonstrated that oaks are currently underrepresented in smaller size classes, which is an indication of tree recruitment failure (Abrams 1992; Nowacki and Abrams 2008; McEwan et al. 2011). These studies concluded that the reduction of oak importance will be accompanied by an increase of importance of shade-tolerant species such as red maple (Lorimer 1984; Tift and Fajvan 1999), which may reduce landscape-scale biodiversity and require new management practices to mitigate undesirable compositional transitions (Loftis and McGee 1993).
An Old-Growth Pine-Oak Community

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The Ridge and Valley physiographic province of the Appalachian Mountains, which is characterized by folded layers of sedimentary rock forming long, parallel ridges of sandstone interspersed with valleys of shale or limestone (DeSelm 1984). MFP is located on Horseleg Mountain, a ridge underlain by Armuchee chert and Conasauga shale (DeSelm 1984). Soils at MFP are shallow, well-drained, silt loams formed from shale residuum (Web Soil Survey 2010). Elevations within MFP range from 200–300 m above sea level. The study area has a humid continental climate with mild winters and hot summers. Mean monthly temperatures in this region range from

Forest Preserve. Specifically, our research goals were to: (1) quantify stand structure and composition, (2) reconstruct disturbance history, and (3) identify the relationships between disturbance history and stand structure to better understand the successional trajectory of MFP.

STUDY SITE

Marshall Forest Preserve consists of approximately 120 ha of minimally-disturbed, old-growth forest located in the city of Rome, Georgia in the northwest part of the state (34° 15' N, 85° 12’ W) (Figure 2). MFP is located in the southern portion of the Ridge and Valley physiographic province of the Appalachian Mountains, which is characterized by folded layers of sedimentary rock forming long, parallel ridges of sandstone interspersed with valleys of shale or limestone (DeSelm 1984). MFP is located on Horseleg Mountain, a ridge underlain by Armuchee chert and Conasauga shale (DeSelm 1984). Soils at MFP are shallow, well-drained, silt loams formed from shale residuum (Web Soil Survey 2010). Elevations within MFP range from 200–300 m above sea level. The study area has a humid continental climate with mild winters and hot summers. Mean monthly temperatures in this region range from

Figure 2. Map of the Marshall Forest Preserve study area (black circle) in Rome, Georgia and the distribution of physiographic provinces in the southeastern United States.
5° C in January to 25° C in July. Mean annual precipitation is approximately 1100 mm, and is evenly distributed throughout the year (PRISM 2004).

The vegetation in MFP is primarily pine-oak forest dominated by shortleaf pine and chestnut oak. Mockernut hickory (*Carya tomentosa* Nutt.), shagbark hickory (*Carya ovata* (Mill.) K. Koch.), northern red oak (*Quercus rubra* L.), southern red oak (*Quercus falcata* Michx.), sourwood (*Oxydendrum arboretum* (L.) DC.), white oak (*Quercus alba* L.), and tulip poplar (*Liriodendron tulipifera* L.) are also minor components of the canopy, especially in mesic locations lower on the north-facing slope of the ridge. In the understory, red maple and black gum (*Nyssa sylvatica* Marsh.) are common, and flowering dogwood (*Cornus florida* L.) and black cherry (*Prunus serotina* Ehrh.) are occasionally found. Longleaf pine in MFP is primarily interspersed in the canopy with shortleaf pine and chestnut oak near the ridgetop on the southwest-facing slope. However, only about 23 individual longleaf pines are scattered across the site. We encountered no longleaf pine in our plots while sampling.

Commercial logging did not occur in Marshall Forest Preserve (DeSelm 1984), but evidence of some timber harvest is discernible from remnant stumps scattered mostly along the southern boundary of the preserve. MFP was designated a National Natural Landmark by the U.S. government in 1966 and the property is currently managed by The Nature Conservancy.

**METHODS**

To quantify stand structure of the pine-oak community in MFP, we randomly established 12 plots (0.01 ha area). In each plot, we identified each tree (stems with diameter > 5 cm at breast height) to species and recorded diameter at breast height (dbh) and crown class. Crown class categories (dominant, co-dominant, intermediate, and overtopped) were based on the amount of light intercepted by the canopy of each tree (Oliver and Larson 1996). We also recorded dbh and decay class for all snags (standing dead trees) to quantify the abundance of coarse woody debris and decay dynamics. Snags were placed into one of five decay classes (1–5, with 5 being the most decayed) based on categories adapted from Maser and others (1979). We determined stand age structure by collecting increment cores from all trees in the plots. All live trees were cored at a height of 30 cm above ground level parallel to the contour of the slope to prevent sampling of reaction wood. Tree counts and diameters were used to calculate importance values of all species. Importance value ranges from 0 to 200, and is an index of relative abundance and relative dominance calculated using tree density and basal area (Husch et al. 2003).

All increment cores were dried and mounted using standard techniques (Stokes and Smiley 1968), then sanded using progressively finer sandpaper until cell structure of the wood was clearly visible under a binocular dissecting microscope. Samples were scanned with a high-resolution digital scanner (EPSON, Expression 10000XL) at 1200 dpi. Ring widths were measured and samples were visually crossdated using the WinDENDRO™ system (version 2009C). Visual crossdating was statistically confirmed using the program COFECHA (Holmes
trees (Pederson 2010). We crossdated these cores using the same techniques as for cores collected within plots. We detrended and standardized cores using the program ARSTAN (Cook 1985) to remove age-related growth trends in the tree-ring series and combine series into standardized tree-ring chronologies. Each series was detrended by fitting a negative exponential or negative slope linear curve to the raw ring-width measurements. Each ring-width measurement was divided by the corresponding value of the fitted curve to produce a standardized index. Autoregressive models were applied to each measurement series to remove autocorrelation, and the series were averaged to create residual chronologies. The index chronologies and individual series of shortleaf pine and chestnut oak were then used for analyses of historical canopy disturbance.

We used standard dendroecological techniques to determine the date and magnitude of canopy disturbances. Identifying release events in radial growth patterns of overstory trees is the primary technique to reconstruct canopy disturbance events (Lorimer 1980, 1985; Nowacki and Abrams 1997; Frélich 2002). Release events are commonly identified using a percent growth equation (Nowacki and Abrams 1997; 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 ≥ 25 percent (minor) or ≥ 50 percent (major) of the 10-year running mean (Nowacki and Abrams 1997) and sustained for a minimum of three years (Hart and Grissino-Mayer 2008).
RESULTS

Stand Composition

Stands at MFP are dominated by shortleaf pine and chestnut oak, with mockernut hickory and red maple as important associates. The total basal area of live stems (≥ 5 cm dbh) was 58 m² ha⁻¹ and the total density of the stand was 946 individuals ha⁻¹ (Table 1). The four species with the highest importance values were shortleaf pine, chestnut oak, mockernut hickory, and red maple. Shortleaf pine and chestnut oak were the most dominant species based on basal area and the most abundant species based on relative density. Although red maple and mockernut hickory did not account for much basal area in the stand, these species attained high importance values because of their high densities (158 stems ha⁻¹ and 149 stems ha⁻¹ respectively).

Red maple accounted for nearly all of the sapling-sized regeneration in the stand. The density of all saplings in the understory was 315 stems ha⁻¹, while the density of red maple saplings was 249 stems ha⁻¹ (Table 2). Of all the tree species sampled at MFP, only red maple, mockernut hickory, chestnut oak, and flowering dogwood produced sapling-sized regeneration. The majority of seedlings in plots were also red maple. The density of red maple seedlings was 1,458 seedlings ha⁻¹.

Table 1. Density, dominance, and importance values of all live stems ≥ 5 cm dbh in an old-growth forest at Marshall Forest Preserve, Georgia.

<table>
<thead>
<tr>
<th>Species Name</th>
<th>Common Name</th>
<th>Density (stems ha⁻¹)</th>
<th>Relative density</th>
<th>Basal area (m² ha⁻¹)</th>
<th>Relative dominance</th>
<th>Importance Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinus echinata</td>
<td>shortleaf pine</td>
<td>199</td>
<td>22.12</td>
<td>27.23</td>
<td>46.81</td>
<td>34.47</td>
</tr>
<tr>
<td>Quercus montana</td>
<td>chestnut oak</td>
<td>208</td>
<td>21.24</td>
<td>16.93</td>
<td>29.11</td>
<td>25.18</td>
</tr>
<tr>
<td>Carya tomentosa</td>
<td>mockernut hickory</td>
<td>149</td>
<td>15.93</td>
<td>2.84</td>
<td>4.88</td>
<td>10.4</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>red maple</td>
<td>158</td>
<td>15.93</td>
<td>1.5</td>
<td>2.58</td>
<td>9.25</td>
</tr>
<tr>
<td>Prunus serotina</td>
<td>black cherry</td>
<td>33</td>
<td>3.54</td>
<td>0.68</td>
<td>1.17</td>
<td>2.35</td>
</tr>
<tr>
<td>Pinus taeda</td>
<td>loblolly pine</td>
<td>17</td>
<td>1.77</td>
<td>3.63</td>
<td>6.25</td>
<td>4.01</td>
</tr>
<tr>
<td>Oxydendron arborescens</td>
<td>sourwood</td>
<td>58</td>
<td>6.19</td>
<td>0.54</td>
<td>0.93</td>
<td>3.56</td>
</tr>
<tr>
<td>Quercus alba</td>
<td>white oak</td>
<td>33</td>
<td>3.54</td>
<td>2.58</td>
<td>4.44</td>
<td>3.99</td>
</tr>
<tr>
<td>Cornus florida</td>
<td>flowering dogwood</td>
<td>33</td>
<td>3.54</td>
<td>0.17</td>
<td>0.29</td>
<td>1.92</td>
</tr>
<tr>
<td>Quercus stellata</td>
<td>post oak</td>
<td>8</td>
<td>0.88</td>
<td>0.22</td>
<td>0.38</td>
<td>0.63</td>
</tr>
<tr>
<td>Liriodendron tulipifera</td>
<td>yellow poplar</td>
<td>17</td>
<td>1.77</td>
<td>1.55</td>
<td>2.67</td>
<td>2.22</td>
</tr>
<tr>
<td>Nyssa sylvatica</td>
<td>blackgum</td>
<td>17</td>
<td>1.77</td>
<td>0.15</td>
<td>0.26</td>
<td>1.02</td>
</tr>
<tr>
<td>Cercis canadensis</td>
<td>eastern redbud</td>
<td>8</td>
<td>0.88</td>
<td>0.04</td>
<td>0.08</td>
<td>0.48</td>
</tr>
<tr>
<td>Ostrya virginiana</td>
<td>American hophornbeam</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>946</td>
<td>100.00</td>
<td>58.16</td>
<td>100.00</td>
<td>100.00</td>
</tr>
</tbody>
</table>
Chestnut oak and mockernut hickory also produced seedlings in excess of 400 seedlings per hectare, but the rates of survival between seedling and sapling stages for both mockernut hickory and chestnut oak were less than half of the survival rate of red maple seedlings. Shortleaf pine produced only 17 seedlings ha\(^{-1}\), and we encountered no shortleaf pine saplings.

**Stand Structure**

The canopy of the stand was entirely dominated by pine and oak species. Shortleaf pine and chestnut oak were abundant in the dominant and co-dominant crown classes, and a few individuals of loblolly pine (*Pinus taeda* L.) also reached the co-dominant class (Figure 3). Mockernut hickory and red maple were...
the most abundant species in subcanopy positions. We found no mockernut hickory or red maple individuals in the co-dominant or dominant categories. Most individuals in the overtopped category were red maple followed by mockernut hickory. Other species commonly encountered in the overtopped crown class category included sourwood, blackgum, flowering dogwood, and black cherry.

All species except shortleaf pine were represented in the 5–10 cm size class (Figure 4). The shortleaf pine group had a bimodal distribution with peaks in the 30–35 cm and 40–45 cm dbh classes. None of the shortleaf pine individuals appeared in the largest size classes. Chestnut oak was the only species to appear in the largest and nearly every size class except for the 45–50 cm dbh class. The mockernut hickory and red maple groups had similar size distributions. Both were most abundant in the smallest size classes and had few individuals reaching a diameter larger than 20 cm. The “others” group had a majority of trees in the smallest two categories. There were several individuals represented in the 30–35 cm and 35–40 cm dbh classes.

The age structure of MFP is characterized by the sequential establishment of different tree species (Figure 4). Over the last century, a succession of establishment occurred beginning with shortleaf pine, followed by chestnut oak, mockernut hickory, and finally red maple. The oldest tree sampled in stand structure plots was a chestnut oak with an inner date of 1851. The next oldest trees, both shortleaf pines, had inner dates of 1857. Shortleaf pine recruitment was continuous from 1880 through the 1940s and after this period no shortleaf pine individuals established. Besides a few individual chestnut oak individuals that established in the 1800s, establishment was characterized by two discrete pulses of regeneration beginning in the 1900s and 1930s. No recruitment of chestnut oak was recorded after the 1940s. The oldest mockernut hickory established in 1863 and until 1919 no other recruitment was recorded. Recruitment of hickory was unimodal with a peak of establishment in the 1940s. Red maple establishment was also unimodal, with no maples establishing prior to 1924. A peak of maple establishment occurred during the 1960s. The majority of individuals comprising the “others” category was sourwood (O. arboretum). Sourwood establishment reached a peak in the 1940s coinciding with a pulse of hickory regeneration.

The density and basal area of standing dead trees in the stand were both small (Table 3), and snags were mostly in advanced stages of decay (Figure 5). The majority of the basal area of dead trees in the stand consisted of large (> 20 cm dbh) shortleaf pine in highly decayed categories with no bark and few branches attached (Table 3; Figure 5); however we also encountered a few small red maple and sourwood among the dead trees. These were generally understory trees and in most cases had dead leaves or small tips of branches attached.

**Tree-ring Chronologies**

We successfully developed well-replicated tree-ring chronologies for chestnut oak and shortleaf pine (Figure 6). The average interseries correlation for the oak samples (n = 32) was 0.66 and the
Figure 4. Diameter and age distributions per hectare for all species sampled in an old-growth forest at Marshall Forest Preserve, Georgia. The arrows indicate separate ice storm events in 1901, 1902, 1908, 1932, 1938, and 1960. Please note scale differences between species. For a list of “others” species see Table 1.
Table 3. Density (stems ha\(^{-1}\)) and basal area (m\(^2\) ha\(^{-1}\)) by diameter at breast height (dbh) for live trees and snags in an old-growth forest at Marshall Forest Preserve, GA.

<table>
<thead>
<tr>
<th>DBH (cm)</th>
<th>Density (stems ha(^{-1}))</th>
<th>Basal area (m(^2) ha(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Live trees</td>
<td>Snags</td>
</tr>
<tr>
<td>≥ 5</td>
<td>249</td>
<td>66</td>
</tr>
<tr>
<td>≥ 10</td>
<td>273</td>
<td>42</td>
</tr>
<tr>
<td>≥ 20</td>
<td>125</td>
<td>25</td>
</tr>
<tr>
<td>≥ 30</td>
<td>158</td>
<td>8</td>
</tr>
<tr>
<td>≥ 40</td>
<td>66</td>
<td>8</td>
</tr>
<tr>
<td>≥ 50</td>
<td>75</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>946</td>
<td>149</td>
</tr>
</tbody>
</table>
Figure 6. Residual tree-ring chronologies and number of samples ($n$) for chestnut oak (top) and shortleaf pine (bottom) sampled from an old-growth forest at Marshall Forest Preserve, Georgia. Please note Index scale differences between species.
mean sensitivity was 0.24. Of the 125 segments tested using COFECHA, none were flagged indicating that all segments were statistically significant with segments of the same period. The measured tree-ring series extended 140 years from 1869 to 2008. Shortleaf pine also crossdated with a high level of confidence. The 32 dated series from shortleaf pine produced a 222-year chronology (1787–2008) with high average interseries correlation (0.56, P < 0.0001) and mean sensitivity (0.27), and only 14 segments were flagged by COFECHA as problematic (7 percent). Upon reexamination of the flagged segments, we determined that these specimens were free of crossdating errors and were correctly dated.

The largest negative index value (a year with an anomalously small radial growth increment) in the shortleaf pine chronology occurred in 1960, a year with a documented ice-storm that inflicted severe damage to trees at MFP. Another year in which an ice-storm occurred, 1932, was the second-largest negative departure from the mean index value in the shortleaf pine chronology. Negative ring-width anomalies were not detected in the chestnut oak chronology in years with ice-storm occurrences.

**Disturbance History**

Nearly all the chestnut oaks sampled (31 of 32 individuals) experienced periods of suppressed growth (Figure 7). We found 103 minor suppressions in all trees and an average of 3.32 suppressions per tree. Of the 32 pine series analyzed, all experienced suppressions and there were 219 suppressions overall and 6.84 suppressions per tree. Of the 32 pines, 31 experienced release events, with 166 release events occurring overall. Per tree, an average of 5.18 release events occurred. Oaks experienced a widespread release event in the 1890s and early 1900s as well as in the 1930s. The oaks also exhibited a significant suppression in the late 1970s. Pines experienced similar release events in the 1890s and 1900s, but with a smaller percentage of individuals responding. They also exhibited a small suppression in the first decade of the 20th century. Several suppressions in the pines were observed in the 1920s, 1930s, 1950s, 1960s, and late 1970s. Just before the suppression in the 1950s, major and minor release events occurred in pines.

Widespread oak release events, with the highest percentages of individuals experiencing growth releases, coincided with documented ice storms. A high percentage of oaks experienced both major and minor releases in the early 1900s after ice storm events occurred in 1901 and 1902. Another release occurred in the late 1930s, a decade that experienced ice storms in 1932 and 1935. Finally, a series of releases were experienced by 10–20 percent of oaks in the early 1960s following a severe ice storm in 1960. No pattern of releases was detected in shortleaf pine during these ice-storm years, but a few suppressions with fewer than 20 percent of individuals responding were detected in ice storm years in pines.

Decadal patterns of tree establishment also coincided with these periods of widespread canopy disturbances. Establishment of chestnut oak was characterized by a bimodal distribution with the first peak of establishment occurring after the ice storms of the early 1900s, and the second peak coinciding with the 1930s ice
Figure 7. Minor (A) and major (B) release and suppression events detected during the period 1896–2008 using the 10-year running mean method for 16 chestnut oak (white line) individuals and 16 shortleaf pine (black area) individuals sampled in an old-growth forest at the Marshall Forest Preserve, Georgia. Please note scale differences between species.
storms (Figure 4). A pulse of establishment of mockernut hickory followed the establishment of oak in the 1940s. A peak in red maple establishment occurred in the 1960s following the severe ice storm of 1960.

**Discussion**

The pattern of disturbance experienced by the old-growth stand at the Marshall Forest Preserve has resulted in a compositional shift in tree establishment from shortleaf pine and chestnut oak to mockernut hickory and, most recently, red maple. The age-class distributions of species clearly show a trend of succession, where no pines have established since 1944 and no oaks have established since 1955, while red maple has been continuously establishing since the mid 20th century. Hickory and maple make up the majority of stems in the understory, and the red maple component in particular consists of high densities of small diameter trees. Red maple also accounts for most of the tree regeneration with high densities of seedlings, many of which survive into saplings and are recruited to understory and sub-canopy positions in the stand. The recent increase in understory maple individuals—the earliest red maple establishment date was 1925—suggests a lack of understory disturbance that would otherwise prevent the establishment and survival of maples.

Active suppression of fires beginning in the early to mid 20th century has often been implicated as the main cause of decline of oak-pine regeneration and successional transitions to red maple dominated stands (Abrams 1992; Nowacki and Abrams 2008), and this may also be the case at MFP. During sampling of stand structure, we noticed basal fire scars on many of the large, mature pines and standing dead pines. The injuries were typical of recurring fires because many of the injured stems contained multiple fire scars. This suggests fire was an important historical disturbance agent at MFP. However, no fires have been documented in the preserve since at least 1920. The lack of pine and oak regeneration at this site may be related to the absence of fire, which would have eliminated shade tolerant competitors and allowed regeneration of oak and pine, maintaining the stand in an earlier successional stage.

While disturbance from fire was probably important historically, the major canopy disturbance agent affecting radial growth and tree recruitment in MFP during the 20th century was likely ice storms. Ice storms occur when freezing rain forms a coating of ice, or glaze, on trees and other surfaces (Gay and Davis 1993). Globally, the conditions for these ice events are most common in eastern North America, and ice storms can cause substantial damage to trees in the mixed deciduous forests of the southeast United States (Bennett 1959; Lafon and Speer 2002; Knight 2003). Layers of ice that accumulate on trees cause structural damage or mortality by breaking branches or stems. Radial growth is reduced in trees affected by ice damage because they have reduced photosynthetic capacity through the loss of leaf area and must allocate resources to recovery from injury rather than to secondary growth. Travis and Meentemeyer (1991) noted that pines were much more susceptible to ice storm damage than hardwoods because of the additional leaf area available for ice accumulation during the winter months. Ice-coated needles
add substantial weight to limbs causing limb breakage or damage to root systems from excessive leaning or bending of the stem. In this type of situation where pines experience extensive damage and gaps in the pine canopy are opened to expansion by hardwoods, a suppression in pine radial growth and an associated growth release in oaks would be expected.

In our analysis of radial growth in canopy pines and oaks, we found widespread growth releases (> 20 percent of trees responding) in oaks that coincided with documented ice storms in this region of northwest Georgia. In a few of the years with ice storms (e.g. 1902, 1960), we also detected suppressions in pines, but these suppressions did not affect as many individuals as oak releases. A previous dendroecological analysis of stand disturbance at MFP also indicated that an ice storm in 1960 resulted in a major radial growth release in oak, and a concurrent suppression in pine (Knight 2003). Travis and Meentemeyer (1991) conducted a study of ice damage on loblolly and shortleaf pines in Virginia. They found that reduced radial growth only occurred during the growing season immediately following an ice storm, and the ice damage rarely induced prolonged, multi-year suppressions. Our criteria for major and minor suppressions required a sustained reduction in growth for three years relative to a moving average. Thus, one-year growth reductions in pines would not be detected as suppressions, and this may account for a lack of pine suppressions associated with documented ice storm events in our analysis. Additionally, canopy trees tend to respond less dramatically than understory trees to gap formation, and growth releases in understory trees are generally more reliable than suppressions in canopy trees for detecting canopy disturbances (Lorimer 1980; Lorimer and Frelich 1989). Because shortleaf pine establishment preceded chestnut oak at MFP, oaks presumably occupied less dominant positions in the canopy and would be more likely than pines to respond to disturbances. Our results are consistent with these findings in that widespread growth releases were consistently detected in chestnut oaks following years with documented ice storms.

Growth releases in understory trees and suppressions in overstory trees do not allow for the identification of the cause of canopy disturbances (Lorimer and Frelich 1989). For example, strong winds are capable of damaging trees and producing gaps in forest canopies (Brewer and Merritt 1978). However, in wind-damaged forests, broken branches and snapped stems are less common than uprooting of trees (Foster 1988). At MFP, we did not observe the pit-and-mound topography indicative of trees uprooted by windthrow (Schaetzl et al. 1989; Ulanova 2000), and we therefore concluded that ice storms are the most likely cause of canopy disturbance at MFP.

The effect of ice storms on the stand composition of MFP has been to accelerate the successional trajectory from pine and oak to red maple dominance. Canopy disturbances from ice storms have variously been considered to either retard or accelerate the pace of succession in southeastern forests (Whitney and Johnson 1984). Ice storms have been thought to impede the succession of shade-tolerant species by opening gaps in the canopy and allowing light to reach the understory permitting the regeneration of early successional shade-intolerant species such as oak and pine (Downs
the implementation of any prescribed fire program will be difficult due to the highly urbanized environment in which the preserve is situated.

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REFERENCES


An Old-Growth Pine-Oak Community


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