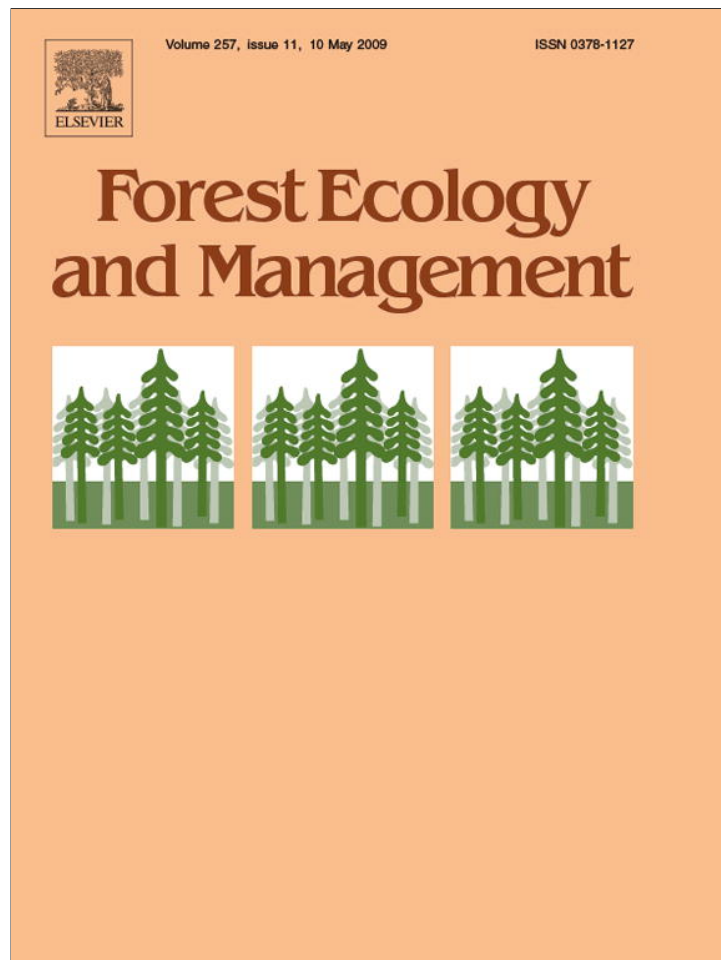


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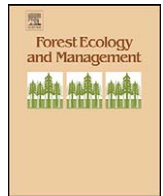
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Identifying dendroecological growth releases in American beech, jack pine, and white oak: Within-tree sampling strategy

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ABSTRACT

The objective of this project was to identify the timing of growth release events detected from tree ring widths and compare whether two cores taken from the same tree reconstructed the same disturbance history. This research question is important because current dendroecological reconstructions of canopy disturbance rely on sampling one core per tree; however, the variation of releases from different cores from the same tree has never been evaluated. We sampled two increment cores from 20 jack pine, 17 white oak, and 19 American beech and identified release events with two commonly employed methods: radial growth averaging technique and boundary line criteria. In jack pine, 85% of the paired cores showed identical releases with the radial growth averaging technique, but 15% of the paired cores varied in reconstructed growth releases. In the jack pine, no releases were identified with the boundary line criteria for any of the paired cores. In the white oak, 65% had identical releases identified with the radial growth averaging technique and 35% of the pairs showed differences. The boundary line criteria for white oak had agreement between releases for 76% of the pairs and different release histories for 24% of the pairs. In the American beech, we were only able to use the radial growth averaging technique and this method showed identical release timing for 79% of the paired cores and differences in 21% of the paired cores. This level of within-tree growth variation is unlikely to influence identification of stand-wide disturbances; however, for reconstructions of small-scale disturbances it is likely to under-represent disturbance events. Therefore, for small-scale disturbance reconstructions, we recommend dendroecologists consider sampling two cores per tree instead of the standard sample of one core per tree.

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1. Introduction

Dendroecologists have developed a number of techniques for identifying disturbance-related growth releases in the tree ring record. The goal of each of these techniques is to distinguish disturbance-related releases from climate-induced increases in growth. Early techniques hinged on the assumption that in comparison to climate-induced signals, releases due to disturbance tended to be more vigorous and sustained as the tree occupied newly formed canopy gaps (Lorimer, 1985; Lorimer and Frelich, 1989; Nowacki and Abrams, 1997). Among the most widely applied approaches is radial growth averaging, in which releases are identified as sustained pulses in relative growth rate; this technique has been employed in a number of forest ecosystems to reconstruct historical gap dynamics, canopy recruitment rates, and disturbance frequency (Piovesan et al.,

2005; Zhang et al., 2007; Gutiérrez et al., 2008; Pederson et al., 2008). The specifics of these criteria vary widely according to species and study objective with for example, the most stringent thresholds established to detect severe disturbances. The Nowacki and Abrams (1997) criteria for overstory oak have been among the most thoroughly investigated, and validation studies have shown that peak radial growth response corresponds to the disturbance date, and that the magnitude of release response, in terms of percent-growth change, corresponds to the degree of crown release (Rentch et al., 2002, 2003). An extension of the running mean techniques, the boundary line release criteria proposed by Black and Abrams (2003) incorporates the effects of prior growth history, in an attempt to better standardize releases across various age, crown, and size classes and potentially species (Splechtna et al., 2005; Nagel et al., 2007; Bhuta et al., 2009). In the recently developed “absolute increase” method, the release threshold for a species is set in terms of absolute growth rate, which indirectly incorporates the effects of prior growth rate and species on release magnitude (Fraver and White, 2005). Alternatively, the “divergence” technique attempts to separate growth patterns unique to

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individual from those of the population in order to identify the formation of fine-scale canopy gaps (Thompson et al., 2007). In another novel methodology, Druckenbrod (2005) employed autoregressive modeling as a mean to identify steps and pulses in growth as evidence of releases as well as suppressions.

The recent focus on methods for identifying disturbance-related release events in the tree ring record led us to question how important is sample collection in disturbance reconstruction? Unlike many tree ring based climate reconstructions, most disturbance reconstructions depend upon a single sample per tree (Abrams et al., 1998; Orwig et al., 2001; Rozas, 2004; Busby et al., 2008a; Kincaid and Parker, 2008; Pederson et al., 2008). This is an important difference because the underlying assumption is that a single core sampled from any aspect on the stem will accurately reflect the tree-level, and ultimately stand-level, disturbance history (Fritts, 1991). However, this assumption seems to be challenged by research which shows that growth occurs at different rates and times around the circumference of a tree stem (Ogata et al., 2002; Gričar and Čufar, 2008) and is considered when determining the number of increment cores to extract to accurately calculate basal area increment (Biging and Wensel, 1988; Gregoire et al., 1990). Thus, our research goal was to determine whether two radii sampled from different sides of a tree will record the same disturbance history. If the answer is no, then all of the fine-tuning of release identification techniques at the analysis stage is for naught until researchers can account for within-tree growth variation. In this study, we address this issue in three diverse species, jack pine (*Pinus banksiana*), white oak (*Quercus alba*), and American beech (*Fagus grandifolia*), which includes conifer and deciduous species as well as a range of understory tolerance levels. All three of these species have been employed in reconstructing disturbance histories and therefore had a proven record for responsiveness to disturbance events in past research (Abrams and Copenheaver, 1999; Copenheaver and Abrams, 2003; Druckenbrod, 2005; Fraver and White, 2005).

2. Materials and methods

2.1. Study sites

American beech was sampled from the Zoar State Forest in King William County, Virginia (Table 1). This 153 ha forest is managed by the Virginia Department of Forestry and has been in their ownership since 1987. The total annual precipitation is 1100 mm and the average temperature in winter is 3 °C and the average temperature in summer is 25 °C. The stand that was sampled was on the river terrace overlooking the Mattaponi River and was dominated by *Carya*, *Fagus*, and *Quercus* and was known to have been selectively harvested in the early 1900s (Copenheaver et al., 2007).

Jack pine was sampled from land managed by the Michigan Department of Natural Resources in Roscommon County, Michigan (Table 1). The total annual precipitation is 810 mm and the average winter temperature is 6 °C and the average summer temperature is 18 °C. The stand was east of Robinson Lake and consisted of naturally regenerated jackpine with an understory of bearberry (*Arctostaphylos uvaursi*) and blueberry (*Vaccinium angustifolium*). There was a small windthrown area in the northeastern section of the stand and trees were not sampled from this section.

White oak was sampled from Buffalo Mountain Natural Area Preserve in Floyd County, Virginia (Table 1). This 200 ha forest is managed by the Virginia Natural Heritage Program. The total annual precipitation is 1046 mm and the average winter temperature is 1.4 °C and the average summer temperature is 20.2 °C. The stand was on the top of Buffalo Mountain (1190 masl) and a mixture of closed-canopy *Quercus*–*Carya* forest interspersed with open grass-dominated glade communities (Copenheaver et al., 2004).

2.2. Field and laboratory work

At each study site, a total of 20 trees were cored twice at stump height (0.5 m). For the beech and the white pine, samples were collected at 180° from each other and for the jack pine, samples were collected at 90° from each other. Trees were selected because of their dominant or co-dominant canopy positions. After collection, all cores were air dried, glued onto wooden core holders, and sanded to allow examination of cellular structure under a dissecting microscope. Cores were excluded from further analysis if they had reaction wood, rot, or branch scars that obscured their annual growth rings. The cores from each site, were cross-dated using narrow years as signature years (Yamaguchi, 1991) and special care was given to the jack pine because of their propensity for false and light ring formation (Volney and Mallett, 1992; Copenheaver et al., 2006). Following visual cross-dating, ring widths of all cores were measured using a TA Tree Ring Measurement System (Velmex Inc., Bloomfield, NY). The cross-dating of the tree ring measurements was then verified with the dating verification program, COFECHA, available through the Dendrochronology Program Library. Any flagged cores were re-examined and dating was corrected. In the white oak, there were three trees for which at least one of the cores was not able to be used because of large sections of rot which prevented accurate dating and measuring; therefore, all subsequent analysis was conducted on 17 pairs of white oaks. In the American beech there was one core with a large branch scar and therefore all subsequent analysis for that species was conducted on 19 pairs of cores. The analysis for the jack pine had 20 pairs of cores.

2.3. Data analysis

To compare the within-tree variation in release events, we opted to use the two most commonly applied release criteria: the radial growth averaging technique (Lorimer and Frelich, 1989; Nowacki and Abrams, 1997) and the boundary line technique (Black and Abrams, 2003, 2004) and compare timing of releases identified within a tree for both techniques. The objective in comparing the two cores from a single tree was to assess whether the number and timing of releases was the same between the two cores; however, because the timing of releases can vary slightly due to individual growth patterns we allowed the timing of a release to count as “the same” if the two release dates were within 5 years of each other. Early work on release criteria focused on establishing the transition date for when a tree moved from an understory to an overstory position, however, subsequent research has used a modification of this approach to identify growth releases in overstory trees. Therefore, we employed a modified

Table 1
Environmental characteristics of the three sites where tree cores were sampled.

Species cored	Soil	Topographic position	Elevation (masl)	Lat./long.
American beech	Loamy sand	River terrace	8	34°47'N, 77°6'W
Jack pine	Sand	Glacial outwash plain	350	44°13'N, 84°46'W
White oak	Loam	Mountain top	1190	36°45'N, 80°28'W

Table 2

Tree ring data sources used in the development of the prior-growth boundary lines for jack pine. International tree ring data bank is abbreviated as ITRDB.

Site	Source	Contributor
13B	Copenheaver et al. (2006)	Copenheaver
Bolen Lake	ITRDB	Beriault, Sauchyn, Stroich
Fleming Island, Cree Lake	ITRDB	Beriault, Sauchyn, Stroich
Gunisao Lake	ITRDB	Schweingruber
Ithingo	ITRDB	Beriault, Sauchyn, Stroich
M1	Copenheaver et al. (2006)	Copenheaver
M2	Copenheaver et al. (2006)	Copenheaver
MacIntyre Lake	ITRDB	Beriault, Sauchyn, Stroich
McGugan Island, Highrock Lake	ITRDB	Beriault, Sauchyn, Stroich
Nelson House	ITRDB	Campbell
Prince Albert	ITRDB	Campbell
Sanford Island, Reindeer Lake	ITRDB	Beriault, Sauchyn, Stroich
Wood Buffalo National Park Site NL	ITRDB	Larsen, Moser
Wood Buffalo National Park Site PR	ITRDB	Larsen, Moser

Nowacki and Abrams (1997) radial growth averaging technique where 10-year running averages of tree ring width were calculated and percent-growth change of these running averages were assessed for release events. A major release was defined as a 50% growth increase sustained for a minimum of 10 years and a moderate growth release was defined as a 25% growth increase sustained for a minimum of 10 years. In the analysis of whether a pair of cores carried the same release signal, there was no distinction made between a major and moderate release.

The boundary line release criteria had already been established for white oak (Black and Abrams, 2004), but had not been established for either American beech or jack pine. The establishment of the boundary line for a new species requires a substantial number of cross-dated chronologies to determine the limits of the growth response for an individual species. Unfortunately, data did not exist for American beech. However for jack pine, we were able to combine tree ring chronologies available on the International Tree Ring Database (ITRDB) with existing jack pine chronologies available in our laboratory archives (Copenheaver et al., 2006) to generate a sample size sufficient for calculating a new boundary line for this species (Table 2). From this set of tree ring widths, the same percent change formula employed for the radial growth averaging technique was calculated. Then, the prior growth (average radial growth from the previous 10 years) was also calculated for each tree ring series. The paired percent-growth change and prior growth were plotted and separated into 0.5 mm segments. The top 10 points within each segment were averaged and fitted to a curve which became the boundary line for identifying releases in that species.

3. Results

3.1. Jack pine

The 40 jack pine cores (2 cores per tree from 20 trees) had a series intercorrelation of 0.573 and a mean sensitivity of 0.321. The trees from this site were fairly young and the chronology spanned 74 years from 1923 to 1996. The radial growth averaging technique did not identify many release events in the jack pine. Trees sharing the same release response in both cores included: 15 jack pine (75%) that had no releases and 2 jack pine (10%) that had release events that occurred in both cores at the same time (Table 3). Three of the jack pine (15%) had release events that were only identified for one of the two cores. The trees that differed in their release identification between the two cores had similar growth patterns for most of the chronology length, but during the

Table 3

Variation in release identification within trees for jack pine sampled in northern lower Michigan, white oak sampled in southcentral Virginia, and American beech sampled in eastern Virginia.

Species and method	Same release signal in both cores	Different release signal between cores
Jack pine		
Radial growth averaging	85% (n = 17)	15% (n = 3)
Boundary line	100% (n = 20)	0% (n = 0)
White oak		
Radial growth averaging	65% (n = 11)	35% (n = 6)
Boundary line	76% (n = 13)	24% (n = 4)
American beech		
Radial growth averaging	79% (n = 15)	21% (n = 4)

period of release events differed in the timing and magnitude of growth (Fig. 1).

Using the jack pine growth information available on the ITRDB and archived by the authors, the first boundary line release equation was developed for jack pine:

$$y = 617.1 e^{1.69x}$$

where y represents growth change and x represents percent-growth change. However, this new boundary line identified no release events in any of the jack pine cores (Table 3).

3.2. White oak

The 34 white oak cores (2 cores per tree from 17 trees) had a series intercorrelation of 0.556 and a mean sensitivity of 0.255. Many of trees from this site were fairly old and the chronology spanned 313 years from 1690 to 2002. The radial growth averaging technique yielded 7 trees (41%) that had no release events identified in either core and 4 trees (24%) that had release events that occurred in both cores at the same time (Table 3). Thus, the remaining six white oaks (35%) had different release events identified for the two cores sampled from the same tree. In some instances, the cores had some common release events coupled with other events that only were identified for one of the two cores (Fig. 2). In other instances, one core would show no release events while the other core did. The boundary line release criteria

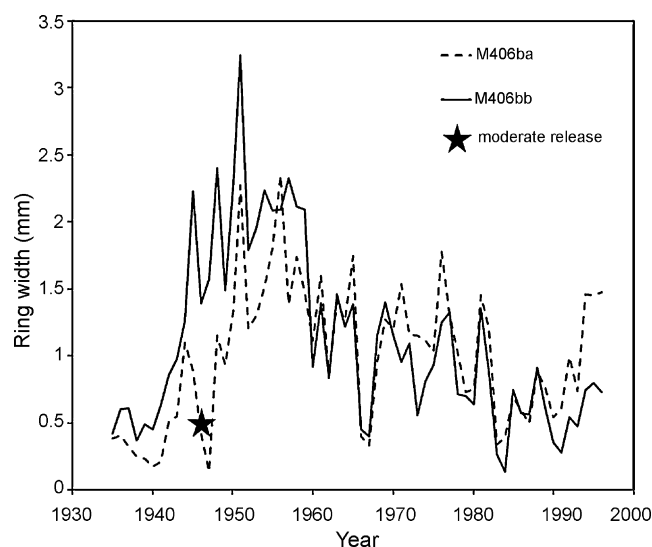


Fig. 1. Ring width chronologies of two cores taken from the same jack pine tree. The cores were taken at 90° from each other and one core had a release event identified by the radial growth averaging technique that was not identified in the other core.

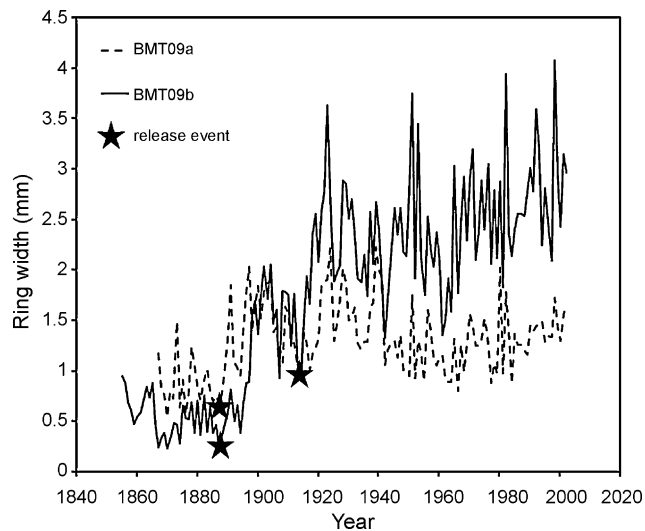


Fig. 2. Ring width chronologies of two cores taken from the same white oak tree. The one core showed two release events (1892 and 1896) based on the boundary line criteria for release detection, however, in the other core no release events were identified.

identified 10 white oaks (59%) that had no release events in either core and 3 trees (17%) that had release events with the same timing in both cores. Four white oaks had either one or two release events that were present in one core, but absent from the other (Fig. 3).

3.3. American beech

The 38 American beech cores (2 cores per tree from 19 trees) had a series intercorrelation of 0.667 and a mean sensitivity of 0.350. The length of the chronology was 147 years and spanned from 1858 to 2004. According to the radial growth averaging technique, the American beech experienced a very strong common release signal in the late 1930s that was identified as a major or moderate release in all of trees, although not all of the cores. Fifteen American beech (79%) had release events in the late 1930s that occurred in both cores. Four American beech (21%) had release events in the late 1930s that were identified in only one of the two

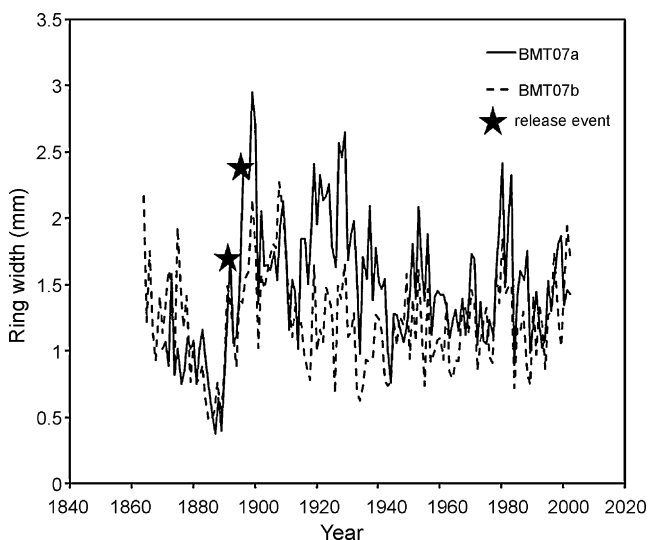


Fig. 3. Ring width chronologies of two cores taken from the same white oak tree. The cores were taken at 180° from each other and both cores identified a release event in 1886 using the radial growth averaging technique for release identification; however, only the radii shown with the solid line (BMT09b) showed a release in 1913.

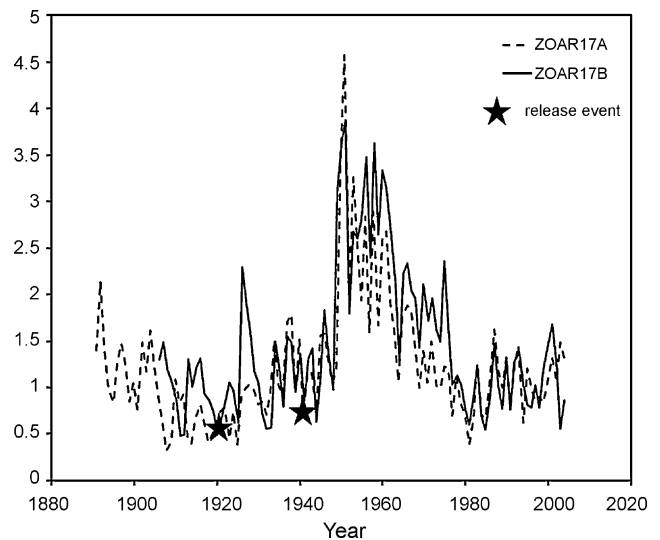


Fig. 4. Ring width chronologies of two cores taken from the same American beech tree. Using the radial growth averaging technique, core 17A experienced a moderate release event in 1920 and core 17B experienced a major release event in 1941.

cores. In some cases, one of the two cores had a release event that initiated prior to the 1930s and was sustained through the following decade. This continuous trajectory of increasing growth masked the second release event in the late 1930s, explaining some of the within-tree variability in release history (Fig. 4).

4. Discussion

Non-concentric growth of annual rings has been widely documented in the field of dendrochronology and consequently a number of techniques have been developed to estimate pith date from cores that fail to reach the center of the stem, e.g. estimating distance from the pith for core samples where the pith has been missed (Villalba and Veblen, 1997). However, the implications of non-concentric growth in dendroecological reconstructions of disturbance history had never been evaluated. The pith not being in the center of the tree is not a problem for release criteria per se; however, if the tree grows at different relative rates around the bole, this pattern of growth could complicate release identification methods. This research demonstrated that in jack pine, white oak, and American beech a majority of the stems carried the same release record regardless of where on the stem the increment core was sampled; but a proportion of the trees (15–35%) had within-tree differences that recorded a variation in the number and timing of release events (Table 3). The question for dendrochronologists is whether it is a scientific concern that for 15–35% of trees, selection of core location will alter the reconstructed disturbance history. The answer will likely vary depending upon the type of research question being addressed.

The current practice for identification of stand-wide disturbances events is to identify a 5–10-year period when at least 25% of the trees demonstrated a release event and this will be sufficient to identify a stand-wide disturbance. There is no expectation that a 100% of the sampled stems demonstrate a release (Nowacki and Abrams, 1997; Pederson et al., 2008). In most situations the 25% cutoff is a conservative value and a much higher percentage of trees demonstrate a release event during a stand-wide disturbance (Busby et al., 2008b; Hart et al., 2008). Therefore, the variation of within-tree release identification will be unlikely to substantially alter the identification of large-scale stand-wide disturbance events and in most situations it will be acceptable to continue

to sample only one core per tree in these types of disturbance reconstructions.

However, for research focused on reconstructing small-scale, individual, tree-level disturbance events, the within-tree growth differences could prove to be more important. For example, Gutiérrez et al. (2008) worked within a forest type where there has not been a stand-wide disturbance event in over 450 years, yet individual tree disturbances were relatively common. In this situation and ones similar to it, researchers may want to take a preliminary collection of cores (when the travel to the research site is not unreasonable) and conduct a preliminary within-tree variation assessment. If the variation is only 15% (our low end) then it is likely not worth the effort of taking two cores per tree; however, if the variation is up to 35% (our high end) it may be worth taking two cores per tree and conducting the release analysis on both cores and counting any releases that appear in either one of the two cores as a legitimate release experienced by that tree. As an example, in the white oak from Buffalo Mountain, when the one set of cores were compared with the other paired cores and release events were reconstructed, each set of cores had many common release events, but each set had one unique release event. These release events were recorded by only one tree and most likely represented fine-scale disturbance that would have been otherwise missed. There are two ways to interpret release events present in only one of two cores sampled from the same tree. The approach favored by the authors is that a release identified in only one core is still a valid growth release, but because of within-tree growth variation perhaps due to uneven canopy distribution, variation in light availability around the circumference of the stem, or damage that occurred on only one face of the stem (Makinen et al., 2007; Petriřan et al., 2009) the release was only expressed on one side of the stem. The alternative view is that a true release is only recorded when it is present in both cores. Interestingly there was a relationship between major and moderate releases and likelihood of a release to appear in both cores. All releases that were present in only a single core were moderate releases; thus confirming that these releases were more limited in scale.

Another area of dendrochronology where the results of this study should be considered is in examinations of the timing of intra-annual wood formation. These studies link how environmental signals trigger or suppress tree growth and have relevance for understanding how climate change may alter tree growth patterns (Čufar et al., 2008). There are three basic techniques for measuring rates of intra-annual wood formation: pinning, dendrometers, and repeated microcore sampling (Jalil et al., 1998; Lisi et al., 2008; Nöjd et al., 2008). It is in the latter technique where differences in relative non-concentric growth could alter results if the cores are collected from different sides of the stem. Currently, some studies collect microcores from a fairly narrow region on one side of the stem (Nöjd et al., 2008), but others use a spiraling technique where the core collection is spaced 2–3 cm apart with the intention of avoiding sample sites from earlier in the growing season (Thibeault-Martel et al., 2008). This sampling assumes that xylem formation occurs equally along all radii—an assumption that was also held to be true for release criteria and the dependence upon one sample per tree. However, the results from this study would indicate that for some species, radial growth occurs around the bole at different relative rates (Figs. 1–4). Thus, for dating the timing of intra-annual wood formation clustered sampling may actually be a better approach because it eliminates any variation that would be caused by location around the bole and for identification of release events.

Two limitations of this current study are that we only sampled individuals identified as being in dominant and co-dominant canopy classes and only collected increment cores from a single height along the stem. Annual radial growth in suppressed trees

can be more variable in allocation along the length of a stem (Niklasson, 2002), more prone to missing rings (Grundmann et al., 2008), and less likely to produce false rings during years when dominant and co-dominant trees from the same site form false rings (Copenheaver et al., 2006). Therefore, it should not be assumed that the findings from this study can be automatically transferred to trees in suppressed or intermediate canopy classes. Trees from these canopy classes will have to undergo a separate examination. Similarly, earlier studies indicated that sampling height is an equally important aspect of sampling strategy (Gutsell and Johnson, 2002; Peters et al., 2002) and the results from this study cannot explain whether identification of release events will vary with coring height.

The data analysis for this project resulted in an unintentional comparison of release criteria. This comparison should be viewed with an understanding that the sampling design for this study was not intended to be a thorough comparison of release criteria, à la Rubino and McCarthy (2004), nevertheless, our results indicated that the boundary line release criteria is a more conservative approach for identifying releases. This was especially notable in the jack pine where the radial growth averaging approach identified 15% of the sampled cores had release events, but the boundary line approach identified no cores with release events (Table 3).

5. Conclusion

Dendroecologists typically collect one core per tree with the assumption that a single core sampled from one location on the bole will represent growth releases and suppressions experienced throughout the tree. The results of this study show that for some species, this method of sampling is likely to result in missing some of the fine-scale growth responses to gap dynamics. Thus, depending upon the research objectives, dendroecologists should consider the option of taking two cores per tree to ensure that a reliable record of canopy dynamics can be reconstructed from the tree ring record.

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