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Causation of false ring formation in *Pinus banksiana*: A comparison of age, canopy class, climate and growth rate

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Abstract

False rings may provide a new source of proxy data for historical environmental conditions once the causes of their formation are understood. The objective of this research was to compare tree age, canopy class, temperature, precipitation, and growth rate as potential causal factors in false ring formation in *Pinus banksiana* Lambert. Our data consisted of 180 *P. banksiana* tree cores from three stands in northern lower Michigan. All cores were cross-dated and measured and false rings were identified by anatomical features within the wood. Frequency of false rings varied, with 48%, 78%, and 80% of the cores having at least one false ring in the three stands. Although there was within-stand synchrony in the timing of false ring formation no significant correlations existed between temperature and precipitation records and frequency of false ring production. Event years (periods of high false ring formation) were identified and superposed epoch analysis detected significantly higher growth rates preceded periods of false ring formation at one of the study sites. Canopy class had a significant influence on a tree's likelihood of producing false rings: suppressed trees were not likely to produce false rings while codominant and intermediate trees were more likely to produce false rings. Tree age also influences propensity of false ring production with rings formed during the early years of a tree's life being more likely to contain false rings than rings formed later in life. Based on the results of this study, we recommend that dendroecologists include false ring analysis in their historical stand reconstructions to improve their ability to distinguish between releases in growth triggered by canopy gaps (associated with formation of false rings) versus releases in growth triggered by climate (no association with false rings).

Keywords: Dendrochronology; Intra-annual bands of latewood; *Pinus banksiana*; Dendroclimatology

1. Introduction

False ring formation, a common source of error in tree ring research, is triggered by drought during the growing season (Fritts, 1976; Ewel and Parendes, 1984; Yamaguchi, 1991); the drought-stressed tree produces smaller-diameter, thick-walled latewood cells. Later in the growing season, moister conditions allow the tree to return to the production of large-diameter, thin-walled earlywood cells. This series of events results in the formation of an intra-annual band of latewood, commonly known as a false ring. False rings do not form uniformly throughout the tree because the chemical signal to form latewood originates from the active, lateral meristem. Therefore, branches and portions of the stem that are near actively growing branches are more likely to form false rings than lower, branchless sections of the stem (Fritts, 1976). Younger trees and trees with faster growth rates are also more prone to false ring formation (Vogel et al., 2001).

Propensity and seasonality of drought-induced false rings varies across sites and species. In *Nothofagus pumilio* Krasser in Patagonia, false rings were caused by a dry, warm spring followed by a wet, warm summer (Masiokas and Villalba, 2004). In *Pinus nigra* Arnold in Vienna, false rings formed during years with less than half of the average precipitation for the month of May (Wimmer et al., 2000). *Larix sibirica* Ledeb. in Mongolia, *Tectona grandis* Linn. in India, and *Picea abies* (L.) Karst. in France formed false rings when trees experienced mid-growing season drought stress from soil water deficits (Priya and Bhat, 1998; Treter et al., 2002; Bouriaud et al., 2005). Stresses other than drought that have been attributed to

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the formation of false rings include unusually high levels of air pollution, periodic flooding, and mild frosts experienced in late spring and early summer (Young et al., 1993; Kurczynska et al., 1997; Kozlov and Kisternaya, 2004). Some studies have linked insect defoliation to false ring formation while others have found no connection (Priya and Bhat, 1998; Salleo et al., 2003). Under greenhouse conditions, Lloyd et al. (1996) triggered false ring formation in potted *Abies balsamea* (L.) Miller late in the growing season by exposing the trees to warm temperatures and a 15-h photoperiod. All of these studies indicate that false ring formation is triggered by specific environmental conditions. Once the relationship between the trigger and false ring formation is established, false rings will serve as strong proxy data for reconstructing droughts, flooding, frosts, or insect outbreaks.

The most common method for dendrochronologists to identify false rings is by anatomical features. In conifers, false rings appear as a narrow band of thick-walled tracheids (latewood) surrounded on both sides by thin-walled, large diameter tracheids (earlywood) (Kuo and McGinnes, 1973). The boundary between the earlywood cells that follow the false ring exhibits a more gradual increase in cell diameter and decrease in cell wall thickness than the abrupt change in cell diameter associated with a true ring boundary (Fritts, 1976). The location of the false ring within the annual ring correlates to the timing of the mechanism that triggers the false ring to form. For example, in *Juniperus virginiana* L. an early spring drought will cause a false ring to form at the beginning of the earlywood zone, while a late summer drought will cause the false ring to form in the latewood zone of the ring (Kuo and McGinnes, 1973). Typically, a computer-based dating verification program supplements the visual identification of false rings (Yamaguchi and Allen, 1992); this approach allows researchers to correctly identify false rings and accurately date tree ring series.

Pinus banksiana, a species prone to false rings and light rings (rings with extremely narrow latewood bands), has developed into an important species for dendrochronology (Volney and Mallett, 1992; Simard and Payette, 2001; Copenheaver and Abrams, 2003; Green et al., 2004). The tree's sensitivity to climate and association with xeric sites makes it a good candidate for dendroclimatology studies (Brooks et al., 1998; Tardif et al., 2001; Girardin and Tardif, 2005); however, its relatively short lifespan precludes its use as a proxy record for long-term climate reconstruction. Nonetheless, the species' frequency of false rings may prove to be valuable if these anatomical features are used as indicators of historical environmental conditions (Wimmer et al., 2000). Thus, identifying the causal agents of false ring formation in *P. banksiana* will provide another tool for dendrochronologists to interpret the climatic signal in the tree ring record.

Our study objective was to identify exogenous or endogenous causes of false ring formation in *P. banksiana* in northern lower Michigan. We tested for relationships between frequency of false ring formation and precipitation, temperature, growth rate, canopy class, and tree age to identify the causal factors of false ring formation in *P. banksiana*.

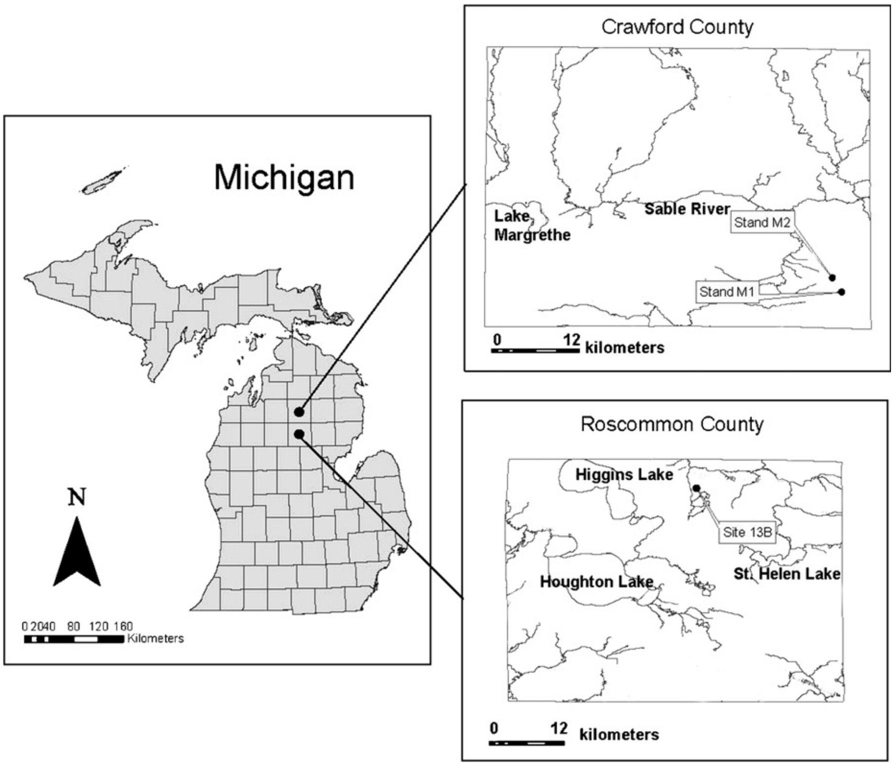

Fig. 1. The three study sites were located in northern-lower Michigan.

2. Study area and methods

2.1. Study area

The three study areas (M1, M2, and 13B) were located in northern-lower Michigan, with two sites in Crawford County and one site in Roscommon County (Fig. 1). The mean summer and winter temperatures are 18 and −6 °C, respectively. The average total annual precipitation is 81 cm. The soil type of the three study sites is Grayling sand which is characterized as sandy, excessively well-drained glacial outwash (Veatch, 1924; Werlein, 1998). The topography is relatively level and the elevation ranged from 350 to 360 m. The dominant vegetation is classified as Pine Community which historically has had a high frequency of fire and been dominated by *P. banksiana* on xeric sites (Barnes and Wagner, 1996). Logging and frequent fire during early European settlement and subsequent fire suppression has resulted in a community dominated by *P. banksiana* and drought-tolerant hardwoods such as oaks (*Quercus*) and aspen (*Populus*).

The study sites were selected because they contained mature *P. banksiana* stands on land owned by the Michigan Department of Natural Resources. Stand 13B is part of a long-term succession study established in 1979 (Abrams et al., 1985; Abrams and Scott, 1989) and at the time of sampling had experienced a moderate blow-down along its northern edge. Stand M1 consists of *P. banksiana* in the overstory and mid-story and an understory dominated by Ericaceae including *Arctostaphylos uva-ursi* (L.) Sprengel, *Epigaea repens* L., *Gaultheria procumbens* L., and *Vaccinium angustifolium* Aiton. Stand M2 has an overstory dominated by *P. banksiana* with an understory of *Amelanchier arborea* (Michx. f.) Fern., *A. uva-ursi*, *E. repens*, *G. procumbens*, *Prunus pumila* L., and *V. angustifolium*. Both M1 and M2 have dense populations of Allegheny mound ants (*Formica exsectoides* Forel), which indicates the *P. banksiana* of the area are experiencing high levels of parasitism from aphids, *Cinara banksiana* Pepper & Tissot, and scales, *Toumeyella parvicornus* Cockerell (Bishop and Bristow, 2003).

2.2. Field methods

Multiple transects were established to span each stand's width. Along each transect, at random intervals, point-centered quarter plots were established and the nearest tree in each quarter was sampled. Data collected on each tree included the species, distance to the tree from point center, and the diameter at breast height. Two cores were removed from the base of each tree with an increment borer and the crown class was classified as dominant, codominant, intermediate, or overtopped. Dominant trees were defined as individuals that received sunlight on the tops and sides of their crowns; codominant received sunlight on the tops of their crowns; intermediate trees received sunlight on a portion of the tops of their crowns and through gaps in the canopy, and overtopped trees received only indirect light (Nyland, 2002). For trees less than 8 cm in diameter, the tree was destructively sampled and a disk was cut from the base of the tree.

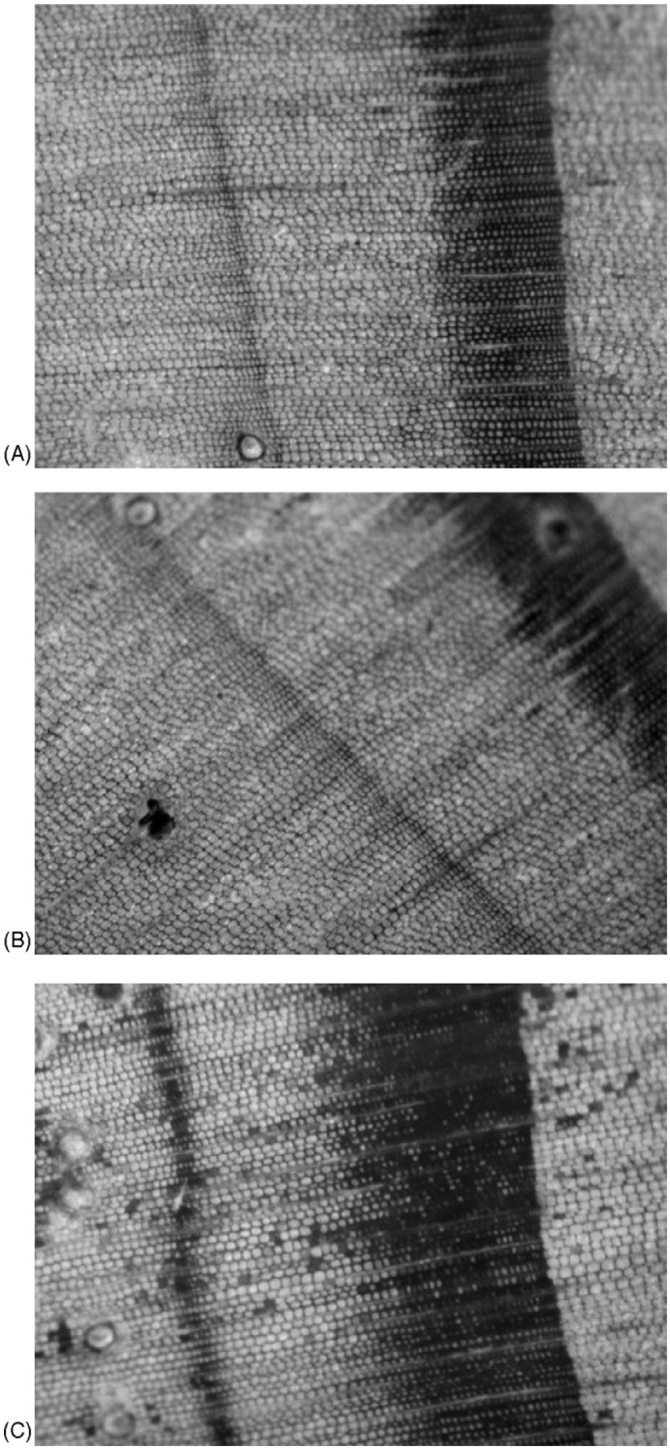

Fig. 2. False rings found in the *Pinus banksiana* cores. In all examples, the false rings are located to the left of the true ring boundary.

2.3. Laboratory methods

All cores and disks were air dried and sanded until the cells could be seen clearly under a microscope. The cores and disks were cross-dated using narrow rings as indicator years

Table 1
Characteristics of the *Pinus banksiana* tree ring series used in this study

	Stand name		
	M1	M2	13B
Number of series	60	60	60
Percent of series that had at least one false ring	48%	78%	80%
Percent of series that had at least two false rings	25%	57%	60%
Maximum tree age (years)	77	79	91
Percent of series within each canopy class			
Dominant	10%	7%	30%
Codominant	40%	47%	40%
Intermediate	27%	23%	19%
Overtopped	23%	23%	11%

(Yamaguchi, 1991); in all stands good indicator years were present at least every 20 years. During the cross-dating process, the presence of any false rings, identified by the presence of an interannual band of latewood, were noted (Fig. 2). After visual cross-dating, the tree ring widths were measured on a TA Unislide Tree Ring Measurement System (Velmex Inc.) to the nearest 0.002 mm. The dating of these raw ring widths was verified with the COFECHA program and any errors identified by the program were rectified. Stand 13B had an average series intercorrelation of 0.526 and an average mean sensitivity of 0.300. Stand M1 had an average series intercorrelation of 0.592 and an average mean sensitivity of 0.429. Stand M2 had an average series intercorrelation of 0.494 and a mean sensitivity of 0.405.

2.4. Data analyses

To identify synchrony in false ring formation, years with the highest occurrence of false rings were identified. Temperature and precipitation records were correlated with frequency of false ring production to identify patterns between climate and false ring formation. To identify the relationship between growth rate and false ring formation, we used superposed epoch analysis. Event years were identified when at least five series had false rings present and an event window of the 5 years prior and 4 years after the false ring event years were analyzed for significant increases or decreases in growth by comparison to a bootstrap simulation of 1000 trials of randomly selected sequences of 9 years using the EVENT program (Holmes and Swetnam, 1994). We were only able to use the superposed epoch analysis in Stands M1 and M2 because Stand 13B had its only event years (1933 and 1936) during a period of the chronology in which the sample size was too small to conduct the analysis.

To identify the relationship between canopy class and false ring formation, the frequency of false rings across all four-canopy class positions was compared with a χ^2-test. The requirements of the χ^2-test meant that the frequency of false rings had to be compressed into three frequency classes: 0 false rings; 1–2 false rings; or more than 3 false rings. We also had to combine all three sites into one dataset for this analysis, which meant that any site-to-site variability was lost. Thus, the χ^2-test identified the likelihood that a particular canopy class would produce no false rings, 1–2 false rings; or more than 3 false rings. A significance level of $P < 0.05$ was used for the χ^2-tests. To identify the relationship between tree age and false ring formation, the biological age of the tree was compared with frequency of false ring formation.

3. Results

3.1. Characteristics of false ring formation

Stands 13B and M2 had the highest number of false rings in the tree cores with 80% of the cores sampled from Stand 13B having at least one false ring and 78% of the cores sampled

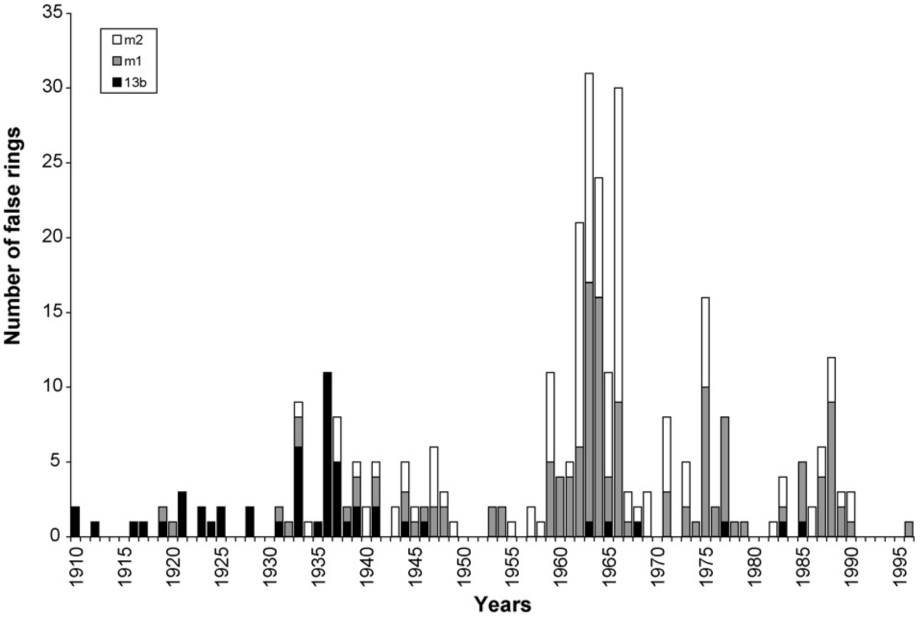

Fig. 3. Synchrony of false ring formation across the three study sites.

from Stand M2 having at least one false ring (Table 1). Many of the cores had multiple false rings and it appears that certain trees were more susceptible to false ring formation than others. For example, the four trees of one point-centered quarter plot in Stand M1 experienced similar growing conditions, yet demonstrated a range from 2 false rings on a tree that was 44 years old to 10 false rings on a tree that was 52 years old. The three stands were similar in age structure with the oldest tree in Stand M1 beginning growth in 1919, the oldest tree in Stand M2 beginning growth in 1917, and the oldest tree in Stand 13B beginning growth in 1909.

There was synchrony in the false ring formation within stands (Fig. 3). Stand 13B had a higher proportion of its false rings formed in the 1920s and 1930s while Stands M1 and M2 formed most of their false rings in the 1960s. There were specific event years during which many trees formed false rings in synchrony. For example, in 1963 at Stand M1 false rings occurred in 16 series. Within the years measured at Stand M1, 50% had at least one tree that exhibited a false ring; at Stand M2 44% of the years had at least one tree with a false ring; and at Stand 13B, 30% of the years had at least one tree with a false ring. Therefore, the pattern of false ring formation at all three stands maintained a steady background level of one or two false rings punctuated with event years during which many of the trees formed false rings in synchrony.

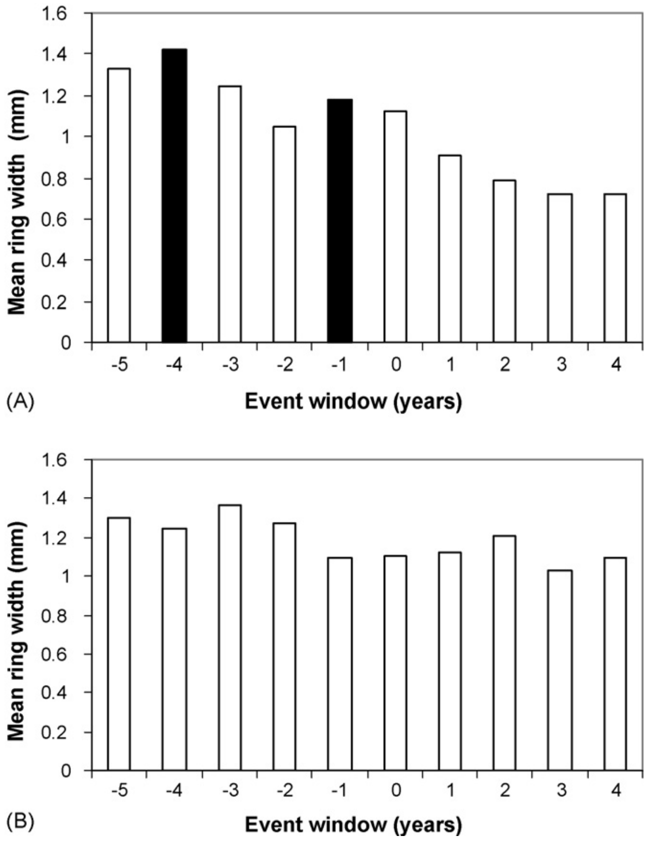

Fig. 4. Superposed epoch analysis of event years during false ring formation from Stands (A) M1 and (B) M2. The significantly (95% confidence) higher growth rates prior to the false ring are shown in black in Stand M1.

3.2. Climate and false rings

There was no significant correlation (Pearson's correlation coefficient = 0.003) between precipitation and frequency of false ring production for trees from Stand 13B, nor was there a significant relationship between temperature and false ring production (Pearson's correlation coefficient = 0.063). Trees from Stand M1 also had no significant correlation between precipitation (Pearson's correlation coefficient = 0.075) or temperature (Pearson's correlation coefficient = −0.038) and false ring frequency. Similarly, for the trees from Stand M2 there was no significant correlation between precipitation (Pearson's correlation coefficient = −0.002) or temperature (Pearson's correlation coefficient = 0.037) and false ring frequency.

3.3. Growth rate and false rings

Stand M1 had 7 years that were classified as event years because they had at least five series with false rings: 1962, 1963, 1964, 1966, 1975, 1977, and 1988. Stand M2 also had seven event years: 1959, 1962, 1963, 1964, 1965, 1966, and 1975. Stand 13B had two event years: 1933 and 1936. The superposed epoch analysis from Stand M1 classified the ring width from 1 and 4 years before the formation of a false ring to be statistically wider than would be found from a random sample (Fig. 4). There were no statistically significant differences in the ring width associated with false ring formation either prior to or after the event years of Stand M2 (Fig. 4). There were not enough series from the event years of Stand 13B to conduct superposed epoch analysis from this chronology.

3.4. Canopy class and false rings

More codominant trees were sampled than the other three canopy classes; however, by combining the data from the three

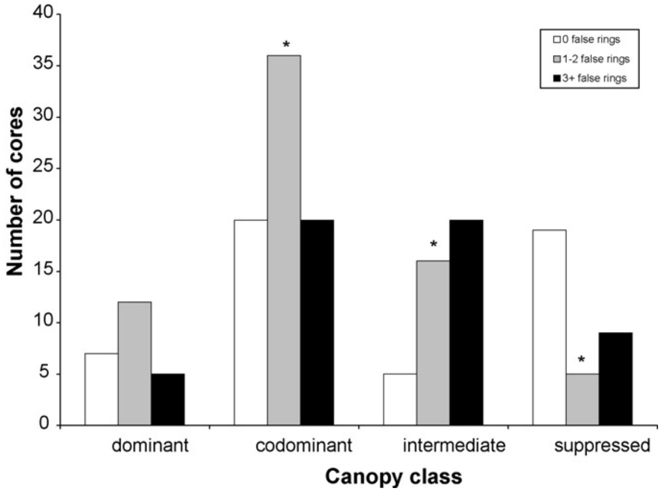

Fig. 5. Frequency of false rings across the four canopy classes. The asterisk on top of the codominant, intermediate, and suppressed canopy classes indicates a significant difference in the likelihood of trees within that canopy class to produce different numbers of false rings. Please note that the sample size varied across canopy classes.

stands we achieved fairly even sampling across the other three canopy classes (Table 1). Trees within the dominant canopy class did not have a significant difference in the proportion of trees that had no false rings, 1–2 false rings, or 3 or more false rings ($P = 0.02$; Fig. 5). The other three canopy classes had significant variations in their likelihood to form false rings. Codominant trees were more likely to produce 1–2 false rings ($P = 0.03$), intermediate trees were more likely to produce 3 or more false rings ($P = 0.01$), and suppressed trees were more likely to produce no false rings ($P = 0.01$).

3.5. Tree age and false rings

Younger trees were more susceptible to false ring formation than older trees (Fig. 6). This does not imply that older trees did not form false rings; several trees formed false rings in their 80s. However, the sample size decreased with increasing age, which artificially amplified the trees with false rings in the older age classes. Therefore, it should not be assumed that older trees were producing false rings at the same rate as younger trees. Instead the small sample size increased the importance of the rare false ring that formed in the older trees. For example, there were only 13 trees that were at least 80 years old and one of these trees had a false ring in the 80th year thus appearing as a peak in false ring formation at age 80 (Fig. 6).

4. Discussion

4.1. Implications for dendroclimatology

It has been suggested that false rings may serve as an additional piece of proxy data to be used in combination with other dendrochronology measurements for reconstructing historical climate or uncovering relationships between growth and climate (Wimmer et al., 2000). Although the potential for this remains in other species, in *P. banksiana* it appears that the formation of false rings is directed more by canopy position, growth rate, and tree age than by external climatic triggers. The lack of a relationship between false ring formation and climatic factors does not imply that *P. banksiana* has no value as a species for dendroclimatic analysis, but it does indicate that the more traditional measurements, e.g., ring width, earlywood width, latewood width, and woody density, may be better suited.

Although the relationships between false rings and climate were not significant, the results of this study elucidate the importance of cross-dating *P. banksiana* samples used for dendroclimatology studies to eliminate dating errors caused by false rings (Fig. 3). Dendrochronolgists should be especially diligent in looking for false rings when working with rings from the early part of the tree's growth because of the propensity of young trees to form false rings (Fig. 6) or when working with cores taken from codominant or intermediate canopy classes (Fig. 5).

4.2. Implications for dendroecology

Dendroecology strives to quantify the variability in historical forest disturbance patterns (Fritts and Swetnam, 1989). One of the more highly debated, but essential techniques in this process is the identification of gap-triggered releases in ring width patterns. The scientific literature is awash with techniques developed to separate gap-triggered growth releases from climate-initiated growth releases (Lorimer and Frelich, 1989; Nowacki and Abrams, 1997; Wu et al., 1999; Black and Abrams, 2003, 2004; Druckenbrod, 2005; Fraver and White, 2005). These various techniques for identifying growth releases have been applied to many different species across a wide geographic range and have proven to be a useful tool for interpreting disturbance regimes (Cao and Ohkubo, 1999; Abrams et al., 2000; Copenheaver et al., 2002; Rozas, 2003). Unfortunately, when the various techniques are applied to the

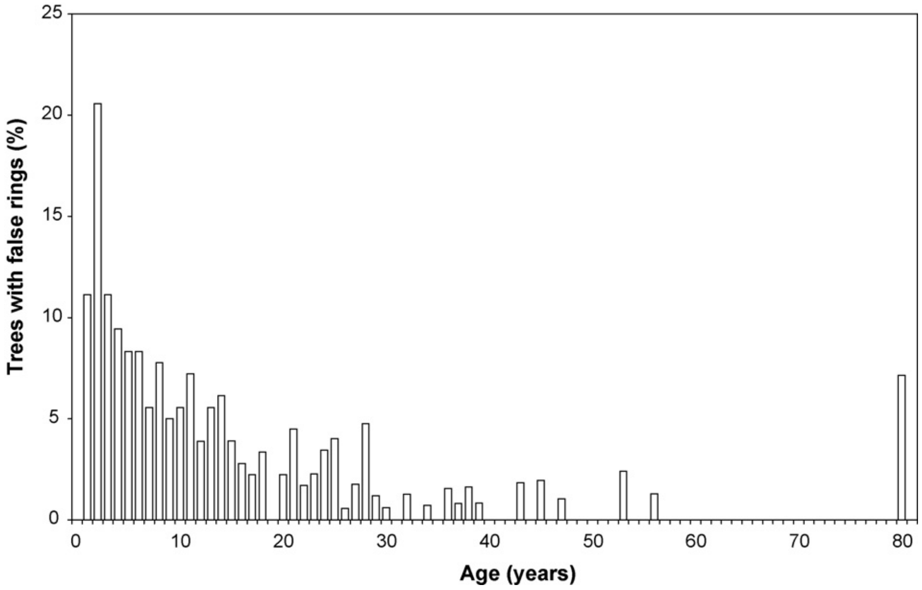

Fig. 6. Percent of trees with false rings in relation to age of the tree.

same dataset they predict substantially different disturbance regimes (Rubino and McCarthy, 2004).

Instead of relying exclusively upon ring width data to identify release events it may be useful to combine ring width data with wood anatomical features, specifically false rings. Trees that are in an intermediate canopy position (and thus likely to be released in a gap dynamics event) are more prone to false rings (Fig. 5). Therefore, a tree which exhibits frequent false rings (indicating a intermediate canopy position) followed by a radial growth release (indicating movement of that tree into a canopy cap) would be strong evidence that the release was caused by canopy ascension. Calculating the frequency of canopy ascension dates would reveal the disturbance regime of that area (Lorimer et al., 1988). Clearly the coupling of radial growth and false ring patterns to determine release events would only be applicable in species for which the formation of false rings was common and for which an established relationship between canopy class and false rings existed. However, for species that are not prone to false ring formation, other tree ring anomalies, e.g., partial rings and missing rings, also occur at higher rates in overtopped trees and therefore they may be just as useful for dendroecologists (Lorimer et al., 1999).

5. Conclusions

This study provides a comprehensive examination of causal factors for false ring formation in *P. banksiana*. False ring formation in *P. banksiana* appears to be more common when trees are young or in the codominant or intermediate canopy position. There was an even split in patterns of growth rate between the two stands, one of which had significantly faster growth rates prior to event years with frequent false rings and the other which had no significant changes in growth before or after false ring event years. In contrast to many other studies, this study found no significant relationship between temperature or precipitation and false ring formation. These results indicate that false rings may not be particularly useful for dendroclimatologists, but there is a strong potential for their use in dendroecology for reconstructing historical stand development patterns.

Acknowledgements

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