



# Canopy disturbance history of old-growth *Quercus alba* sites in the eastern United States: Examination of long-term trends and broad-scale patterns

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## ARTICLE INFO

### Article history:

Received 1 July 2011

Received in revised form 23 September 2011

Accepted 18 November 2011

### Keywords:

Disturbance regimes

*Quercus* (oak)

Succession

Dendroecology

Hardwood forests

## ABSTRACT

In the Eastern Deciduous Forest Formation, disturbance regimes are dominated by localized events that remove relatively small portions of the forest canopy, increasing growing space and resource availability for residual trees. Numerous local-scale canopy disturbance reconstructions have been developed and have shaped our understanding of natural disturbance frequency, community dynamics, and changes in forest systems through time. We analyzed tree-ring series from 44 *Quercus alba* old-growth sites located throughout the species' distributional range with the ultimate goal of identifying long-term, broad-scale changes in canopy disturbance regime characteristics throughout the tree-ring record. We documented large gap-scale disturbances via the identification of release events with a five-year duration. To account for unequal sample sizes and tree ages, we calculated the mean releases tree<sup>-1</sup> century<sup>-1</sup> and a ratio of releases to sample sizes for all sites and forest regions. The disturbance chronology contained 311 release events and displayed several pulses in release and establishment frequency that were likely related to stand developmental processes, drought, and anthropogenic impacts. Throughout the 44 old-growth *Q. alba* sites, a steady decline in large gap-scale disturbances beginning in the mid-1600s was apparent in the both the mean releases tree<sup>-1</sup> century<sup>-1</sup> and ratio of releases to sample sizes. This gradual decrease in canopy disturbance is neither the result of forest developmental processes occurring in synchrony throughout the 44 sites nor a result of tree age. Possible broad-scale phenomena that may explain this decline in canopy disturbance include changes in drought frequency and intensity, changes in anthropogenic land use (i.e. timber harvesting and localized fire), and the extinction of *Ectopistes migratorius* (Passenger Pigeon). Prior to the decline of *E. migratorius* in the late 19th Century, the species exerted a profound influence on eastern hardwood forest composition and structure through canopy disturbance. The decline of large gap-scale disturbance is concomitant with the loss of the species. The widespread successional shift reported in *Quercus* stands throughout the Eastern Deciduous Forest may be partly explained by the decrease in large gap-scale disturbance. If land managers aim to mimic the hypothesized canopy disturbance from centuries prior, a combination of harvest prescriptions should be employed to result in both more and larger gaps. Single-tree, group-selection, and shelterwood harvests may mimic the hypothesized impact of *E. migratorius* on eastern hardwood forests (i.e. medium to large gap-scale and incomplete stand-scale disturbances). These larger, more frequent gaps may facilitate the regeneration of mid-successional taxa such as *Quercus*.

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## 1. Introduction

Disturbances impart lasting legacies on forest composition, structure, and successional trajectories (Foster et al., 1998, 2002; Lorimer, 1980). In the Eastern Deciduous Forest Formation of North America, disturbance regimes are dominated by localized events that remove relatively small portions of the forest canopy, increasing growing space and resource availability for residual

trees (Runkle, 1990). As light is the most common limiting factor in eastern hardwood forests (Oliver and Larson, 1996), gap-scale to intermediate-scale disturbances that increase understory light levels are critical for the presence of shade-intolerant and intermediately-tolerant species (Canham et al., 1990). Canopy disturbance reconstructions are useful to elucidate the processes that have shaped forest development (Lorimer, 1985). Numerous local-scale canopy disturbance reconstructions have been developed and have shaped our understanding of natural disturbance frequency, community dynamics, and changes in forest systems through time (Abrams et al., 1995; Hart and Grissino-Mayer, 2008; Lorimer, 1985; Lorimer and Frelich, 1989). However, the

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broad-scale effects of disturbance regime variability remain largely uninvestigated.

Throughout the eastern US and across a variety of site conditions, a widespread successional shift has been documented in which canopy *Quercus* have failed to regenerate and smaller size classes are increasingly dominated by shade-tolerant, mesophytic species (Nowacki and Abrams, 2008). Since *Quercus* is mid-successional and only moderately tolerant of shade, a long-term, broad-scale analysis of canopy disturbance characteristics may provide insight into the apparent successional shift. We analyzed tree-ring series from 44 *Quercus alba* L. old-growth sites located throughout the species' distributional range. We chose to analyze *Q. alba* because the species is a common component of hardwood forests in eastern North America (Abrams, 2003; Rogers, 1990), the species (and genus) is commonly used to reconstruct stand disturbance histories (Abrams et al., 1995; Hart and Grissino-Mayer, 2008; Hart et al., 2008; Nowacki and Abrams, 1997), and the International Tree Ring Data Bank (ITRDB, 2005, <http://www.ncdc.noaa.gov/paleo/treering.html>; Grissino-Mayer and Fritts, 1997) contains chronologies located throughout the species' range.

The ultimate goal of our research was to analyze changes in canopy disturbance regime characteristics throughout the old-growth *Q. alba* tree-ring record. The specific objectives of this study were to: (1) construct an old-growth *Q. alba* disturbance chronology from the identification of release events in tree-ring series and (2) analyze release characteristics (i.e. release frequency, disturbance return interval, mean releases tree<sup>-1</sup> century<sup>-1</sup>, ratio of releases to sample size, and frequency of widespread disturbance episodes) across time and space (i.e. at site, forest region, and range levels). As our goal and objectives were broader in scope than many localized canopy disturbance reconstructions, we used different methods to elucidate disturbance history. Therefore, our results are not meant for comparison with reconstructions in the eastern US that used different methods to reconstruct stand disturbance histories. Our results were viewed in context of providing information on *Quercus* decline and management implications were provided.

## 2. Material and methods

We obtained *Q. alba* tree-ring chronologies from the ITRDB to examine the historical canopy disturbance regime throughout the species' range. Tree-ring chronologies from the ITRDB have undergone intense scrutiny to ensure accurate crossdating and to reduce measurement error (Grissino-Mayer and Fritts, 1997). We used the raw ring-width measurements from all *Q. alba* chronologies that analyzed live standing trees, contained a minimum 10 individuals, and had a minimum of two series per tree ( $n = 44$  chronologies; Table 1). Tree-core samples were collected perpendicular to slope in areas with relief (Cleaveland and Duvick, 1992; LeBlanc and Terrell, 2009). We assumed inner dates were approximate establishment dates. Buchanan and Hart (2011) analyzed the same 44 chronologies to examine intra-tree release discrepancies in *Q. alba* individuals. Additionally, LeBlanc and Terrell (2009) and Goldblum (2010) analyzed portions of the same dataset 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 1768 tree-ring series) were suitable for analysis.

To quantify radial growth release characteristics, we analyzed the raw ring-width measurements for percent growth change using the ten-year running mean method developed by Nowacki and Abrams (1997). Changes in raw ring-widths were analyzed with respect to the running mean of the previous and subsequent 10 years (20 years cumulatively). Release events were identified as periods in which raw ring-width was  $\geq 25\%$  (minor) or  $\geq 50\%$  (major) of

the ten-year preceding and superseding mean, sustained for a minimum of 5 years (i.e. a minimum five consecutive years with raw-ring widths at least 25% greater than the respective ten-year running mean values). A radial growth increase of at least 25% over the 10-year running mean directly corresponds to an increase in sun exposure of at least 25–40% of the tree crown (Nowacki and Abrams, 1997; Rentch et al., 2002). In our study, the additional 25–40% of the tree crown remained exposed for at least 5 years after the disturbance. We excluded the first and last 10 years of each series from analysis as this method requires a ten-year window prior and subsequent to each individual growth ring analyzed.

Though a myriad of release identification methods exist (see Rubino and McCarthy, 2004), we selected the ten-year running mean as it was developed using overstory *Quercus* species in complex-stage stands of eastern North America and has been empirically tested and verified (Nowacki and Abrams, 1997; Rentch et al., 2002). Furthermore, we chose a release duration criterion that was more conservative than many used in disturbance reconstructions in the eastern US (e.g. Lorimer and Frelich, 1989; Nowacki and Abrams, 1997; Rentch et al., 2002) in attempt to only capture large gap-scale disturbances in which growing space and resource availability were substantially heightened for a minimum 5 years. We contend the release duration provides an analogue for gap residence time, which, in turn, corresponds to gap size (though the exact gap size cannot be determined). Larger, longer-lasting canopy gaps have a greater probability of closure via ascension to a higher canopy class by individuals in the gap environment (Clinton et al., 1994; Dahir and Lorimer, 1996; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011; Runkle, 1982). Indeed, establishment of woody species is often limited to the first 5 years following canopy gap creation (Canham and Marks, 1985; Oliver, 1981). As *Quercus* species are only moderately tolerant of shade, gaps that are large enough to provide at least 5 years of increased sunlight and to likely close by subcanopy height growth represent important mechanisms in the maintenance of *Quercus* regeneration in closed-canopy forests. We note that the inclusion of a five-year duration requirement will inherently provide lower release frequency values as compared to other disturbance reconstructions that do not include a duration requirement. It follows that results from this study should not be compared to studies with objectives and corresponding methods that differ from those presented here. We acknowledge that what we are defining here as large gap-scale disturbance may have in fact been closer to what may be considered incomplete stand-scale events (Oliver and Larson, 1996).

We used the ten-year running mean method to identify releases in both of the paired tree-ring series from all 844 individuals. 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, 2011; Copenheaver et al., 2009). Contemporaneous releases occurring in both of the paired series were counted as a single release event. We 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 5 years or less were considered simultaneous). The release frequency of all individuals was then totaled to construct canopy disturbance chronologies at the stand, forest region, and range-wide levels. We analyzed the disturbance chronologies to identify widespread disturbance events at all spatial scales. We considered disturbances to be widespread if  $\geq 25\%$  of all trees exhibited a simultaneous release within a five-year window (Hart et al., 2008; Nowacki and Abrams, 1997; Rubino and McCarthy, 2004).

To describe release characteristics, we used the following measures: mean disturbance return interval (MDRI) and Weibull median

**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. McClenahan; 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. McClenahan; 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 74.57° W	16	1674–1982	225.68 (±7.65 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)

return interval (WMRI), mean releases tree<sup>-1</sup> century<sup>-1</sup> (MRTC), and a ratio of release frequency to sample size (R:n). We analyzed the distribution of disturbance interval data to determine whether the MDRI or WMRI was most appropriate for each forest region (i.e. MDRI was used for normally distributed return interval data, WMRI was used for return interval data best modeled by the Weibull distribution; Grissino-Mayer, 1999; Rentch et al., 2003a). MRTC and R:n are relativized descriptors of canopy disturbance and allow for comparisons of disturbance chronologies of different lengths and sample sizes. The MRTC provides insight into disturbance frequency while mitigating the influence of variable tree ages and sample sizes of forest stands and regions (Rubino and McCarthy, 2004). The R:n ratio also mitigates the influence of sample size in release frequency comparisons by providing the number of releases per individual tree. For example, a site with 20 documented release events from 40 sample trees would have an R:n ratio of 0.5:1 (i.e. when relativized, each individual exhibited 0.5 release events during stand history). To calculate relativized values at the region and range levels, we used the mean of stand-level results. We made qualitative comparisons between the forest regions because sample sizes were too small and variable for statistical analyses.

### 3. Results

#### 3.1. Release characteristics

From the 1768 tree-ring series analyzed, we documented 311 release events of which 300 were minor in magnitude and 11 were major in magnitude (Table 2; Fig. 2). 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 years (±0.04 SE) and 5.36 years (±0.20 SE), respectively. Using the five-year threshold to distinguish intra-tree releases as resulting from separate disturbance events, the maximum release initiation discrepancy was 2 years (documented in a single tree from the Cameron Woods chronology), with all others being a single year. The minimum lag time that exceeded the five-year threshold was 18 years. 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

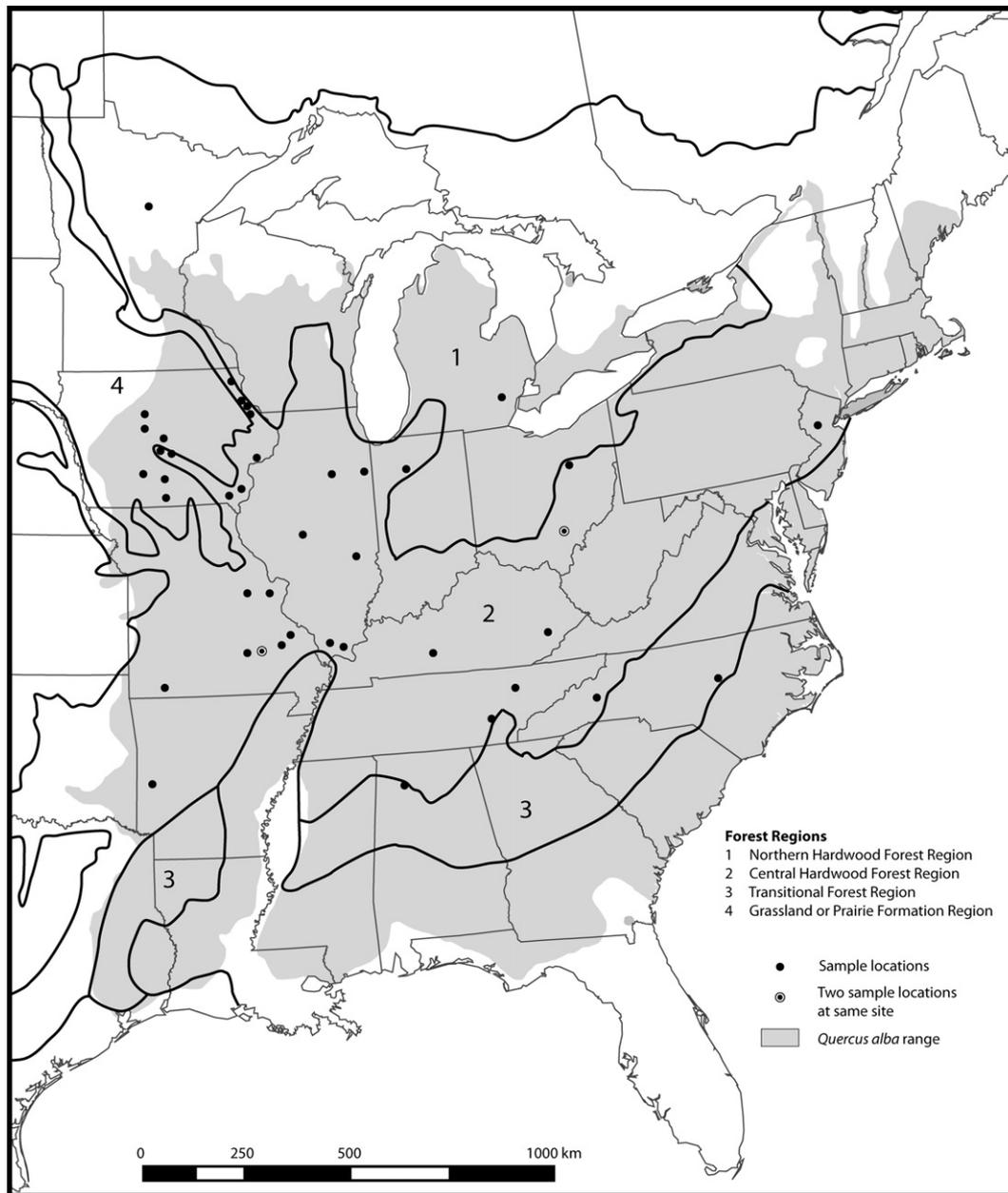


Fig. 1. Map showing the distributional range of *Quercus alba* and the locations of the 44 sites analyzed.

a release within 50 years of tree establishment, 108 never exhibited a subsequent release event.

### 3.2. Forest region

The Central Hardwood Forest Region had the highest sample size with 34 sites comprised of 663 trees (Table 3). The Northern Hardwood Forest Region contained the lowest sample size with 28 trees from two sites. The Transitional Forest Region also contained two sites but was comprised of 30 individuals. The Grassland or Prairie Formation Region featured six sites containing 163 trees. The Central Hardwood Forest Region exhibited the highest release frequency ( $n = 227$ ) followed by the Grassland or Prairie Region ( $n = 51$ ). The Transitional Forest Region exhibited the lowest release frequency ( $n = 16$ ). In the Northern Hardwood Region, 15 (54%) trees exhibited at least one release event and three individuals (10%) exhibited multiple release episodes. In the Central

Hardwood Region, 187 (28%) individuals documented a growth release event and 32 (5%) trees exhibited multiple releases. Twelve (40%) individuals within the Transitional Forest Regions exhibited at least one release episode and four (13%) trees documented multiple release events. In the Grassland or Prairie Region, 43 (26%) trees documented a minimum of one release episode whereas seven (4%) individuals documented multiple release events.

No widespread release episodes were found within any of the four forest regions. The shortest disturbance interval occurred in the Central Hardwood Region (WMRI of 1.96 years) and the longest disturbance interval occurred in the Transitional Region (MDRI of 16.42 years). The Grassland or Prairie Region exhibited the lowest MRTC with a value of 0.18 ( $\pm 0.03$  SE) and the Northern Hardwood Region exhibited the highest MRTC with a value of 0.41 ( $\pm 0.30$  SE). The Grassland or Prairie Region R:n of 0.29:1 was the lowest between the four regions. The Northern Hardwood Forest Region featured the highest R:n value with a ratio of 0.58:1.

**Table 2**  
Release characteristics for the 44 *Quercus alba* ITRDB collections: release frequency, mean releases tree<sup>-1</sup> century<sup>-1</sup>, mean disturbance return interval (MDRI), stand-wide releases, and ratio of release frequency to sample size (R:n).

Site name	Release frequency		Mean releases Tree <sup>-1</sup> century <sup>-1</sup>	MDRI	Stand-wide Releases	R:n
	Minor	Major				
Andrew Johnson Woods	9	–	0.17 (±0.05 SE)	37.78	–	0.50:1
Babler State Park	11	–	0.20 (±0.06 SE)	29.09	–	0.41:1
Backbone State Park	1	–	0.07 (±0.07 SE)	223.00	–	0.09:1
Blackfork Mountain	7	–	0.26 (±0.08 SE)	44.43	–	0.54:1
Buffalo Beats North Clay Lens Prairie Soil	3	–	0.10 (±0.06 SE)	98.33	–	0.11:1
Buffalo Beats North Ridgetop Forest Site	4	–	0.20 (±0.09 SE)	30.00	–	0.19:1
Cameron Woods	7	–	0.56 (±0.22 SE)	16.57	–	0.58:1
Cass Lake B	14	1	0.72 (±0.15 SE)	12.27	–	0.88:1
Cranbrook Institute	3	–	0.11 (±0.06 SE)	127.67	–	0.27:1
Current River Natural Area	8	1	0.23 (±0.12 SE)	36.22	–	0.53:1
Current River Natural Area Recollection	3	–	0.13 (±0.06 SE)	110.33	–	0.33:1
Dolliver Memorial State Park	4	1	0.15 (±0.07 SE)	55.40	–	0.36:1
Duvick Backwoods	6	1	0.55 (±0.23 SE)	15.86	1	0.44:1
Fern Clyffe State Park	4	1	0.08 (±0.03 SE)	61.40	–	0.23:1
Fox Ridge State Park	4	–	0.09 (±0.06 SE)	71.75	–	0.22:1
Geode State Park	12	–	0.39 (±0.13 SE)	20.08	1	0.75:1
Giant City State Park	14	1	0.28 (±0.07 SE)	20.67	–	0.60:1
Greasy Creek	5	–	0.35 (±0.14 SE)	37.20	–	0.33:1
Hampton Hills	5	–	0.26 (±0.15 SE)	39.40	–	0.31:1
Hutcheson Forest	1	–	0.03 (±0.03 SE)	289.00	–	0.06:1
Jack's Fork	9	–	0.28 (±0.09 SE)	20.67	–	0.30:1
Kankakee River State Park	5	1	0.22 (±0.09 SE)	45.83	–	0.40:1
Lacey-Keosauqua State Park	5	1	0.24 (±0.09 SE)	41.17	–	0.50:1
Lake Anquabi State Park	12	–	0.31 (±0.12 SE)	32.25	–	0.46:1
Ledges State Park	25	–	0.25 (±0.15 SE)	11.46	–	0.43:1
Lilley Cornett Tract	5	–	0.12 (±0.05 SE)	60.60	–	0.33:1
Lincoln's New Salem State Park	4	–	0.06 (±0.03 SE)	72.50	–	0.14:1
Linville Gorge	5	–	0.11 (±0.04 SE)	68.20	–	0.29:1
Lower Rock Creek	3	–	0.10 (±0.05 SE)	78.33	–	0.18:1
Mammoth Cave Recollect	4	1	0.15 (±0.05 SE)	51.00	1	0.36:1
Merritt Forest State Preserve	8	–	0.33 (±0.12 SE)	31.25	–	0.50:1
Nine Eagles State Park	2	–	0.15 (±0.10 SE)	145.50	–	0.15:1
Norris Dam State Park	9	–	0.13 (±0.04 SE)	36.44	–	0.28:1
Pammel State Park	20	–	0.19 (±0.04 SE)	16.25	–	0.38:1
Piney Creek Pocket Wilderness	4	–	0.17 (±0.11 SE)	78.00	–	0.27:1
Pulaski Woods	2	–	0.09 (±0.06 SE)	137.00	–	0.18:1
Roaring River	1	–	0.03 (±0.03 SE)	239.00	–	0.07:1
Saylorville Dam	8	1	0.23 (±0.10 SE)	33.33	–	0.26:1
Sipsey Wilderness	11	–	0.33 (±0.09 SE)	26.09	–	0.79:1
Starved Rock State Park	15	1	0.16 (±0.05 SE)	20.50	–	0.38:1
Wegener Woods	4	–	0.14 (±0.06 SE)	68.00	–	0.31:1
White Pine Hollow State Preserve	5	–	0.13 (±0.07 SE)	66.00	–	0.33:1
Woodman Hollow State Preserve	3	–	0.07 (±0.04 SE)	86.67	–	0.13:1
Yellow River State Forest	6	–	0.24 (±0.08 SE)	49.67	–	0.50:1

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. 3). 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 and during the 1940s whereas tree establishment peaked during 1740–1789 and subsequently during the 1870s and 1890s. Based on long-term trends in MRTC values and the R:n ratio, large gap-scale disturbances in the Central Hardwood and Grassland or Prairie Regions began to decline from ca. 1650 until the end of the record (Fig. 4). This pattern was not evident in the Northern Hardwood and Transitional Forest Regions.

### 3.3. Range

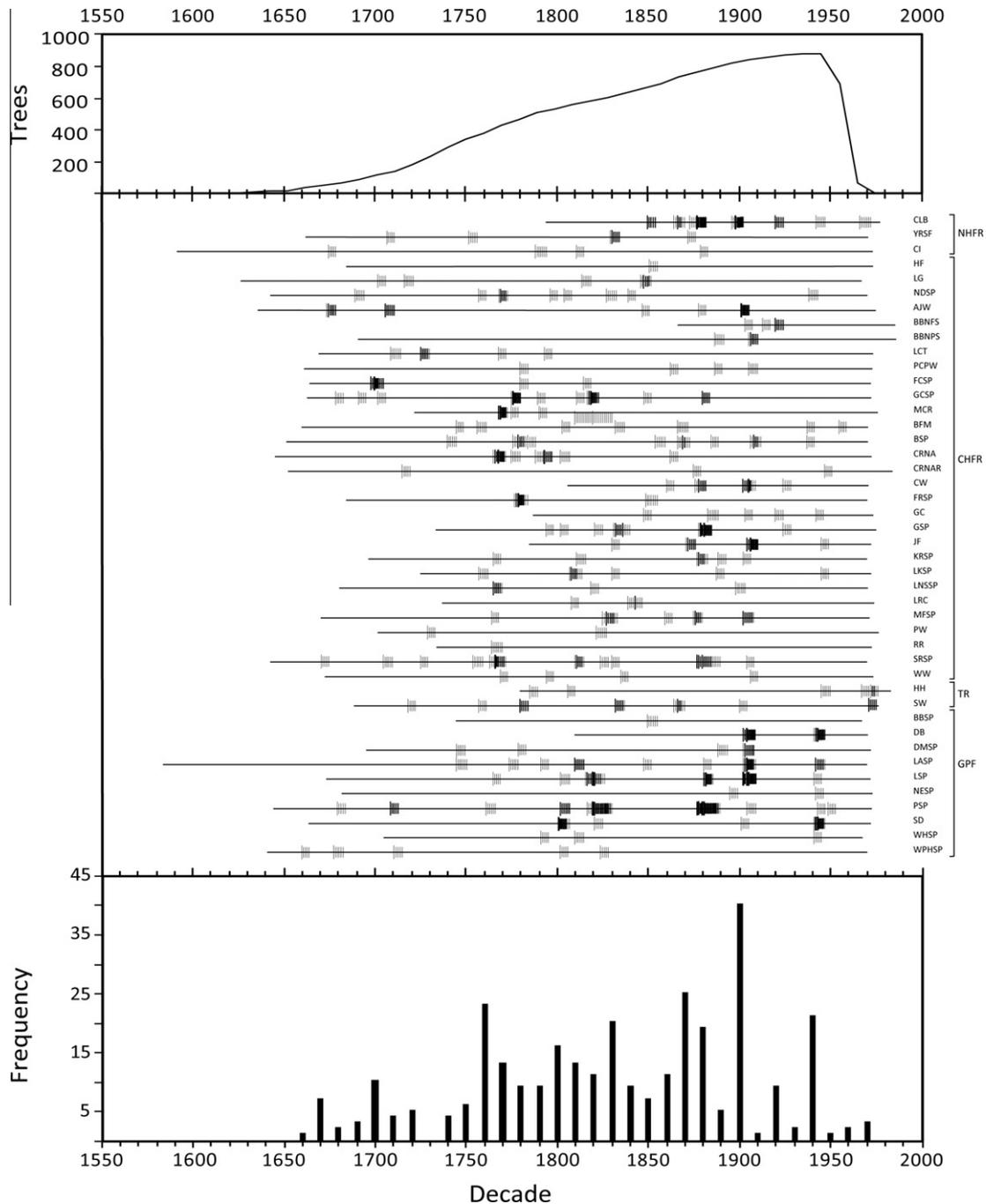
At the range level, the release record extended from 1584 to 1985. Individual MRTC values throughout the *Q. alba* distribution

ranged from 0 to 2.78 with a mean value of 0.21 (±0.01 SE). The range-wide mean R:n ratio (calculated from the stand-level results) was 0.36:1 (±0.03 SE). Range-wide release frequency exhibited peak values during the 1760s, 1830s, 1870s, 1900s, and 1940s (Fig. 5). Range-wide establishment was highest during a period from 1720 to 1799 and exhibited a subsequent pulse of lesser magnitude from 1840 to 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. Based on long-term trends in MRTC values and the R:n ratio, large gap-scale disturbances in the *Q. alba* range have steadily declined from the mid-1600s to the end of the tree-ring record (Fig. 6).

## 4. Discussion

### 4.1. Release characteristics

Radial growth release events recorded in the tree-ring record provide information regarding historical canopy disturbance regimes at fine spatial and temporal resolutions. For our study, we aimed to only document large gap-scale disturbance events in



**Fig. 2.** The release frequency from the 44 *Q. alba* ITRDB chronologies. 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 durations. A composite of release events is shown across the bottom and the range-wide sample depth is shown across the top.

which the voids were likely filled by subcanopy height growth (Hart and Grissino-Mayer, 2009; Runkle, 1982; Webster and Lorimer, 2005). For intermediate shade tolerant taxa such as *Quercus*, these larger, longer-lasting gaps serve as important mechanisms for regeneration. As the goal of our study was to analyze disturbance history with regard to the pervasive *Quercus* regeneration problem in Eastern forests, the documentation of large gap-scale disturbances (via the inclusion of the five-year release duration criterion) best suited these goals. We contend the five-year duration criterion serves as an analogue for gap residence time and thus, gap size (though we had no means of determining actual gap size). Larger gaps provide increased probability for closure via the ascension

to higher canopy classes of individuals in the gap environment (Clinton et al., 1994; Dahir and Lorimer, 1996; Hart and Grissino-Mayer, 2008, 2009; Richards and Hart, 2011; Runkle, 1982). We are confident we documented large gap-scale disturbances as the mean release duration value of 5.39 ( $\pm 0.04$  SE) only minimally exceeds the five-year criterion.

As a result of the conservative duration criterion, the total release frequency throughout the 44 *Q. alba* old-growth sites was relatively low when compared to other site-specific studies in the region that used more liberal criteria ( $n = 311$  events from 1574 to 1985; see studies reviewed in Rubino and McCarthy, 2004). As the objectives of this study were broader in scope than most

**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. Data reported for mean releases tree<sup>-1</sup> century<sup>-1</sup> and ratio of releases to sample size (R:n) 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 <sup>-1</sup> century <sup>-1</sup>	Disturbance return interval	R:n
Northern Hardwood Forest Region	2	28	198.43 (±17.05 SE)	17	0.41 (±0.30 SE)	13.69 <sup>a</sup>	0.58:1
Central Hardwood Forest Region	34	663	201.83 (±2.88 SE)	227	0.20 (±0.02 SE)	1.96 <sup>b</sup>	0.34:1
Transitional Forest Region	2	30	190.70 (±13.73 SE)	16	0.29 (±0.03 SE)	21.17 <sup>a</sup>	0.42:1
Grassland or Prairie Formation	6	163	185.70 (±5.81 SE)	51	0.18 (±0.03 SE)	6.06 <sup>b</sup>	0.29:1

<sup>a</sup> Mean disturbance return interval.

<sup>b</sup> Weibull median disturbance return interval.

localized reconstructions, we developed methods to identify only disturbances of a certain magnitude (i.e. large gap-scale events) as these events represent important mechanisms for *Quercus* regeneration. Therefore, results from this study should not be directly compared to reconstructions derived from different release identification criteria. The methods we used were specific to our goals. Moreover, the results should not be interpreted as being exhaustive of all disturbance and release events that occurred during the respective stand histories. Rather, they represent only what we define as large gap-scale disturbances. For instance, 70% of trees in our study did not exhibit a release event identified by the ten-year running mean with a five-year duration criterion. This does not imply that 70% of the trees never experienced a release event; rather, 70% of the sampled *Q. alba* trees never experienced a large gap-scale disturbance. Certainly some of the trees that did not record a large gap-scale disturbance established in a gap environment and did not experience a subsequent release; but other trees ascended to the canopy via a series of small canopy gaps.

#### 4.2. Forest region

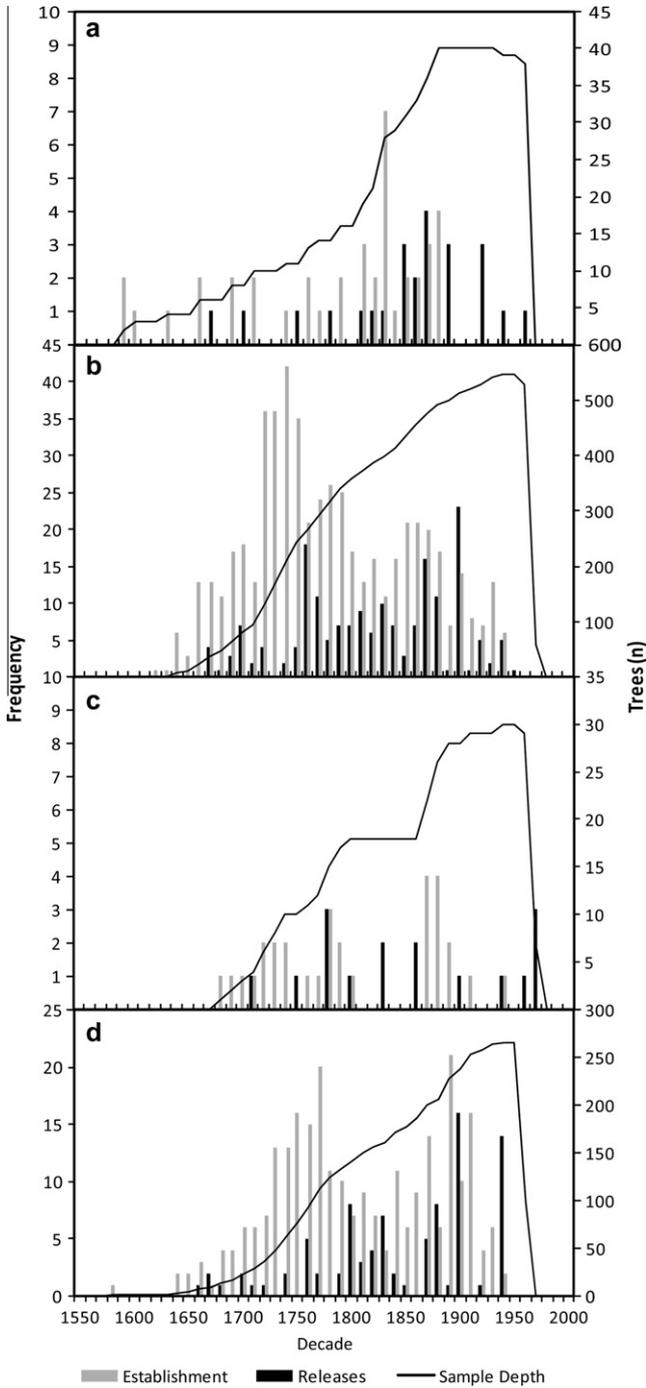
The Northern Hardwood Region exhibited the highest values in both of the relativized disturbance parameters. Conversely, the Central Hardwood Region featured the second lowest MRTC value and R:n ratio. Therefore, though the Central Hardwood Region exhibited the highest release frequency ( $n = 227$ ) and shortest disturbance return interval (WMRI of 1.96 years), the relativized factors revealed the region experienced one of the lowest levels of large gap-scale disturbance. This discrepancy makes clear the importance of relativized release descriptors in accounting for unequal sample sizes (e.g. number of trees per stand, number of stands per region) and tree age variability. These descriptors were especially useful here since we could not statistically compare release characteristics between regions. We recommend the use of relativized release descriptors in canopy disturbance reconstructions as the measurements allow for unbiased comparisons between sites of differing sample sizes and ages (see Rubino and McCarthy, 2004). Additionally, we suggest the standardization of disturbance return intervals; these calculations should be based on the distribution of disturbance interval data (see Rentch et al., 2003a).

Several temporal trends in release and establishment frequency were noted throughout the four regions. In all forest regions except the Northern Hardwood, both establishment and release frequency exhibited pulses during a period from 1720 to 1789. This multi-decadal period of increased establishment and release frequency coincided with the 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 from early European explorers and colonizers (Denevan, 1992; Ramenofsky,

1987). This period of depopulation effectively caused a cessation in Native American land-use practices (e.g. tree girdling and fire to favor mast trees and pasturage (Abrams and Nowacki, 2008)) throughout much of the eastern US (Guyette et al., 2002; McEwan et al., 2011). Thus, in the century prior to broad-scale European settlement, reforestation occurred throughout the region. We suggest the relatively high rates of establishment and release frequency between 1720 and 1789 documented in the tree-ring record corresponded to this period of Native American depopulation.

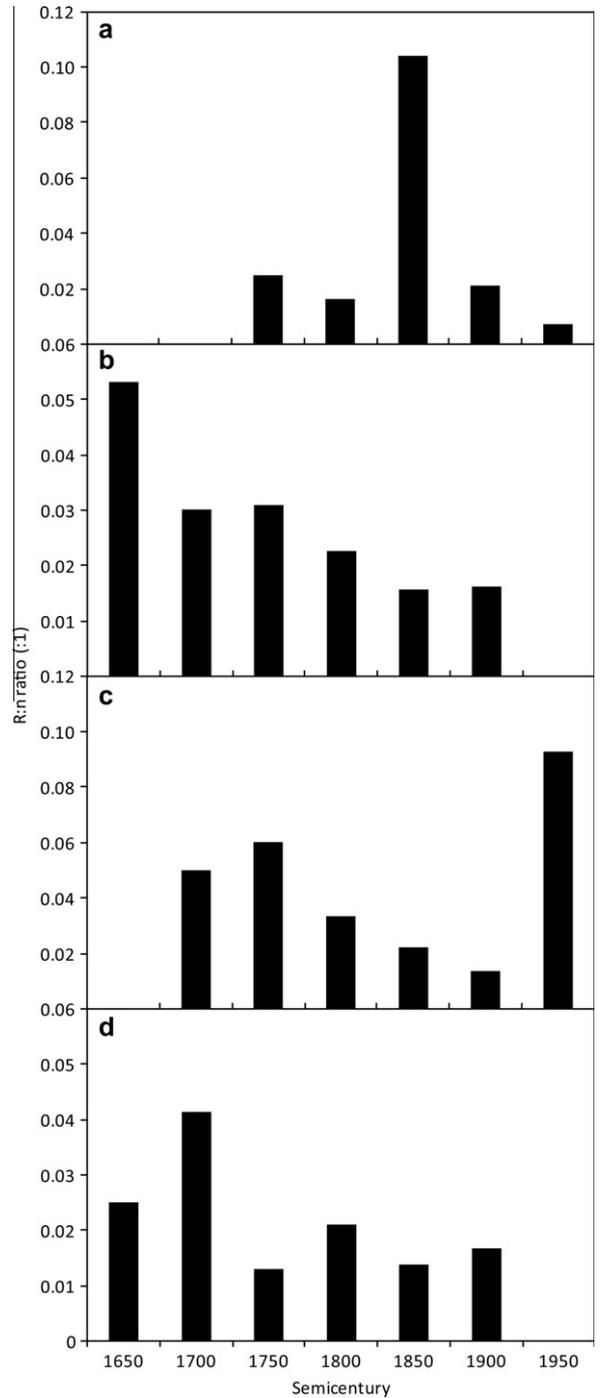
In these three regions, pulses in release frequency in the 1760s and 1780s possibly represented self-thinning occurring in the recently established stands or were related to a high frequency of moderate droughts. Self-thinning is the result of both the increasing size of neighbors and a decreased tolerance to low light as trees age (Zeide, 2010) and has been shown to increase productivity of residual trees ca. 40 years after establishment (Hart and Grissino-Mayer, 2008; Hart et al., 2011). At this stage in stand development, growing space is fully utilized and the space made available by removed individuals is filled by larger trees with superior crown positions (Oliver and Larson, 1996; Hart et al., 2011). The hypothesis that these release pulses represented self-thinning is supported by the fact that 49% of all releases occurred within 50 years of tree establishment. Furthermore, during this thirty-year period of increased release frequency, large portions of Central Hardwood and Transitional Forest Regions experienced periods of moderate drought 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). We speculate in the subsequent wetter years, remnant trees positively responded to the increased resource availability resulting from both the large 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 frequency suddenly increased. Both of these occurrences coincide with the period of settlement for the region and therefore likely resulted from the sudden increase in land-use intensity and spatial extent by European settlers (Gerlach, 1970; Stambaugh and Guyette, 2006). Multiple studies recognize that significant portions of the Northern Hardwood Forest Region were cleared for timber during the mid-19th Century (Frelich and Reich, 2002; Whitney, 1994). After the removal of individuals for timber, we speculate remnant trees responded with increased radial growth and new trees established in the resultant gaps.



**Fig. 3.** The establishment frequency, release frequency, and sample depth (secondary y-axis values) for the Northern Hardwood Forest Region (a), Central Hardwood Forest Region (b), Transitional Forest Region (c), and Grassland or Prairie Region (d). Note the different primary y-axis values and secondary y-axis values.

The Central Hardwood, Transitional, and Grassland or Prairie regions exhibited multiple decades of increased establishment and release frequency during a period from 1850 to 1919. The increased establishment during the early portion of this period likely corresponded to widespread settlement of the regions (Gerlach, 1970) and the associated increase in logging for wood products. Moderate multi-year droughts beginning in both 1856 and 1872 (Cook and Krusic, 2004; McEwan et al., 2011) 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



**Fig. 4.** The ratio of releases to sample size (R:n) in 50-year bins for the Northern Hardwood Forest Region (a), Central Hardwood Forest Region (b), Transitional Forest Region (c), and Grassland or Prairie Region (d). Note the different y-axis values.

eastern US peaked (Whitney, 1994). Though many of the stands in our dataset are considered old growth based on the tree age, we speculate many of these stands experienced selective cutting during this period of intense logging (Parker, 1989; Whitney, 1994).

All regions excepting the Transitional Forest Region continued to display high rates of establishment and release frequency during the early 20th Century. These pulses were likely the result of continued selective cutting and the onset of *Castanea dentata* population decimation by the fungal pathogen *Cryphonectria parasitica* (Murrill) Barr. in stands where the species was present (Agrawal

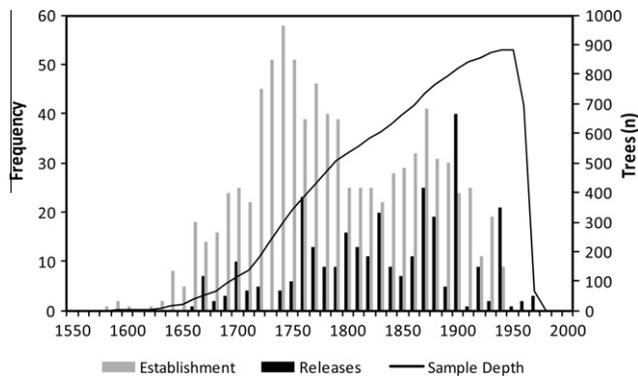


Fig. 5. The establishment frequency, release frequency, and sample depth (secondary y-axis) for the 44 analyzed *Quercus alba* sites in the eastern United States.

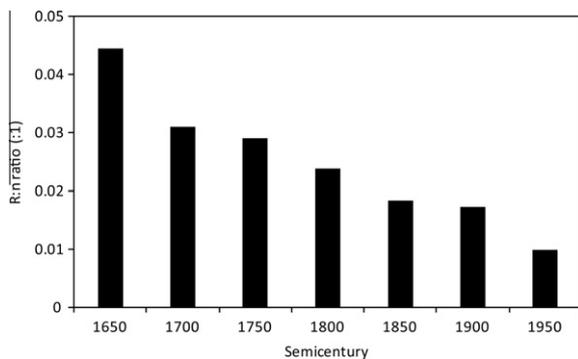


Fig. 6. The ratio of releases to sample size (R:n) in 50-year bins for the 44 analyzed *Quercus alba* sites.

and Stephenson, 1995; Hart et al., 2008; McEwan et al., 2011). As this pathogen spread throughout the eastern US, genera such as *Quercus* and *Acer* were able to fill the niche vacated by *C. dentata* (McCarthy and Bailey, 1996; Woods and Shanks, 1959) and this increase in growth and establishment is evident in the tree-ring record. The decimation of *C. dentata* has 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 to 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, we speculate the significant pulse in release frequency in the Grassland or Prairie Region corresponded to drought-induced tree mortality and subsequent increased growth by remnant individuals.

Beginning in the mid-1600s, the MRTC values and R:n ratios for both the Central Hardwood and Grassland or Prairie Regions exhibited a steady decline in the frequency of large gap-scale disturbances. The Northern Hardwood and Transitional Regions did not display this trend in relativized values. However, both regions contained only two sites and we therefore suspect the patterns are not representative of the entirety of these two regions.

#### 4.3. Range

Several widespread temporal trends of establishment and release frequency were identified from the collective 44 *Q. alba*

old-growth sites. The establishment frequency exhibited a bimodal temporal distribution with a peak from 1720 to 1799 and a subsequent pulse of lesser magnitude from 1840 to 1919. As these peaks were well defined, we speculate that these two periods represented open-origin establishment subsequent to stand-scale or incomplete stand-scale disturbance where most of the overstory was removed. The pulses in release and establishment frequency identified within the four regions were evident when analyzed at the range scale. Prior to the establishment peak beginning in 1720, establishment frequency was relatively sparse until 1650 when a constant level of “background” establishment (i.e. background disturbance) was begun. Similarly, the release frequency exhibited a constant level of background disturbance from ca. 1650–1900.

To account for the variable sample sizes throughout the record's extent, we used MRTC values and the R:n ratio to analyze general trends in large gap-scale disturbances. While some variability was apparent between forest regions, at the range-level the frequency of large gap-scale disturbance events decreased steadily from the mid-1600s until the end of the tree-ring record. It is possible the gradual decrease in large gap-scale disturbances was an artifact of tree age as older individuals may not respond positively to increased resources and growing space (Nowacki and Abrams, 1997). However, we think this is unlikely for two reasons. First, old *Quercus* trees have been shown to increase radial growth in accord with increased resource availability (McEwan and McCarthy, 2008; Orwig and Abrams, 1994). Indeed, we documented a release in a 275-year old tree and 89 trees in our dataset exhibited releases at 100 years of age or more. Second, not all individuals were old during the latter portion of the tree-ring record. Over half of the trees analyzed were under 200 years of age in the mid-1900s and thus, should not have been affected by the possibility of reduced phenotypic plasticity.

The decline in large gap-scale disturbance frequency over the past three centuries in old-growth *Q. alba* stands may have been a function of stand development processes or attributed to a broad-scale phenomenon not related to forest dynamics. As forests age, we would expect large gap-scale disturbances to become more common (Hart and Grissino-Mayer, 2009; Oliver and Larson, 1996; Runkle, 1991). As the pattern detected throughout the *Q. alba* sites displays a gradual decline in disturbances of this magnitude, we suspect the trend is not related to forest developmental processes. Additionally, the *Q. alba* stands occurred over a large area and had variable establishment dates. Therefore, at any given point in time, the developmental stages of the sites were not in synchrony and would not produce a uniform trend in release frequency. Furthermore, if establishment dates were relatively similar, we would expect the uniform trend would be one of increasing large gap-scale disturbances over time. Therefore, while the mechanisms are unknown, we speculate that this pattern resulted from a sub-continental phenomenon.

The decline in large gap-scale disturbances appears to be caused by a range-wide phenomenon and we speculate potential explanatory mechanisms include: drought, anthropogenic timber harvesting, human-set fires (specifically, spot fires that created sizeable canopy voids over time), and *Ectopistes migratorius* L. (Passenger Pigeon) extinction. The severity and general frequency of drought in the eastern US has decreased in the last five centuries (Cook and Krusic, 2004; McEwan et al., 2011). Fewer and/or less severe droughts should generally result in a lower rate of forest canopy disturbance. Human use of and impact on forest resources have changed considerably over this period as well. While these forests support old trees, we suspect they have been high-graded and influenced by anthropogenic fire (Frelich and Reich, 2002; Martin, 1992; Nowacki and Abrams, 1992; Whitney, 1994). Most old-growth hardwood forests in the eastern US currently receive

some protection from these anthropogenic disturbances (Parker, 1989). Cessation of selective cutting and fire would have contributed to the decline in large gap-scale disturbances that we documented in this study. While changes in drought and human disturbances have certainly influenced canopy disturbance regimes, the most pronounced change was the loss of *E. migratorious* and their associated impacts on forest ecosystems.

Before the demise of *E. migratorious*, the species range spanned the Eastern Deciduous Forest from the Gulf of Mexico to Hudson Bay and from the Atlantic Coast to the Great Plains, and covered 7.25 million km<sup>2</sup> (Schorger, 1955). The population was estimated to be 3–5 billion at settlement, a size that approximates the total number of birds that currently inhabit North America (Ellsworth and McComb, 2003; Schorger, 1955; Webb, 1986). The birds travelled in flocks of up to hundreds of millions and it has been said their passing would obscure the sun for days (Blockstein and Tordoff, 1985). The *E. migratorious* roosts covered up to 10,000 ha and were inhabited by an estimated average of 105,000 birds ha<sup>-1</sup> (Ellsworth and McComb, 2003). The nest sites comprised a cumulative 200,000 ha and generally were inhabited by 617 adults ha<sup>-1</sup> (Schorger, 1937). The physical damage (i.e. branch and stem breakage) and chemical damage (i.e. over-fertilization by pigeon excrement) caused by roosting would result in large gap-scale and incomplete stand-scale disturbance (Ellsworth and McComb, 2003). An 1810 account of a roost in Missouri was described as having the appearance of “having suffered from a hurricane or tornado” (McKinley, 1960). The bird’s nesting sites created mid-sized and large canopy gaps (Ellsworth and McComb, 2003). Indeed, individual trees could support up to 100 nests in which the cumulative weight of the birds would break branches and collapse entire trees (Blockstein and Tordoff, 1985; Ellsworth and McComb, 2003). Within the nesting areas (ranging in size up to 2000 km<sup>2</sup>), every suitable tree was inhabited by at least one nest (Blockstein and Tordoff, 1985; Ellsworth and McComb, 2003). Ellsworth and McComb (2003) estimated that 97,250 km<sup>2</sup> of the Northern and Central Hardwood Forest Regions were affected by nesting disturbances in a given year.

The canopy voids created by both roosting and nesting would have favored shade intolerant and moderately intolerant species (Ellsworth and McComb, 2003). The return interval of nesting disturbance was 12–13 years and would have affected 8% of the breeding area annually (Ellsworth and McComb, 2003). The estimated percentage of land disturbed by *E. migratorious* activity exceeds the land percentage disturbed by chronic background disturbance agents such as ice and wind storms (Beckage et al., 2000; Ellsworth and McComb, 2003; Hart and Grissino-Mayer, 2009; Runkle, 1982). Additionally, coarse woody debris inputs caused by *E. migratorious* branch and stem breakage increased forest fuel loadings throughout the region which may have increased fire frequency and intensity (Ellsworth and McComb, 2003). The impact of *E. migratorious* was widespread throughout eastern North America as the birds migrated extensively to locate sites with abundant mast (Ellsworth and McComb, 2003).

An abrupt decline of *E. migratorious* began in 1871, the population was all but decimated by 1900, and the last individual (“Martha”) died in 1914 (Blockstein and Tordoff, 1985; Webb, 1986). While the striking decline did not begin until the 1870s, increased human population density in eastern North America certainly had deleterious impacts on *E. migratorious* populations. For example, netting as a harvesting technique dates to the 1600s and a single net could capture over 100 birds (Blockstein and Tordoff, 1985). Additionally, *E. migratorious* preferred nesting in unbroken expanses of old hardwood forests and was likely susceptible to habitat fragmentation caused by anthropogenic land clearance (Jackson and Jackson, 2007). Moreover, *E. migratorious* had an enormous demand for mast and would have been vulnerable to human

competition for favored fruits (e.g. *Fagus grandifolia* Ehrh., *Quercus* spp., *C. dentata*; Blockstein and Tordoff, 1985; Schorger, 1955). Therefore, we suspect the decline of *E. migratorious* was well established prior to the drastic population decimation that began in the late 1800s.

The decline of *E. migratorious* corresponds to the decline in frequency of large gap-scale disturbances documented in the tree-ring record. The background disturbance level noted in our study is likely primarily the result of wind and ice storm damage, mechanisms that have not changed significantly over the period of observation. In the early portion of the record, increased levels of release frequency, beyond those created by the background disturbance mechanisms, were possibly caused by droughts of higher frequency and intensity, more widespread and frequent human impacts, and damage caused by *E. migratorious*. We hypothesize the decline in large gap-scale disturbance is most strongly linked to the extinction of *E. migratorious*. However, we stress that this relationship is speculative as it is based on secondary data and other published studies analyzing the history and impact of *E. migratorious*.

The widespread successional shift reported in *Quercus* stands throughout the Eastern Deciduous Forest may be partly explained by a decrease in large gap-scale disturbance. *Quercus* is only moderately tolerant of shade and is considered mid-successional (Abrams, 2003; Rentch et al., 2003b). Its perpetuation in forests is dependent upon canopy removal sufficiently large to allow recruitment that is uninhibited by an intact understory of shade-tolerant species. A decline in the frequency and size of canopy gaps would inhibit *Quercus* regeneration and canopy recruitment and favor the establishment of shade-tolerant species. We speculate the decline and eventual extinction of *E. migratorious* caused a drastic change in canopy disturbance characteristics and may have had significant implications for community composition, structure, and successional patterns. Certainly, changes in other disturbance agents likely also played a role in this documented compositional shift (notably, changes in fire regimes; Nowacki and Abrams, 2008). We stress that the extinction of *E. migratorious* was not the sole driver of the decline in gap-scale disturbances nor does the decrease in gap-scale disturbance alone fully explain *Quercus* regeneration failure and the proliferation of shade-tolerant mesophytes in the understory. Rather, it is likely one of a host of interacting factors that have contributed to the observed compositional change (Abrams, 2003; Lorimer, 1993; McEwan et al., 2011).

## 5. Management implications

In the Eastern Deciduous Forest, harvesting prescriptions have been developed to mimic the natural occurrence of gap-scale disturbances caused by wind and ice events (Coates and Burton, 1997). Following such guidelines, approximately 1–2% of the forest canopy should be opened annually to mimic gaps caused by these agents (Runkle, 1985, 1991). However, this gap land fraction only captures the rate and extent of canopy disturbance occurring after the extinction of *E. migratorious*, ca. 1900. Our results reveal a decreasing frequency of large gap-scale disturbances concomitant with the decline and extinction of *E. migratorious* and, to a lesser extent, changes in drought and anthropogenic disturbance. Prior to 1900, these disturbances were more common and we hypothesize were, in large part, a result of nesting and roosting activity of *E. migratorious*. Indeed, within the breeding range, 8% of the land area was in gap environments annually (Ellsworth and McComb, 2003). Therefore, if land managers aim to mimic the hypothesized canopy disturbance from centuries prior, a combination of harvest prescriptions should be employed to result in both more and larger gaps. Single-tree, group-selection, and shelterwood harvests may

mimic the hypothesized impact of *E. migratorious* on eastern hardwood forests (i.e. medium to large gap-scale and incomplete stand-scale disturbances). These larger, more frequent gaps may facilitate the regeneration of mid-successional taxa such as *Quercus* (Loftis, 1990). Some *Quercus* forests are now being managed for old-growth characteristics, biodiversity, and various aesthetic values and these managers may be reluctant to harvest timber (Johnson, 2004). However, removing timber via single-tree, group-selection, and shelterwood harvests may actually mimic canopy gaps caused by a disturbance agent that is now extinct and return forest composition and structure to within their historic range of variability.

## Acknowledgements

We would like to thank the many contributors of *Quercus alba* chronologies to the ITRDB. We also thank the University of Alabama Cartographic Research Laboratory for assistance with figure preparation; Ian Comstock for assistance with database management; and David Shankman, Gregory Starr, Jacob Richards, and two anonymous reviewers for helpful comments on earlier drafts of the manuscript.

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