DISTURBANCE, SUCCESSION, AND STRUCTURAL DEVELOPMENT OF AN UPLAND HARDWOOD FOREST ON THE INTERIOR LOW PLATEAU, TENNESSEE

Justin L. Hart, Merrit M. Cowden, Scott J. Torreano, and J. Patrick R. Vestal[1]

Abstract.—We quantified species composition, stand structure, canopy disturbance history, and *Quercus* establishment and canopy accession patterns in 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. Prior to 1880, the majority of *Quercus* trees established in closed canopy conditions, whereas after 1880 most *Quercus* trees 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 event coincided with an establishment pulse of largely understory taxa, and the 1945 event corresponded with an establishment pulse of *A. saccharum*.

INTRODUCTION

Late-successional hardwood stands throughout the temperate zone are noted for their unique structural characteristics, which are often described as complex (Hale et al. 1999, Johnson 2004, Oliver and Larson 1996). 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, 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). 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. 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.

METHODS

Our study was conducted on the Hill Forest State Natural Area (HFNA) located 20 km southwest of Nashville, TN. The 91 ha reserve is managed as a state natural area by the Tennessee Department of Environment and Conservation. Our study was specifically focused within a ca. 60 ha portion within the core section of the reserve. To quantify forest composition and structure, we established 27 separate 0.04 ha fixed-radius plots throughout the inner core of the HFNA. On each plot we recorded species, crown class, and diameter at breast height (d.b.h.;

[1] Associate Professor (JLH) and graduate student (MMC), University of Alabama, Tuscaloosa, AL 35487; Professor (SJT), University of the South; Staff Scientist (JPRV), Tennessee Department of Environment and Conservation. JLH is corresponding author: to contact, call 205-348-1673 or email at hart013@ua.edu.

diameter measured ca. 1.4 m above the ground) of all stems ≥5 cm d.b.h. to quantify species composition and stand structural characteristics. We used increment borers to extract tree core samples from all trees ≥20 cm d.b.h. and the four trees ≥5 cm but <20 cm d.b.h. located 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* (*Q. prinus*, *Q. rubra*, *Q. alba*, and *Q. velutina*) canopy trees immediately adjacent to our inventory plots that exhibited characteristics associated with old trees such as low stem taper, high stem sinuosity, and low crown volume (Pederson 2010).

Once all tree rings on our *Quercus* core samples were visually dated, we measured raw ring widths of all overstory *Quercus* series (n = 56) to the nearest 0.001 mm using a Velmex measuring stage (Velmex, Inc., Bloomfield, NY) interfaced with Measure J2X® software (VoorTech Consulting, n.d.). 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 (Grissino-Mayer 2001, Holmes 1983). We then analyzed changes in raw ring widths with respect to the running mean of the previous and subsequent 10 years (Nowacki and Abrams 1997). Release events were identified as periods in which raw ring width was ≥25 percent (minor) or ≥50 percent (major) of the 10-year preceding and subsequent mean, sustained for a minimum of 3 years (Hart and Grissino-Mayer 2008, Hart et al. 2008, Hart 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 percent of the study plots (Hart and Grissino-Mayer 2008, Nowacki and Abrams 1997, Rubino and McCarthy 2004). Trees with mean radial growth rates of ≥2.00 mm/year for the first 10 years were considered to be of gap origin, and those with mean radial growth rates of <2.00 mm/year for the first 10 years were classed as understory origin (Hart and Grissino-Mayer 2008, McEwan and McCarthy 2008, Ruffner and Abrams 1998). We subsequently determined if and when the trees experienced growth releases identified by the 10-year running mean method. We combined the recruitment strategy classes with the detection of subsequent release event(s) to assign all *Quercus* trees ≥20 cm d.b.h. to an establishment and canopy accession strategy class: gap origin-no release, gap origin-gap release, or understory origin-gap release (Hart et al. 2012, Rentch et al. 2003).

RESULTS AND DISCUSSION

Species richness of woody stems ≥5 cm d.b.h. was 29, diversity (H') was 2.61, and evenness (J) was 0.78. Basal area was 24.0 m^2/ha and tree density was 426 stems/ha. The most important species (based on relative density and dominance) were *Acer saccharum* and *Quercus prinus,* and the most dominant species was *Quercus prinus*. The diameter structure of all trees in the forest revealed an inverse J-shape from small size classes to large size classes. The mean q-factor was 1.38. We documented 20 trees/ha ≥60 cm d.b.h. and 8 trees/ha ≥70 cm d.b.h. The oldest tree we documented was a *Q. prinus* with an inner date at breast height of 1841. *Quercus* establishment was continuous from the mid-1800s through the 1950s. However, establishment was greatest from 1890 through the 1910s, with 45 percent of all *Quercus* trees in our sample becoming established during this 30-year period.

Of the 56 overstory *Quercus* trees analyzed for disturbance history, 46 (82 percent) exhibited at least one release event. In total, 101 release events (89 percent minor and 11 percent major releases) were detected from these individuals. A total of 33 trees (59 percent of samples analyzed) experienced multiple releases, including 15 trees (27 percent) with three or more releases during their lifespans. The mean release duration was 5 years for all *Quercus* combined. The longest period between release initiation events after 1900 was 10 years. Release initiations often occurred in consecutive years; the longest periods of consecutive initiations were 1968-1975 and 1942-1947. The single year with the highest frequency of release initiations was 1945 (n = 14 release initiations). The mean release initiation return interval was 3 years.

We documented three forest-wide disturbances during stand development. These episodes were initiated in 1922, 1945, and 1973. Synchronous release initiations across broad areas indicated exogenous disturbances such as strong winds, ice storms, or selective timber harvesting prior to establishment as a natural area resulted in the removal of canopy trees throughout much of the forest. Although trees may have been removed individually or in small groups, these disturbances can be considered intermediate-stand scale events because trees were removed from throughout the forest at a rate well above that of background mortality. From the late-1800s to the end of the record, decadal release to sample size percentages (i.e., the percentage of living trees at least 10 years of age that exhibited a radial growth release) 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. Of the 56 overstory *Quercus* trees analyzed, 31 (55 percent) established in a canopy gap and 25 (45 percent) established under a closed forest canopy. Early in stand development, most *Quercus* trees established in closed canopy environments. Prior to 1880, only two *Quercus* trees established in high light environments. In contrast, nine *Quercus* trees established in low light environments prior to 1880. Establishment of gap origin trees peaked from the 1890s to the 1910s. Of the *Quercus* trees that established in the understory of a closed canopy, the mean period of suppression was 28 years, and the longest residence time in the understory prior to overstory release was 62 years observed in a *Q. alba*. We did not observe differences in establishment or accession across *Leucobalanus* and *Erythrobalanus* groups.

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