RESEARCH ARTICLE

Forest Dynamics in a Natural Area of the Southern Ridge and Valley, Tennessee

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ABSTRACT: This study was initiated to document forest development in the oldest natural area in the Ridge and Valley of east Tennessee. The Ijams Nature Reserve was established in 1910 and provided the opportunity to document secondary succession of the oldest upland forest reserve in the region. We established forest inventory plots in the original land holding of the Ijams family 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 disturbance regime of the reserve. The forest was dominated by *Quercus alba* and *Liriodendron tulipifera* while *Acer saccharum* and *Fagus grandifolia* had high densities in the understory. *Liriodendron tulipifera* was the most important species in the stand because it colonized the site following agricultural abandonment and subsequently established in small canopy gaps. The stand had a reverse J-shaped diameter structure typical of regenerating forests. The forest experienced one stand-wide disturbance event likely attributed to the decline of *Castanea dentata* in the 1920s. The return interval of stand-wide disturbances was much longer than what has been reported in other eastern hardwood forests. With the exception of this one stand-wide release, the disturbance regime was characterized by localized, asynchronous events that influenced only neighboring trees. Under the current disturbance regime, composition of the stand is projected to change as shade-tolerant mesophytes in the understory (*A. saccharum* and *F. grandifolia*) are recruited to larger size classes. This phenomenon has been widely reported throughout the eastern United States and is most commonly linked to active fire suppression. However, the forest of the Ijams Nature Reserve has not burned during development and still shows a marked change in species composition even with no change in the fire disturbance regime. We propose the composition shift is related to understory facilitation by disturbance oriented canopy species that have created conditions favorable for the establishment of mesophytes and by the loss of *C. dentata* that resulted in canopy gaps.

Index terms: dendroecology, disturbance, *Liriodendron tulipifera, Quercus*, Ridge and Valley, succession

INTRODUCTION

The southern section of the Ridge and Valley physiographic province extends from northeast Tennessee through northern Georgia to the terminus of the Appalachian Highlands in central Alabama. The natural vegetation of the southern Ridge and Valley was originally described as *Quercus-Castanea* (Braun 1950), but is now dominated by mixed *Quercus* and *Carya* species (Keever 1953; DeSelm et al. 1969; McCormick and Platt 1980; Stephenson et al. 1993). The contemporary forests of the region have been heavily impacted by anthropogenic disturbances. The majority of forested land in the southern Ridge and Valley was cleared for settlement, timber, row cropping, and grazing during the nineteenth and twentieth centuries. Some lands have remained in non-forest uses while others have been allowed to develop into mature forests via secondary succession. The majority of forest stands in this region are relatively young (< 100 y) and few old-growth remnants remain. Many of these forests are even-aged and have experienced considerable anthropogenic disturbances during their growth and development, such as selective timber harvesting and grazing.

While many reserves in the region were not established until the 1930s, the Ijams Nature Reserve (INR) was established in 1910 to create a natural area for conservation and recreation and is the oldest upland forest reserve in the region. Reserve status has allowed the forest to mature with minimal anthropogenic disturbance; and because the property was owned and managed by two naturalists, records of forest history have been maintained. The INR provides a unique opportunity to study the growth and development of one of the oldest secondary upland forests in the region that has been in reserve management for almost one century.

Throughout the Eastern Deciduous Forest Region, the documentation of successional processes is important because the majority of the landscape consists of secondary forests that have developed following widespread timber removal and intense human impacts during the eighteenth, nineteenth, and twentieth centuries. Land use practices have been important controls on forest vegetation patterns of post-European settlement landscapes as many forest stands are not returning to their pre-European settlement conditions. This phenomenon is largely attributed to prior land uses (e.g., burning, forest clearing, grazing, row cropping) and altered disturbance regimes that have disrupted vegetation-environment relationships (Fralish et al. 1991; Abrams et al. 1995; Abrams and McCay 1996; Cowell 1998; Foster et al. 1998; Fuller et al. 1998; Motzkin et al. 1999). To comprehensively understand growth and development of modern forest communities, researchers must consider the land use and disturbance history of the study site (Raup 1966; Cronon 1983; Foster 1988; Christensen 1989; Foster 1992; Whitney 1994; Ruffner and Abrams 1998; Lafon et al. 2000; Foster 2002; Frelich 2002; Foster et al. 2003).

A widespread pattern of successional change has been reported throughout the eastern United States (Lorimer 1984; Abrams and Downs 1990; Loftis and McGee 1993; McCarthy and Bailey 1996; Abrams 2003; Pierce et al. 2006). A lack of *Quercus* regeneration and increased mesophytic dominance (especially *Acer* species) has been linked to active fire suppression that began in the early 1900s (McCarthy *et al*. 1987; Crow 1988; Cho and Boerner 1991; Goebel and Hix 1997). However, some sites undergoing composition shifts do not have a history of repeated burns and have developed entirely in the absence of fire. In these ecosystems, processes other than fire must be examined to explain observed successional patterns. Stands at the INR fall under this category and provide an opportunity to document relatively long-term secondary succession of an upland hardwood forest under reserve management that has developed in the absence of fire. By quantifying species composition, stand structure, and disturbance history we can elucidate the processes responsible for the documented successional pattern. The specific objectives of our study were to: (1) quantitatively describe species composition and structural attributes, (2) determine the disturbance history of the forest using dendroecological techniques, and (3) document the role of land use and disturbance history on the successional pathway of a mature hardwood forest in the Ridge and Valley of east Tennessee.

Land Use History

Historical inhabitants, such as the Cherokee and Creek, traveled through the Tennessee Valley and used resources on an ephemeral, task specific basis (Stueckrath 1859). While their influence on the landscape is not quantified, the prevalence of disturbance-oriented vegetation across the region at settlement suggests possible burning and widespread land clearing. The region was known for excellent hunting grounds, and the proximity of the Tennessee River offered additional transportation and commercial advantages (Stueckrath 1859).

Although anthropogenic disturbances have occurred for millennia in the southern Ridge and Valley, European settlement of the region intensified human modification of the landscape (Delcourt and Delcourt 2000). Europeans began to settle the area and establish land claims soon after the Revolutionary War (U.S. Department of Agriculture 1955). Land ownership and transferal records of the property currently in the INR were obtained from the Knox County Courthouse, Office of the Property Assessor, and the East Tennessee Historical Society. The original land grant was provided to William Brown in 1826 by the state of Tennessee, and the records showed the land was always owned by private individuals (Table 1). Although the records were of limited value because of the lack of detailed land use information (such as number of livestock), they did provide data on the original witness trees used to mark the property boundary. The boundary trees listed were: *Quercus alba* L. (three individuals), *Q. velutina* Lam., *Castanea dentata* (Marsh.) Borkh., and one *Carya* species. The ownership records indicated the land was cleared for agriculture sometime after 1826 (although it likely experienced prior anthropogenic disturbances) and was used for subsistence farming until the property was purchased by Harry P. and Alice Y. Ijams in 1910. The Ijams bought the land for $1000 and converted a resident barn

Table 1. Land-use history of the Ijams Nature Reserve in the Ridge and Valley of east Tennessee.

Date	Land-Use Practice	Forest Impact
Before 1790	Cherokee hunting grounds	Hunting pressure and understory burning
After 1790	European settlement	Timber cut to build homes, roads, and railroads in the Knoxville area
1794	Knoxville established	Log buildings erected, trade center of east Tennessee
1826–1910	William Brown and Johnson family	Land granted from Tennessee, subsistence agriculture, forest cutting, and grazing
1910–1964	Harry and Alice Ijams create reserve	Built home and developed the 8-hectare property into a nature reserve
1965	Ijams land deeded to Knoxville	Managed by Knoxville Garden Club, Knox County Council of Garden Clubs, and the City of Knoxville
1976–present	Ijams Nature Center, Inc.	Formally incorporated as a non-profit organization and became an interpretation and education center
1990	Ijams land purchase	25 hectares of adjoining land purchased with Knoxville and Tennessee Funds

into their living quarters. The original land parcel established as a nature reserve was donated to the City of Knoxville in 1965. The property is managed by the board of directors of Ijams Nature Center, Incorporated, which is a non-profit organization founded in 1976.

Currently, the primary land use of the INR is recreational. Anthropogenic disturbances are limited to maintenance of light, single-track trails. Trees and limbs that fall across trails are cut if required and moved to serve as trail borders. Park visitors are requested to remain on trails to prevent the trampling of herbaceous vegetation and seedlings. We did not find fire scars on any living or dead trees. Field observations included the analysis of tree cross sections that had been cut to prevent trail obstruction. Although soil charcoal was not quantified, soil was collected at the site for additional analyses and no charcoal was documented in our 30 samples. Furthermore, no fires were recorded in field notes maintained by reserve managers. Based on these observations, we are confident that the INR has not burned since reserve establishment in 1910.

METHODS

Study Area

The INR is located in Knox County, Tennessee, in the eastern portion of the state (Figure 1). The original reserve was only 8 ha, but additional lands were acquired and the reserve now consists of 65 ha. The study site is located within the Ridge and Valley physiographic province of the Appalachian Highlands (Fenneman 1938). The province lies east of the Cumberland Plateau and west of the Blue Ridge Mountains. At this latitude, the Ridge and Valley province is ca. 64 km wide. The underlying geology consists of Cambrian and Ordovician limestones, dolomites, shales, and silty sandstones (Miller 1974). Severe folding, faulting, and differential weathering of bedrock have resulted in a system of parallel ridges consisting of resistant sediments and valleys composed of softer limestones and shales that have northeast to southwest oriented axes (Miller 1974; Griffith et al. 1997). The INR contains extensive karst features. Depth to bedrock varies from 1-3.5 m. The soils of the study site are of the rolling phase of the Tellico loam. Soils of the area are moderately acidic and have moderately high moisture holding capacity (U.S. Department of Agriculture 1955). The elevation of our study plots varied

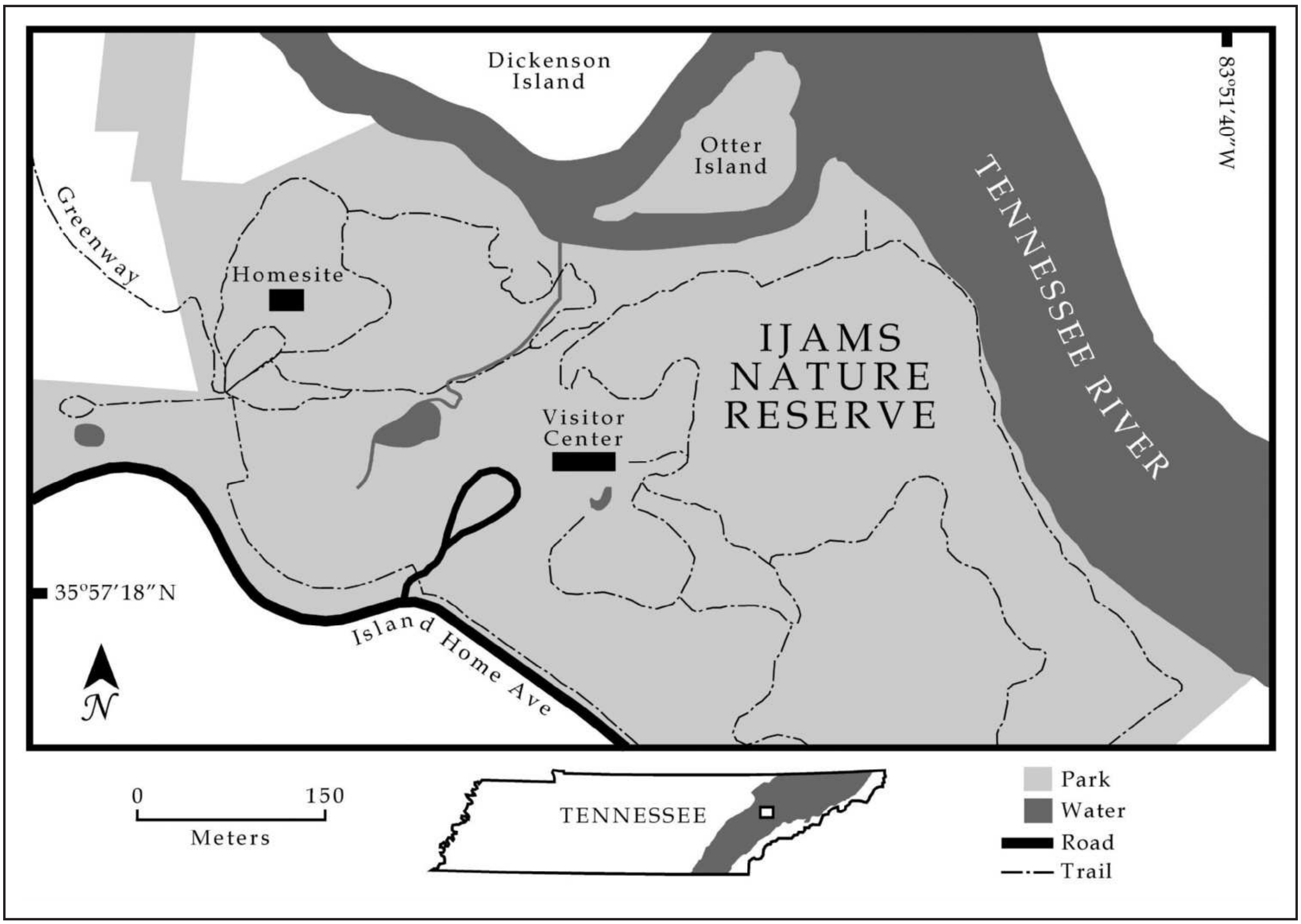

Figure 1. Map of Ijams Nature Reserve in the Ridge and Valley physiographic province in east Tennessee.

from 250-275 m.

The climate is classified as humid mesothermal (Thornthwaite 1948), with long-hot summers and short-mild winters. The average frost-free period is 201 days (early-April to late-October) and mean annual temperature is 14 °C. The July average is 25 °C and the January average is 2 °C (National Oceanic and Atmospheric Administration 2004). In winter, soils may freeze to a depth of no more than 5 cm and generally remain frozen for no more than a few hours (U.S. Department of Agriculture 1955). Mean annual precipitation is 135 cm and mean annual snowfall is 5 cm (National Oceanic and Atmospheric Administration 2004). The area receives steady precipitation throughout the year with no distinct dry season. Spring, summer, and early fall are characterized by heavy rains that are often accompanied by moderate to severe thunderstorms.

The study area is a component of the Ridge and Valley Ecoregion (Southern Shale Valleys, ecoregion level IV) (Omernik 1987). Braun (1950) classified the area as part of the *Quercus*-*Castanea* Forest Region with mesophytic forests occurring in ravines. Most *C. dentata* trees in the area were killed by *Cryphonectria parasitica* (Murr.) Carr. (chestnut blight) before 1930 (U.S. Department of Agriculture 1955). In the southern Appalachians, *C. dentata* was replaced by *Quercus* as well as *Carya* species especially on upland sites (Keever 1953; Woods and Shanks 1959; DeSelm et al. 1969; McCormick and Platt 1980). *Quercus* stands are common on upland sites of the southern Ridge and Valley. *Quercus alba* and *Q. montana* Willd. often dominate stands with other *Quercus* and *Carya* species. *Liriodendron tulipifera* L. and mixed *Pinus* species are common during early stages of succession (Martin and DeSelm 1976; Stephenson et al. 1993).

Field Methods

We randomly established ten 0.0625 ha square plots (25 m x 25 m) in the original land holding of the Ijams family to document forest conditions. Plots represented different aspects, slope positions, and slope gradients. In each plot we recorded species, crown class, and diameter at breast height (dbh, ca. 1.4 m above the surface) for all stems 5 cm dbh to quantify species composition and the vertical and diameter structure of the stand. Crown class categories (overtopped, intermediate, codominant, and dominant) were based on the amount and direction of intercepted light (Oliver and Larson 1996). To characterize richness of the seedling layer, all woody species < 1 m ht were recorded in all plots. We also documented all alien species. Within each plot 4-7 trees were cored at breast height with increment borers to evaluate stand age, recruitment pulses, and radial growth patterns. In each plot, we also documented all snags and logs on the forest floor to quantify the abundance of coarse woody debris and decay dynamics. All logs were measured and placed into one of four decay classes (1-4, with 4 being the most decayed) following criteria adapted from McCarthy and Bailey (1994).

Laboratory Methods

Tree cores were prepared and processed using the methods outlined in Stokes and Smiley (1996). The cores were air-dried, glued to wooden mounts, and then sanded to reveal the cellular structure of the wood (Orvis and Grissino-Mayer 2002) before being dated with the aid of a dissecting microscope. *Quercus* individuals were selected to analyze forest disturbance history 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 disturbance history in the eastern United States (McCarthy and Bailey 1996; Nowacki and Abrams 1997; Rubino and McCarthy 2004). For all *Quercus* series (n = 37), we measured ring widths to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software. The measurement series were visually compared and statistically analyzed to ensure accurate crossdating (i.e., to ensure each growth ring was labeled with the appropriate 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 created from the remaining series. Any segment that falls below a significance threshold is flagged by the program. All flagged segments were re-inspected for incorrect crossdating. The program ARSTAN (Cook 1985) was used to standardize the raw ring measurements to document periods of above and below average growth at the stand level. The raw data were detrended using a 30-year smoothing spline. The standard chronology was developed by dividing actual tree-ring measurements by predicted values generated by the deterministic linear growth models fit to each series.

Dendroecological techniques are commonly used to quantify the magnitude and frequency of forest disturbance events (Fritts and Sweatnam 1989; Abrams and Nowacki 1992; Orwig and Abrams 1995; Black and Abrams 2005). The identification of release episodes is one of the fundamental dendroecological approaches for quantifying the disturbance history of a stand (Lorimer and Frelich 1989; Nowacki and Abrams 1994; Ruffner and Abrams 1998; Frelich 2002; Rubino and McCarthy 2004). Minor and major release events, defined as changes in radial growth relative to a pre-determined criterion, were calculated using a percent growth change equation (Nowacki and Abrams 1997; Schuler and Fajvan 1999; Rubino and McCarthy 2004). We analyzed changes in raw ring width with respect to the running median of the previous and subsequent 10 years. Release events were identified as periods in which raw ring width was ≥ 25% (minor) or ≥ 50% (major) of the 10 years preceding and superseding median, sustained for a minimum of three years (Rubino and McCarthy 2004). Release data were displayed using FHX2 software to visually display release events spatially and temporally (Grissino-Mayer 1995). The FHX2 software displays release events by individual trees and as a composite to investigate disturbance at the stand level. The use of FHX2 software to develop disturbance chronologies from tree-ring widths versus scar information demonstrates a new technique in dendroecology. Vegetation was analyzed by standard descriptors of density, basal area (dominance), importance, richness, the Shannon diversity index (*H'*), and evenness (*J*) (Cottam and Curtis 1956; Ludwig and Reynolds 1988).

RESULTS

Forest Composition

The four most important species were *L. tulipifera*, *Fagus grandifolia* Ehrh., *Q. alba*, and *Acer saccharum* Marsh. (Table 2). *Fraxinus americana* L., *Cornus florida* L., *Q. velutina*, *Carya ovata* (Mill.) K. Koch, and *Quercus rubra* L. were also important contributors to the forest stand. Density of trees ≥ 5 cm dbh was 555 stems/ha (Table 3). The total basal area of overstory trees was 34.04 m^2/ha. Species richness of stems ≥ 5 cm dbh was 30, diversity (*H'*) was 2.97,

Table 2. Density, dominance, and importance of trees (≥ 5 cm dbh) at Ijams Nature Reserve, Tennessee. Values shown are per hectare.

Species	Density (stems/ha)	Relative density	Dominance (m^2/ha)	Relative dominance	Relative importance
Liriodendron tulipifera	49.6	8.93	5.37	15.77	12.35
Fagus grandifolia	68.8	12.39	3.08	9.06	10.73
Quercus alba	19.2	3.46	5.66	16.63	10.04
Acer saccharum	81.6	14.70	1.55	4.54	9.62
Fraxinus americana	38.4	6.92	1.23	3.62	5.27
Cornus florida	48.0	8.65	0.34	1.01	4.83
Quercus velutina	12.8	2.31	2.45	7.21	4.76
Carya ovata	20.8	3.75	1.84	5.41	4.58
Quercus rubra	17.6	3.17	1.83	5.38	4.28
Quercus coccinea Muenchh.	9.6	1.73	2.00	5.88	3.81
Quercus falcata	6.4	1.15	2.11	6.20	3.67
Nyssa sylvatica Marsh.	24.0	4.32	0.94	2.76	3.54
Pinus virginiana	12.8	2.31	1.41	4.14	3.22
Quercus montana	16.0	2.88	1.00	2.94	2.91
Ulmus americana L.	24.0	4.32	0.34	0.99	2.66
Acer rubrum	17.6	3.17	0.30	0.88	2.02
Pinus echinata	4.8	0.86	1.07	3.13	2.00
Juniperus virginiana	9.6	1.73	0.45	1.32	1.53
Ostrya virginiana (Mill.) K. Koch	14.4	2.59	0.09	0.26	1.43
Carya glabra Mill.	9.6	1.73	0.33	0.98	1.36
Oxydendrum arboreum (L.) DC.	8.0	1.44	0.14	0.40	0.92
Prunus serotina Ehrh.	8.0	1.44	0.12	0.35	0.90
Cercis canadensis	6.4	1.15	0.06	0.17	0.66
Tilia americana L.	4.8	0.86	0.09	0.27	0.57
Albizia julibrissin	4.8	0.86	0.05	0.16	0.51
Carpinus caroliniana Walt.	4.8	0.86	0.03	0.08	0.47
Carya tomentosa (Poir.) Nutt.	4.8	0.86	0.02	0.06	0.46
Robinia pseudoacacia L.	3.2	0.58	0.08	0.23	0.40
Aesculus flava Ait.	3.2	0.58	0.02	0.06	0.32
Celtis occidentalis L.	1.6	0.29	0.04	0.11	0.20
Totals	**555.2**	**100**	**34.04**	**100**	**100**

Table 3. Diversity, structural, and compositional measures of trees (≥ 5 cm dbh) at Ijams Nature Reserve, Tennessee.

Parameter	Value
Density (stems/ha)	555
Basal area (m²/ha)	34.04
Species richness	30
Diversity (*H′*)	2.97
Evenness (*J*)	0.87

and evenness (*J*) was 0.87 (Table 3).

The most abundant species based on relative density were *A. saccharum* and *F. grandifolia* (Table 2). A second tier of species with high densities included *L. tulipifera*, *C. florida*, and *F. americana*. The most dominant trees in the stand based on basal area were *Q. alba* and *L. tulipifera* (Table 2), with a second tier that included *F. grandifolia*, *Q. velutina*, and *Quercus falcata* Michx.

Richness in the seedling layer (< 1 m ht) was 20. We did not quantify the density or percent cover of seedlings, but visual observation indicated *A. saccharum*, *Acer rubrum* L., *F. grandifolia*, *C. florida*, and *Cercis canadensis* L. were most common. Only three species occurred in the seedling layer that we did not document as established individuals: *Asimina triloba* (L.) Dunal, *Ilex opaca* Ait., and *Sassafras albidum* (Nutt.) Nees. We found four alien species within our study plots including an *Albizia julibrissin* Durazz in the overstory, *Ligustrum japonicum* Thunb. in the understory, and *Hedera helix* L. and *Vinca minor* L. in the seedling layer.

We documented 66 individuals in our plots with dominant positions in the canopy representing 13 species. *Liriodendron tulipifera* and *Q. alba* were the most common species with dominant positions in the canopy, representing 22.7% and 13.6% of canopy dominants, respectively. A total of 54 individuals representing 12 species occupied codominant positions in the canopy. *Liriodendron tulipifera* (18.5%), *F. americana* (16.6%), and *C. ovata* (14.8%) were the most common canopy codominants. A total of 107 individuals were overtopped with *C. florida* (25.2%) and *A. saccharum* (19.6%) being the most abundant. When standardized at the hectare level, a pattern is revealed for the four most important trees. *Quercus alba* and *L. tulipifera*, the most dominant species, had the majority of individuals in dominant canopy positions with no individuals that were overtopped (Figure 2). *Fagus grandifolia* and *A. saccharum*, the most abundant species, had the majority of individuals in intermediate and overtopped positions (Figure 2).

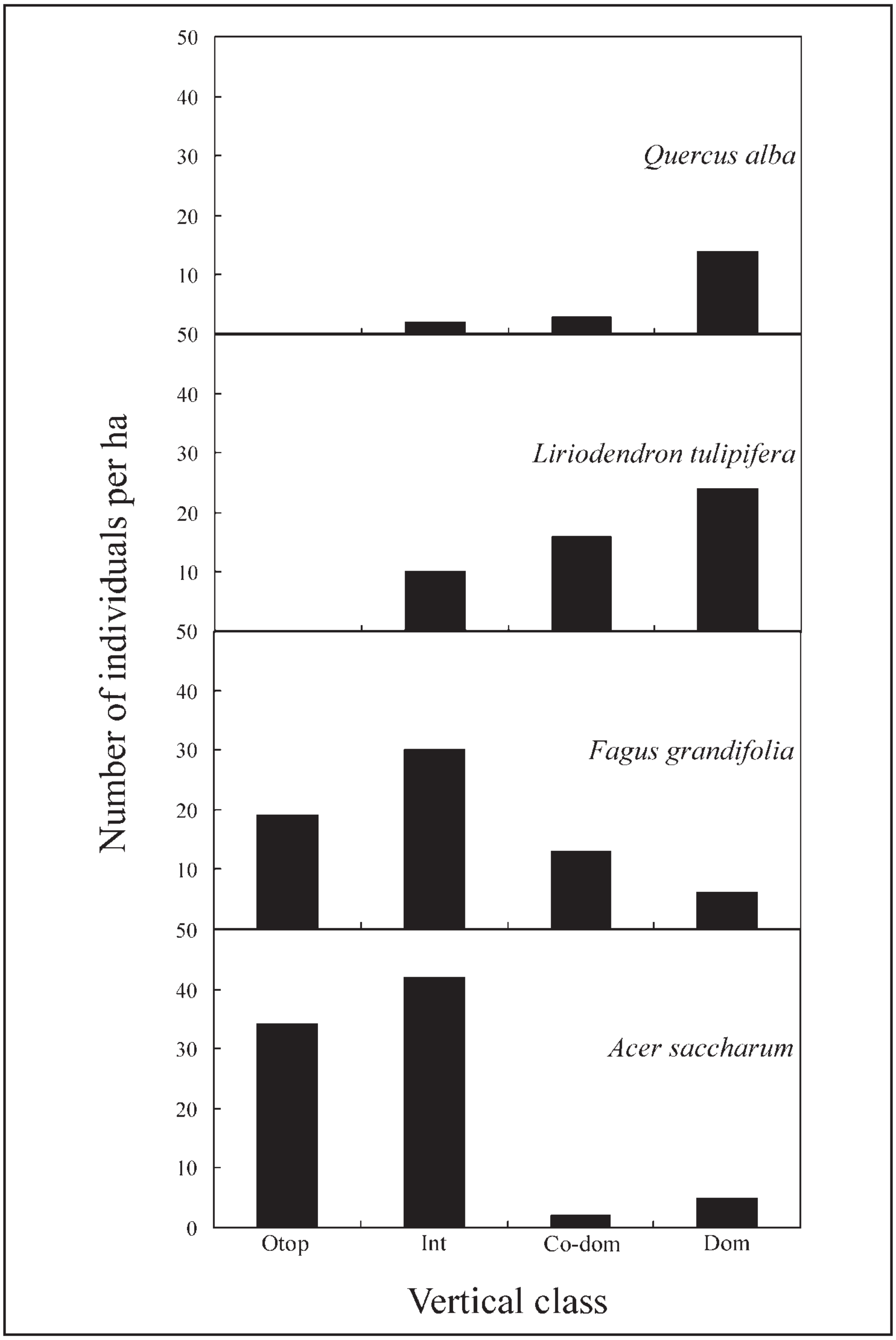

Figure 2. Canopy class distributions for the four most important species in Ijams Nature Reserve, Tennessee. Categories are based on the amount and direction of intercepted light (Oliver and Larson 1996). Otop: overtopped, Int: intermediate, Codom: codominant, Dom: dominant.

Stand Structure

The largest individual recorded was a *Q. alba* at 98.5 cm dbh and the second largest individual was a *Q. falcata* at 82 cm. These were the only trees > 80 cm in diameter. The largest diameter for a *L. tulipifera* tree was 77.5 cm, the largest *F. grandifolia* was 64 cm, and the largest *A. saccharum* was 36 cm. The diameter distribution of all stems in the stand was indicative of a mature transitional forest (Figure 3). Of the four most important species, only *Q. alba* occurred in the largest diameter class (Figure 3). *Quercus alba* occurred in nine of the 16 size classes spread throughout the range, but did not occur in a high density in any one class. *Liriodendron tulipifera* had a rather uniform diameter distribution (Figure 3). The species occurred in all but four size classes. Notably, *L. tulipifera* was missing in the smallest size class. *Fagus grandifolia* and *A. saccharum* had similar diameter structures. Both species exhibited reverse J-shaped distributions, where the number of individuals was greatest in the smallest size class and density generally declined with increasing size. This diameter structure is indicative of regenerating species. No species had individuals that occurred in every diameter class.

Of the 57 trees cored, all but one could be accurately dated. The oldest tree establishment was a *L. tulipifera* with an inner date of 1854 (Figure 4). The next oldest trees, a *C. ovata* and a *Q. alba*, were both established in 1857. There was continual establishment of individuals throughout the development of the stand with a recruitment pulse in the 1920s. Although we did not quantify radial growth during the juvenile stage for our sampled trees, visual observation of radial growth patterns of the oldest trees indicate they established in open areas with no overstory vegetation. The first 20 years of growth of the oldest individuals were complacent with minimal year-to-year variability.

To document the ratio of live and dead trees, we standardized the values at the hectare level. The number of live trees greatly exceeded the number of snags and logs on the forest floor (Figure 5). Density of snags and logs was similar, with 75 snags and 94 logs per hectare. The majority of coarse woody debris was in an advanced state of decay (Figure 6). The large amount of woody debris in decay class 3 indicated a forest disturbance or disturbances that removed trees within a short period.

Disturbance History

We are confident all *Quercus* individuals were accurately crossdated. The interseries correlation of the 37 *Quercus* series (from 36 individuals) was significant at

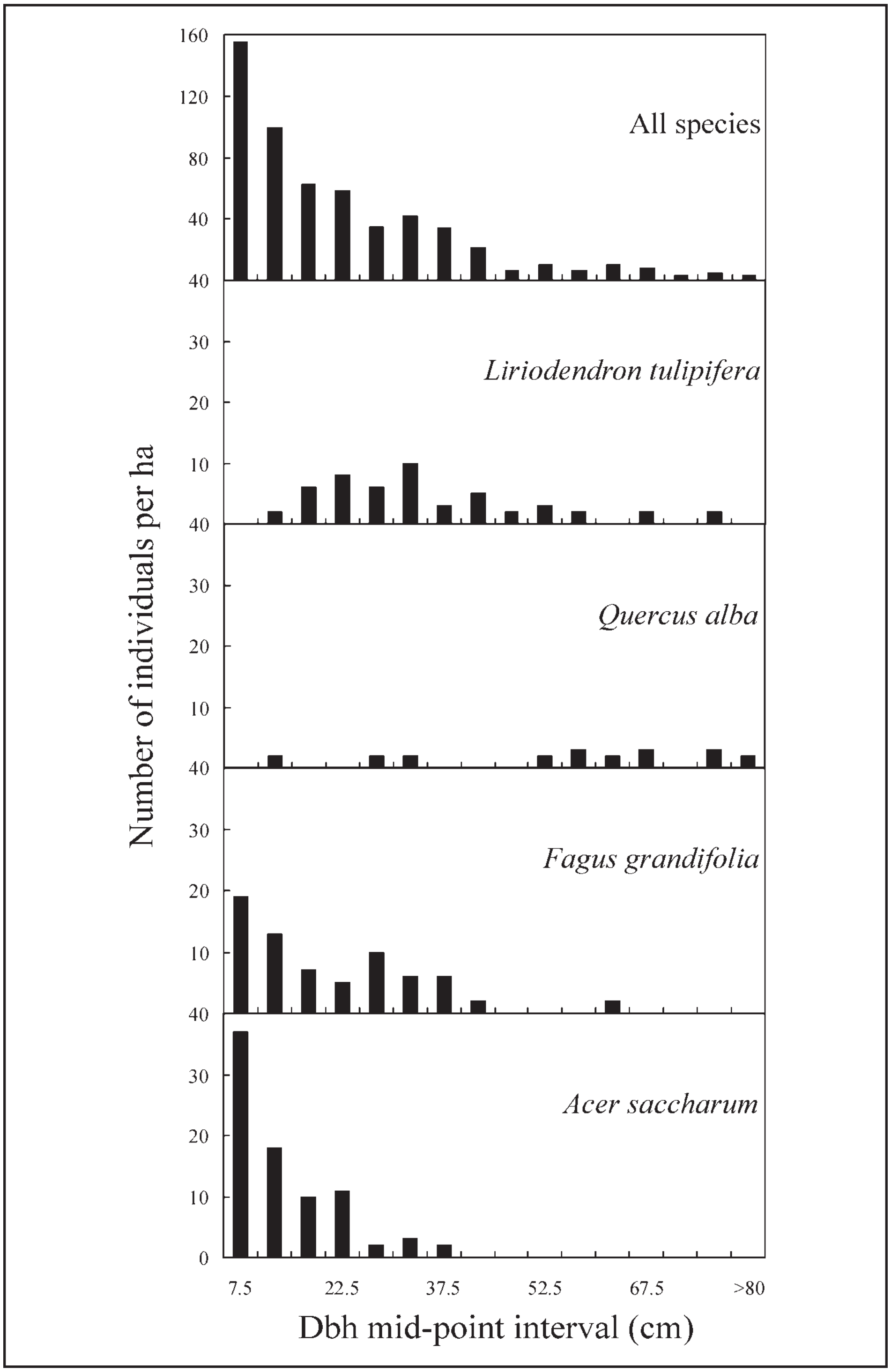

Figure 3. Number of trees (≥ 5 cm dbh) per ha for all species and the four most important species in Ijams Nature Reserve, Tennessee. Each dbh interval includes all stems ± 2.5 cm of the stated value with the exception of the > 80 category.

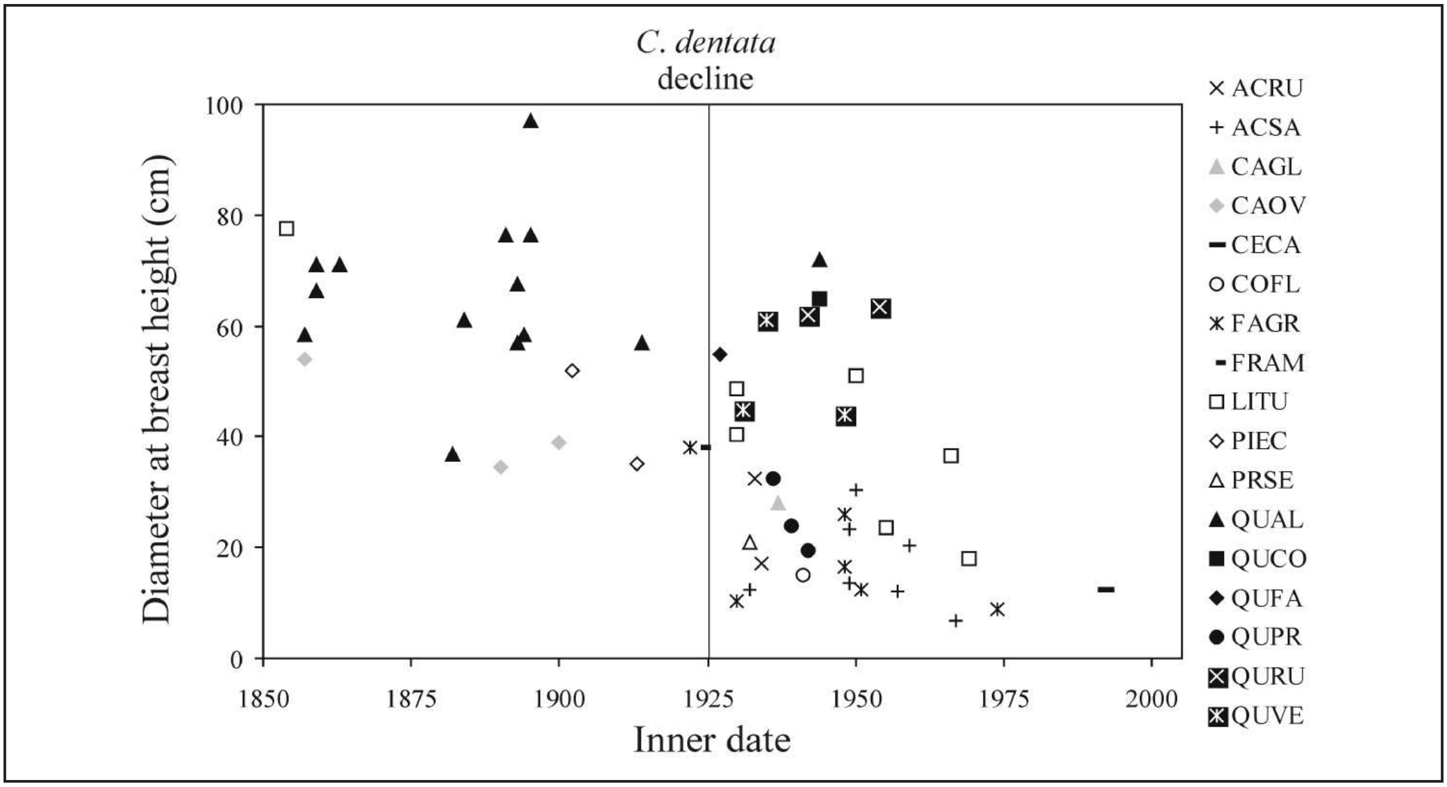

Figure 4. Diameter-age relationships for all cored trees that could be accurately dated in Ijams Nature Reserve, Tennessee. Species acronyms are based on the first two letters of the genus and the first two letters of the specific epithet (see Table 2 for complete binomials).

0.54. A total of 143 segments were tested by COFECHA of which 18 (12.5%) were flagged (indicating they were not statistically significant with the other segments of the same period). Average mean sensitivity was 0.21, which is typical for *Quercus* in the southeastern United States. The measured tree-ring series extended 149 years from 1857-2005. A composite radial-growth chronology was created where mean growth was standardized to equal 1.0. The composite chronology extends from 1859-2005. The first two years of the oldest individual were truncated so the earliest year (1859) had a sample depth of three individuals (Figure 7). The standardized chronology showed above average secondary growth from 1880-1890, during the 1920s, and from 1940-1980.

Of the 36 *Quercus* individuals analyzed using the 10-yr running median method, 28 (78%) exhibited release events. A total of 52 release events were detected from the 36 individuals with some trees experiencing multiple releases during their lifespan (Figure 8). All release events detected using the 10-yr running median method were visually checked for accuracy using the raw ring-width measurements for the 36 different *Quercus* individuals. Of the 52 detected release events, 41 (79%) were minor and 11 (21%) were major. One individual (a *Q. montana*) experienced four separate release events during its life (1919-2005, Figure 9a) and seven individuals experienced three separate release events (Figure 9b). Greatest percent growth change over the 10-yr running median was 318% experienced by a *Q. alba* (Figure 9c). Two release events were detected with sustained increased radial growth of over 100% (experienced by two *Q. alba* trees, Figures. 9c and 9d). These two events were sustained for three and four years and were not contemporary with one another. The longest release dura-

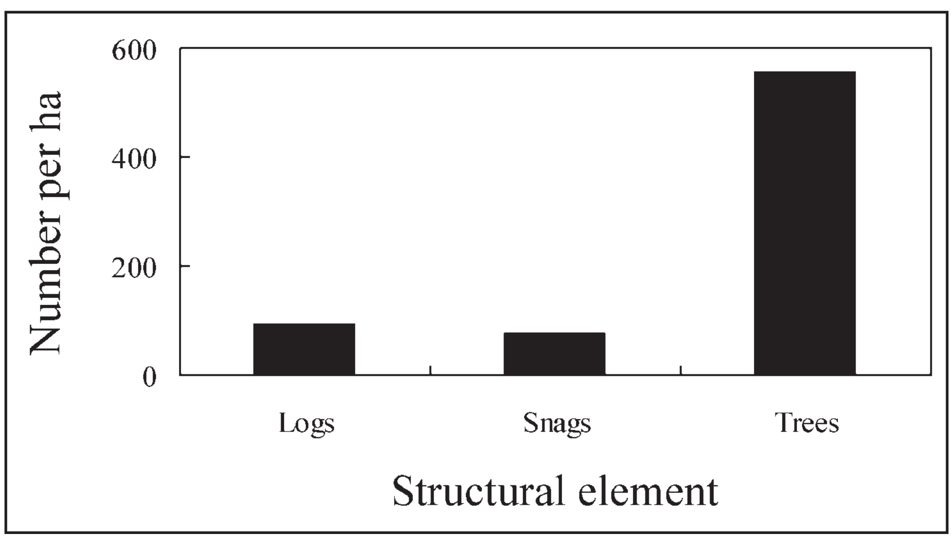

Figure 5. Number of logs, snags, and trees per hectare at Ijams Nature Reserve in east Tennessee.

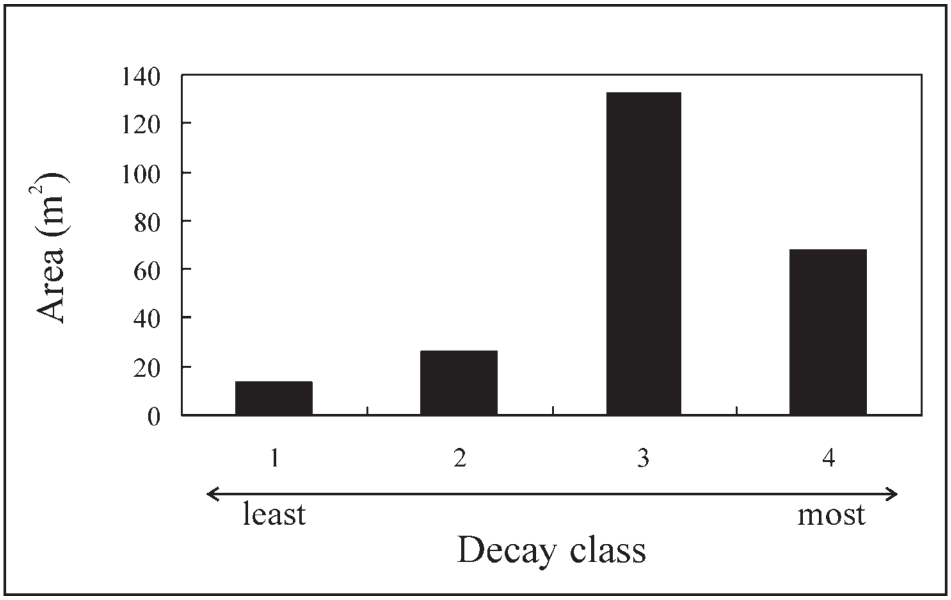

Figure 6. Decay class distributions for coarse woody debris at Ijams Nature Reserve in east Tennessee. Categories are based on the presence of small limbs, bark, fungi, and soundness of the material (adapted from McCarthy and Bailey 1994).

tion was seven years and observed in two individuals. The mean release duration was 3.87 years ± 1.1 (SD), which was just above our minimum sustained threshold of three years. The longest period between release events was 10 years and the shortest period was one year. In several instances, releases occurred in consecutive years (e.g., 1920-1923, Figure 8 composite). The mean release return interval was 3.5 years ± 2.7 (SD).

To determine if release events were stand-wide or local, we analyzed the temporal pattern of release episodes. Stand-wide disturbances were defined as release episodes where a minimum of 25% of individuals experienced simultaneous release (Nowacki and Abrams 1997; Rubino and McCarthy 2004). A stand-wide release event indicates an exogenous disturbance that removed overstory trees at a large spatial scale (e.g., ice storms, high wind events, insect attack). Only one stand-wide release was observed and it occurred between 1920 and 1927, with the majority of release episodes occurring in 1921-1923. During this stand-wide episode, 60% of all individuals living at that time experienced a release. In general, release events were asynchronous throughout the stand, occurring at a variable temporal scale. Asynchronous release events indicate a disturbance regime characterized by small, local-scale events such as single tree-fall gaps (Lorimer 1980; Orwig and Abrams 1994).

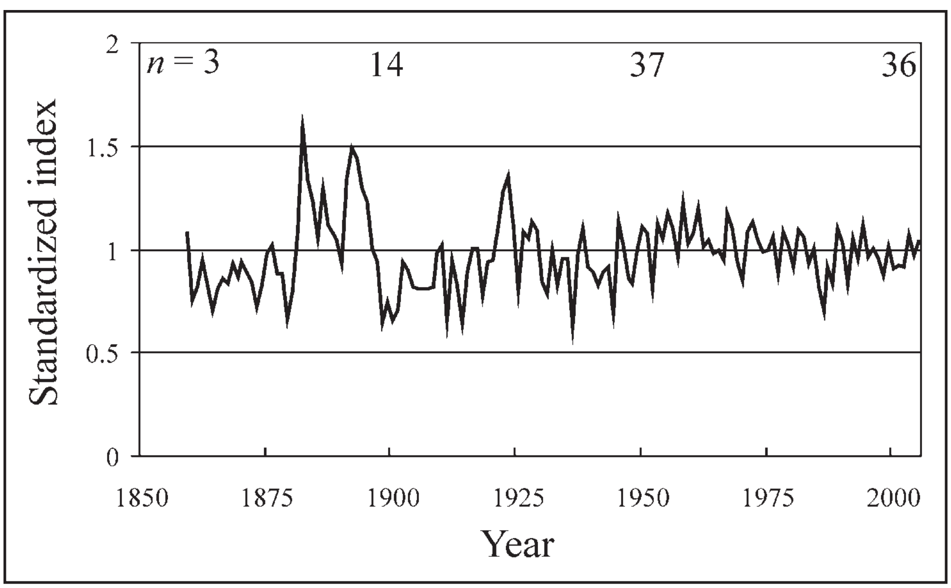

Figure 7. Composite ring-width index generated from all *Quercus* series sampled at Ijams Nature Reserve with mean growth standardized to 1.0 (*n* = number of series at that time).

DISCUSSION

Composition and Structure

The stand had a reverse J-shaped diameter structure, indicating the forest is regenerating (Smith et al. 1996). However, the composition of species most abundant in the understory did not match the composition of species in the overstory. Barring a large-scale disturbance, successional change is apparent. The forest canopy was dominated by *L. tulipifera*, *Q. alba*, *F. americana*, and *C. ovata*. However, stem density was highest for *A. saccharum* and *F. grandifolia*. The forest is currently in a stage of understory reinitiation as defined by Oliver and Larson (1996) as individuals present in the understory are being recruited to larger size classes. In the absence of a major disturbance, *A. saccharum* and *F. grandifolia* will likely increase in dominance as individuals overtopped in the understory are recruited to codominant and dominant positions in the forest canopy. These shade tolerant species may remain suppressed in the understory until the formation of canopy gaps allows for their recruitment.

Liriodendron tulipifera was the most important tree in the study site. In the southeastern United States, *L. tulipifera* commonly establishes after agricultural abandonment or other large-scale disturbances that remove overstory vegetation (Clebsch and Busing 1989; Shankman 1990; Elliott et al. 1998; Lafon 2004). The species is also able to establish after small canopy disturbances and is a com-

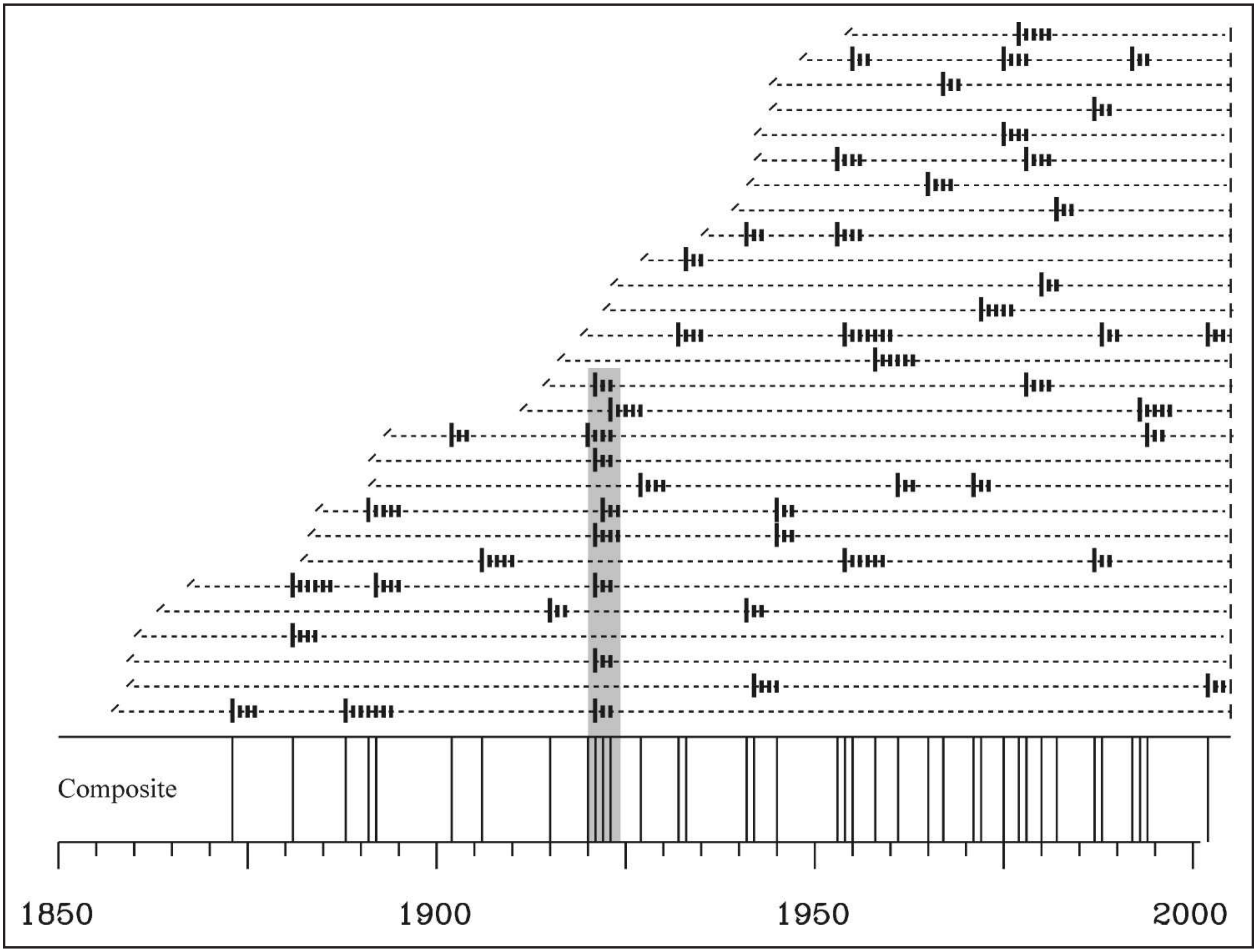

Figure 8. Detected release events using the 10-yr running median method for 36 *Quercus* individuals sampled at Ijams Nature Reserve in east Tennessee. Each horizontal line represents the record from one individual tree, long vertical bars indicate release events, and short vertical bars indicate release duration. Gray area indicates stand-wide release of early 1920s. A composite of release events for the study site is shown across the bottom.

mon component of old-growth forests in the southern Appalachians (Clebsch and Busing 1989; Lafon 2004). The size of the gap needed for *L. tulipifera* establishment likely varies according to biotic and abiotic site conditions. The species can establish and reach the canopy in larger gaps, but cannot withstand the periodic growth suppression that may occur in smaller gaps (i.e., gap closure before *L. tulipifera* reaches the canopy) (Buckner and McCracken 1978; Runkle 1981; Orwig and Abrams 1994; Busing 1995). The age and diameter structure of *L. tulipifera* in our study plots indicated the species established during the early stages of old field succession and subsequently established in small canopy gaps (Figure 4).

Alien species have colonized and presented problems at specific sites in the reserve, which is not surprising because the INR is located on the periphery of the Knoxville, Tennessee, metropolitan area. We documented the establishment of one woody alien, *A. julibrissin* (15 cm dbh), and we also documented the occurrence of *L. japonicum* in the understory (< 1 m ht). Both of these woody species are able to persist in the understory of a closed canopy, are able to survive in a suite of environmental conditions, and are invasive (Miller 2003). *Albizzia julibrissin* likely escaped cultivation on the property, while *L. japonicum* likely colonized the site by animal (likely avian) dispersed seed. We only documented two woody alien individuals in our study plots, and we do not believe they are having a significant influence on forest community dynamics. However, if these invasions are not remedied, they could present future problems for reserve managers. This is especially true for *L. japonicum* that can establish a dense, impenetrable understory that may preclude forest regeneration. The herbaceous layer of the INR was also inhabited by two notable alien species, both of which are groundcovers. There was a small cluster (*ca.* 80 m^2) of *H. helix* as well as several scattered patches of *V. minor*. Both of these species are shade tolerant

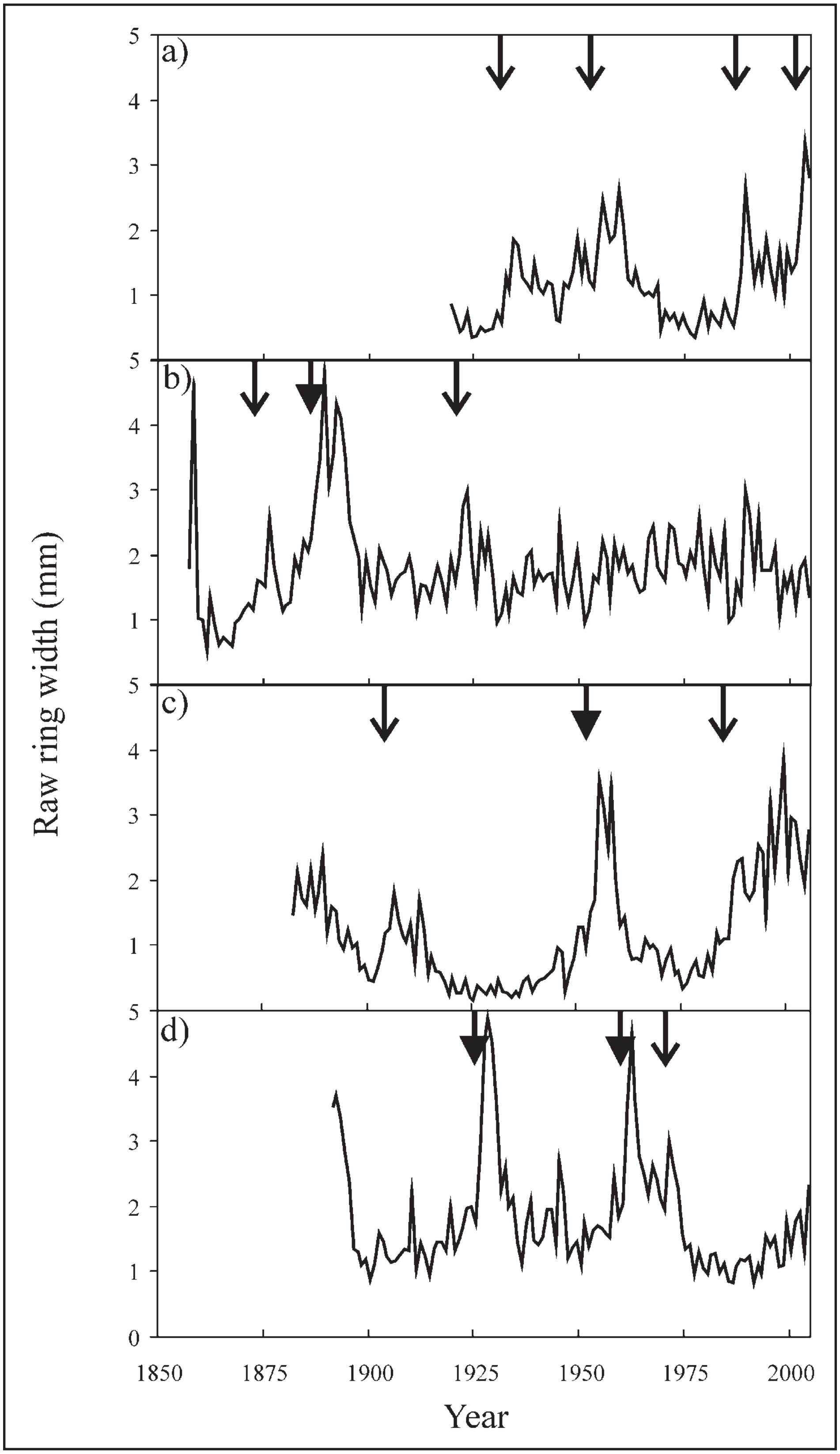

Figure 9. Raw-ring width measurements for individuals sampled at Ijams Nature Reserve. Open arrow indicates minor release and filled arrow indicates major release episodes. a) *Q. montana* with 4 release events, b) *Q. alba* with 3 release events (oldest *Quercus* individual sampled), c) *Q. alba* with a growth change of 318% and change of over 100% sustained for 4 years, d) *Q. alba* with growth change of over 100% sustained for 3 years.

and can be invasive (Miller 2003), but they did not appear to be influencing forest dynamics (i.e., regeneration or disturbance patterns).

The age structure indicated the stand experienced two establishment pulses that may be related to land use. Three of our study plots were located on steep slopes (60-75% slope) that would not have allowed for row cropping. The timber was likely removed from the slopes in the mid-1800s and then allowed to progress through secondary succession without further disturbance. The steep slopes contained the oldest trees we documented, which were *Quercus*. The oldest *Pinus* individuals we documented established in the early twentieth century (Figure 4) around the time the Ijams family acquired the property. These individuals were located on relatively flat surfaces that would have been well-suited for agriculture. Following agricultural abandonment on upland sites in the region, *P. echinata* Mill. and *P. virginiana* Mill. are typically the first woody species to establish and dominate a site. Following *Pinus* senescence, composition shifts to hardwoods (Billings 1938; Lafon et al. 2000). Because *Pinus* still occurred in the overstory, we believe this site was allowed to develop following the abandonment of agriculture at the turn of the century. In contrast, sites with steep slopes were not farmed and allowed to develop immediately following timber removal around 1850. Agriculture as a historic land use was also apparent by the importance of *L. tulipifera*. Stands dominated by the species are not common on sites without a history of anthropogenic disturbance (Lafon 2004) although exceptions do occur (e.g., Joyce Kilmer Memorial Forest, North Carolina).

Disturbance History

Only one stand-wide release episode was detected in the study site. This stand-wide disturbance occurred in the 1920s and may have been the result of *C. dentata* decline. Other studies in the Appalachians have also documented radial growth increases in *Quercus* species during this time in the Ridge and Valley of Virginia (Agrawal and Stephenson 1995) and in western Maryland

(McCarthy and Bailey 1996). Although we documented no *C. dentata* stump sprouts, we know the species occurred on the site because of the original 1820s land survey records.

Despite the stand-wide disturbance that occurred in the 1920s, forest disturbance events were largely asynchronous, occurring at a variable temporal scale. The occurrence of only one stand-wide disturbance in the 150-year record of the forest indicates that the return interval of stand-wide disturbance events at the INR is much longer than what has been reported elsewhere in the eastern U.S. Other studies in *Quercus*-dominated forests that have used similar release detection methods have found stand-wide disturbance events to occur approximately every 20-30 years (Nowacki and Abrams 1997; Rubino and McCarthy 2004). However, only one stand-wide disturbance was documented during 80 years of forest development by Hart and Grissino-Mayer in secondary hardwood stands on the Cumberland Plateau of Tennessee (Hart and Grissino-Mayer 2008). Because no events occurred in all sampled trees and many release episodes occurred in a single individual, we believe gap-phase dynamics were the primary disturbance events that influenced forest development in the INR. These release events likely resulted from small canopy disturbances that involved the partial or total death of one or a few canopy individuals (Nowacki and Abrams 1997; Rubino and McCarthy 2004; Black and Abrams 2005). Interestingly, at least one major storm event that impacted the region was not recorded in the tree-ring series. On 12-15 March 1993, over 30 cm of snow fell in Knox County causing damage to natural and human structures. However, this storm caused only minimal forest damage at the INR as only one individual exhibited a release in 1993 and one in 1994 (Figure 8).

The duration of increased radial growth following a canopy disturbance varied among individuals and events, but, in general, was approximately four years; and the maximum time between disturbance events was a decade. As forests mature, the distance between large individuals increases and dominant trees occupy more canopy area. As trees are removed from the canopy during early stages of succession, the resulting gaps are small relative to canopy gaps in old-growth stands. The small gaps should close at faster rates than larger gaps in older forests. It is important to note that release events do not necessarily indicate tree recruitment as some release events may be coincident with lateral crown expansion (Rubino and McCarthy 2004). This may be especially true during the early stages of forest development. As forests mature, gap size should increase and so should the time required to fill the canopy void. As gap size increases, so should the likelihood that release events indicate recruitment over lateral crown expansion.

Succession and Disturbance

The species composition shift documented at the INR supports other studies throughout the eastern U.S. where *Quercus-Carya* dominated systems are being replaced by *Acer-Fagus* (e.g., Fralish et al. 1991; Abrams 1992; Ruffner and Abrams 1998; van de Gevel and Ruffner 2006). Most studies have linked successional shifts to active fire suppression that has allowed for the establishment of mesophytic and fire-sensitive species in the understory (Crow 1988; Loftis 1990; Abrams 1992; Brose et al. 2001; Lorimer 2001). Stands at the INR have developed entirely in the absence of fire, but are still projected to support more mesophytic and fire-intolerant species in the future. In this case, the successional shift does not correspond to active fire suppression by reserve managers. The current canopy dominant individuals at the INR are of disturbance oriented species that established on the site following timber removal and agricultural abandonment. Undoubtedly, during stand initiation, site conditions (e.g., soil fertility) were less favorable than present conditions. Throughout stand development, understory and soil conditions have been modified by the canopy through modifications in light, moisture, and temperature and through leaf litter and coarse woody debris inputs (Callaway 1995; Stachowicz 2001; Bruno et al. 2003). We hypothesize this facilitation created conditions favorable for the establishment of mesophytic species that generally dominate on higher quality sites. These facilitative processes combined with the loss of *C. dentata* may explain the successional shift evident in the reserve. Establishment dates of the oldest *A. saccharum*, *A. rubrum*, and *F. grandifolia* individuals coincide with the loss of *C. dentata*. We propose facilitation and not solely fire suppression may be responsible for successional changes in other hardwood forests of the eastern United States where composition shifts do not coincide with fire suppression. In such forests, successional change likely follows modifications to understory and soil conditions during stand development, not the removal of fire. Poor site conditions (caused by row cropping, grazing, annual burning, etc.) at the time of stand initiation are ameliorated during the growth of the stand. This facilitation by the present forest (i.e., the nurse plants) allows for the establishment of mesophytes that cannot compete with *Quercus* species, *L. tulipifera,* and other disturbance-oriented taxa on lower quality sites.

CONCLUSIONS

The goal of our study was to quantify species composition, stand structure, disturbance patterns, and the successional trajectory for the oldest hardwood forest reserve in the southern Ridge and Valley of Tennessee. The stand was dominated by *Q. alba* and *L. tulipifera*. The relative importance of *L. tulipifera* was attributed to its status as a pioneering species and its ability to establish in canopy gaps caused by the senescence of dominant individuals. The understory contained a high abundance of *A. saccharum* and *F. grandifolia*.

The forest experienced one stand-wide release episode in the 1920s that we attributed to the decline of *C. dentata*. This stand-wide disturbance was contemporary with other release episodes that have been reported in the Appalachian Highlands. The return interval of stand-wide disturbance events at INR is much longer than what has been reported for similar forest types in the eastern U.S. (Nowacki and Abrams 1997; Rubino and McCarthy 2004). With the exception of this one stand-wide release, the disturbance regime was characterized by localized, asynchronous events that involved only neighboring individuals, indicating the disturbance regime consists almost solely of gap-phase processes. Although many of these canopy disturbances were likely filled via lateral branch growth, some were large enough to allow for the establishment of *L. tulipifera*.

In the absence of large-scale disturbance, the composition of the forest is projected to change as *A. saccharum* and *F. grandifolia* will be recruited to larger size classes. These findings support other studies throughout the eastern United States. However, the composition shift at the INR does not coincide with fire suppression, as fire has not occurred during the development of the current stand. We attribute this successional shift to facilitative processes that ameliorated the poor site conditions that existed after agricultural abandonment combined with the loss of *C. dentata*. We suggest modifications to understory and soil conditions allowed for the establishment of mesophytic species that cannot compete on lower quality sites, such as those that often result from agricultural land practices.

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