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# A methodological analysis of canopy disturbance reconstructions using *Quercus alba*

**Megan L. Buchanan and Justin L. Hart**

**Abstract:** Forest disturbance history reconstructions in the eastern US commonly rely on the analysis of a single tree-ring series per individual. However, this method can result in an underrepresentation of radial growth releases and canopy disturbance events. We analyzed paired tree-ring series from 884 *Quercus alba* L. individuals to quantify discrepant patterns of intratree release frequency, magnitude, and initiation years. We also developed a model for *Q. alba* that accounts for this underrepresentation of releases. Of the 884 trees analyzed, 216 exhibited radial growth releases. Only 13 of these 216 trees recorded the same canopy disturbance events in both series. Through analysis of a single growth-ring series per tree, a minimum of 39 and a maximum of 241 releases could be detected from the trees in the data set. Of the total number of release events, 238 (85%) occurred only in one of the paired tree-ring series. For stand development studies requiring the frequency of canopy disturbance alone, a multiplicative factor of 1.72 can provide the information necessary without deviating from the standard practice in the eastern US of collecting and analyzing a single increment core per tree. Studies requiring spatially and temporally explicit information regarding disturbance should extract and analyze two or more tree-ring series per individual.

**Résumé :** La reconstitution de l'historique des perturbations forestières dans l'est des États-Unis repose généralement sur une seule série dendrochronologique par individu. Cependant, cette méthode peut entraîner la sous-représentation des épisodes de perturbation du couvert et de reprise de la croissance radiale à la suite d'un dégagement. Nous avons analysé les séries dendrochronologies appariées de 884 tiges de *Quercus alba* L. pour quantifier les patrons divergents de l'année du début, de l'ampleur et de la fréquence des dégagements dans chaque arbre. Nous avons aussi développé un modèle pour *Q. alba* qui tient compte de la sous-représentation des dégagements. Des 884 arbres analysés, 216 montraient une reprise de la croissance radiale à la suite de dégagements. Seulement 13 des 216 arbres avaient enregistré les mêmes épisodes de perturbation du couvert dans les deux séries. Avec l'analyse d'une seule série dendrochronologique par arbre, un minimum de 39 et un maximum de 241 dégagements pouvaient être détectés à partir des arbres contenus dans le jeu de données. Du nombre total d'épisodes de dégagement, 238 (85 %) sont apparus seulement dans une des séries dendrochronologiques appariées. Dans le cas des études sur le développement du peuplement qui requièrent seulement la fréquence des perturbations du couvert, un facteur de multiplication de 1,72 peut fournir l'information nécessaire, sans dévier le la pratique standard dans l'est des États-Unis qui consiste à collecter et analyser une seule carotte de bois par arbre. Dans le cas des études qui requièrent une information explicite dans le temps et dans l'espace au sujet des perturbations, on devrait extraire et analyser deux séries dendrochronologiques ou plus par individu.

[Traduit par la Rédaction]



## Introduction

The identification of release events in radial growth patterns of trees is a fundamental dendroecological technique used to reconstruct the disturbance history of forest environments at multiple scales (Lorimer 1985; Fraver and White 2005). The timing, magnitude, and spatial extent of past canopy disturbance events can be determined through analysis of radial growth patterns of remnant trees (Fritts and Swetnam 1989; Hart et al. 2010). A number of methods exist to quantify radial growth release events (Rubino and McCarthy 2004; Copenheaver et al. 2009); however, the most prevalent method defines dendroecological release events as changes in radial growth relative to a predetermined criterion using a percentage growth change equation (Nowacki and Abrams 1997).

The reconstruction of forest disturbance history is necessary to elucidate stand development patterns and to enhance

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the understanding of successional processes that influence forest environments (Goebel and Hix 1997; Hart and Grissino-Mayer 2008). The results of such reconstructions enable researchers to determine processes that have shaped the composition and structure of forest stands at both local and regional scales (Lorimer and Frelich 1989; Black and Abrams 2005). The knowledge ascertained through the reconstruction process can then be used by resource managers to mimic historical disturbance regimes.

The importance of disturbance history reconstruction necessitates that the identification of radial growth releases derived from the tree-ring record be an accurate representation of canopy disturbance events. However, competition, differing levels of resource availability surrounding the bole (e.g., uneven canopy distribution, variation in light quantity and quality), or damage to one aspect of the tree serve to produce variable radial growth patterns resulting in nonconcentric tree-ring formation (Biging and Wensel 1988; Copenheaver et al. 2009). As such, a tree-ring sample extracted from one aspect of an individual may exhibit different radial growth patterns than a tree-ring sample extracted from a different radius of the same tree. Analyses of two tree-ring series from a single individual have confirmed this variability (Rentch et al. 2002) and have documented discrepant frequencies of growth release events between the two series (Copenheaver et al. 2009). Therefore, analysis of only a single tree-ring series per individual, as is most common for canopy disturbance reconstructions in the eastern US, can lead to an underrepresentation of radial growth release episodes and of canopy disturbance events. We analyzed intratree radial growth variation across the range of *Quercus alba* L. with the ultimate goal of documenting the spatial extent and magnitude of this underrepresentation. We used the results of our findings to develop a simple model to account for this underrepresentation and eliminate the need to collect and analyze multiple tree-ring series per individual for studies requiring an accurate frequency of canopy disturbance events alone. The radial-growth series contained within the International Tree-Ring Data Bank (ITRDB; http://www.ngdc.noaa.gov/paleo/treering.html) allowed us to quantify intratree radial growth release discrepancies and the effect that this variability has on disturbance reconstruction research.

We 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), the species was identified by Copenheaver et al. (2009) as having discrepant growth releases between two series of the same tree, and the ITRDB contains chronologies located throughout the species' range. Therefore, the results of our study are widely applicable to dendroecological investigations conducted in *Quercus* forests of eastern North America and provide a framework for developing similar models for other species. The specific objectives of our study were (*i*) to quantify discrepant patterns of release frequency between paired series from the same tree, (*ii*) to document intratree disparities of growth release magnitude, (*iii*) to quantify within-tree differences of release initiation years, and (*iv*) to develop a range-wide model for *Q. alba* that accounts for the underrepresentation of dendroecological growth releases that occurs when analyzing only a single tree-ring series per individual. Our results provide information on the variability inherent in radial growth patterns and include a model that effectively compensates for within-tree radial growth variation using tree-ring chronologies located throughout the *Q. alba* range. The contribution of our study is thus twofold: first, an analysis of intratree release discrepancy patterns to determine if an underrepresentation of release events is a range-wide issue for the species most commonly used in canopy disturbance reconstructions, and second, the development of a simple model to account for the underrepresentation of release events, a variable that is critically important for studies focused on forest stand dynamics. For stand development studies in which the frequency of canopy disturbance events alone is needed, the model provides the information necessary without deviating from the standard canopy disturbance sampling practice in the eastern US of extracting and analyzing one increment core per tree. Additionally, the model can be retroactively applied to prior studies.

## Methods

### Release frequency, magnitude, and initiation lags

To examine release frequency, release magnitude, and release initiation discrepancies of paired tree-ring series from *Q. alba* individuals, we obtained *Q. alba* chronologies from the ITRDB. Tree-ring chronologies featured on the ITRDB have undergone intense scrutiny to ensure accurate crossdating and to minimize measurement error (Grissino-Mayer and Fritts 1997). We used the raw annual ring-width measurements from all *Q. alba* chronologies in the ITRDB that analyzed live standing trees, contained a minimum of 10 individuals, and had a minimum of two series per tree ($n$ = 44 chronologies; Table 1). The majority of these *Q. alba* individuals were selected by investigators for climate – tree growth analyses, and thus, we speculated that these samples represented large, overstory trees hypothesized to be of old age. In areas with relief, tree-core samples were collected perpendicular to slope (Cleaveland and Duvick 1992; LeBlanc and Terrell 2009). Portions of the same data set 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 with some clustering in the midwestern US and one disjunct stand (Fig. 1). From the 44 chronologies, 884 trees (representing 1768 paired tree-ring series) were suitable for our analysis. For each tree, the series were truncated so that only years common to both were included.

To quantify radial growth release characteristics, we analyzed the raw ring-width measurements for percentage growth change using the 10-year running mean method (Nowacki and Abrams 1997). This technique was selected because 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, 2003). We analyzed changes in raw ring widths with respect to the running mean of the previous and subsequent 10 years. Release events were identified as periods in which raw ring width was ≥25% (minor) or ≥50% (major) of the 10-year preceding and superseding mean, sus-

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

| Collection name | Contributor | Coordinates | No. of trees analyzed | Chronology time span | Mean stand age (years) |
|---|---|---|---|---|---|
| Andrew Johnson Woods | E.R. Cook | 40.88°N, 81.75°W | 18 | 1626–1985 | 304 (±8 SE) |
| Babler State Park | D.N. Duvick | 38.60°N, 90.72°W | 27 | 1641–1980 | 216 (±11 SE) |
| Backbone State Park | R. Landers; D.N. Duvick | 42.62°N, 91.57°W | 11 | 1735–1977 | 151 (±11 SE) |
| Blackfork Mountain | D.W. Stahle | 34.72°N, 94.45°W | 13 | 1650–1980 | 218 (±10 SE) |
| Buffalo Beats North Clay Lens Prairie Soil | J.R. McClenahen; D.B. Houston | 39.45°N, 82.15°W | 28 | 1681–1995 | 106 (±10 SE) |
| Buffalo Beats North Ridge-top Forest Site | J.R. McClenahen; D.B. Houston | 39.45°N, 82.15°W | 21 | 1856–1995 | 119 (±4 SE) |
| Cameron Woods | D.N. Duvick | 41.65°N, 90.73°W | 12 | 1845–1980 | 118 (±5 SE) |
| Cass Lake B | L.J. Graumlich | 47.27°N, 94.38°W | 17 | 1785–1988 | 147 (±7 SE) |
| Cranbrook Institute | E.R. Cook | 42.67°N, 83.42°W | 11 | 1581–1983 | 272 (±23 SE) |
| Current River Natural Area | D.N. Duvick | 37.27°N, 91.27°W | 17 | 1636–1981 | 226 (±8 SE) |
| Current River Natural Area Recollection[a] | R.P. Guyette | 37.27°N, 91.27°W | 9 | 1588–1992 | 247 (±7 SE) |
| Dolliver Memorial State Park | D.N. Duvick | 42.38°N, 94.08°W | 14 | 1685–1981 | 197 (±20 SE) |
| Duvick Backwoods | D.N. Duvick | 41.68°N, 93.68°W | 16 | 1654–1980 | 111 (±7 SE) |
| Fern Clyffe State Park | D.N. Duvick | 37.53°N, 88.98°W | 22 | 1655–1981 | 187 (±24 SE) |
| Fox Ridge State Park | D.N. Duvick | 39.42°N, 88.17°W | 18 | 1674–1980 | 210 (±13 SE) |
| Geode State Park | D.N. Duvick | 40.83°N, 91.37°W | 16 | 1724–1984 | 213 (±12 SE) |
| Giant City State Park | D.N. Duvick | 37.60°N, 89.20°W | 25 | 1652–1981 | 244 (±7 SE) |
| Greasy Creek | D.N. Duvick | 37.72°N, 90.20°W | 15 | 1777–1982 | 144 (±8 SE) |
| Hampton Hills | A.C. Barefoot | 35.82°N, 78.68°W | 16 | 1770–1992 | 133 (±12 SE) |
| Hutchenson Forest | E.R. Cook | 40.50°N, 74.57°W | 16 | 1674–1982 | 226 (±8 SE) |
| Jack's Fork | D.N. Duvick | 37.12°N, 91.50°W | 30 | 1776–1981 | 123 (±8 SE) |
| Kankakee River State Park | D.N. Duvick | 41.22°N, 88.00°W | 15 | 1686–1980 | 197 (±17 SE) |
| Lacey-Keosauqua State Park | D.N. Duvick | 40.72°N, 91.97°W | 12 | 1715–1981 | 190 (±15 SE) |
| Lake Anquabi State Park | D.N. Duvick | 41.28°N, 93.58°W | 26 | 1574–1980 | 195 (±16 SE) |
| Ledges State Park | D.N. Duvick | 42.00°N, 93.88°W | 61 | 1663–1981 | 182 (±10 SE) |
| Lilley Cornett Tract | E.R. Cook | 37.08°N, 83.00°W | 15 | 1660–1982 | 276 (±7 SE) |
| Lincoln's New Salem State Park | D.N. Duvick | 39.97°N, 89.85°W | 29 | 1671–1979 | 196 (±11 SE) |

**Table 1** (*concluded*).

| Collection name | Contributor | Coordinates | No. of trees analyzed | Chronology time span | Mean stand age (years) |
|---|---|---|---|---|---|
| Linville Gorge | E.R. Cook | 35.88°N, 81.93°W | 17 | 1617–1977 | 256 (±13 SE) |
| Lower Rock Creek | D.N. Duvick | 37.50°N, 90.50°W | 17 | 1728–1982 | 197 (±9 SE) |
| Mammoth Cave Recollect | E.R. Cook | 37.18°N, 86.10°W | 14 | 1649–1985 | 244 (±7 SE) |
| Merritt Forest State Preserve | D.N. Duvick | 42.70°N, 91.13°W | 16 | 1711–1980 | 182 (±12 SE) |
| Nine Eagles State Park | D.N. Duvick | 40.62°N, 93.75°W | 13 | 1672–1982 | 137 (±17 SE) |
| Norris Dam State Park | D.N. Duvick | 36.22°N, 84.08°W | 32 | 1633–1980 | 247 (±9 SE) |
| Pammel State Park | D.N. Duvick | 41.28°N, 94.07°W | 52 | 1635–1981 | 194 (±10 SE) |
| Piney Creek Pocket Wilderness | D.N. Duvick | 35.70°N, 84.88°W | 15 | 1651–1982 | 159 (±21 SE) |
| Pulaski Woods | E.R. Cook | 41.05°N, 86.70°W | 11 | 1692–1985 | 224 (±15 SE) |
| Roaring River | D.W. Stahle | 36.60°N, 93.82°W | 14 | 1724–1982 | 198 (±7 SE) |
| Saylorville Dam | D.N. Duvick | 41.72°N, 93.70°W | 34 | 1654–1981 | 158 (±13 SE) |
| Sipsey Wilderness | E.R. Cook | 34.33°N, 87.45°W | 14 | 1679–1985 | 252 (±9 SE) |
| Starved Rock State Park | D.N. Duvick | 41.30°N, 89.00°W | 42 | 1633–1980 | 244 (±5 SE) |
| Wegener Woods | D.W. Stahle | 38.65°N, 91.50°W | 12 | 1662–1982 | 229 (±11 SE) |
| White Pine Hollow State Preserve | D.N. Duvick | 42.63°N, 91.13°W | 15 | 1631–1973 | 225 (±12 SE) |
| Woodman Hollow State Preserve | D.N. Duvick | 42.42°N, 94.10°W | 24 | 1695–1979 | 120 (±8 SE) |
| Yellow River State Forest | D.N. Duvick | 43.18°N, 91.25°W | 12 | 1651–1980 | 212 (±19 SE) |

[a]Only the series not analyzed in the Current River Natural Area collection were analyzed for the Current River Natural Area Recollection chronology.



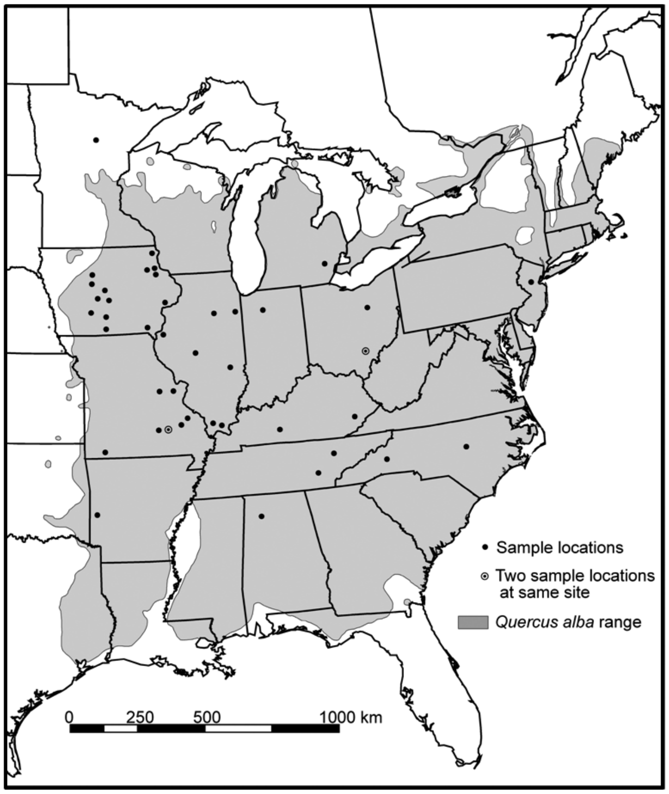
tained for a minimum of five years (Nowacki and Abrams 1997). The first and last 10 years common to each series were excluded from our analysis because this method requires a 10-year window prior and subsequent to each individual growth ring analyzed. We used a five-year threshold to identify releases recorded in both of the paired series as resulting from the same disturbance event (i.e., intratree releases exhibiting an initiation lag time of five years or less were considered simultaneous).

Intratree radial growth release discrepancies were compared at the series, tree, stand, and data-set level. We enumerated the minor and major growth release events in all series and noted the duration of each release. For each tree in the data set, we compared release initiation dates and durations to quantify growth release discrepancies between the two corresponding series. We tabulated the minimum and maximum release frequency value that could be documented based on the analysis of a single tree-ring series per individual. We then totaled these values for each stand and for the 884 trees across all sites included in our data set.

## Release frequency factor

To create a model that predicts the maximum (i.e., actual) frequency of release events in *Q. alba* stands in eastern North America, we used the total minimum and maximum release frequency values, regardless of magnitude, from all trees in our data set to calculate the mean number of detected growth releases. We did not separate the frequency values by magnitude because the small number of major releases precluded a robust model for releases of this category. In addition, we deemed the total number of releases as being more important to quantify than the number of releases by magnitude because this value encompasses all canopy disturbance events. If only a single growth series was analyzed from all sampled trees, it is statistically improbable that the minimum or maximum number of release events would be detected, but rather an average of the two. Thus, we determined the mean release frequency (i.e., the number of releases likely to be detected by analyzing only one increment core per tree) by averaging the total minimum and maximum release frequency values. We then used the following equation to develop a multiplica-

**Fig. 1.** Map showing the range of *Quercus alba* and the locations of the 44 tree-ring collections from the ITRDB used in our radial growth release analysis.




tive release frequency factor (RFF) that predicts the maximum number of release events given the mean release frequency:

$$[1] \qquad \mathrm{RFF} = \frac{\text{maximum release frequency}}{\text{mean release frequency}}$$

The RFF can be multiplied by the number of growth release events documented by analysis of a single radial growth series per *Q. alba* tree to predict the total number of release events that would be detected by analyzing an additional sample per individual. As we developed the RFF using only *Q. alba* tree-ring chronologies, the RFF is only verifiably accurate for canopy disturbance reconstructions that use *Q. alba*. We contend that the large sample size used in this study ensures the accuracy of the RFF. Therefore, multiplying the number of releases represented in the tree-ring series by the RFF will produce a more accurate release frequency by accounting for the ring-width variability exhibited across radii of the tree bole.

## Results

### Release frequency, magnitude, and initiation lags

From the 1768 tree-ring series analyzed, we documented 280 radial growth release events of which 271 (97%) were classified as minor releases and nine (3%) were classified as major releases. Of the 884 trees analyzed, 216 (24%) exhibited dendroecological releases in at least one of the tree-ring series. At the stand level, only two tree-ring chronologies did not contain individuals that exhibited radial growth releases (Buffalo Beats North Clay Lens Prairie Soil chronology and Roaring River chronology). From the 884 trees analyzed, the minimum number of releases that could be detected by analysis of a single tree-ring series per individual was 39, and the maximum number of release events that could be detected was 241. The maximum detectable value was 518% greater than the minimum possible value.

At the tree level, only 31 (14%) of the 216 individuals exhibiting release events showed the same release frequency for both the minimum and maximum possible values (Table 2). Of these 31 trees, 13 (34%) contained simultaneous releases that corresponded to the same canopy disturbance event. Thus, only 13 (6%) of the 216 trees that exhibited growth release events documented the same disturbance history in both series. The greatest range between the minimum and maximum number of releases for a single individual was two release events (documented in 11 trees). At the stand level, all chronologies that contained at least one tree with a radial growth release ($n$ = 42) exhibited a discrepant number of release events between the minimum and maximum possible frequency values (Table 3). The greatest range between the minimum and maximum number of releases that could have been documented from a collection was 18 minor release events (Pammel State Park chronology) and one major release event (documented in five chronologies). However, these were the most extreme situations, and discrepancies of a lesser extent were more common (Fig. 2).

At the data-set level, 237 (87%) of the 271 minor release events occurred in only one of the paired series and 30 (11%) occurred simultaneously in both series (i.e., releases occurred in both of the paired series with initiation dates separated by five years or less). Of the nine major release events, one (11%) occurred in only one of the paired series and four (44%) occurred simultaneously in both series. In four instances, a minor release event occurred in tandem with a major release event in the corresponding series (this accounts for 2% of the minor release record and 44% of the major release record).

The mean release duration for minor events was 5.39 years (±0.04 SE). The longest sustained minor release was seven years and was observed in 21 tree-ring series. The mean release duration for major episodes was 5.44 years (±0.18 SE). The maximum sustained release duration was six years and was exhibited in four tree-ring series. The mean release duration for all events regardless of magnitude classification was 5.39 years (±0.04 SE).

Of the 15 synchronous minor release events, two episodes exhibited lag times of one year and one episode exhibited a lag time of two years. One of the two simultaneous major release events exhibited a lag time of one year. Of the four synchronous release events that registered as both minor and major magnitudes in corresponding series, two exhibited lag times of one year. In total, six (30%) of the 20 synchronous release events exhibited release initiation year discrepancies. Using the five-year threshold to distinguish releases as resulting from separate disturbance events, the maximum release initiation discrepancy was two years (documented in a single tree from the Cameron Woods chronology), with all others being a single year. The minimum lag time that exceeded our threshold was 18 years.

**Table 2.** Results from the tree and data-set level analysis of release frequency and release disparity between two tree-ring series from the same individual.

| Results | Total | Minor | Major |
|---|---|---|---|
| Trees | 884 | | |
| Trees with releases | 216 | | |
| Trees with same disturbance history in both series | 13 | | |
| Releases | 280 | 271 | 9 |
| Releases recorded in only one series | 238 | 237 | 1 |
| Releases recorded simultaneously in both series[a] | 42 | 30 | 4 |
| Minimum release frequency detected from analysis of a single tree-ring series | 39 | 37 | 2 |
| Maximum release frequency detected from analysis of a single tree-ring series | 241 | 234 | 7 |

[a]Four release events (comprising eight total releases) occurred simultaneously in both series but registered as differing magnitudes between the series. This accounts for the remainder of the simultaneous release events.

### Release frequency factor

For releases classified as minor growth change events, the minimum and maximum number of releases at the data-set level that could be detected by analysis of a single series per tree were 37 and 234, respectively. For radial growth releases classified as major events, the minimum and maximum number of releases that could be detected by analysis of a single series per tree were two and seven, respectively. In total, we found that a minimum of 39 release events and a maximum of 241 could be detected from the 884 trees in the data set. Thus, we hypothesized that a researcher using a random sample of one growth series per tree would detect 140 radial growth releases (i.e., the mean of the two extremes). Therefore, by using the RFF equation, we calculated that a multiplicative factor of 1.72 could be used to discover the maximum number of growth release events that would have been detected if two growth series per tree were analyzed.

We tested the efficacy of the RFF by applying the 1.72 multiplicative factor to the mean release frequency of each stand in our data set. The RFF accurately predicted the maximum release frequency for 26 (62%) of the 42 stands exhibiting release events. For stands in which the RFF did not accurately predict the maximum release frequency, the mean difference between the RFF predicted value and the actual frequency was 1.09 releases. Therefore, for instances in which the RFF was incorrect, the predicted value error was approximately one release event. As such, we assert that multiplying the number of release events detected from analysis of a single radial growth series per tree by the RFF of 1.72 will allow researchers to ascertain a more accurate number of canopy disturbance events that have occurred during stand development.

## Discussion

### Release frequency, magnitude, and initiation lags

The frequency of minor and major radial growth release events for a stand provides information necessary for the reconstruction of canopy disturbance events at fine and coarse scales (Lorimer 1985; Rentch et al. 2002). The nonconcentric nature of annual growth rings complicates the disturbance reconstruction process as separate radii produce different ring widths (Fritts 2001; Copenheaver et al. 2009). As such, the actual disturbance history of a stand can be difficult or impossible to ascertain through analysis of annual rings from only one increment core per tree, a complication made apparent by the fact that 95% of the stands that we analyzed showed a discrepant release frequency (the remaining 5% ($n$ = two chronologies) had the same release frequency as both records exhibited zero growth releases).

The complications in disturbance reconstruction resulting from the nonconcentricity of radial growth rings are further evidenced by the quantity of releases that occurred in only one of the paired tree-ring series. In this study, 87% of minor release events and 11% of major release events occurred in only one of the series pairs. Therefore, disturbance reconstructions could potentially grossly underestimate the frequency of canopy disturbance events. For example, we documented a discrepancy of 18 minor release events from 53 individuals spanning 347 years from the Pammel State Park chronology. This discrepancy, and others of lesser extent throughout the data set, reflects both the inconsistency inherent in radial growth-ring widths and the influence of release magnitude on this variability. As only 11% of minor releases, yet 44% of major releases, occurred simultaneously in both tree-ring series, we infer that releases of greater magnitude increase the probability of co-occurrence in both of the paired series. However, this pattern may be the result of sample size or the release detection criteria that we used.

The individuals that comprised our data set were initially selected for dendroclimatological studies; therefore, we speculated that the trees were sampled because they represented large, overstory trees hypothesized to be of old age. It is possible that the climate signal in these series is stronger than the competition signal. Furthermore, though old trees contain relatively long forest history records, they are less likely to respond to canopy disturbance events (Hilt 1979; Fritts 2001). Thus, radial growth releases may be underrepresented in the latter portion of the tree-ring record (Nowacki and Abrams 1997). Additionally, disturbance mechanisms and canopy gap characteristics differ throughout the range of *Q. alba*. We acknowledge that the clustering of sample locations in the midwestern US may introduce a disproportionate amount of the disturbance agents common to this region into the data set.

The nonconcentric nature of tree-ring formation and the intratree release frequency disparity may be the result of several processes, working independently or collaboratively. The extent of an individual's radial growth is sensitive to the growing space surrounding the bole (Oliver and Larson

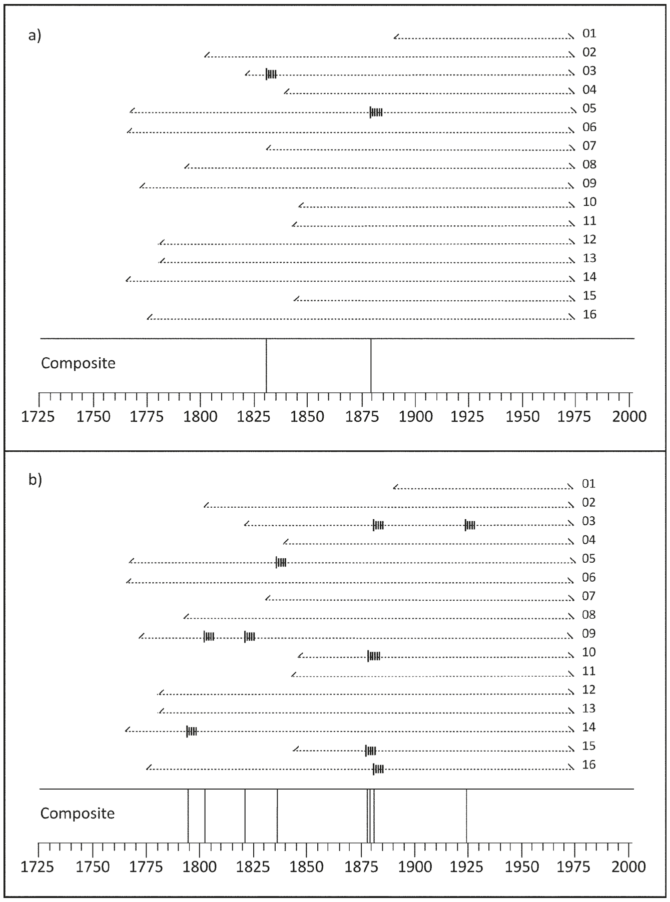
**Table 3.** Minimum and maximum radial growth release frequency values for minor and major events from the 44 ITRDB *Quercus alba* collections. The minimum value represents the lowest frequency of releases and the maximum value represents the highest frequency of releases that could have been detected from analyzing only one tree-ring series per tree.

| | Minor release frequency | | Major release frequency | |
|---|---|---|---|---|
| Site name | Minimum | Maximum | Minimum | Maximum |
| Andrew Johnson Woods | 0 | 5 | 0 | 0 |
| Babler State Park | 1 | 8 | 0 | 0 |
| Backbone State Park | 0 | 1 | 0 | 0 |
| Blackfork Mountain | 1 | 7 | 0 | 0 |
| Buffalo Beats North Clay Lens Prairie soil | 0 | 0 | 0 | 0 |
| Buffalo Beats North Ridgetop Forest site | 1 | 4 | 0 | 0 |
| Cameron Woods | 1 | 7 | 0 | 0 |
| Cass Lake B | 2 | 10 | 0 | 0 |
| Cranbrook Institute | 0 | 3 | 0 | 0 |
| Current River Natural Area | 1 | 4 | 1 | 1 |
| Current River Natural Area Recollection[a] | 0 | 2 | 0 | 0 |
| Dolliver Memorial State Park | 1 | 4 | 0 | 1 |
| Duvick Backwoods | 3 | 5 | 0 | 0 |
| Fern Clyffe State Park | 0 | 4 | 1 | 1 |
| Fox Ridge State Park | 0 | 4 | 0 | 0 |
| Geode State Park | 2 | 9 | 0 | 0 |
| Giant City State Park | 1 | 9 | 0 | 1 |
| Greasy Creek | 0 | 4 | 0 | 0 |
| Hampton Hills | 1 | 5 | 0 | 0 |
| Hutchenson Forest | 0 | 1 | 0 | 0 |
| Jack's Fork | 1 | 8 | 0 | 0 |
| Kankakee River State Park | 0 | 5 | 0 | 1 |
| Lacey-Keosauqua State Park | 1 | 3 | 0 | 1 |
| Lake Anquabi State Park | 3 | 9 | 0 | 0 |
| Ledges State Park | 6 | 19 | 0 | 0 |
| Lilley Cornett Tract | 0 | 3 | 0 | 0 |
| Lincoln's New Salem State Park | 1 | 3 | 0 | 0 |
| Linville Gorge | 0 | 3 | 0 | 0 |
| Lower Rock Creek | 0 | 3 | 0 | 0 |
| Mammoth Cave Recollect | 0 | 4 | 0 | 0 |
| Merritt Forest State Preserve | 2 | 6 | 0 | 0 |
| Nine Eagles State Park | 0 | 1 | 0 | 0 |
| Norris Dam State Park | 0 | 8 | 0 | 0 |
| Pammel State Park | 0 | 18 | 0 | 0 |
| Piney Creek Pocket Wilderness | 0 | 3 | 0 | 0 |
| Pulaski Woods | 0 | 1 | 0 | 0 |
| Roaring River | 0 | 0 | 0 | 0 |
| Saylorville Dam | 2 | 6 | 0 | 0 |
| Sipsey Wilderness | 1 | 7 | 0 | 0 |
| Starved Rock State Park | 3 | 14 | 0 | 1 |
| Wegener Woods | 0 | 4 | 0 | 0 |
| White Pine Hollow State Preserve | 1 | 3 | 0 | 0 |
| Woodman Hollow State Preserve | 0 | 2 | 0 | 0 |
| Yellow River State Forest | 0 | 5 | 0 | 0 |

[a]Only the series not analyzed in the Current River Natural Area collection were analyzed for the Current River Natural Area Recollection chronology.

1996). Neighboring trees benefit from increased growing space on one or all aspects following the disturbance-initiated removal of a canopy individual. This increase in growing space also provides the disturbance-adjacent individuals with decreased competition and increased insolation on the aspect(s) adjacent to the canopy void. As these growth-increasing factors may only benefit one aspect of an individual, secondary growth may only increase on one aspect. Therefore, growth release events do not have an equal probability of being recorded on all radii of an individual. Additionally, trees surrounding canopy gaps may exhibit canopy displacement in which individual canopies migrate toward gap center and the trees are no longer vertically oriented (Muth and Bazzaz 2002). These perimeter trees may

**Fig. 2.** Detected radial growth release events using the 10-year running mean method for the Geode State Park ITRDB collection. The collection contained two tree-ring series for each of the 16 *Quercus alba* individuals and was analyzed to elucidate (*a*) the minimum release frequency and (*b*) the maximum release frequency that could be detected based on analysis of a single series per tree. Each horizontal line represents the record for one individual tree-ring series. Long vertical bars indicate release events and short vertical bars indicate release durations. A composite of release events is shown across the bottom of both graphs. For this collection, the number of release events likely to be documented by an analysis of one tree-ring series per individual was five release events (i.e., the approximate mean). Therefore, the multiplicative release frequency factor of 1.72 correctly predicts an actual frequency value of nine release events.




increase radial growth on one aspect to improve mechanical stability (Muth and Bazzaz 2002). Topographic relief also influences the concentricity of radial growth in the form of reaction wood (Fritts 2001).

The results also provided information on intratree discrepant release initiation signals. We found that when simultaneous releases did occur in both series, the release initiation was temporally synchronous in 71% of the growth release episodes. For the releases that exhibited a lag time between the two series, the most frequent lag time was one year and the maximum lag time was two years (observed in a single individual). We suggest that release initiation dates for *Q. alba* need not be adjusted when analyzing a single growth series per tree as the releases likely indicate the exact calendar year of physiological response and have a maximum error of two years.

### Release frequency factor

The discrepancies between two tree-ring series from the same individual demonstrated that the disturbance history derived from only one series was not an accurate reflection of canopy disturbance and subsequent radial growth response. The difference between the minimum and maximum frequency of releases at the tree, stand, and data-set level indicated that the analysis of only a single tree-ring series per individual does not produce the accurate frequency of canopy disturbance events. As a result of this inaccuracy, we recommend that researchers extract and analyze a minimum of two increment cores per tree for studies in which the exact calendar years of disturbance events are required to accomplish research objectives. Alternatively, for stand development studies only requiring the frequency of canopy disturbances, the RFF alleviates the intratree release discrepancy that we found to be pervasive throughout the *Q. alba* range. We therefore suggest that researchers interested in discerning an accurate number of canopy disturbances during stand development in *Q. alba* forests can continue to extract one increment core per tree as long as the RFF of 1.72 is used to account for the underrepresentation of radial growth releases. Canopy disturbance frequency during stand development is an important driver of species composition and stand structure; thus, this value is important in forest development studies. However, study-specific objectives should dictate sampling and analytical procedures. We stress that if researchers need spatially and temporally explicit canopy disturbance characteristics, they should extract and analyze at least two increment cores per tree.

We contend that the large sample size used to develop the RFF ensures that the proposed model will effectively predict the actual number of releases for a given stand and therefore greatly reduce the inaccuracy that we found to be inherent in analyzing only one series per tree. We propose that the research presented here be used as a model to conduct similar studies focused on other species, particularly those often used in disturbance history reconstructions. Our research demonstrates that the analysis of a single increment core per tree results in an underrepresentation of growth releases and canopy disturbance events. We developed the RFF to alleviate this underrepresentation. For stand development studies in which the frequency of canopy disturbance events alone is necessary, the RFF provides the required information for disturbance reconstruction without sampling an additional increment core per tree.

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