A RANGE-WIDE DISTURBANCE HISTORY
FOR *QUERCUS ALBA*
IN THE EASTERN US

by

MEGAN LINDSAY BUCHANAN

A THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Geography
in the Graduate School of
The University of Alabama

TUSCALOOSA, ALABAMA

2011

ABSTRACT

Throughout much of the eastern US, forests are undergoing a transition from *Quercus* to *Acer-Fagus* dominance. While the pattern has been reported in many site-specific analyses and is often linked to changes in disturbance regimes, a landscape-level analysis of historical establishment and disturbance throughout the region has not been conducted. I used tree-ring chronologies to analyze the disturbance history from old-growth *Q. alba* sites located throughout the species' range with the ultimate goal of determining the environmental conditions and disturbance dynamics that existed throughout the latter period of *Quercus* dominance and early period of *Quercus* decline. My analysis provided regional- and range-wide data regarding the frequency of disturbance throughout the development of old-growth *Q. alba* stands. In general, the temporal distribution of tree establishment dates was bimodal and corresponded to the period of Native American depopulation and the period following European settlement. Drought, *Castanea dentata* decline, and logging activities also significantly contributed to the long-term, range-wide disturbance regime.

Regional discrepancies in release characteristics were identified. The Northern Hardwood Forest Region featured the highest level of disturbance as compared to all other regions. The Central Hardwood Forest Region exhibited the second lowest rate of disturbance (as evidenced by the relativized release descriptors). In general, high-magnitude disturbances occurred throughout the *Q. alba* range every 234–556 years. My findings confirm that *Quercus* dominance throughout the latter part of the Holocene was maintained, in part, by high magnitude disturbance events ca. every 400 years. Such high magnitude disturbances remove many

disturbance-intolerant species, fragment large areas of the canopy, cause significant damage to subcanopy individuals, and allow disturbance-oriented and mid-successional taxa, such as *Quercus,* to establish. This return interval for high magnitude disturbance events can be imitated by land managers throughout the region in effort to promote *Quercus* regeneration.

ACKNOWLEDGMENTS

I would like to thank the many contributors of *Quercus alba* chronologies to the ITRDB. I also thank Laura Wesley and Craig Remington of the University of Alabama Cartographic Research Laboratory for assistance with figure preparation, Ian Comstock for assistance with database management, and Jacob Richards for helpful comments on earlier drafts of the manuscript. I especially thank Dr. Justin Hart for his invaluable guidance throughout the entire research process. Additionally I sincerely thank Drs. David Shankman, and Gregory Starr for their valued assistance and service on my thesis committee.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. Introduction

Throughout much of the Holocene epoch, *Quercus* species have dominated forests in the eastern United States (Abrams, 1992; Abrams, 2002; McWilliams et al., 2002). The importance of the genus has been widely documented throughout a variety of forest regions and site types. However, many forest regions historically dominated by *Quercus* species have undergone recent shifts in composition in which the importance of *Quercus*, especially *Quercus alba* L., is declining (Abrams, 2003). Throughout the East, *Quercus* species have exhibited an apparent regeneration failure concomitant with increased density of more mesic, shade-tolerant species such as *Fagus grandifolia* Ehrh., *Acer saccharum* Marsh., and *Acer rubrum* L. throughout all size classes (Lorimer, 1984; Abrams et al., 1995; McCarthy and Bailey, 1996; McEwan et al., 2010). In light of this widespread successional shift, a broad-scale analysis of historical *Quercus* forest dynamics is warranted.

Long-term oscillations in canopy disturbance characteristics such as frequency, magnitude, and spatial extent, impart lasting legacies upon forest composition, structure, and successional trajectories. Since the onset of European settlement, increased land-use intensity and spatial extent have drastically altered the disturbance regime dynamics occurring in *Quercus* forests (Foster et al., 1998, 2002; Abrams, 2003). Low magnitude disturbance regimes such as surface fires and windthrow events have been documented to support the historical dominance of *Quercus* species, especially *Quercus alba* (Abrams, 2003). However, the frequency, magnitude, and extent of disturbance such as these have been altered since the onset of European settlement; in particular, direct and indirect anthropogenic impacts during the late 19th and early 20th

Centuries have imparted changes in forest composition, structure, and disturbance throughout the eastern US (Foster et al., 1998; Abrams, 2003).

Numerous local-scale canopy disturbance reconstructions throughout the region have been conducted and have empirically identified mechanisms that have historically maintained *Quercus* dominance as well as mechanisms that favor the recruitment and regeneration of mesic taxa (e.g. Nowacki and Abrams, 1994; Abrams et al., 1995; Goebel and Hix, 1997; Rentch et al., 2002). However, the broad-scale effects of disturbance regime variability remain largely uninvestigated. My study fills this void with an analysis of *Q. alba* tree-ring chronologies from many of the remaining old-growth stands located throughout the species' range. As the distributional range of *Q. alba* encompasses the entirety of the eastern US, the historical disturbance regime characteristics uncovered through analysis of the old-growth *Q. alba* tree-ring record are representative not only of the disturbance dynamics occurring in old-growth *Q. alba* stands, but also of all eastern *Quercus* forests. Comparisons of disturbance characteristics between the four forest regions within the *Q. alba* range (Northern Hardwood Forest Region, Central Hardwood Forest Region, Transitional Forest Region, and Grassland or Prairie Formation Region) also provided information regarding the spatial variability of disturbance regimes.

For my research, I used *Q. alba* tree-ring chronologies to determine the long-term dynamics of historical disturbance regimes throughout the eastern US. I chose to analyze *Q. alba* because the species is a common component of hardwood forests in eastern North America (Rogers, 1990; Abrams, 2003), the species (and genus) is commonly used to reconstruct stand disturbance histories (Nowacki and Abrams, 1997; Rubino and McCarthy, 2000; Hart and

Grissino-Mayer, 2008; Hart et al., 2008), and the International Tree Ring Data Bank (ITRDB; Grissino-Mayer and Fritts, 1996) contains chronologies located throughout the species' range.

The ultimate goal of my research was to develop a broad-scale, long-term understanding regarding *Quercus* forest dynamics in the eastern US. The specific objectives of this study were to: (1) construct an old-growth *Q. alba* disturbance chronology from the identification of release events using the ten-year running mean method; (2) determine the release characteristics (i.e. release frequency, mean releases tree^{-1} century^{-1}, mean disturbance return interval, stand-wide disturbance frequency, and a ratio of sample size to releases) for each site and forest region; (3) identify range-wide and regional disturbance regime patterns and develop a mechanistic understanding of the causal factors (e.g. stand age, land-use history, atmospheric disturbance frequency, and *Castanea dentata* March. decline). The results of my research provided a long-term, broad-scale perspective of the disturbance regime dynamics in old-growth *Q. alba* stands. The results from these stands can be scaled-up to the region level as the sites are representative of the environmental conditions and disturbance characteristics that existed throughout the region during the past ca. 400 years. Furthermore, the long-term disturbance characteristics identified in my study provide practical information to land management agencies aiming to maintain *Quercus* importance via the imitation of historical disturbance regimes.

2. *Quercus alba*

Quercus alba is a common component to every major forest type throughout the US eastern deciduous forest (Abrams, 2003). Throughout the East, the species is commonly associated with other *Quercus* species and *Carya* species and reaches peak dominance in the oak-hickory and oak-pine forest types (Braun, 1950). *Quercus alba* flowers and disseminates pollen in the spring whereas acorns reach the ground and germinate in the fall (Rogers, 1990). Acorn production is irregular and good acorn crops generally occur every four to ten years (an occurrence largely dependent on spring temperature fluxes; Rogers, 1990). Sexual maturity for the species is size-dependent but commonly occurs in closed-canopy forests when individuals are over 40 years of age (Rogers, 1990). *Quercus alba* is considered moderately shade tolerant and has several morphological and physiological adaptations that allow the species to tolerate fire and drought (e.g. thick bark, deep rooting, wound compartmentalization, sprouting ability, high stomatal density; Rogers, 1990; Abrams, 2003). The species exhibits slower growth rates than other *Quercus* species common to eastern deciduous forests (e.g. *Quercus prinus* L., *Quercus rubra* L.); a factor that has possibly contributed to the decline of the species in recent decades (Abrams, 2003). Therefore, in deeply shaded understory positions, the slow-growing *Q. alba* is often overtopped by competitors (Braun, 1950; Abrams, 2003). As a result of these phenological, morphological, and physiological characteristics, *Q. alba* generally does best in areas with low magnitude disturbance regimes, including surface fires, and gap-phase regeneration (Abrams, 2003).

3. Methods

3.1 Radial growth release analyses

To examine the historical disturbance regime dynamics throughout the range of *Q. alba*, I obtained *Q. alba* chronologies from the ITRDB (http://www.ncdc.noaa.gov/paleo/treering.html). Tree-ring chronologies featured on the ITRDB have undergone intense scrutiny to ensure accurate crossdating and to minimize measurement error (Grissino-Mayer and Fritts, 1996). I used the raw annual ring-width measurements from all *Q. alba* chronologies in the ITRDB that analyzed live standing trees, contained a minimum ten individuals, and had a minimum of two series per tree (n = 44 chronologies; Table 1). In areas with relief, tree-core samples were collected perpendicular to slope (Cleaveland and Duvick, 1992; LeBlanc and Terrell, 2009). Portions of the same dataset were analyzed by LeBlanc and Terrell (2009) and Goldblum (2010) in range-wide dendroclimatological studies of *Q. alba*. The sample network provided adequate spatial coverage from the *Q. alba* range (including one disjunct population; Fig. 1). From the 44 chronologies, 884 trees (representing 1,768 tree-ring series) were suitable for analysis.

To quantify radial growth release characteristics, I analyzed the raw ring-width measurements for percent growth change using the ten-year running mean method (Nowacki and Abrams, 1997). I analyzed changes in raw-ring widths with respect to the running mean of the previous and subsequent ten years. Release events were identified as periods in which raw ring width was ≥ 25% (minor) or ≥ 50% (major) of the ten-year preceding and superseding mean, sustained for a minimum of five years (Nowacki and Abrams, 1997). The first and last ten years of each series were excluded from analysis as this method requires a ten-year window prior and

Table 1. Descriptive data for the 44 *Quercus alba* ITRDB collections: Data reported for chronology time spans and mean stand ages were derived from the entirety of the chronology, including trees and years not analyzed for growth release events.

Site Name	Contributor	Coordinates	Number of Trees Analyzed	Years Represented	Mean Stand Age
Andrew Johnson Woods	E.R. Cook	40.88°N 81.75° W	18	1626-1985	304.46 (± 7.82 SE)
Babler State Park	D.N. Duvick	38.6° N 90.72° W	27	1641-1980	216.46 (± 11.03 SE)
Backbone State Park	R. Landers; D.N. Duvick	42.62° N 91.57° W	11	1735-1977	151.18 (± 11.08 SE)
Blackfork Mountain	D.W. Stahle	34.72° N 94.45° W	13	1650-1980	218.29 (± 9.65 SE)
Buffalo Beats North Clay Lens Prairie Soil	J.R. McClenahen; D.B. Houston	39.45° N 82.15° W	28	1681-1995	106.06 (± 9.79 SE)
Buffalo Beats North Ridgetop Forest Site	J.R. McClenahen; D.B. Houston	39.45° N 82.15° W	21	1856-1995	119.33 (± 3.86 SE)
Cameron Woods	D.N. Duvick	41.65° N 90.73° W	12	1845-1980	118.00 (± 4.75 SE)
Cass Lake B	L.J. Graumlich	47.27° N 94.38° W	17	1785-1988	147.06 (± 7.06 SE)
Cranbrook Institute	E.R. Cook	42.67° N 83.42° W	11	1581-1983	272.21 (± 23.45 SE)
Current River Natural Area	D.N. Duvick	37.27° N 91.27° W	17	1636-1981	226.25 (± 8.36 SE)
Current River Natural Area Recollection	R.P. Guyette	37.27° N 91.27° W	9	1588-1992	246.96 (± 6.81 SE)
Dolliver Memorial State Park	D.N. Duvick	42.38° N 94.08° W	14	1685-1981	197.07 (± 19.70 SE)
Duvick Backwoods	D.N. Duvick	41.68° N 93.68° W	16	1654-1980	111.47 (± 7.04 SE)
Fern Clyffe State Park	D.N. Duvick	37.53° N 88.98° W	22	1655-1981	186.65 (± 24.11 SE)
Fox Ridge State Park	D.N. Duvick	39.42° N 88.17° W	18	1674-1980	209.68 (± 12.97 SE)
Geode State Park	D.N. Duvick	40.83° N 91.37° W	16	1724-1984	212.59 (± 11.57 SE)
Giant City State Park	D.N. Duvick	37.6° N 89.2° W	25	1652-1981	243.85 (± 7.43 SE)
Greasy Creek	D.N. Duvick	37.72° N 90.2° W	15	1777-1982	143.87 (± 7.82 SE)
Hampton Hills	A.C. Barefoot	35.82° N 78.68° W	16	1770-1992	133.31 (± 11.87 SE)
Hutcheson Forest	E.R. Cook	40.5° N	16	1674-1982	225.68 (± 7.65

		74.57° W			SE)
Jack’s Fork	D.N. Duvick	37.12° N 91.5° W	30	1776-1981	123.37 (± 7.84 SE)
Kankakee River State Park	D.N. Duvick	41.22° N 88° W	15	1686-1980	197.33 (± 16.53 SE)
Lacey-Keosauqua State Park	D.N. Duvick	40.72° N 91.97° W	12	1715-1981	189.53 (± 14.96 SE)
Lake Anquabi State Park	D.N. Duvick	41.28° N 93.58° W	26	1574-1980	195.19 (± 15.54 SE)
Ledges State Park	D.N. Duvick	42° N 93.88° W	61	1663-1981	182.47 (± 10.19 SE)
Lilley Cornett Tract	E.R. Cook	37.08° N 83° W	15	1660-1982	276.00 (± 6.98 SE)
Lincoln’s New Salem State Park	D.N. Duvick	39.97° N 89.85° W	29	1671-1979	196.00 (± 11.37 SE)
Linville Gorge	E.R. Cook	35.88° N 81.93° W	17	1617-1977	256.35 (± 12.80 SE)
Lower Rock Creek	D.N. Duvick	37.5° N 90.5° W	17	1728-1982	196.88 (± 8.82 SE)
Mammoth Cave Recollect	E.R. Cook	37.18° N 86.1° W	14	1649-1985	244.25 (± 6.69 SE)
Merritt Forest State Preserve	D.N. Duvick	42.7° N 91.13° W	16	1711-1980	181.76 (± 11.95 SE)
Nine Eagles State Park	D.N. Duvick	40.62° N 93.75° W	13	1672-1982	137.15 (± 16.88 SE)
Norris Dam State Park	D.N. Duvick	36.22° N 84.08° W	32	1633-1980	247.38 (± 8.72 SE)
Pammel State Park	D.N. Duvick	41.28° N 94.07° W	52	1635-1981	194.14 (± 9.88 SE)
Piney Creek Pocket Wilderness	D.N. Duvick	35.7° N 84.88° W	15	1651-1982	159.13 (± 21.09 SE)
Pulaski Woods	E.R. Cook	41.05° N 86.7° W	11	1692-1985	224.09 (± 14.66 SE)
Roaring River	D.W. Stahle	36.6° N 93.82° W	14	1724-1982	197.61 (± 7.10 SE)
Saylorville Dam	D.N. Duvick	41.72° N 93.7° W	34	1654-1981	157.68 (± 13.18 SE)
Sipsey Wilderness	E.R. Cook	34.33° N 87.45° W	14	1679-1985	252.06 (± 8.78 SE)
Starved Rock State Park	D.N. Duvick	41.3° N 89° W	42	1633-1980	244.47 (± 4.99 SE)
Wegener Woods	D.W. Stahle	38.65° N 91.5° W	12	1662-1982	229.23 (± 10.72 SE)
White Pine Hollow State Preserve	D.N. Duvick	42.63° N 91.13° W	15	1631-1973	224.50 (± 11.72 SE)
Woodman Hollow State Preserve	D.N. Duvick	42.42° N 94.1° W	24	1695-1979	119.68 (± 7.86 SE)
Yellow River State Forest	D.N. Duvick	43.18° N 91.25° W	12	1651-1980	212.42 (± 19.21 SE)

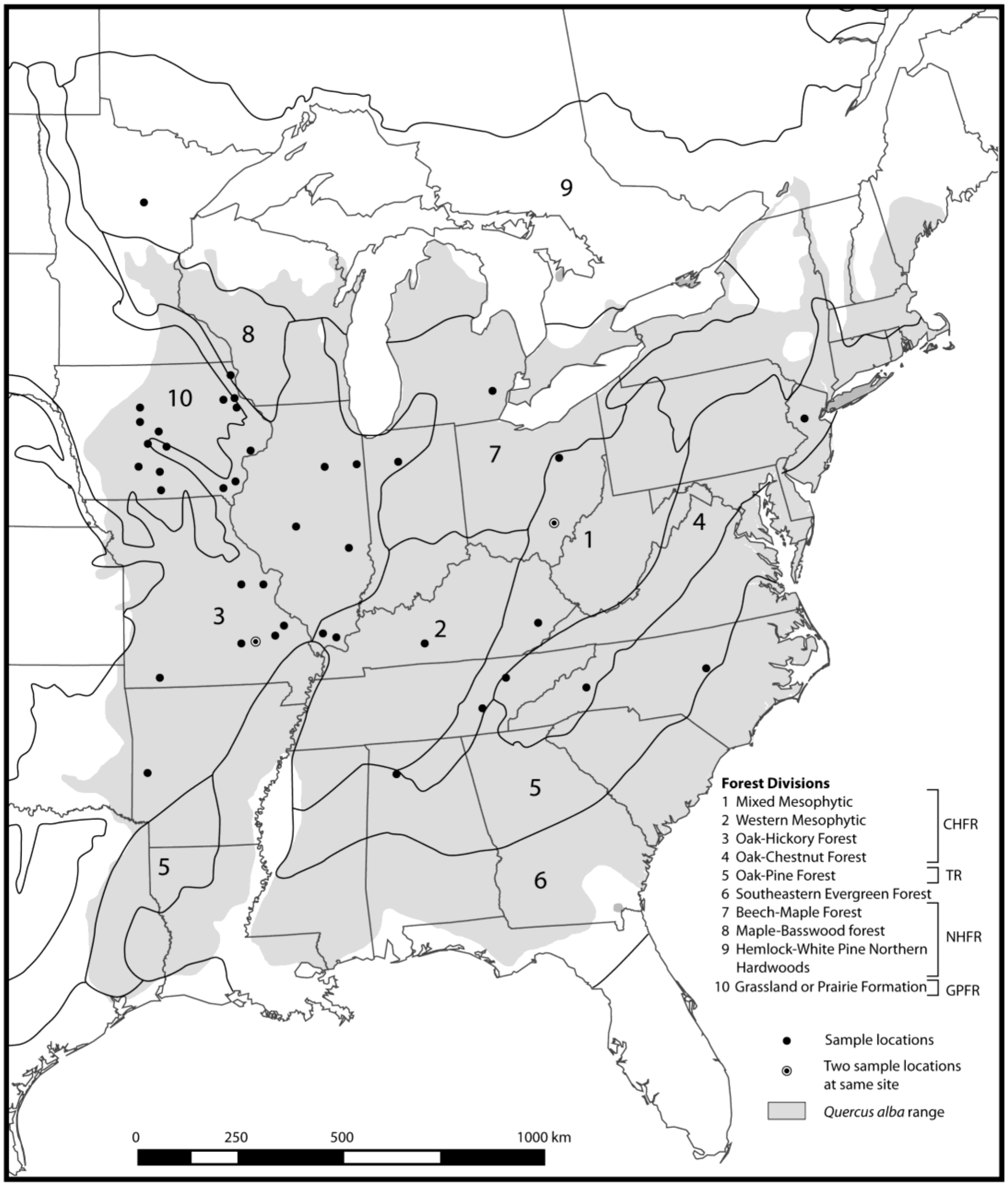

Fig. 1. Map showing the *Quercus alba* range and 44 site locations: Brackets represent the Central Hardwood Forest Region (CHFR), Transitional Forest Region (TR), Northern Hardwood Forest Region (NHFR), and Grassland or Prairie Formation Region (GPFR).

subsequent to each individual growth ring analyzed. Though a myriad of release identification methods exist (Rubino and McCarthy, 2004), I selected these specific criteria as they were developed using overstory *Quercus* species in complex-stage stands of eastern North America and have been empirically tested and verified (Nowacki and Abrams, 1997; Rentch et al., 2002, 2003). Furthermore, I chose a release duration criterion that was more conservative than many used in disturbance reconstructions in the eastern US (e.g. Schwartz and Hermann, 1999; Hart et al., 2008; Hart and Grissino-Mayer, 2009) to only capture the high magnitude disturbance events that create large canopy gaps in which growing space and resource availability are heightened for a minimum of five years. Establishment of woody species is often limited to the 1–5 years following canopy gap creation (Canham and Marks, 1985) and species density within gaps often peaks between gap ages of 7–12 years (Runkle, 1982). These longer-lasting canopy gaps, represented by the longer duration criterion, are indicative of relatively large canopy disturbance events and provide a greater potential for new species to establish and therefore directly alter successional trajectories (Runkle, 1982; Clinton et al., 1994; Hart and Grissino-Mayer, 2009).

I used the ten-year running mean method to identify releases in both of the paired tree-ring series from all 844 individuals. Contemporaneous releases occurring in both of the paired series were counted as a single release event. I used a five-year threshold to identify releases recorded in both of the paired series as resulting from the same disturbance event (i.e. intra-tree releases exhibiting an initiation lag-time of five years or less were considered simultaneous). Release detection analyses were performed on both of the paired tree-ring series as to avoid the underrepresentation of release events associated with the analysis of only a single increment core per tree (Buchanan and Hart, in press). The release frequency of all individuals was then totaled to construct canopy disturbance chronologies at the stand- and forest region-levels. I analyzed the disturbance chronologies to identify widespread disturbance events at both spatial scales. I considered disturbances to be widespread if ≥ 25% of all trees exhibited a simultaneous release within a five-year threshold (Nowacki and Abrams, 1997; Rubino and McCarthy, 2004; Hart et al., 2008).

To compare release characteristics, and thus disturbance regime characteristics, throughout the *Q. alba* range, I used a relativized number of release events for each individual, stand, and forest region. At all three spatial scales, I calculated the mean releases tree^{-1} century^{-1} (MRTC) as this value provides insight into disturbance frequency and tree sensitivity to disturbance while mitigating the influence of the varying tree ages and stand sample sizes throughout the dataset (Rubino and McCarthy, 2004). Additionally, I determined the mean disturbance return interval (MDRI) for each stand and forest region to elucidate the recurrence frequency of canopy disturbances occurring throughout stand development in the eastern US. To provide further insight into the spatial patterns of disturbance, I also calculated the ratio of sample size to release frequency (n:R) for each forest region. At the forest region level, the MRTC, MDRI, and n:R values were calculated by averaging the stand-level values of all sites within each respective region. I then searched relevant literature to investigate possible causal mechanisms for spatial and temporal patterns of release frequency, MRTC, MDRI, and n:R (e.g. land-use history, atmospheric disturbance frequency, drought, and *C. dentata* decline).

3.2 Statistical analyses

As the 44 sites featured differing sample sizes (i.e. number of trees) and mean stand ages, I analyzed the statistical relationships between these two variables and the release characteristic variables. I analyzed the relationship between mean stand age and the stand-level release frequency, MRTC, and MDRI using Pearson correlation analysis in SAS 9.1. Similarly, I used Pearson correlation analysis to determine the relationship between stand sample size and stand-level release frequency, MRTC, and MDRI. At the forest region level, I used ANOVA to compare the variance in mean age, sample size, MRTC, and MDRI values between the four forest regions. I used stand-level values for this analysis (i.e. the Northern Hardwood Region had 3 data entries for each parameter, the Central Hardwood Region had 29 entries, the Transitional Region had 2 entries, and the Grassland or Prairie Region had 10 data entries).

4. Results

4.1 Tree

From the 1,768 tree-ring series analyzed, I documented 311 release events of which 300 were minor in magnitude and 11 were major in magnitude. Of the 884 trees in the dataset, 269 (30%) exhibited at least one release event. Of the 269 trees exhibiting a release event, 34 trees recorded two release events and seven trees recorded three release events. The mean release duration was 5.39 years (± 0.04 SE) whereas the mean duration for minor and major release events was 5.40 (± 0.04 SE) and 5.36 (± 0.20 SE), respectively. Of the 311 total release events, 153 episodes (49%) from 144 trees (53% of all trees exhibiting a release event) occurred within 50 years of tree establishment. From the 144 trees that exhibited a release within 50 years of tree establishment, 108 never exhibited a subsequent release event.

4.2 Stand

All 44 stands exhibited at least one release event. The maximum release frequency was 26 events (n = 1 stand; Table 2) and the minimum frequency was one release event (n = 3 stands). Release frequency was significantly correlated with stand sample size ($r = 0.77$, $P < 0.0001$) and was not significantly correlated with mean stand age ($P = 0.49$). Two sites featured one widespread disturbance event (Duvick Backwoods, Iowa and Geode State Park, Iowa). Though both stands that experienced widespread disturbance events were in close proximity, the disturbances were not synchronous. The stand-level MRTC was significantly correlated with mean stand age ($r = -0.35$, $P = 0.02$) and values ranged from 0.03 (± 0.03 SE; Hutcheson Forest,

Table 2: Release characteristics for the 44 ITRDB *Quercus alba* collections.

Site Name	Release Frequency		Mean Releases Tree^{-1} Century^{-1}	MDRI	Stand-Wide Releases
	Minor	Major			
Andrew Johnson Woods	9	—	0.17 (± 0.05 SE)	37.78	—
Babler State Park	11	—	0.20 (± 0.06 SE)	29.09	—
Backbone State Park	1	—	0.07 (± 0.07 SE)	223.00	—
Blackfork Mountain	7	—	0.26 (± 0.08 SE)	44.43	—
Buffalo Beats North Clay Lens Prairie Soil	3	—	0.10 (± 0.06 SE)	98.33	—
Buffalo Beats North Ridgetop Forest Site	4	—	0.20 (± 0.09 SE)	30.00	—
Cameron Woods	7	—	0.56 (± 0.22 SE)	16.57	—
Cass Lake B	12	1	0.72 (± 0.15 SE)	12.27	—
Cranbrook Institute	3	—	0.11 (± 0.06 SE)	127.67	—
Current River Natural Area	8	1	0.23 (± 0.12 SE)	36.22	—
Current River Natural Area Recollection	3	—	0.13 (± 0.06 SE)	110.33	—
Dolliver Memorial State Park	4	1	0.15 (± 0.07 SE)	55.40	—
Duvick Backwoods	6	1	0.55 (± 0.23 SE)	15.86	1
Fern Clyffe State Park	4	1	0.08 (± 0.03 SE)	61.40	—
Fox Ridge State Park	4	—	0.09 (± 0.06 SE)	71.75	—
Geode State Park	12	—	0.39 (± 0.13 SE)	20.08	1
Giant City State Park	14	1	0.28 (± 0.07 SE)	20.67	—
Greasy Creek	5	—	0.35 (± 0.14 SE)	37.20	—
Hampton Hills	5	—	0.26 (± 0.15 SE)	39.40	—
Hutcheson Forest	1	—	0.03 (± 0.03 SE)	289.00	—
Jack’s Fork	9	—	0.28 (± 0.09 SE)	20.67	—
Kankakee River State Park	5	1	0.22 (± 0.09 SE)	45.83	—
Lacey-Keosauqua State Park	5	1	0.24 (± 0.09 SE)	41.17	—
Lake Anquabi State Park	12	—	0.31 (± 0.12 SE)	32.25	—
Ledges State Park	26	—	0.25 (± 0.15 SE)	11.46	—
Lilley Cornett Tract	5	—	0.12 (± 0.05 SE)	60.60	—
Lincoln’s New Salem State Park	4	—	0.06 (± 0.03 SE)	72.50	—
Linville Gorge	5	—	0.11 (± 0.04 SE)	68.20	—
Lower Rock Creek	3	—	0.10 (± 0.05 SE)	78.33	—
Mammoth Cave Recollect	4	1	0.15 (± 0.05 SE)	51.00	1
Merritt Forest State Preserve	8	—	0.33 (± 0.12 SE)	31.25	—
Nine Eagles State Park	2	—	0.15 (± 0.10 SE)	145.50	—
Norris Dam State Park	9	—	0.13 (± 0.04 SE)	36.44	—
Pammel State Park	20	—	0.19 (± 0.04 SE)	16.25	—
Piney Creek Pocket Wilderness	4	—	0.17 (± 0.11 SE)	78.00	—
Pulaski Woods	2	—	0.09 (± 0.06 SE)	137.00	—
Roaring River	1	—	0.03 (± 0.03 SE)	239.00	—
Saylorville Dam	8	1	0.23 (± 0.10 SE)	33.33	—
Sipsey Wilderness	11	—	0.33 (± 0.09 SE)	26.09	—
Starved Rock State Park	15	1	0.16 (± 0.05 SE)	20.50	—
Wegener Woods	4	—	0.14 (± 0.06 SE)	68.00	—
White Pine Hollow State Preserve	5	—	0.13 (± 0.07 SE)	66.00	—
Woodman Hollow State Preserve	3	—	0.07 (± 0.04 SE)	86.67	—
Yellow River State Forest	6	—	0.24 (± 0.08 SE)	49.67	—

New Jersey and Roaring River, Missouri) to 0.72 (± 0.15 SE; Cass Lake B, Minnesota). The Hutcheson Forest collection also exhibited the highest MDRI (289.00 years) whereas the Cass Lake B collection located in Minnesota featured the lowest MDRI (12.27 years). Stand-level MDRI was significantly correlated with stand sample size (r = -0.34, P= 0.02).

4.3 Forest region

At the forest region-level, the Central Hardwood Forest Region exhibited the highest release frequency (n = 227; Table 3) followed by the Grassland Prairie Formation Region (n = 51). The Transitional Forest Region exhibited the lowest release frequency (n = 16). The Grassland or Prairie Region exhibited the lowest MRTC with a value of 0.18 (± 0.03 SE) and the Northern Hardwood Region exhibited the highest MRTC with a value of 0.41 (± 0.30 SE). The shortest MDRI occurred in the Transition Region (32.75 years) whereas the longest MDRI occurred in the Northern Hardwood Forest Region (75.02 years). The Grassland or Prairie Region n:R of 4.31:1 was the highest between the four regions. The Transitional Region exhibited the lowest n:R with a ratio of 2.24:1. Importantly, neither mean stand age nor sample size different significantly between the regions.

The Northern Hardwood Region experienced pulses in release frequency during the 1850s, 1870s, 1890s, and 1920s whereas establishment dates exhibited a pulse in the 1830s (Fig. 2). Release frequency in the Central Hardwood Region was highest in the 1760s and from 1870–1889 and 1900–1909. Establishment in this region peaked from 1720–1759, 1770–1799, and 1850–1889. The Transitional Region experienced elevated release frequency values in the 1780s, 1830s, 1860s, and 1970s with the highest establishment rates during the 1780s and from 1870–1889. In the Grassland or Prairie Region, release frequency was highest from 1900–1909

Table 3. Descriptive data and release characteristics for the four forest regions: Data reported for mean region age was derived from the entirety of all series, including years not analyzed for growth release events. Date reported for mean releases tree^{-1} century^{-1}, MDRI, and n:R represent the average values from all sites within each respective region.

Forest Region	Number of Sites	Number of Trees	Mean Region Age	Number of Releases	Mean Releases Tree^{-1} Century^{-1}	MDRI	n:R
Northern Hardwood Forest Region	2	28	198.43 (±17.05 SE)	17	0.41 (±0.30 SE)	75.02	3.32:1
Central Hardwood Forest Region	34	663	201.83 (±2.88 SE)	227	0.20 (±0.02 SE)	68.16	4.22:1
Transitional Forest Region	2	30	190.70 (±13.73 SE)	16	0.29 (±0.03 SE)	32.75	2.24:1
Grassland or Prairie Formation	6	163	185.70 (±5.81 SE)	51	0.18 (±0.03 SE)	61.58	4.31:1

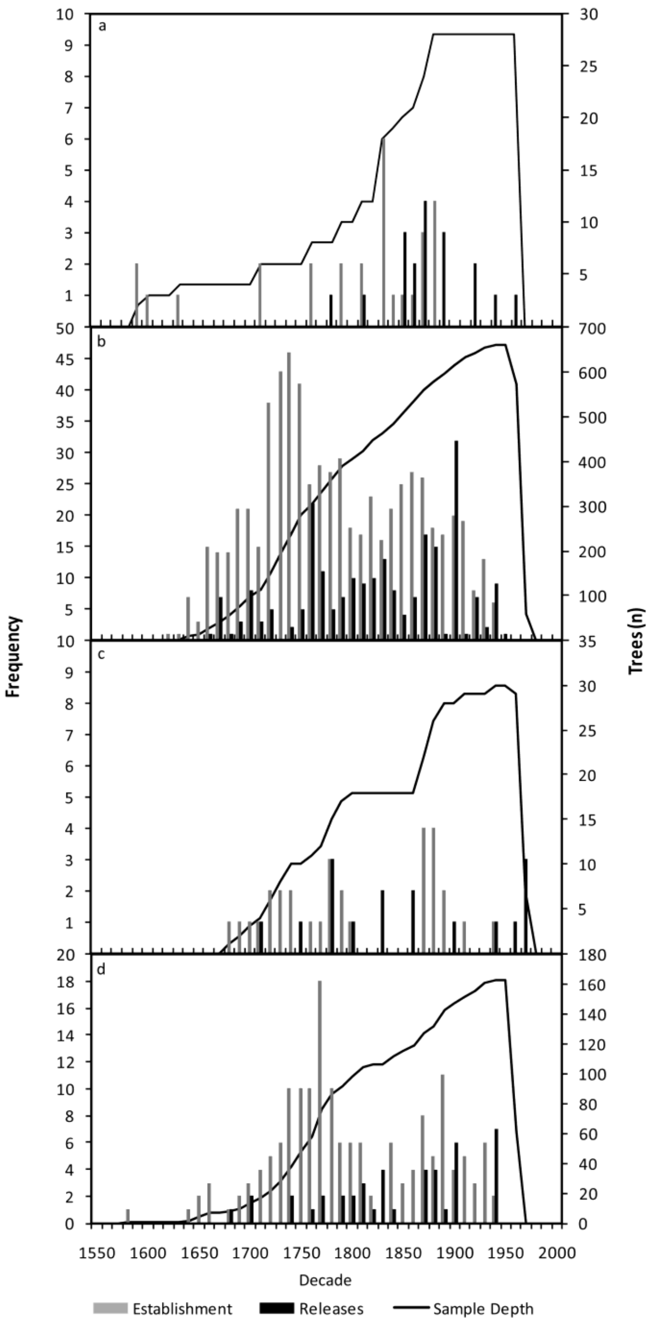

Fig. 2. Establishment frequency, release frequency, and sample depth for the four forest regions: Northern Hardwood Forest Region (a), Central Hardwood Forest Region (b), Transitional Forest Region (c), and Grassland of Prairie Formation Region (d). Establishment and release frequency values correspond to the primary y-axis whereas sample depth values correspond to the secondary y-axis. Note the different primary y-axis and secondary y-axis scales.

and during the 1940s whereas tree establishment peaked during 1740–1789 and subsequently during the 1870s and 1890s.

4.4 Range

At the range level, the release record extended from 1584 to 1985. Range-wide release frequency exhibited peak values during the 1760s, 1830s, 1870s, 1900s, and 1940s (Fig. 3). Range-wide establishment dates were highest during a period from 1720–1799 and exhibited a subsequent pulse of lesser magnitude from 1840–1919. A relatively constant level of "background" establishment existed from ca. 1690 to 1939. Similarly, a constant level of "background" release frequency occurred from ca. 1700–1900.

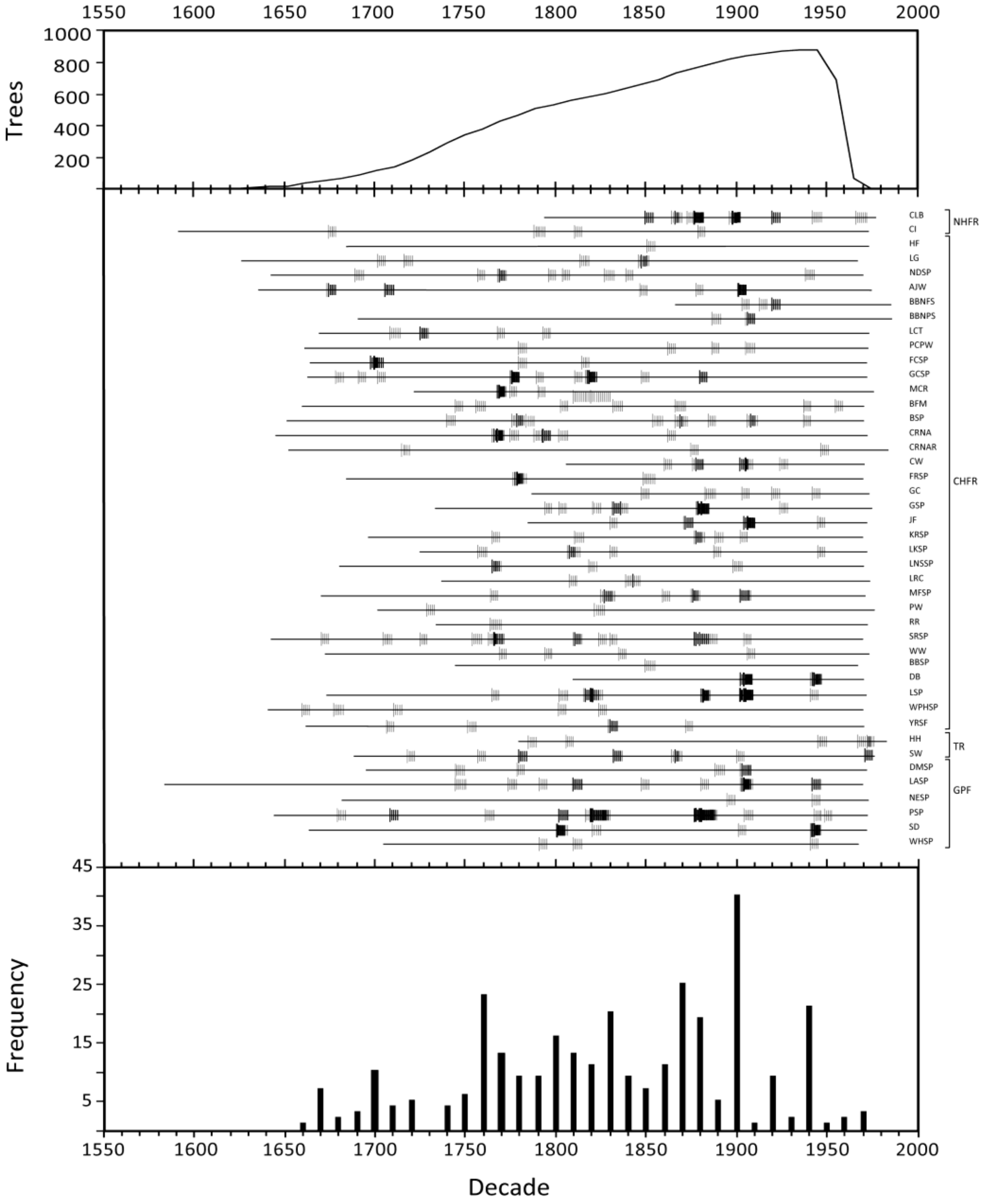

Fig. 3. The release frequency and dates from the 44 *Quercus alba* ITRDB collections: Each horizontal line represents the record for one site. The site name abbreviation and corresponding forest region are given to the right of the horizontal line. Long vertical bars indicate release events and short vertical bars indicate release duration. The thinnest vertical bars indicate one tree exhibiting a release, the intermediate vertical bars represent two trees exhibiting a release, and the thickest vertical bars indicate three or more trees exhibiting a release event. A composite of all release events is shown across the bottom of the graph and the range-wide sample depth is shown across the top.

5. Discussion

5.1 Tree

Radial growth release events recorded in the tree-ring record provide information regarding historical disturbance regimes at fine spatial and temporal resolution. For my study, I aimed to analyze only the high magnitude disturbance events that occurred during stand development in old-growth *Q. alba* stands located throughout the eastern US. Such disturbance events, whether exogenous or endogenous, generally create larger voids in the canopy subsequent to tree removal (Oliver and Larson, 1996). For this study, these larger canopy gaps are indicative of at least 35–40% of the canopy of the released tree being exposed to increased sunlight for a minimum of five years (Nowacki and Abrams, 1997; Rentch et al., 2002). Larger canopy gaps remain on the landscape for longer periods and thus have an enhanced potential to allow increased species recruitment thereby directly altering successional trajectories (Runkle, 1982; Clinton et al., 1994; Hart and Grissino-Mayer, 2009). Additionally, the five-year duration threshold coincides with the general length of time species establishment occurs within canopy gaps subsequent to disturbance (Canham and Marks, 1985). Furthermore, canopy gaps have been documented to exhibit peak species densities between gap ages of 7–12 years. As such, the five-year duration criterion (i.e. minimum gap age threshold) successfully captures only the canopy gaps that allow significant levels of species recruitment. As a result of the conservative duration criterion, the total release frequency (i.e. disturbance frequency) throughout the 44 *Q. alba* was relatively low (n = 311 events throughout the *Q. alba* range from 1574 to 1985). Had a more liberal duration criterion been used (e.g. four years), the release frequency would have more than doubled and thereby potentially masked region- and range-wide patterns of high magnitude disturbances. As the mean release duration value of 5.39 (± 0.04 SE) only minimally exceeds the five-year criterion, I am confident that only high magnitude disturbance events that greatly influence stand dynamics were analyzed.

Interestingly, 144 (54%) of the 269 trees exhibiting release events featured a release episode within 50 years of tree establishment. I hypothesize that this early-onset of release episodes, and thus of canopy disturbances, corresponds to stand self-thinning. Self-thinning has been documented in eastern *Quercus* forests to occur ca. 40 years post-stand establishment (Hart and Grissino-Mayer, 2008; Hart et al., 2011). At this time, the self-thinning process becomes discernable the tree-ring record as the high frequency of mortality exerts a relatively strong influence on the productivity of remnant individuals. Self-thinning occurs several decades after a stand-initiating disturbance event. During this phase of stand development, new individuals are prevented from successfully establishing underneath a dense, closed canopy and the increasing diameter of the even-aged stand causes many existing individuals die because of limited growing space (Oliver and Larson, 1996; Zeide 2010). In this study, the death of existing individuals ca. 40–50 years after the respective stand establishment dates provides evidence of the self-thinning process. I therefore speculate that stand-replacing disturbance events have occurred in a majority of the old-growth *Q. alba* stands in this dataset. However, as the gaps created by the death of 50-year old individuals are not large, other disturbance agents were likely operating simultaneously to produce this trend.

5.2 Stand

Release frequency at the stand scale ranged from a single event to 26 canopy disturbances occurring at one site (Ledges State Park, Iowa). The three sites that exhibited only one release event (Backbone State Park, Iowa; Hutcheson Forest, New Jersey; and Roaring River, Missouri) featured sample sizes below the mean sample size of 20.09 trees (n = 11, 16, and 14, respectively). As release frequency was positively correlated with sample size, it is possible the low release frequency is an artifact of the number of trees sampled. However, numerous sites exhibited multiple release events despite small sample sizes (e.g. Cameron Woods, Iowa exhibited seven release events from 12 sampled trees). Therefore, the low release frequency exhibited at these sites could possibly be the result of a spatially-restricted sampling scheme in which sampled trees were located within a relatively small geographic area possessing site-specific factors that made the sampled stands less susceptible to disturbance and/or the trees less likely to record disturbance in radial growth patterns (e.g. mesic conditions, protected slope position). Ledges State Park, Iowa featured the maximum release frequency of 26 events and also exhibited the largest sample size (n = 61 trees). Similar to the collections with the lowest release frequency, the high frequency value could be an artifact of the large sample size. However, the site's 0.25 MRTC value, a parameter that mitigates the influences of sample size, was within the upper 30% of all sites. Therefore, I again speculate that site-specific factors likely rendered the stand more susceptible to disturbance and the trees more likely to record the events (e.g. ridgetop position, west-facing slopes, shallow soils). Indeed, Ledges State Park features dissected topography with canyons and bluffs creating many ridgetop and upper-slope positions in which trees are more exposed to strong wind events (Johnson-Groh, 1985; Johnson-Groh and Farrar, 1985).

The only two stands that exhibited widespread release events were Duvick Backwoods, Iowa and Geode State Park, Iowa. Interestingly, the tree-ring record at both sites was derived from 16 trees, a sample size below the range-wide mean. Therefore, although release frequency and sample size were positively correlated, the only two instances of widespread disturbance occurred in stands with relatively low sample sizes.

The two stands with the lowest MRTC values (Hutcheson Forest, New Jersey and Roaring River, Missouri) both exhibited only a single release event and thus the low MRTC values are expected. Cass Lake B, Minnesota exhibited the highest MRTC value of 0.72 (i.e. a given tree exhibits a release event every ca. 139 years). The Cass Lake B mean stand age was 147.06 years (± 7.06 SE), an age below the range-wide mean stand age of 178.37 (± 2.52 SE). Cass Lake B also featured the shortest MDRI and a relatively high frequency of release events (n = 12). The site is located just outside of the northwest boundary of the *Q. alba* range; an area in which *Q. alba* individuals have documented mean sensitivity values higher than those throughout the remainder of the range (Sakulich et al., 2011). As the site is geographically situated outside the contiguous range in which conditions are most favorable, the stand is likely even more sensitive and susceptible to environmental variability (e.g. disturbance events, drought) and individuals are more likely to respond to canopy fragmentation by increasing radial growth (Fritts, 2001).

However, the maximum MRTC value exhibited at the Cass Lake B site is possibly an artifact of mean stand age as the two factors exhibited a significant negative correlation. Younger stands generally exhibited higher MRTC values as these stands have likely undergone frequent endogenous canopy disturbances during the period of self-thinning (Oliver and Larson, 1996). When calculating the relativized MRTC value, only this elevated disturbance frequency rate is captured. However, release frequency has been shown to decrease in older-aged stands as these trees have reduced phenotypic plasticity and are therefore less likely to capitalize on increased growing space and resource availability as evidenced by increased radial growth (Nowacki and Abrams, 1997; Fritts, 2001; Hart et al., 2010). Therefore, younger stands may exhibit exaggerated MRTC values as the release frequency rate has not yet declined with increasing age. Nonetheless, this possible bias does not negate the likely relationship between the high release frequency at Cass Lake B and its location being outside the contiguous *Q. alba* range.

Similarly, the short MDRI values at Cass Lake B and other sites could be the result of sample size as the variables were negatively correlated. The MDRI value is not relativized and therefore introduces possible sample-size bias into the return-interval calculations. At the stand-level, this bias is possibly amplified as sample sizes are inherently the lowest and also more variable than at the forest-region scale.

5.3 Forest region

Analysis at the forest region-level allowed for the comparison of regional differences in disturbance characteristics and the identification of spatial and temporal trends. The Northern Hardwood Region exhibited the highest and second highest values in both of the relativized disturbance parameters: MRTC and n:R, respectively. Conversely, the Central Hardwood Region featured the second lowest MRTC value and n:R ratio. Therefore, although the Central Hardwood Region exhibited the highest release frequency, the relativized factors revealed the region experienced one of the lowest levels of disturbance. However, though the mean stand sample sizes did not differ significantly between the regions, I acknowledge that the large range in region sample size precludes statistically robust comparisons at the forest region level.

A host of factors likely contribute to the high level of disturbance in the Northern Hardwood Region; factors that are not encountered in the other forest regions. The Northern Hardwood Region occupies the northern extent of the *Q. alba* range and, as a result of this high latitude and proximity to the polar jet stream, experiences an increased frequency of winter storm events (Zishka and Smith, 1980). These frequent storm events, especially during winter months, cause increased instances of windthrow at both fine and broad spatial scales (e.g. Foster, 1988; Peterson and Pickett, 1991; Canham et al., 2001). Furthermore, the dominant species in the region likely contribute to the increased rates of canopy disturbance. Both *F. grandifolia* and *Acer* species occur at high densities throughout parts of the region (i.e. the Beech-Maple and Maple-Basswood forest divisions). As these taxa are more shallow-rooted than the *Quercus* species within the old-growth *Q. alba* stands, they are more vulnerable to drought, surface fire, and uprooting from windthrow (Abrams, 1998). The evergreen species *Tsuga canadensis* (L.) Carr. and *Pinus strobus* L. are also more abundant in the Northern Hardwood Region (i.e. the Hemlock-White Pine Northern Hardwoods Forest district) than in the Central Hardwood Region. These two species feature foliage year round and are therefore more susceptible to high wind events during the winter season; indeed, *T. canadensis* windthrow has been documented as a common occurrence in the region (Foster, 1988; Davis et al., 1996). *Pinus strobus* is also one of the tallest trees in eastern North America and features soft wood making the species susceptible to snapping (Foster, 1988). Furthermore, stands within the Northern Hardwood Forest Region often experience snow and ice loading, both of which commonly cause stem and bole breakage (Duguay et al., 2001).

Several temporal trends in release and establishment frequency were noted throughout all four regions. Establishment frequency in the Central Hardwood Region exhibited a pulse from 1720–1759 and the Grassland of Prairie Formation Region exhibited a subsequent pulse in establishment frequency from 1740–1789. Additionally, release frequency in the Central Hardwood and Transitional Forest regions exhibited pulses in the 1760s and 1780s, respectively. This multi-decadal period of significantly increased establishment and release frequency coincides with period of drastically reduced Native American population density (ca. 1650–1760; Ramenofsky, 1987). Native American populations throughout eastern North America plummeted after introduction of infectious diseases (e.g. smallpox) from early European colonizers (Ramenofsky, 1987; Denevan, 1992). This period of depopulation effectively caused a cessation in Native American land-use practices throughout the East. Thus, in the century prior to European settlement, reforestation occurred throughout much of the region, as evidenced by both the high rates of establishment between 1720 and 1789. In the Central Hardwood and Transitional Regions, the subsequent pulses in release frequency in the 1760s and 1780s, respectively, likely represent self-thinning occurring in the recently established stands as this process generally beings ca. 40 years after establishment (Hart and Grissino-Mayer, 2008). This hypothesis is strengthened by the fact that 49% of all releases occurred within 50 years of tree establishment and therefore represent widespread stand-level self-thinning. Furthermore, during the twenty-year period of increased release frequency, large portions of Central Hardwood and Transitional Forest Regions experienced moderate high-frequency drought periods followed by significantly wetter years as indicated by reconstructed Palmer Drought Severity Index (PDSI) values (PDSI values ranging from -3.0 to -1.0 during the drought years and ranging from 1.0 to 4.0 during the wetter years; Cook and Krusic, 2004). Moderate, periodic droughts potentially caused increased overstory mortality either directly or indirectly as water stressed trees in eastern *Quercus* forests have been shown to exhibit reduced growth and vigor and be susceptible to other killing agents such as soil fungi that damage root systems (e.g. *Armillaria mellea* Vahl ex Fr.; Clinton et al., 1993, 1994; Klos et al., 2009; Hart and Kupfer, in review). In the subsequent wetter years, remnant trees responded to the increased resource availability resulting from both the canopy gaps and the increased moisture availability.

In the Northern Hardwood Forest Region, establishment frequency was relatively sparse until a pulse of establishment occurred in the 1830s. Similarly, release frequency in the region was relatively sparse until the 1850s when release frequency suddenly increased. Both of these occurrences coincide with the period of settlement for the region and therefore likely result from the sudden increase in land-use intensity and spatial extent by European settlers (Exploration and Settlement 1835–1850, 1966).

All regions except the Northern Hardwood Region exhibited multiple decades of increased establishment and release frequency during a period from 1850 to 1919. The increased establishment during the early potion of this period corresponds to settlement of the region (Exploration and Settlement 1850–1890, 1966) and the corresponding increase in land use extent and intensity for both building and agriculture. Moderate multi-year droughts beginning in both 1856 and 1872 (Cook and Krusic, 2004) likely contributed to the increased mortality and subsequent periods of increased establishment and release frequency throughout these regions. During the early 20th Century, logging activity throughout the eastern US was nearing a peak in intensity (Whitney, 1994). Though many of the stands in the dataset were classified as old growth by the respective ITRDB contributors, I speculate many of these stands experienced selective cutting (whether by diameter limit cutting or species-specific cutting) during this period of intense logging.

As all regions excepting the Transitional Forest Region exhibited high rates of establishment and release frequency during the early 20th Century, it is likely these pulses in tree recruitment and growth corresponded to the selective cutting of neighboring individuals or cohorts. Additionally, increased establishment and release frequency occurring in these three regions from 1900–1929 likely corresponds to onset of *C. dentata* population decimation by the fungal pathogen *Cryphonectria parasitica* (Murrill) Barr. (Agrawal and Stephenson, 1995; Hart et al., 2008; McEwan et al., in press). As this pathogen spread throughout the eastern US, genera such as *Quercus* and *Acer* were able to fill the niche vacated by *C. dentata* (Woods and Shanks, 1959; McEwan et al., in press). The decimation of *C. dentata* has also been documented in the radial growth of remnant trees from sites in Tennessee (Hart et al., 2008), Virginia (Agrawal and Stephenson, 1995), and Maryland (McCarthy and Bailey, 1996).

The Grassland or Prairie Region exhibited a significant pulse in release frequency during the 1940s. A majority of the sites within this region are located in Iowa. Iowa experienced drought conditions from 1939–1940 (PDSI values ranging from -2 to -4; Cook and Krusic, 2004) followed by generally wet conditions for the remainder of the decade. Drought conditions were less intense or non-existent throughout the other regions at this time; therefore, I speculate the significant pulse in release frequency in the Grassland or Prairie Region directly corresponds to drought-induced tree mortality and subsequent increased growth exhibited by remnant individuals.

5.4 Range

Results at the range level allowed for broad-scale analysis of disturbance characteristics throughout the eastern US. Several widespread temporal trends of establishment and release frequency were identified. The cumulative establishment frequency from the 44 *Q. alba* old-growth sites exhibited a bimodal temporal distribution with a peak from 1720–1799 and a subsequent pulse of lesser magnitude from 1840–1919 (Fig. 4). Prior to the peak beginning in 1720, establishment frequency was relatively sparse until 1650 when constant level of "background" establishment was begun. The range-wide background establishment rate is likely the result of multiple disturbance mechanisms interacting at varying spatial and temporal scales: *Ectopistes migratorious* L. (Passenger Pigeon) decline, stand high-grading, settlement activities, agriculture land clearance, *C. dentata* decline, insect outbreaks, small localized wind events, surface fire that removes fire-sensitive species and increases local resource availability, and general region-level natural background mortality (Whitney, 1994; Ruffner and Abrams 1998; McEwan et al., in press).

The first, higher magnitude peak in establishment (1720–1799) corresponds to the aforementioned period of Native American depopulation (ca. 1650–1760) and subsequent decrease in land-use extent and intensity. A pulse in release frequency in the 1760s likely represents self-thinning in the newly established stands (ca. 40 years post-establishment; Hart and Grissino-Mayer, 2008). Though, again, this pulse attributed to self-thinning is likely also the result of simultaneous disturbance events that create larger canopy voids than the removal of 50-year old individuals. Following this period of reforestation, establishment frequency decreased to a constant level of background establishment (i.e. background disturbance) between 1790 and 1849. A second pulse in release frequency during the 1830s preceded the second peak in

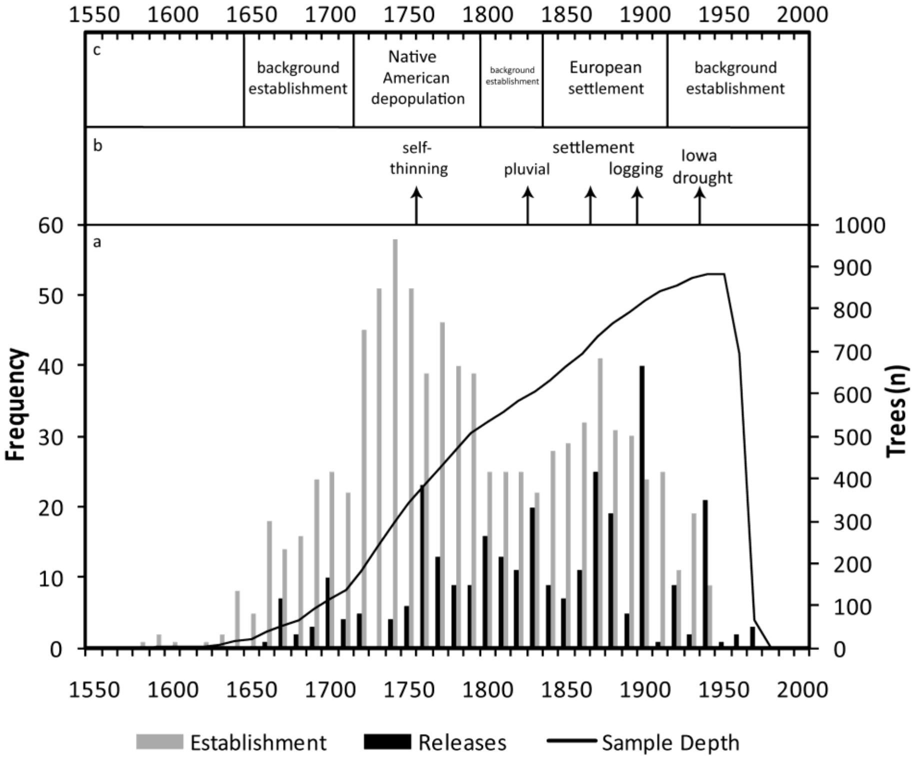

Fig. 4. Establishment frequency, release frequency, and sample depth for the 44 sites: The establishment frequency, release frequency, and sample depth (secondary y-axis) (a); the main pulses in release frequency and their likely causes (b); and the main trends in tree establishment and their likely explanations (c).

establishment frequency beginning in the 1840s and corresponds to a pluvial period (i.e. increased moisture availability) in the eastern US (Cook and Krusic, 2004; McEwan et al., in press). The second peak in establishment frequency from 1840–1919 coincides with the westward expansion of human settlement (Exploration and Settlement 1835–1850, 1850–1890, 1966) and regional development throughout the eastern US (e.g. intense agriculture, clear- or selective-cutting for building materials; Stambaugh and Guyette, 2006). A third pulse in release frequency occurred during the 1870s and likely corresponds to both settlement activities and a multi-year drought that began in 1872 (Cook and Krusic, 204; McEwan et al., in press).

The largest pulse in release frequency occurred between 1900 and 1909. This high frequency of release events presumably represents intense logging activity throughout the region and, to a lesser extent, canopy disturbance arising from the decline of *C. dentata* (at this time, the population decimation was not at its full extent; Lorimer, 1980; Woods and Shanks, 1959). Importantly, the release frequency nearly ceases subsequent to 1900 excepting the final pulse in release frequency in the 1940s. This decrease in release frequency throughout the old-age *Q. alba* stands is concomitant with the decline of *Quercus* dominance throughout the eastern US. Therefore, a decreased frequency of high-magnitude disturbance could be a possible contributor to the compositional shift documented throughout eastern *Quercus* forests in recent decades. However, this cessation could possibly be an artifact of the old age of the sampled trees as trees exhibit decreased phenotypic plasticity with increasing age (Nowacki and Abrams, 1997; Fritts, 2001; Hart et al., 2010)

Subsequent to 1919, tree establishment rates resume to background disturbance levels until tapering off at 1940. However, the apparent cessation of establishment in 1940 is solely an artifact of sample collection rather than environmental factors. A large majority of tree-ring series in the dataset was sampled during the 1980s and 1990s and therefore trees establishing subsequent to 1940 were likely not sampled because of their young age. A fifth pulse in release frequency was identified in the 1940s. As mentioned before, the Grassland or Prairie Region experienced a moderate drought followed by five years of wetter conditions (Cook and Krusic, 2004). This climatic factor, in tandem with high grading throughout the region and *C. dentate* decline in the eastern portion of the range, likely led to the increased disturbance frequency during the 1940s.

Throughout the range of *Q. alba*, the mean releases per tree every 100 years ranged from 0.18 (Grassland or Prairie Formation Region) to 0.41 (Northern Hardwood and Grassland or Prairie Formation Regions). Therefore, any given *Q. alba* individual is likely to experience a high-magnitude canopy disturbance event every 244–556 years. This range of disturbance recurrence exceeds the documented canopy disturbance return interval in the eastern US (i.e. every 50–200 years; Runkle, 1984, 1985; Foster, 1988). This longer return interval was expected as I only documented high-magnitude events that create a patchwork landscape and are generally less frequent than localized disturbances (Lorimer, 1980; Foster, 1988; Rentch et al., 2003). The data presented here confirm that historical *Quercus* dominance throughout much of the Holocene was maintained, in part, by high-magnitude disturbance events ca. every 400 years. These high magnitude disturbances remove many disturbance-intolerant species, fragment large areas of the canopy, cause significant damage to subcanopy individuals, and allow disturbance-oriented and mid-successional taxa such as *Quercus* to establish.

However, with an increased abundance of mesic, shade-tolerant taxa throughout the central portions of the *Q. alba* range, *Quercus* species are failing to regenerate as they cannot establish and recruit under a layer of supcanopy mesic species. In the Northern Hardwood

Region, *Quercus* is generally less dominant and mesic taxa such as *A. saccharum* and *F. grandifolia* are more important. As these species are also increasing in importance throughout the Central Hardwood Region, and as this region had one of the lowest level of disturbance, *Quercus* regeneration will likely continue to decline without the presence of frequent, high-magnitude disturbance. I suspect that the high-magnitude disturbance events occurring throughout the period of *Quercus* dominance also removed significant portions of the understory vegetation. The removal of subcanopy vegetation, in addition to canopy individuals, increases the regeneration prospects of shade-intolerant *Quercus* species by allowing more sunlight to reach the understory and forest floor. Experimental midstory thinning in the Central Hardwood Region has shown successful *Quercus* regeneration on certain site types (Brose and Van Lear, 1998; Loftis, 1990; Iverson et al., 2008). Broad-scale experiments have yet to be conducted but I contend the removal of both overstory and understory individuals, as would occur in high-magnitude disturbance events, would improve the regeneration potential of *Quercus* species.

6. Conclusion

The long-term, broad-scale perspective of disturbance history throughout the *Q. alba* range provided insight into the disturbance characteristics that prevailed during the latter period of *Quercus* dominance in the eastern US. The ca. 400-year record presented in this study provides disturbance regime characteristics for both the latter period of Quercus dominance as well as the onset of Quercus decline. Importantly, I noted a decrease in the "background disturbance" rates in the late 19th and early 20th Centuries, the period in which the compositional shift from *Quercus* to mesic taxa occurred. This decrease signifies a reduction in the frequency of high magnitude disturbance events throughout the eastern deciduous forest region. Furthermore, my analysis provided information regarding regional- and range-wide temporal trends in disturbance. In general, the temporal distribution of tree establishment dates was bimodal and corresponded to the period of Native American depopulation and the period following European settlement. Reforestation during both of these establishment peaks was generally followed by pulses of increased release frequency that signified self-thinning within the newly established stands. Drought, *C. dentata* decline, and logging activities also significantly contributed to the long-term, range-wide disturbance regime.

Regional discrepancies in release characteristics were identified. The Northern Hardwood Forest region featured the highest level of disturbance as compared to all other regions. Surprisingly, the Central Hardwood Forest Region exhibited the second lowest rate of disturbance (as evidenced by the lowest MRTC value and n:R ratio). In general, disturbances occured throughout the *Q. alba* range every 244–556 years. This return interval for high magnitude disturbance events can be imitated by land managers in effort to promote *Quercus* regeneration. However, significant portions of understory vegetation likely need to be removed as I suspect the high-magnitude disturbance during the period of historical *Quercus* dominance removed more than just the overstory vegetation. Removal of multiple forest strata should improve the regeneration potential of *Quercus* throughout the eastern US.

7. References

Abrams, M.D. 1992. Fire and the development of oak forests. BioScience 42: 346–353.

Abrams, M.D. 1998. The red maple paradox. BioScience 48: 355–364.

Abrams, M.D. 2002. The postglacial history of oak forests in eastern North America. In: McShea, W.J., and Healy, W.M. (Eds.), Oak Forest Ecosystems: Ecology and Management for Wildlife. The John Hopkins University Press, Baltimore, pp. 34–45.

Abrams, M.D. 2003. Where has all the white oak gone? BioScience 53: 927–393.

Abrams, M.D., D.A. Orwig, and T.E. Demeo. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white pine-mixed oak forest in the southern Appalachians, USA. Journal of Ecology 83: 123–133.

Agrawal, A. and Stephenson, S.L. 1995. Recent successional changes in a former chestnut-dominated forest in southwestern Virginia. Castanea 60: 107 – 113.

Brose, P.H. and Van Lear, D.H. 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Canadian Journal of Forest Research 28: 331–339.

Buchanan, M.B., and Hart, J.L. A methodological analysis of canopy disturbance reconstructions using *Quercus alba*. Canadian Journal of Forest Research. In press.

Canham, C.D., and Marks, P.L. 1985. The response of woody plants to disturbance: patterns of establishment and growth. In: Pickett, S.T.A., and White, P.S. (Eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego, pp.197–217.

Canham, C.D., Papaik, M.J., and Latty, E.K. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. Canadian Journal of Forest Research 31: 1–10.

Cleaveland, M.K. and Duvick, D.N. 1992. Iowa climate reconstructed from tree rings 1640–1982. Water Resources Research 28: 2607–2615.

Clinton, B.D., Boring, L.R., and Swank, W.T. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. Ecology 74: 1551–1558.

Clinton, B.D., Boring, L.R., and Swank, W.T. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the Southern Appalachians: influences of topographic position and evergreen understory. American Midland Naturalist 132: 308–319.

Cook, E.R., and Krusic, P.J. 2004. The North American drought atlas. Lamont-Doherty Earth Observatory and the National Science Foundation, Web document accessed 9 February 2011: <http://iridl.ldeo.columbia.edu/SOURCES/.LDEO/.TRL/.NADA2004/.pdsi-atlas.html>, accessed 9 February 2011.

Davis, M.B., Parshall, T.E., and Ferrari, J.B. 1996. Landscape heterogeneity of hemlock-hardwood forest in northern Michigan. In: Davis, M.B. (ed.), Eastern Old-Growth Forests. Island Press, Washington, pp. 291–304.

Denevan, W.M. 1992. The pristine myth: the landscape of the Americas in 1492. Annals of the Association of American Geographers 82: 369–385.

Duguay, S.M., Arii, K., Hooper, M., and Lechowicz, M.J. 2001. Ice storm damage and early recovery in an old-growth forest. Environmental Monitoring and Assessment 67: 97–108.

Exploration and Settlement 1835–1850 [Map]. 1966. Retrieved from University of Texas Libraries, Perry-Castaneda Library Map Collection. Accessed 9 February 2011.

Exploration and Settlement 1850–1890 [Map]. 1966. Retrieved from University of Texas Libraries, Perry-Castaneda Library Map Collection. Accessed 9 February 2011.

Foster, D.R. 1988. Species and stand response to catastrophic wind in Central New England, U.S.A. Journal of Ecology 76: 135–151.

Foster, D.R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. Ecosystems 1: 96–119.

Foster, D.R., S. Clayden, D.A. Orwig, B. Hall, and S. Barry. 2002. Oak, chestnut and fire: climatic and cultural controls of long-term forest dynamics in New England, USA. Journal of Biogeography 29: 1359–1379.

Fritts, H.C. 2001. Tree Rings and Climate. Blackburn Press, Caldwell, New Jersey.

Goebel, P.C. and Hix, D.M. 1997. Changes in the composition and structure of mixed-oak, second-growth forest ecosystems during the understory reinitiation stage of stand development. Ecoscience 4: 327–339.

Goldblum, D. 2010. The geography of white oak's (*Quercus alba* L.) response to climatic variables in North America and speculation on its sensitivity to climate change across its range. Dendrochronologia 28: 73–83.

Grissino-Mayer, H.D. and Fritts, H.C. 1997. The International Tree-Ring Data Bank: An enhanced global database serving the global scientific community. Holocene 7: 235–238.

Hart, J.L., and Grissino-Mayer, H.D. 2008. Vegetation patterns and dendroecology of a mixed hardwood forest on the Cumberland Plateau: Implications for stand development. Forest Ecology and Management 255: 1960–1975.

Hart, J.L., and Grissino-Mayer, H.D. 2009. Gap-scale disturbance processes in secondary stands on the Cumberland Plateau, Tennessee, USA. Plant Ecology 201: 131–146.

Hart, J.L., and Kupfer, J.A. in review. Sapling richness and composition in canopy gaps of a southern Appalachian mixed *Quercus* forest.

Hart, J.L., van de Gevel, S.L., and Grissino-Mayer, H.D. 2008. Forest dynamics in a natural area of the southern Ridge and Valley, Tennessee. Natural Areas Journal 28: 275–289.

Hart, J.L., Austin, D.A., and van de Gevel, S.L. 2010. Radial growth responses of three co-occurring species to small canopy disturbances in a secondary hardwood forest on the Cumberland Plateau, Tennessee. Physical Geography 31: 1–22.

Hart, J.L., Bhuta, A.A.R., and Schneider, R.M. 2011. Canopy disturbance patterns in secondary hardwood stands on the Highland Rim of Alabama. Castanea. In press.

Hutchinson, T.F., Long, R.P., Ford, R.D., and Sutherland, E.K. 2008. Fire history and the establishment of oaks and maples in second-growth forests. Canadian Journal of Forest Research 38: 1184–1198.

International Tree-Ring Data Bank (ITRDB). 2005. Data available at http://www.ngdc.noaa.gov/paleo/treering.html.

Iverson, L.R., Hutchinson, T.F., Prasad, A.M., and Peters, M.P. 2008. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. Forest Ecology and Management 244: 3035–3050.

Johnson-Grohl, C.L. 1985. Vegetation communities of Ledges State Park, Boone County, Iowa. Proceedings of the Iowa Academy of Science 92: 129–136.

Johnson-Grohl, C.L., and Farrar, D.R. 1985. Flora and phytogeographical history of Ledges State Park, Boone County, Iowa. Proceedings of the Iowa Academy of Science 92: 137–143.

Klos, R.J., Wang, G.G., Bauerle, W.L., and Rieck, J.R. 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. Ecological Applications 19: 699–708.

LeBlanc, D.C., and Terrell, M.A. 2009. Radial growth response of white oak to climate in eastern North America. Canadian Journal of Forest Research 39: 2180–2192.

Loftis, D.L. 1990. A shelterwood method for regenerating red oak in the southern Appalachians. Forest Science 36: 917–929.

Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61: 1169–1184.

Lorimer, C.G. 1984. Development of the red maple understory in northeastern oak forests. Forest Science 30: 3–22.

McCarthy, B.C., and Bailey, D.R. 1996. Composition, structure, and disturbance history of Crabtree Woods: an old-growth forest of western Maryland. Bulletin of the Torrey Botanical Club 123: 350–365.

McEwan, R.W., and McCarthy, B.C. 2008. Anthropogenic disturbance and the formation of oak savanna in central Kentucky, USA. Journal of Biogeography 35: 965–975.

McEwan, R.W., Dyer, J.M., Pederson, N. in press. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography doi: 10.1111/j.1600-0587.2010.06390.x.

McWilliams, W.H., O'Brien, R.A., Reese, G.C., Waddell, K.L. 2002. Distribution and abundance of oaks in North America. In: McShea, W.J., and Healy, W.M. (Eds.), Oak Forest Ecosystems: Ecology and Management for Wildlife. The John Hopkins University Press, Baltimore, pp. 13–33.

Nowacki, G.J. and M.D. Abrams. 1994. Forest composition, structure, and disturbance history of the Alan Seeger Natural Area, Huntington County, Pennsylvania. Bulletin of the Torrey Botanical Club. 121: 277–291.

Nowacki, G.J. and Abrams, M.D. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecological Monographs 67: 225–249.

Oliver, C.D., and Larson, B.C. 1996. Forest Stand Dynamics, Update edition. John Wiley and Sons, New York.

Peterson, C.J., and Pickett, S.T.A. 1991. Treefall and resprouting following catastrophic windthrow in an old-growth hemlock-hardwoods forest. Forest Ecology and Management 42: 205–217.

Ramenofsky, A.F. 1987. Vectors of Death: the Archeology of European Contact. University of New Mexico Press, Albuquerque, New Mexico.

Rentch, J.S., Desta, F., and Miller, G.W. 2002. Climate, canopy disturbance, and radial growth averaging in a second-growth mixed-oak forest in West Virginia, U.S.A. Canadian Journal of Forest Research 32: 915–927.

Rentch, J.S., Fajvan, M.A., and Hicks Jr., R.R. 2003. Spatial and temporal disturbance characteristics of oak-dominated old-growth stands in the central hardwood forest region. Forest Science 49: 778–789.

Rogers, R. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. Agricultural Handbook 654, U.S. Dept. of Agriculture, Forest Service, Washington, D.C. vol.2.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 63: 1533–1546.

Runkle, J.R. 1984. Development of woody vegetation in treefall gaps in a beech-sugar maple forest. Ecography 7: 157–164.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. In: Pickett, S.T.A., and White, P.S. (Eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego, pp.17–34.

Rubino, D.L. and McCarthy, B.C. 2000. Dendroclimatological analysis of white oak (*Quercus alba* L., Fagaceae) from an old-growth forest of southeastern Ohio, USA. Journal of the Torrey Botanical Society 127: 240–250.

Rubino, D.L. and McCarthy, B.C. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. Dendrochronologia 21: 97–115.

Ruffner, C.M., and Abrams, M.D. 1998. Relating land-use history and climate to the dendroecology of a 326-year-old *Quercus prinus* talus slope forest. Canadian Journal of Forest Research 28: 347–358.

Sakulich, J., Hart, J.L., van de Gevel, S.L., Nagle, N.N., and Grissino-Mayer, H.D. 2011. Modeling spatial variability of climate response in annual growth of eastern North American trees. Scheduled talk, 2011 Annual Meeting of the Association of American Geographers, 12–16 April 2011, Seattle, Washington.

Schwartz, M.W., and Hermann, S.M. 1999. Is slow growth of the endangered *Torreya taxifolia* (Arn.) normal? Journal of the Torrey Botanical Society 126: 307–312.

Stambaugh, M.C., and Guyette, R.P. 2006. Fire regime of an Ozark wilderness area, Arkansas. American Midland Naturalist 156: 237–251.

Whitney, G.G. 1994. From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America From 1500 to the Present. University Press, Cambridge.

Woods, F.W., and Shanks, R.E. 1959. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. Ecology 40: 349–361.

Zeide, B. 2010. Comparison of self-thinning models: an exercise in reasoning. Trees 24: 1117–1126.

Zishka, K.M., and Smith, P.J. 1980. The climatology of cyclones and anticyclones over North America and surrounding ocean environs for January and July, 1950–77. Monthly Weather Review 108: 387–401.