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Source: Castanea, 76(1):55-63. 2011.
Published By: Southern Appalachian Botanical Society
DOI: 10.2179/10-012.1
URL: http://www.bioone.org/doi/full/10.2179/10-012.1

CASTANEA 76(1): 55–63. MARCH 2011

Canopy Disturbance Patterns in Secondary Hardwood Stands on the Highland Rim of Alabama

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ABSTRACT Disturbance regimes of many hardwood forests of the eastern United States in the complex stage of development are characterized by localized canopy disturbance events that change fine-scale biophysical conditions. Recently, research has demonstrated the importance of gap-scale disturbance processes in secondary hardwood stands of the southern Appalachian Highlands. However, information on canopy disturbance patterns during early developmental stages is required from the broader geographic region for a comprehensive understanding of stand dynamics. The goal of this study was to reconstruct canopy disturbance history for mixed hardwood stands on the Highland Rim of Alabama to elucidate disturbance patterns during early development. We analyzed radial growth from 46 *Quercus* individuals to reconstruct canopy disturbance history. The majority (67%) of the trees analyzed exhibited release events. In total, 42 releases were detected and some trees experienced multiple events. Of these releases, 28 (67%) were classed as minor and 14 (33%) were classed as major. Mean release duration was 4.00 years ± 0.21 (SE) and the longest release was sustained for eight years. Based on mean release duration, we speculate that most of the canopy gaps were filled by lateral crown expansion rather than subcanopy height growth. We did not document any forest-wide disturbance events; a pattern that may be a regional phenomenon or may be related to forest age. Canopy disturbances became common after ca. 40 years of development. We propose that the frequency of canopy gaps will decrease and the size and magnitude of individual gaps will increase as the stands mature.

INTRODUCTION In the eastern United States, disturbance regimes of many hardwood forests in the complex stage of development (i.e., with old-growth structures) are characterized by localized canopy disturbance events that result from the removal of a single tree or a small cluster of trees (Lorimer 1980; Barden 1981; Runkle 1981, 1982; Cho and Boerner 1991; Oliver and Larson 1996; Runkle 2000). In these systems, gap-scale disturbance processes promote multi-aged stands with patchy canopy dominance, modify the arrangement of biomass, influence density and diversity patterns, and increase overall forest heterogeneity by changing fine-scale biophysical conditions (Lorimer 1980; Connell 1989; Runkle 1998, 2000; Frelich 2002). The overwhelming majority of localized canopy disturbance studies in mixed hardwood forest systems have focused on stands during the complex stage of development. However, recent research in secondary hardwood stands (i.e., all non-primeval forests prior to a complex stage of development) on the Cumberland Plateau in Tennessee indicated that gap-scale disturbance processes are important mechanisms of change during relatively early stages of stand development (Hart and Grissino-Mayer 2008, 2009). Results from these studies indicated that prior to a complex developmental stage localized canopy disturbance events influence species composition, stand structure, and successional pathways in

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Received February 23, 2010; Accepted June 11, 2010.

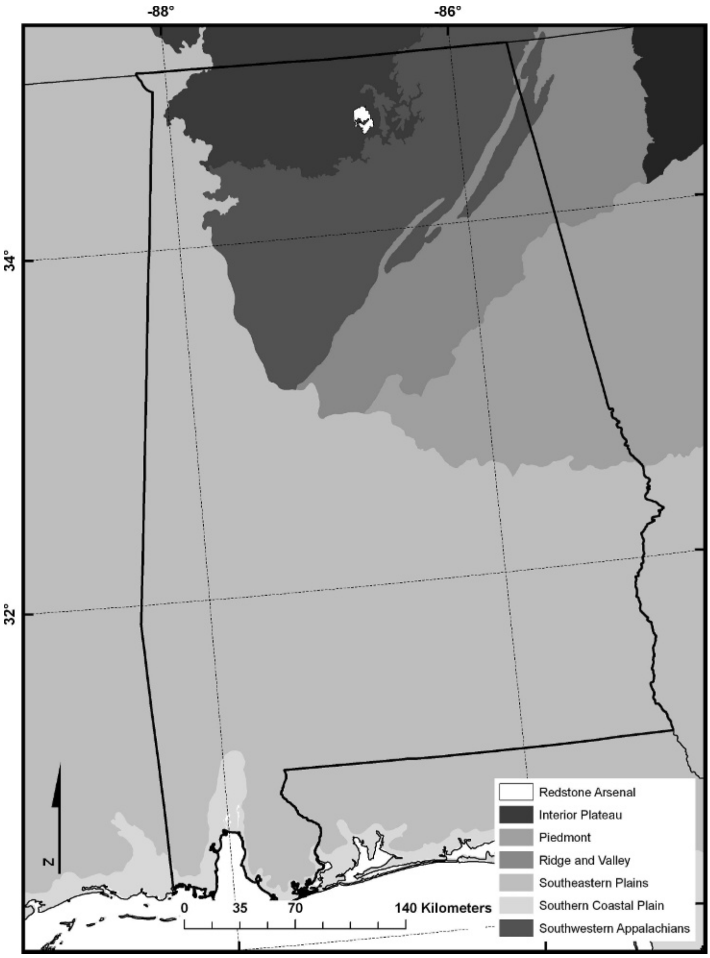

Figure 1. Map showing the location of Redstone Arsenal and level III ecoregions of Alabama and adjacent states (Griffith et al. 2001).

hardwood stands on the Cumberland Plateau. To develop a better understanding of early hardwood forest development, quantitative information on canopy disturbance patterns is required from the broader geographic region (i.e., data from multiple ecoregions).

The primary purpose of this study was to elucidate patterns of localized canopy disturbance events in secondary hardwood stands on the Eastern Highland Rim of northern Alabama. Our research was driven by four questions. 1) What was the frequency of canopy disturbance events recorded in radial growth patterns of canopy *Quercus* trees? 2) What was the magnitude of individual canopy disturbances? 3) Were individual canopy disturbance episodes synchronous or asynchronous? 4) At what point in stand development do canopy disturbance processes become common? The results of our study were compared with findings from forests in other regions to examine general gap-scale disturbance and forest growth and development patterns. Our findings provide quantitative information on canopy disturbance dynamics for a region (i.e., the Highland Rim) where no such data exist.

METHODS

Study Area

This study was conducted on the Redstone Arsenal (RA) in north-central Alabama (Figure 1). The RA is a ca. 13,000 ha landholding managed by the United States Department of the Army. The federal government acquired the original property for RA from agricultural landowners in the early 1940s (Nixon 2002). Approximately 6,340 ha of RA are used for the management of second-growth forest communities. Most of these stands established in the 1930s after the abandonment of agricultural fields (Bhuta et al. unpubl. data). The RA occurs on the weakly dissected plateau–red soils landtype association of the Eastern Highland Rim physiographic section of the Interior Low Plateau province (Fenneman 1938, Smalley 1983). The RA contains gently rolling hills with elevations between 170 to 206 m amsl and local relief is typically less than 30 m. Soils are generally deep, reddish, and well drained. The clayey and loamy soils are derived from alluvium or clayey residuum from moderately high-grade limestone (Smalley 1983). The climate for the region is classified as humid mesothermal with long, moderately hot summers and short mild winters (Thornthwaite 1948). The January average temperature is 5°C and the July average is 27°C (Smalley 1983). Average annual precipitation is 132 cm. March is typically the wettest month and October is typically the driest. The frost-free period extends from early-April to late-October. The area experiences ca. 55 days with thunderstorms annually (Smalley 1983). These events are most common in spring, but may occur throughout the year. The RA lies within the western mesophytic forest region described by Braun (1950). Common dominant species in hardwood stands at RA include: *Quercus phellos* L., *Liquidambar styraciflua* L., *Quercus falcata* Michx., *Celtis occidentalis* L., *Quercus nigra* L., *Quercus velutina* Lam., *Juniperus virginiana* L., *Quercus rubra* L., and *Quercus alba* L. (Bhuta et al. unpubl. data).

Field and Laboratory Methods

Our field sampling was specifically focused in hardwood stands on the RA because the goal of our study was to document canopy disturbance patterns during hardwood stand development. In the field, we collected a total of 46 tree-core samples from overstory *Quercus* individuals (i.e., trees with canopy dominant or codominant positions). We restricted our analyses to *Quercus* trees because they have clear ring boundaries, do not commonly exhibit locally absent or false rings, were dominant canopy species, and have been used successfully in other studies to document canopy disturbance history in the eastern United States (McCarthy and Bailey 1996, Nowacki and Abrams 1997, Rentch et al. 2002, Rentch et al. 2003, Rubino and McCarthy 2004, Hart and Grissino-Mayer 2008, Hart et al. 2008). These trees were all located on established plots used for a prior study on forest vegetation patterns. Plots were randomly placed in stands ≥2 ha in size using the extension Hawth's Analysis Tools in ArcGIS. All trees were cored parallel to slope contour to avoid the sampling of reaction wood in the radial growth patterns (Scurfield 1973, Fritts 2001, Grissino-Mayer 2003) and all cores were collected at breast height. Once extracted, all tree-core samples were placed in labeled straws and transported to the laboratory for radial growth analysis.

All samples were prepared and processed for crossdating and disturbance history reconstruction using the methods outlined in Stokes and Smiley (1996). Tree cores were mounted with cells vertically aligned to provide a transverse view of the wood surface and then sanded with progressively finer abrasives following standard procedures to reveal the anatomical features of the wood before crossdating (Orvis and Grissino-Mayer 2002). Annual growth rings on all samples were visually inspected with the aid of a microscope for patterns of wide and narrow rings and other diagnostic characteristics that could be used to crossdate all series (i.e., assign the exact calendar year of formation to all growth rings). Notable (e.g., unusually narrow or otherwise distinct) rings and/or sequences of rings were documented to aid with dating (Yamaguchi 1991). Annual growth rings on each sample were then assigned calendar years starting with the first ring beneath the bark and continuing backward until the innermost ring or pith was reached. All tree rings were then measured to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software. For crossdating quality control purposes, all measurement series were statistically analyzed to ensure all growth rings were assigned the proper year of formation using the computer program COFECHA (Holmes 1983, Grissino-Mayer 2001). The

COFECHA program uses segmented time series correlation analyses to determine the strength of association between 50-year segments lagged 25 years from each individual series against a master chronology created from the remaining series. All segments that fell below the predetermined significance threshold (r = 0.32, $P > 0.01$) were flagged by the program. Each flagged segment was re-inspected for possible dating errors. This procedure helped to ensure all radial growth rings were assigned to their proper calendar year of formation.

Once we were confident all annual rings from all series were assigned to the proper calendar year of formation we analyzed radial growth patterns for release events to reconstruct canopy disturbance history. The identification of release events (i.e., pulses of increased growth) in radial growth patterns of trees is a widely used technique to reconstruct the disturbance history of a forest (Lorimer 1985, Lorimer and Frelich 1989, Nowacki and Abrams 1994, Frelich 2002, Fraver and White 2005, Copenheaver et al. 2009). The removal of overstory trees modifies biophysical conditions, especially available sunlight. This increase in resource availability is often apparent in the radial growth patterns of residual trees by an increase in annual growth increment. To reconstruct canopy disturbance history for these stands, we quantified minor and major release episodes using a percent growth change equation. Release events were documented as periods in which raw ring width was ≥25% (minor) or ≥50% (major) of the median of the 10 years prior and subsequent (Nowacki and Abrams 1997, Rubino and McCarthy 2004) and were sustained for a minimum of three years (Hart and Grissino-Mayer 2008, Hart et al. 2008). Thus, for each tree ring a 20-year window of radial growth increments was analyzed to document growth rates that exceeded the predetermined thresholds attributed to canopy disturbance events and the subsequent increase in resource availability. To document the extent of disturbance events we analyzed the spatio-temporal patterns of release episodes. For our analyses, we considered forest-wide disturbances as release episodes where a minimum of 25% of the individuals experienced a contemporary release (Nowacki and Abrams 1997, Rubino and McCarthy 2004, Hart and Grissino-Mayer 2008). Release episodes that occur simultaneously in trees from different areas of the study site indicate exogenous disturbance events such as ice storms or high wind events that may remove canopy trees over a large spatial area. Release initiation dates and durations were displayed using FHX2 software to graphically display spatial and temporal characteristics of forest disturbance history (Grissino-Mayer 1995, Hart et al. 2008).

RESULTS AND DISCUSSION The oldest *Quercus* tree analyzed in our study had an inner date at breast height of 1909 and the youngest tree had a date of 1970. Of the 46 *Quercus* trees analyzed for canopy disturbance history, 31 (67%) exhibited release events. A total of 42 release events were detected as some trees experienced multiple releases during their lifespan (Figure 2). Of the 42 detected release events, 28 (67%) were minor and 14 (33%) were major. Two individuals (a *Q. rubra* and a *Q. alba*) experienced three separate release events during their lifespans , Figure 3a and 3b). We found the ages of these individuals of interest. One of these trees with three release episodes was among the oldest individuals analyzed (inner date at breast height of 1922). In older trees we might expect to find multiple release events because of the longer tree-ring record. However, the other tree with three separate release events was much younger (inner date at breast height of 1947). In only 59 years of life, this individual benefited from three separate canopy disturbance events. The longest release duration was eight years and was observed in a *Q. rubra* (Figure 3c). Of note, this release was classed as major because the growth change was greater than 50% of the 10-yr running median. We documented two individuals that experienced releases of seven years.

The mean release duration was 4.00 years ± 0.21 (SE). We found similar release duration periods to what has been documented in *Quercus* individuals within secondary stands on the Cumberland Plateau in Tennessee (Hart and Grissino-Mayer 2008) and the Ridge and Valley of Tennessee (Hart et al. 2008). From the duration of the release, the magnitude of the canopy disturbance event can be inferred. We suggest that most canopy

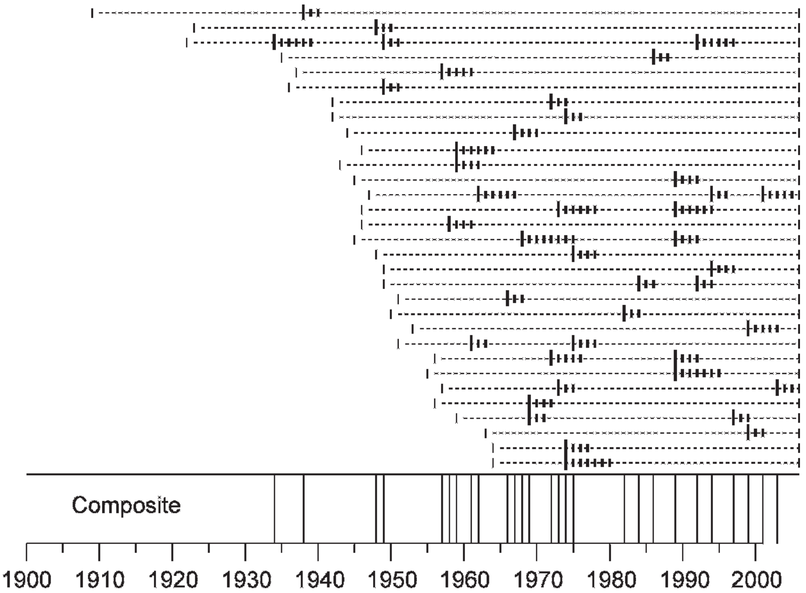

Figure 2. Detected release events using the 10-yr running median method for 31 *Quercus* individuals sampled at Redstone Arsenal, Alabama. Each horizontal line represents the record from one individual tree, long vertical bars indicate release events, and short vertical bars indicate release duration. A composite of release events for the study area is shown across the bottom.

gaps documented in this study closed four years after they were created. These gaps were relatively small and short lived as would be expected in secondary stands prior to a complex stage of development. In young forests, the distance between canopy individuals is short and individual tree crowns occupy relatively small areas of the main forest canopy (Oliver and Larson 1996). Most of the canopy disturbance events documented in our study would not have allowed for the recruitment of understory individuals to the main canopy. We propose that most of the gaps closed by lateral crown expansion rather than height growth of subcanopy individuals (Rubino and McCarthy 2004). This is a pattern we would expect to change as the forest matures. In secondary stands, as trees are removed from the canopy through self-thinning processes, the gaps created are relatively small compared to gaps in older forests (Clebsch and Busing 1989, Yamamoto and Nishimura 1999, Hart and Grissino-Mayer 2009). These small canopy gaps should fill more rapidly than larger gaps in older stands (Dahir and Lorimer 1996). With increased age, larger trees would occur at wider spacings and individual tree crowns would occupy a larger proportion of the forest canopy. As the forest matures, the size of individual canopy gaps should increase and so should the time required for the gap to infill. We hypothesize that larger gaps, which are expected to occur as the stands age, would have a greater likelihood of being filled by subcanopy height growth rather than by lateral crown expansion of gap perimeter trees (Dahir and Lorimer 1996). This process would provide the mechanism required for the stands to develop a complex structure typical of older forests (Oliver and Larson 1996).

The longest period between release initiation events was 10 years and the shortest period was 1 year. In several instances ($n = 8$), releases occurred in consecutive years (e.g., 1948 and 1949, 1957–59, Figure 2). The mean release return interval was 2.67 years ± 0.35 (SE). No forest-wide releases were documented in our analyses. No more than 16% (a period in the late 1970s) of the trees with documented releases experienced simultaneous release events. The lack of a forest-wide release event is interesting. Studies in older mixed *Quercus* forests of the eastern United States have documented that such broad-scale canopy

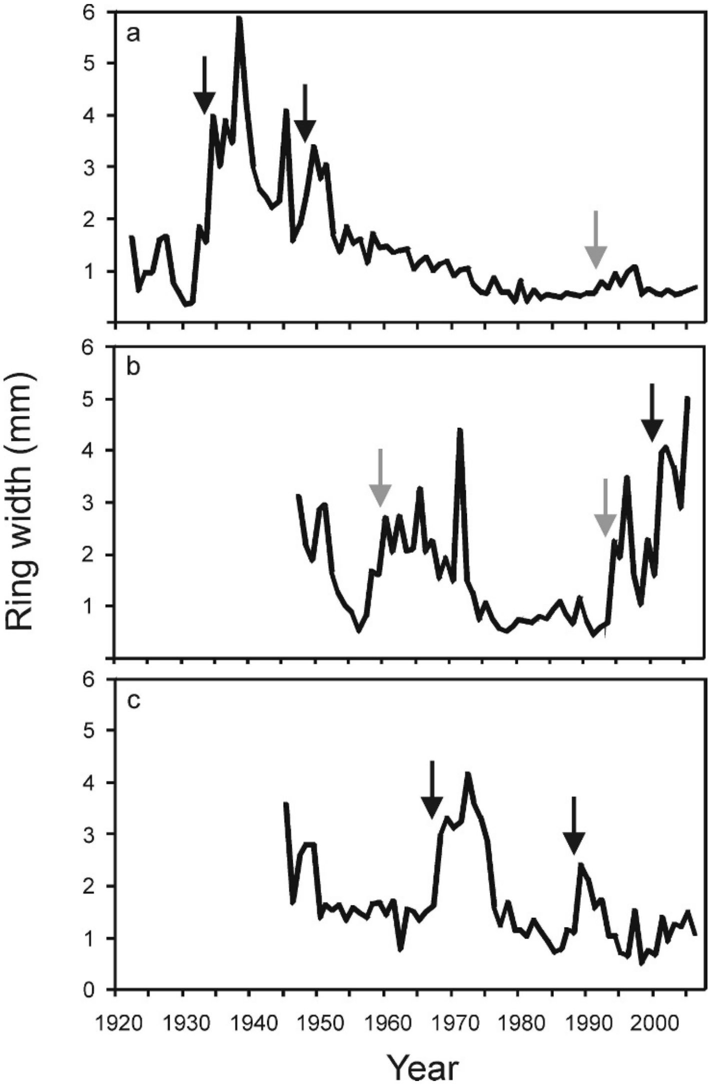

Figure 3. Raw-ring width measurements for selected individuals sampled at Redstone Army Arsenal, Alabama. Black arrows indicate major releases and gray arrows indicate minor release episodes. a) *Quercus rubra* with three release events, b) *Q. alba* with three release events, c) *Q. rubra* with a growth change of >50% sustained for eight years.

disturbances occur every 20 to 30 years (Nowacki and Abrams 1997, Rubino and McCarthy 2004). While this pattern may be related to biophysical site characteristics or weather events such as ice storms, it may also be related to forest age. Studies in younger, secondary hardwood forests in Tennessee found the return intervals of such broad-scale disturbance events to be much longer (Hart and Grissino-Mayer 2008, Hart et al. 2008). In fact, these studies found that such events occurred less than once per century. Perhaps the forest at RA was not sufficiently old to have a high number of canopy trees that were susceptible to death by an extreme weather event, such as high winds or ice loading. In older forests, individual tree crowns occupy a relatively large area of the canopy compared to younger stands. Tree architecture is also quite different between developmental stages. Because of these characteristics, canopy trees in older stands may be more susceptible to removal by exogenous disturbance events. Interestingly, three tornadoes have caused

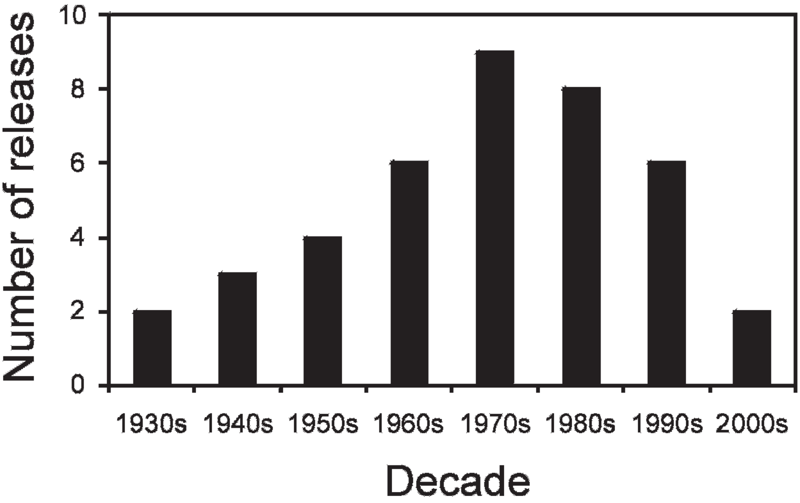

Figure 4. Number of release events per decade at Redstone Arsenal, Alabama. Release events were detected using the 10-year running median method (Nowacki and Abrams 1997, Rubino and McCarthy 2004).

damage to natural and human-built structures on RA. These events occurred in December 1967, April 1974, and November 1989. In addition, the remnants of Hurricane Opal passed through the area causing some damage in 1995. Based on release initiation dates, only two of these four storm events could be possibly related to canopy disturbances. A total of three releases may have been caused by the 1967 event and five releases may have been caused by the 1974 event. However, we cannot definitively say that these two atmospheric disturbances directly removed overstory trees and may be used to explain the documented releases in radial growth patterns of residual trees.

The greatest number of release initiations occurred in the 1970s, followed by the 1980s (Figure 4). A steady increase in the number of release episodes was evident from the 1930s to the apex of release events in the 1970s. While the frequency of release episodes peaked in the 1970s, the number of release events remained relatively high in the 1980s and 1990s and the record for the 2000s was incomplete because the data were collected during the growing season of 2007 (tree-ring measurements ended in 2006). This information is useful to examine the period during forest development when canopy disturbance events become frequent. The majority of the trees in the forest established in the 1930s and the frequency of release events peaked in the 1970s. Our results indicate that localized canopy disturbance events became important drivers of forest change after ca. 40 years of development. This is the same pattern that was observed in secondary hardwood stands in Tennessee (Hart and Grissino-Mayer 2008). At this stage of forest development, the canopy becomes stratified and growing space is fully utilized (Oliver and Larson 1996). Self-thinning is induced by competition and the subsequent growing space made available by tree mortality is accrued by larger trees with superior crown positions (Oliver and Larson 1996, Hart and Grissino-Mayer 2008).

SUMMARY The overall goal of our study was to reconstruct the canopy disturbance history for mixed hardwood stands on the Eastern Highland Rim of Alabama to elucidate patterns of disturbance during forest development. A total of 42 release episodes were detected with some trees experiencing multiple release events. Of these documented releases, 28 (67%) were classed as minor and 14 (33%) were classed as major. Mean release duration was four years and the longest release episode was sustained for eight years. Based on the duration of the events, we speculate that most of the canopy gaps were filled by lateral crown expansion rather than height growth of subcanopy individuals. We did not document any forest-wide disturbance events. Releases were asynchronous occurring at variable spatial and temporal scales. This pattern may be a regional phenomenon or may be related to forest age. Canopy disturbances became common after ca. 40 years of forest development. We propose that the frequency of canopy gaps will decrease and the size and magnitude of each individual gap will increase as the stands mature to develop complex structures.

ACKNOWLEDGMENTS We thank L. Hedrick, R. Chandler, G. Hicks, K. McGuckin, J. Pflueger, P. Swint, and J. Dorr for assistance in the field and J. Oakley and D. Wagner for assistance in the laboratory. M. Buchanan, R. Pine, M. Pyne and R. Reaves provided helpful comments on an earlier draft of the manuscript and G. Hicks provided helpful discussion. Laboratory analyses were funded in part by the College of Arts and Sciences, University of North Alabama.

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