DENSITY FLUCTUATIONS (FALSE RINGS) IN JACK PINE AND BLACK SPRUCE TREES, NOPIMING PROVINCIAL PARK, MANITOBA

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A thesis submitted in partial fulfillment of the Honours Thesis (05.4111/6) Course

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2007

Abstract

In dendrochronology, little research exists on density fluctuations (DFs). This tree-ring anomaly can be used to better understand tree growth and to potentially help reconstruct past climatic events. The main objective of this study was to explore the association between DFs and climate. Sampling was conducted in Nopiming Provincial Park. Five *Pinus banksiana*, Lamb. (jack pine) stands were sampled. In each stand, wood cores were extracted from both *P. banksiana* and *Picea mariana*, [Mill.] BSP (black spruce), when present. After crossdating, all cores were measured for earlywood, latewood, and total ring width. All DFs were identified and their position within a tree ring determined. Both tree species showed similar radial growth and density fluctuation patterns. In *P. banksiana*, DFs were much more abundant in the juvenile period. Results indicated that cool/snowy springs and summers with severe drought were associated with higher frequency of DFs. These anomalies could be formed partly in response to the timing of the start of the growing season as well as to conditions during that growing season that lead to interruption and subsequent resumption of normal growth. It was observed that *P. banksiana* was more sensitive to precipitation and *P. mariana* was more sensitive to temperature.

Acknowledgements

I would like to thank my supervisor, Dr. Jacques Tardif for his support and guidance throughout this project, and for his faith in me. I am very grateful to have had this experience working with him. I thank my committee members Dr. Richard Westwood and Dr. Danny Blair for their advice and feedback, and Brock Epp and Stephen Geitz for their field and lab assistance. My gratitude goes to France Conciatori, without whom my knowledge is this field of study would be very limited. I would also like to thank Dr. Ric Moodie for coordinating the Honours course. This project was made possible through assistance from the Natural Sciences and Enigineering Research Council of Canada and the University of Winnipeg. Drought code indices were provided by Dr. Martin Girardin, and I thank him for sharing those with me. I would also like to thank my husband and best friend Ian, for his unending love, support, and patience.

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1.0 Introduction

Tree growth is affected by the physical conditions in which the trees are growing (such as substrate type) and by variations in environmental conditions such as temperature and precipitation (Fritts 1976; Schweingruber 1996). The influence of these factors can be reflected in the anatomical development and physiological processes involved in the growth of the trees, whose rings can be used to establish the year in which a specific event took place (Fritts 1976). These events may include insect defoliation, volcanic eruptions, low temperatures, and an excess or lack of water. The information embedded in tree ring anatomy can be used to better understand tree growth and also to help reconstruct, for example, past climatic events. However, an understanding of the anatomical variations (anomalies) in tree rings is essential before such reconstructions can take place. Some of the variations that can be used as environmental indicators include narrow or large rings, missing or locally absent rings, frost rings, pale latewood rings, intra-annual density fluctuations and density fluctuations (Fritts 1976 Wimmer 2002). For example, the relationship between pale latewood rings and climate was explored by Tardif *et al.* (2004) in western Manitoba. They found that *Pinus banksiana* Lamb. (jack pine) produced a high frequency of pale latewood rings when early and late summer were cooler than average. Glerum (1970) looked at the formation of "drought rings" in *Picea glauca* [Moench] Voss (white spruce) seedlings. He found that seedlings exposed to severe drought treatment produced rings that were characterized by the presence of an intra-annual band of tracheids which had reduced radial diameters, and that the features of these rings varied depending on their location in the stems of the seedlings.

As softwood trees lay down their xylem throughout the growing season, two different types of wood are formed (Fritts 1976 Wimmer 2002). In the spring and early summer, earlywood (EW) tracheids are laid down. These cells are large in diameter and have thin secondary walls. Later in the growing season, latewood (LW) tracheids are laid down which are smaller in diameter and have thicker walls than the EW cells (Appendix A). According to the Multilingual Glossary of Dendrochronology a density fluctuation (DF) can be defined as a "layer of cells within a tree ring identified by different shape, size, and wall thickness" (Kaennel and Schweingruber 1995). Density fluctuations are also known as double or multiple rings, intra-annual DFs or false rings. There is some debate about the interchangeability of the terms false ring and density fluctuation. The PaleoClimate Glossary defines false rings as "a change in cell structure within an annual growth layer, which resembles the boundary of a true annual ring, making it appear to be two or more growth layers instead of one. Also known as a double ring or an intra-annual ring." (PaleoClimate Glossary 2000). However, Kaennel and Schweingruber (1995) say that the term false ring should only be used for the intra-annual rings that cannot be morphologically distinguished from a true ring. For the purposes of this study, a false ring can be considered to be the extreme degree of a DF. There can be much variation in DFs in terms of their distinctiveness (clarity and intensity) as well as their position within rings and they can be observed anywhere in the EW or LW zones (Kuo and McGinnes, 1973). Anatomical differences in lumen size and shape of tracheids, as well as differences in stable carbon isotopic composition in the latewood-like cells of DFs and those of true LW were also found in *Pinus pinaster* Aiton. (Maritime pine) by De Micco *et al.* (2007).

Density fluctuations and false rings have been reported in both hardwood and softwood tree species. Young *et al.* (1993) looked at flooding regimes and found that *Taxodium distichum* L. (bald cypress) produced false rings. While the specific reasons for false ring formations remain unclear, the degree of this formation in saplings was presumed to be determined by the hydrologic regimes of a site. Those saplings subjected to a treatment of periodic flooding showed major false rings (gradual decrease in cell size and increase in cell wall thickness with a distinct margin defining the terminal boundary) while those under a treatment of continuous flooding showed no major false rings. An association between insect defoliation and false ring formation was also reported for juvenile *Tectona grandis* L.f. (teak), a ring porous species (Priya and Bhat 1997). Priya and Bhat (1998) also found that environmental factors, such as prolonged droughts, and physical factors, such as transplantation, were responsible for false ring formation in *T. grandis*.

It is in softwood species however that DFs have been the most studied. Some of the first studies were aimed at describing false rings (DFs), identifying them and providing insight as to their origin (Schulman 1938, 1939; Glock and Reed 1940; Wendland 1975). Few studies have been done to specifically explore DFs in tree rings, or their association with climate variables. Kuo and McGinnes (1973) speculated that false ring formation in *Juniperus virginiana* L. (eastern red cedar) may be governed by changes in hormonal levels and increased water stress. The authors reported numerous forms of false rings (narrow or wide bands with varying radial diameters and cell wall thicknesses) and demonstrated that false rings may be tangentially or longitudinally discontinuous. Rigling *et al.* (2001) found intra-annual DFs in *Pinus sylvestris* (Scots

pine) in semi-arid environments. All sites under investigation were subject to drought stress, and DFs were found at each. The authors also found that the DFs were useful for ecological distinction between the qualities of sites, for example substrate type and climatic differences. In a subsequent study, Rigling *et al.* (2002) found that seasonal variations in temperature and precipitation produced DFs. These DFs varied in number across sites that differed in drought stress and soil conditions, and also in their position within the ring. False rings were described as being formed by dry conditions by Wimmer *et al.* (2000). They were found to be useful environmental indicator for dendroclimatic studies, particularly in reconstruction of past low rainfall months.

This research project investigated the relationship between DFs in *P. banksiana* and *Picea mariana* [Mill.] BSP (black spruce), growing in Nopiming Provincial Park, Manitoba, and climate, particularly with drought. *Pinus banksiana* is a shade intolerant coniferous tree that is widely distributed throughout Canada and the Boreal forest (Rudolph and Laidly 1990). It grows in a variety of habitats including rock outcrops, low quality sites such as sandy areas, and shallow soils (Farrar 1995). It is well known as a pioneer species in succession and in areas where soil has been uncovered after a fire (Rudolph and Laidly 1990). *Picea mariana* is also a coniferous tree with wide range and abundance in the northern parts of North America (Viereck and Johnston 1990). It is moderately shade tolerant usually found growing in wet poorly drained sites (Farrar 1995), but may be found on a range of soil types from clays to sands to shallow soils overlying bedrock (Viereck and Johnston 1990). *P mariana*, like *P. banksiana*, has serotinous cones and reproduces well after a fire (Farrar 1995). In this study, *P. mariana* was used as a secondary species, to assess if its radial growth was affected in a similar

way to that of *P. banksiana*. Not all species of trees have the same ability to produce DFs (Schweingruber 1988) and this project compared the *P. banksiana* cores with those of *P. mariana*. The main hypothesis predicted that there would be a positive association between the DFs formed in *P. banksiana* and the drought years in Nopiming Provincial Park. It was also predicted that *P. mariana* would show similar radial growth to *P. banksiana*, but a lack of DF production.

2.0 Methodology

2.1 Study Area

The study area is located approximately 200 km north-east of Winnipeg in Nopiming Provincial Park (50°67' N, 95°28' W) in eastern Manitoba (Appendix B). The park has an area of 1,429 km², and is bound on the east by the Manitoba-Ontario border (Manitoba Conservation 2006). Nopiming Park is located on the Canadian Shield and the underlying bedrock consists of Precambrian granites (Manitoba Geological Survey 2002). It is dominated by hills, ridges, granitic outcrops, lakes, and rivers. Soils in the study area include Eutric and Dystric Brunisols, Fibrisols, Mesisols, and Gray Luvisols (Scott 2006). Forest stands are dominated by *Populus tremuloides* Michx. (trembling aspen) and *Betula papyrifera* Marsh. (white birch) mixed with *P. banksiana* and *P. mariana* (Manitoba Conservation 2006). Lichens, mosses and spruce bogs are also commonly found in the park. *Pinus banksiana* dominates on rock outcrops or sandy/gravelly esker ridges due to physiological drought conditions (Scott 2006). Nopiming Park is also characterized by periodic fires that encourage and maintain renewed growth and plant diversity (Manitoba Conservation 2006).

The study area is in the Lac Seul Upland ecoregion of Canada, which is part of the subhumid mid-boreal ecoclimate (Environment Canada 2005). The closest meteorological station to the sites is that of Great Falls, Manitoba (50°28' N, 96°0' W, elevation 248.70 masl, Appendix B). The region is subject to a harsh climate of short hot summers reaching an average maximum temperature of 24.9°C in July, and long cold winters reaching an average minimum temperature of -22.5°C in January (Appendix C). Low levels of precipitation are characteristic, with monthly snowfall ranging from 0.3 to

17.9 cm and monthly rainfall ranging from 0.2 to 88.2 mm over the course of the year (Appendix C) (Environment Canada 2007).

2.2 Sampling Methods and Data Collection

A total of five sites (52L-08, 09, 11, 12, and 13) were sampled in Nopiming Park (Appendix B). Sites 52L08 and 09 were sampled in the fall of 2001 and sites 52L-11, 12, and 13 in June 2006. In the two sites sampled in 2001, wood cores were extracted from living *P. banksiana*. In 52L-08 two cores were extracted from each of 27 trees, and in 52L-09 two cores were extracted from each of 17 trees. In the sites sampled in 2006, two cores were extracted from each of 15 living *P. banksiana* and 15 living *P. mariana*. All cores were extracted near the base of the trees, using a 5 mm increment borer. Two *P. banksiana* snags were also collected at site 52L-11.

The Point Centered Quarter (PCQ) sampling method (Cottam and Curtis 1956) was implemented at all five sites in June of 2006 to quickly assess tree composition. This method is used to identify the various tree species in a community and determine their relative importance (Mitchell 2006). Four 40 m transects were laid out at 90° angles to one another forming a square, and one PCQ was placed every 10 meters (paced distance), totaling 16 points. In each of four quadrants at each of the points, the distance to the nearest tree was measured using a laser hypsometer. Diameter breast height (dbh) was also measured using a dbh tape, and species was noted. Minimum dbh for trees to be considered was 5 cm. For trees on slopes, dbh was measured on the high slope side of the tree. The PCQ data collected was then used to calculate species density (trees/ha) and species basal area (m^2/ha) for each of the species in each of the sites. The tree species

composition among the sites was variable, ranging from one species in site 52L-08 to six species in site 52L-13 (Appendix D). The five sites also differed in total species density; with the lowest value being observed in stand 52L-08. Total species basal area was lowest in site 52L-08 and highest in site 52L-13 (Appendix D).

The three dominant or tallest trees were identified at each site. Height and diameter for each tree was measured using a Suunto clinometer. After determining the distance of the observer to the tree, percent slope to the top and to the base of the tree were measured. *Pinus banksiana* was the dominant tree at four sites (average height range of 7.47 to 8.78 m) and *P. mariana* was dominant in site 52L-13 (average height of 10.27 m) (Appendix D).

Three soil pits were excavated at each site. Depths of the soil pits, LFH, A and B horizons were measured and samples of the three horizons were collected, where present, for analysis. The pH of all soil samples was determined in the laboratory, using the 0.01 M CaCl method (Scott 2006). The soils in all sites were acidic, though values varied between sites and among horizons (Appendix D). The most acidic value was found in the LFH horizon of site 52L-11, while the least acidic value was in the B horizon of site 52L-08. Apparent soil texture was also noted in the field for each horizon in each of the soil pits using the 'feel method' (Scott 2006). The stands selected encompassed a wide range of soil texture, and varied between and among sites. Fine sands, loams, rocks, and organics were among those found in different stands (Appendix D).

2.3 Dendrochronological Methods

In the laboratory all cores were mounted and dried. They were sanded incrementally, increasing the paper grit from 180 to 600. Because the date of formation of the outermost rings of the cores was known, pointer years were determined using a modification of the methods described by Yamaguchi (1991). A pointer year is one in which a distinguishing characteristic, such as a wide or narrow ring, may be found in most or all trees of a species growing in a particular area. Dating and crossdating were carried out on all cores from the sites sampled in 2006, using pencil marks to denote decades, half centuries and centuries, and tree age was determined. Dating and crossdating had previously been carried out on the cores from the sites sampled in 2001 using the same technique. These cores were checked for errors.

Density fluctuations were identified in each core for both species. Each DF was also visually assigned one of three categories describing its distinctiveness (Appendix E). Category 1 (DF 1) included DFs that were hazy and not very intense, category 2 (DF 2) included those that were moderately clear and intense and category 3 (DF 3) included those that were very clear and intense. Using the data generated, the frequency and relative frequency of DFs in time was tabulated for each site and species according to the three DF categories.

2.4 Tree-Ring Chronology Development

In addition to identification of DFs, measurements were taken of the earlywood (EW), latewood (LW), and total ring width (RW) for each core from both tree species and all sites. Measurements were manually taken using a LINTAB 5 linear table and

micrometer to a precision level of ± 0.001 mm. In this project EW and LW were separated according to the qualitative aspect of color change to darker cells (Fritts 1976; Lebourgeois 2000; Wimmer 2002; and Appendix A). For all rings LW was measured from where the darker cells began in the growth ring to where they ended. For years showing DFs, LW was measured from the beginning of the DF cells to the end of the darkened LW cells. This allowed the position of the DFs, when present, within the annual ring to be precisely determined. Density fluctuation position within the rings was determined by calculating the percent latewood (PLW) for each core in each site for both species using the following formula:

$$\text{DF Position/PLW} = \frac{\text{Latewood measurement}}{\text{Total ring width measurement}} \times 100$$

(Appendix F).The program COFECHA (Holmes 1983) was run to validate the crossdating and measurements and to find potential errors. COFECHA achieves this by filtering each measurement series with a short cubic spline, then performs a log transform and derives a master chronology by taking the mean of all filtered and transformed series (Holmes 1983). It then tests each series against the master chronology (which is adjusted each time), and correlations are computed between short segments the series and corresponding segments of the adjusted master chronology (Holmes 1983). If any potential errors were identified, cores were checked for accuracy of dating, measurement and placement of core fragments, and any inaccuracies were corrected. Once all measurement series were validated, tree-ring chronologies were developed. Standardization is a fundamental dendrochronological procedure, in which growth indices are produced from tree ring width measurements prior to averaging (Fritts 1976). Growth rates can vary according to a number of factors including fluctuations in

environmental conditions, systematic changes in tree age, and productivity of the site (Fritts 1976). Standardization was carried out in order to remove the age and size related trends in tree growth and to make the younger, faster growing portion of the tree more comparable to the older, slower growing portion of the tree (Fritts 1976). This was done using a polynomial regression model (cubic spline of 50 years, Appendix G), with a 50% frequency response. A 25-year spline with a frequency response of 50% was used for measurement series where the first standardization did not perform well. Following series standardization, the serial autocorrelation was removed, and the resulting residual series were averaged using a robust averaging procedure to obtain the mean residual chronologies. All measurement series of EW, LW, and RW were standardized in the same way, and tree-ring chronologies (by species and site) were produced using the program ARSTAN (Cook 1985). These procedures resulted in the development of residual EW, LW, and RW chronologies for each species (6) and for each species site combination (24) totaling 30 chronologies. Common interval statistics for the period 1940-2001 were extracted from the *P. banksiana* and *P. mariana* standard and residual chronology ARSTAN output files and compiled into a table.

2.5 Statistical Analyses

2.5.1 Density Fluctuations and Climate

The data compiled from the DF identification (see section 2.3, above) was used to calculate the overall frequency of DFs per year per species. From this data, three DF frequency classes were created: class 1 (0-5%): years with no to low abundance of DFs;

class 2 (5-25%): years with mid abundance of DFs; and class 3 (>25%): years with high occurrence of DFs.

To analyze the DF data, analysis of variance (ANOVA) was used. For all ANOVA, separate analyses were carried out for both species, using the program Systat (Systat Software Inc. 2004). The first two ANOVA were carried out to test whether the number of sites and the distinctiveness of DFs were similar among the three DF frequency classes. When a significant difference was observed among variables ($P \leq 0.050$), a post-hoc Tuckey test was done to determine which groups within the variables were statistically different from one another (Zar 1996). The third ANOVA was used to test whether climate was similar among the three DF frequency classes. A post-hoc Tuckey test was carried out under the same conditions as all other ANOVA.

The climate data used was from the Great Falls meteorological station (Appendix B). This location was chosen because of its proximity to the study area, and the timeline of the data available. Homogenized data sets for monthly and seasonal mean, minimum, and maximum temperature (Vincent and Gullet 1999) as well as those for snow, rain, and total precipitation (Mekis and Hoff 1999) for the period 1922 to 2003 were used. The Canadian Drought Code (CDC) monthly and seasonal average indices calculated for the southern Canadian Boreal forest for the period 1923 to 1996 were also used (Girardin *et al.* 2004). The CDC is a numerical rating of average moisture content of deep organic layers of soil. It accounts for the losses and gains of moisture due to evapotranspiration and precipitation. A rating of 0 indicates that the maximum water holding capacity of the soil has been reached, one of 200 indicates that the drought severity is high, while a rating of 300 indicates that the drought severity is extreme (Girardin and Tardif 2004).

Monthly data was used from May in the year prior to ring formation to August of the year of formation. Seasonal data consisted of the previous summer (June, July, and August), previous fall (September, October, and November), current winter (previous December, current January and February), current spring (March, April, and May), and current summer (June, July, and August)

2.5.2 Tree-Ring Chronologies and Climate

To assess the similarity in the growth pattern between the two species, and also the relationship among the four chronology types (EW, LW, and RW), Pearson correlation analyses were conducted. All correlation analyses were carried out using the program Systat (Systat Software Inc. 2004). To explore the effects of growth in one year of the tree's life on the next year's growth, a Pearson's correlation was also calculated between residual tree-ring chronologies (EW, LW, and RW) with a lag of one year, for each species. A between-species Pearson's correlation was also calculated between residual tree-ring chronologies (EW, LW, and RW) for *P. banksiana* and the same chronologies for *P. mariana*.

Pearson's correlation analyses were also used to determine the association between climate and the tree ring chronologies developed for each species. The climate variables influencing earlywood, latewood, total ring width, and percent latewood were assessed in each species. The correlations were calculated between residual tree ring chronologies (EW, LW, and RW) and monthly and seasonal maximum, minimum, and average temperature, as well as rain, snow, and total precipitation and drought code data. The same climate variables as those described in section 2.5.1 were used.

3.0 Results

3.1 Occurrence of Density Fluctuations

The cumulative relative frequency of DFs shows that they reached a high occurrence in *P. banksiana*, with DFs appearing in a majority of the years for the period 1919-2005 (Figure 1a). Despite showing peak occurrences in the same years (e.g. 1947, 1961, 1979), *P. mariana* generally had more years with low or no DFs (Figure 1b) compared to *P. banksiana*. In both species DFs with low distinctiveness (DF1) have the highest relative frequencies and appear in the greatest number of years. As the DFs increase towards moderate and high distinctiveness (DF2 and DF3) the frequency and the number of years in which they appear decreases (Figure 1). *Picea mariana* produced fewer DF3s compared to *P. banksiana*, which were only observed in 1979, and showed more years when only DF1s were produced. It was observed in both species that when the frequency of DFs increased, there were usually more rings with a greater intensity, for example in 1922 compared with 1954 and 1979 (Figure 1). There are a greater number of years showing DFs and higher frequencies between 1920 and 1950, at a time when trees were young, than between 1950 and 2003, indicating a juvenile effect. This juvenile effect was less pronounced in *P. mariana* , and DFs showed a slightly more even distribution among years than in *P. banksiana* (Figure 1).

The ANOVA indicated that the distinctiveness of DFs (categories DF1, DF2, DF3) for both *P. banksiana* and *P. mariana* differed significantly among the three DF frequency classes (Figures 2a and 2b). In *P. banksiana* the distinctiveness of DFs significantly increased from one abundance class to the next. In *P. mariana* no statistical

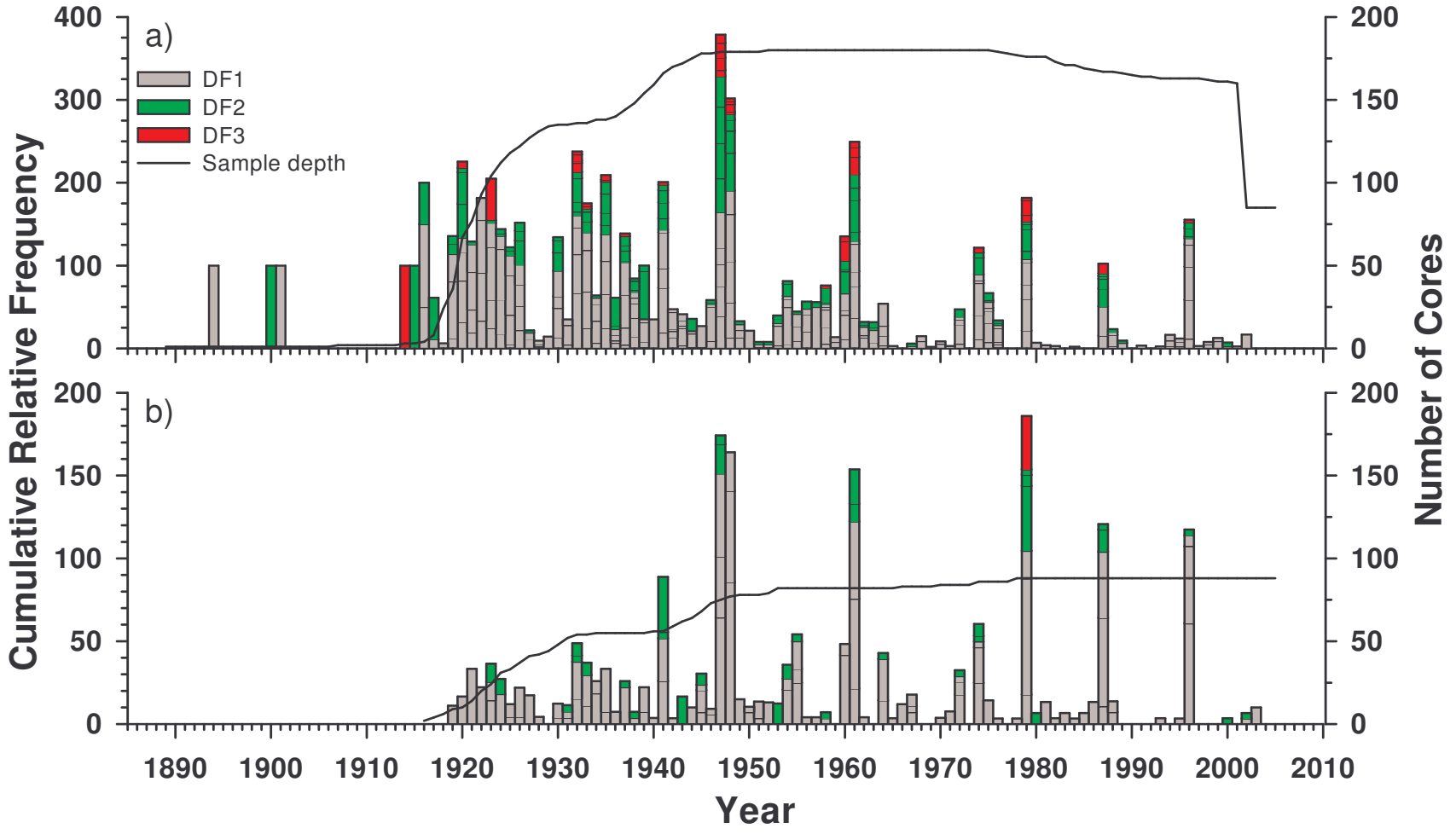

Figure 1: Cumulative relative frequency of density fluctuations in a) *Pinus banksiana* trees (n=5 sites, represented by horizontal lines), and b) *Picea mariana* trees (n=3 sites, represented by horizontal lines). DF1s are hazy density fluctuations with low intensity, DF2s are moderately clear and intense density fluctuations, and DF3s are very clear and intense density fluctuations.

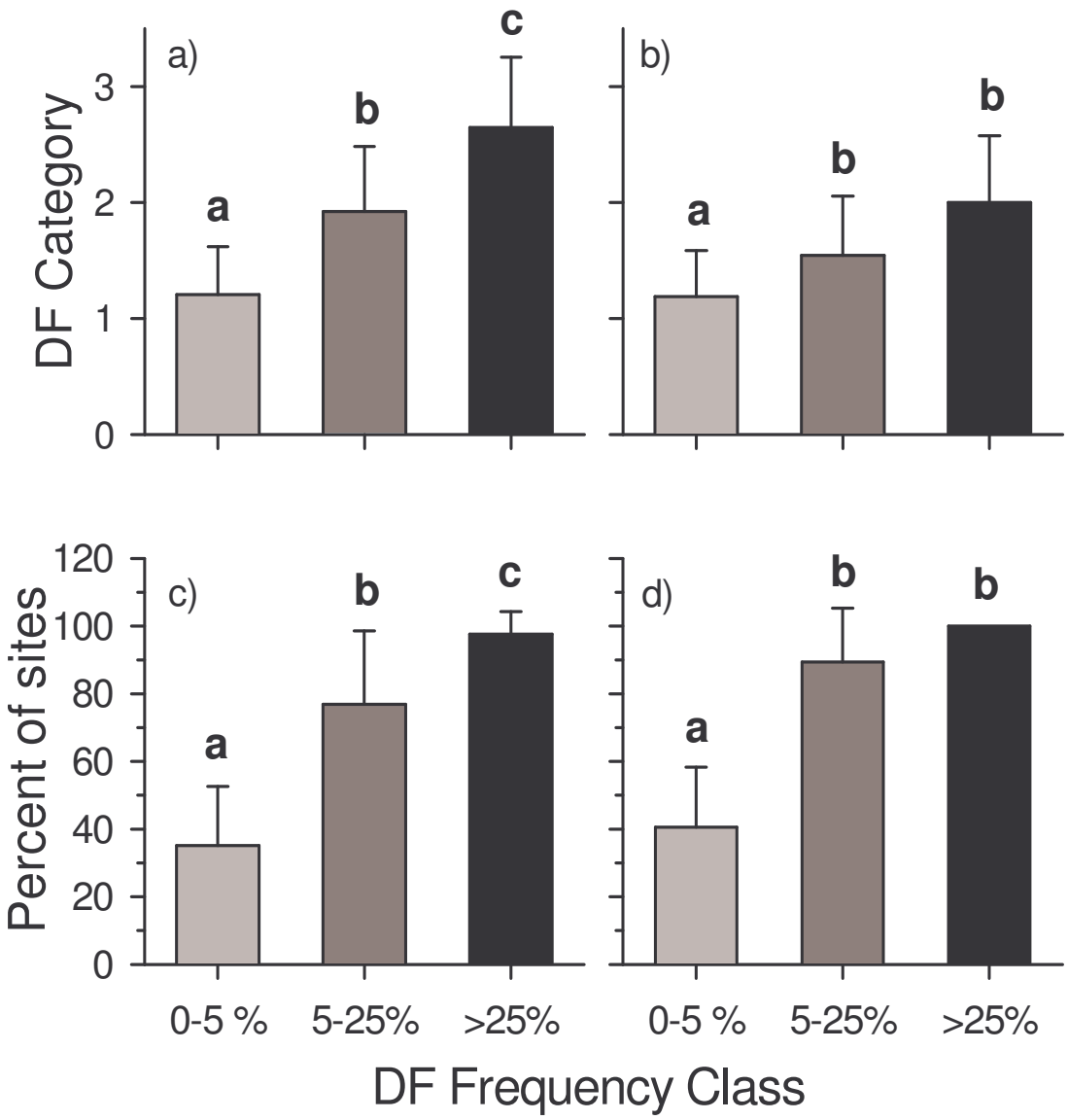

Figure 2: Bar graph of Analysis of Variance (ANOVA) for mean density fluctuation (DF) frequency class compared with density fluctuation (DF) category for a) *Pinus banksiana* and b) *Picea mariana*, and with percent of sites for c) *Pinus banksiana* and d) *Picea mariana*. Error bars represent standard deviation and letters represent significant differences between categories following a Tuckey test ($P \leq 0.05$).

difference in DF distinctiveness was observed between medium and high abundance years, which was expected because DF3s were formed in only one year, but these two classes presented clearer DFs than in the low abundance class. The number of sites represented in years with low-medium-high frequency of DFs was also found to vary significantly (Figures 2c and 2d). In *P. banksiana*, the number of sites represented increased significantly from one frequency class to the next (Figure 2c). Both species showed the same trend as was observed for the distinctiveness of DFs.

3.2 Density Fluctuations and Climate

The ANOVA analysis comparing climate variables among DF frequency classes revealed that years with high frequencies of DFs in *P. banksiana* were characterized by significantly cooler March and spring temperatures, than years with low frequency of DFs (Table 1). The effect of spring conditions on DF frequency was further emphasized as the classes with mid and high DF frequency corresponded to years with significantly higher snowfall in February, March, and spring than years with low DF frequency (Table 1). The correlation with increased May snowfall was significantly higher in the mid than the low DF frequency class, but there was no significant difference between the mid and high DF frequency classes. A similar result was found for February total precipitation. Years with mid and high frequencies of DFs were characterized by significantly higher March total precipitation than years with low frequency of DFs (Table 1).

In addition, significant differences were also observed among the DF frequency classes when looking at summer climate variables. In June and summer, the total precipitation received in years with high frequencies of DFs was significantly lower than

Table 1: Mean and standard deviation for the monthly and seasonal climate variables characterizing years with low (0-5%), mid (5-25%), and high (>25%) density fluctuation frequencies for *Pinus banksiana*. The variables are average temperature, drought code, snowfall , and total precipitation. Bolded values indicate a significant ANOVA analysis ($P \leq 0.05$). Results are read row-wise and letters (a, b, c) represent significant differences ($P \leq 0.05$) between groups following a post-hoc Tuckey test.

Average Temperature (°C)					
Month/Season	0 – 5 %	5 – 25 %	> 25 %	P Value	Squared Multiple R
January	-17.9 ± 3.8	-17.1 ± 3.9	-18.3 ± 3.4	0.569	0.014
February	-13.9 ± 3.7	-15.3 ± 4.3	-15.1 ± 3.6	0.324	0.028
March	**-5.8 ± 3.2 a**	**-7.4 ± 3.5 ab**	**-8.6 ± 2.8 b**	**0.011**	**0.110**
April	3.3 ± 2.5	3.2 ± 2.6	2.2 ± 2.1	0.271	0.033
May	11.3 ± 2.5	10.8 ± 1.9	10.9 ± 2.4	0.724	0.008
June	16.4 ± 1.9	16.6 ± 1.5	16.9 ± 2.0	0.544	0.015
July	19.4 ± 1.3	20.0 ± 1.5	20.08 ± 1.1	0.108	0.055
August	18.4 ± 1.7	18.2 ± 1.3	18.9 ± 1.5	0.306	0.030
Winter	-15.2 ± 2.5	-15.2 ± 2.8	-15.7 ± 2.6	0.809	0.005
Spring	**2.9 ± 1.9 a**	**2.3 ± 1.7 ab**	**1.5 ± 1.7 b**	**0.029**	**0.088**
Summer	18.0 ± 1.3	18.3 ± 0.9	18.6 ± 0.9	0.169	0.045
Drought Code					
April	59.2 ± 93.5	84.8 ± 119.5	80.4 ± 109.0	0.626	0.013
May	671.2 ± 325.6	710.4 ± 286.0	771.8 ± 297.8	0.562	0.016
June	1558.6 ± 575.4	1478.8 ± 487.7	1870.1 ± 475.0	0.063	0.075
July	**2257.3 ± 652.3 a**	**2106.7 ± 509.3 a**	**3030.8 ± 567.4 b**	**0.000**	**0.270**
August	3204.4 ± 957.2	2941.5 ± 652.4	3621.1 ± 919.9	0.053	0.079
Spring	365.2 ± 193.5	397.6 ± 185.8	426.1 ± 183.5	0.553	0.017
Summer	**2340.1 ± 626.8 a**	**2175.7 ± 403.1 a**	**2840.7 ± 517.2 b**	**0.001**	**0.179**
Snow (cm)					
January	20.7 ± 18.5	33.1 ± 24.9	27.8 ± 23.0	0.085	0.064
February	**13.7 ± 11.3 a**	**22.7 ± 12.5 b**	**24.3 ± 18.8 b**	**0.009**	**0.121**
March	**13.1 ± 10.9 a**	**25.5 ± 20.3 b**	**35.3 ± 17.4 b**	**0.000**	**0.240**
April	7.4 ± 10.9	7.9 ± 10.9	8.4 ± 8.7	0.958	0.001
May	**0.4 ± 1.6 a**	**2.3 ± 3.9 b**	**1.0 ± 2.7 ab**	**0.034**	**0.090**
Winter	61.8 ± 31.2	84.5 ± 43.6	74.3 ± 43.4	0.084	0.068
Spring	**21.0 ± 15.7 a**	**35.7 ± 22.2 b**	**44.8 ± 16.2 b**	**0.000**	**0.222**
Total Precipitation (mm)					
January	20.9 ± 18.4	33.1 ± 25.0	27.8 ± 23.0	0.093	0.062
February	**14.0 ± 11.1 a**	**22.9 ± 12.1 b**	**24.4 ± 18.8 ab**	**0.009**	**0.121**
March	**16.7 ± 11.3 a**	**29.5 ± 21.2 b**	**37.2 ± 17.1 b**	**0.000**	**0.210**
April	23.2 ± 16.9	28.1 ± 16.4	28.1 ± 16.4	0.464	0.022
May	50.0 ± 32.1	54.1 ± 37.5	43.3 ± 31.4	0.679	0.011
June	**88.6 ± 46.2 a**	**85.7 ± 34.1 a**	**46.4 ± 33.4 b**	**0.008**	**0.131**
July	76.9 ± 34.9	76.4 ± 35.0	63.1 ± 41.9	0.476	0.021
August	61.0 ± 39.1	69.5 ± 31.3	68.6 ± 32.6	0.625	0.014
Winter	63.3 ± 30.9	85.2 ± 43.0	82.0 ± 36.7	0.060	0.078
Spring	92.1 ± 34.8	116.2 ± 50.4	110.5 ± 43.9	0.114	0.070
Summer	**225.0 ± 72.0 a**	**231.6 ± 48.5 b**	**169.5 ± 49.0 b**	**0.014**	**0.122**

in years with low and mid frequencies (Table 1).The importance of precipitation for the formation of DFs was confirmed with the Canadian drought code being significantly higher in July and summer for years showing a high DF frequency class compared with those showing a low-mid class (Table 1). Maximum temperature in July was also significant (P = 0.042), with no significant differences between the low frequency class (24.62 °C ± 1.55), the mid DF frequency class (25.33 °C ± 1.76), and the high DF frequency class (25.71 °C ± 1.33).

When comparing both species, it was observed that *P. mariana*, also showed an association between increased DF frequency and cooler March and spring average temperatures (Table 2). For *P. mariana*, however, the mid DF frequency class was significantly different from the low class but not from the high class. The association of spring climate with mid and high DF frequency classes for *P. mariana* was also supported (as in *P. banksiana*) by the observed increase in DF frequency in years with higher levels of spring snowfall (Table 2). In contrast with *P. banksiana* however, *P. mariana* was not significantly affected by May snowfall. Despite not being significant at the P=0.05 level but at the P=0.06 level, February and March snowfall was similar in *P. mariana* and *P. banksiana*, and showed a trend of increased snow levels with DF frequency class (Table 2). There was a lack of a significant correlation in *P. mariana* between frequency of DFs and February (P = 0.062) or March (P = 0.168) total precipitation (Table 2).

As with *P. banksiana*, there were also significant differences observed among DF frequency classes in terms of the summer climate variables in *P. mariana*. High

Table 2: Mean and standard deviation for the monthly and seasonal climate variables characterizing years with low (0-5%), mid (5-25%), and high (>25%) density fluctuation frequencies for *Picea mariana*. The variables are average temperature, drought code, snowfall , and total precipitation. Bolded values indicate a significant ANOVA analysis ($P \leq 0.050$). Results are read row-wise and letters (a, b, c) represent significant differences ($P \leq 0.050$) between groups following a post-hoc Tuckey test.

Month/Season	0 – 5 %	5 – 25 %	> 25 %	P Value	Squared Multiple R
Average Temperature (°C)					
January	-17.7 ± 3.9	-17.9 ± 3.6	-17.5 ± 3.5	0.977	0.001
February	-14.5 ± 3.7	-15.0 ± 4.2	-14.5 ± 5.0	0.879	0.003
March	**-6.1 ± 3.2 a**	**-8.6 ± 3.3 b**	**-7.5 ± 2.9 ab**	**0.012**	**0.108**
April	3.3 ± 2.5	2.7 ± 2.1	2.4 ± 3.6	0.423	0.022
May	11.2 ± 2.1	10.8 ± 2.4	10.6 ± 3.0	0.676	0.010
June	16.5 ± 1.8	16.5 ± 1.8	17.4 ± 1.4	0.417	0.022
July	19.6 ± 1.5	19.8 ± 1.3	20.2 ± 0.7	0.530	0.016
August	18.5 ± 1.6	18.3 ± 1.5	18.8 ± 1.7	0.750	0.007
Winter	-15.3 ± 2.5	-15.3 ± 2.6	-15.4 ± 3.4	0.993	0.000
Spring	**2.8 ± 1.8 a**	**1.6 ± 1.4 b**	**1.8 ± 2.8 ab**	**0.024**	**0.092**
Summer	18.2 ± 1.2	18.2 ± 1.0	18.8 ± 0.6	0.349	0.027
Drought Code					
April	64.6 ± 92.4	76.8 ± 100.2	110.4 ± 188.3	0.556	0.016
May	683.9 ± 305.2	748.9 ± 288.3	724.3 ± 382.6	0.717	0.009
June	1519.8 ± 563.0	1715.9 ± 483.4	1768.3 ± 511.3	0.268	0.036
July	**2162.0 ± 610.7 a**	**2624.7 ± 595.5 b**	**3011.9 ± 785.1 b**	**0.001**	**0.184**
August	3111.5 ± 912.2	3292.7 ± 654.4	3563.4 ±1241.9	0.396	0.026
Spring	374.3 ± 184.1	412.9 ± 169.2	417.4 ± 273.5	0.682	0.011
Summer	**2264.4 ± 580.6 a**	**2544.4 ± 464.3 ab**	**2781.2 ± 728.8 b**	**0.033**	**0.092**
Snow (cm)					
January	24.8 ± 21.4	29.8 ± 22.5	26.3 ± 28.2	0.710	0.009
February	16.2 ± 11.9	21.6 ± 14.4	28.1 ± 21.7	0.058	0.075
March	17.5 ± 16.8	26.7 ± 16.7	30.6 ± 21.6	0.052	0.080
April	6.7 ± 10.6	11.7 ± 10.8	5.3 ± 5.5	0.188	0.046
May	0.7 ± 2.1	2.3 ± 4.0	1.7 ± 3.7	0.112	0.059
Winter	70.1 ± 39.4	72.4 ± 37.9	83.6 ± 43.5	0.697	0.010
Spring	**25.3 ± 20.0 a**	**40.8 ± 14.1 b**	**37.6 ± 24.5 b**	**0.020**	**0.116**
Total Precipitation (mm)					
January	25.0 ± 21.3	29.8 ± 22.5	26.3 ± 28.2	0.725	0.009
February	16.5 ± 11.6	21.7 ± 14.3	28.2 ± 21.6	0.062	0.074
March	21.9 ± 17.8	28.0 ± 16.0	33.8 ± 21.7	0.168	0.050
April	22.8 ± 15.7	34.3 ± 18.5	25.7 ± 13.2	0.054	0.082
May	50.3 ± 30.0	45.6 ± 43.7	61.5 ± 37.7	0.596	0.015
June	**90.3 ± 43.2 a**	**68.7 ± 33.4 ab**	**37.1 ± 23.9 b**	**0.003**	**0.155**
July	77.0 ± 36.0	67.1 ± 34.5	71.2 ± 43.2	0.626	0.013
Aug	62.1 ± 36.8	78.3 ± 25.5	56.8 ± 40.8	0.228	0.042
Winter	71.3 ± 38.8	78.3 ± 32.3	83.9 ± 43.6	0.626	0.014
Spring	97.5 ± 37.7	113.8 ± 57.0	121.0 ± 43.3	0.258	0.044
Summer	**228.5 ± 63.9 a**	**208.3 ± 57.4 ab**	**165.1 ± 58.6 b**	**0.040**	**0.093**

frequencies of DFs were observed in years when total precipitation was lower in June and summer, as was found in *P. banksiana* (Table 2). The difference between species however, is that in *P. mariana*, the high DF frequency class was statistically different from the low class, but not the mid class (Table 2).The importance of precipitation on DF formation is again supported in *P. mariana* by the significantly higher drought code indices observed in July and summer in years with high DF frequencies. For July drought code the same trend was seen as in *P. banksiana*, however the summer trend showed that the high DF frequency class was statistically different from the low class but not the mid class (Table 2). In contrast to *P. banksiana*, *P. mariana* showed no significant correlation with July maximum temperature.

3.3 Density Fluctuation Position in the Rings

Variation in the position of the DFs within annual rings was observed both within and among tree species (Figure 3). The overall mean was observed to be close to 40% for both *P. banksiana* and *P. mariana*, and overall there were more years where the DF position was at or below (19 for *P. banksiana* and 15 for *P. mariana*), rather than above (16 for *P. banksiana* and 8 for *P. mariana*) the mean. There were periods in both species when DF positions were above (1915-1923 in *P. banksiana*, and 1919-1926 in *P. mariana*) as well as below (1933-1941 for both species) the mean for several consecutive years. Of the 15 years in which DF3s were observed in *P. banksiana* (Figure 1) the DF position in 7 of these were above the mean, e.g. 1979, and nine below the mean, e.g. 1947 (Figure 3). In *P. mariana*, the solitary year, 1979, showing a DF3 (Figure 1) the DF position was at the mean (Figure 3).

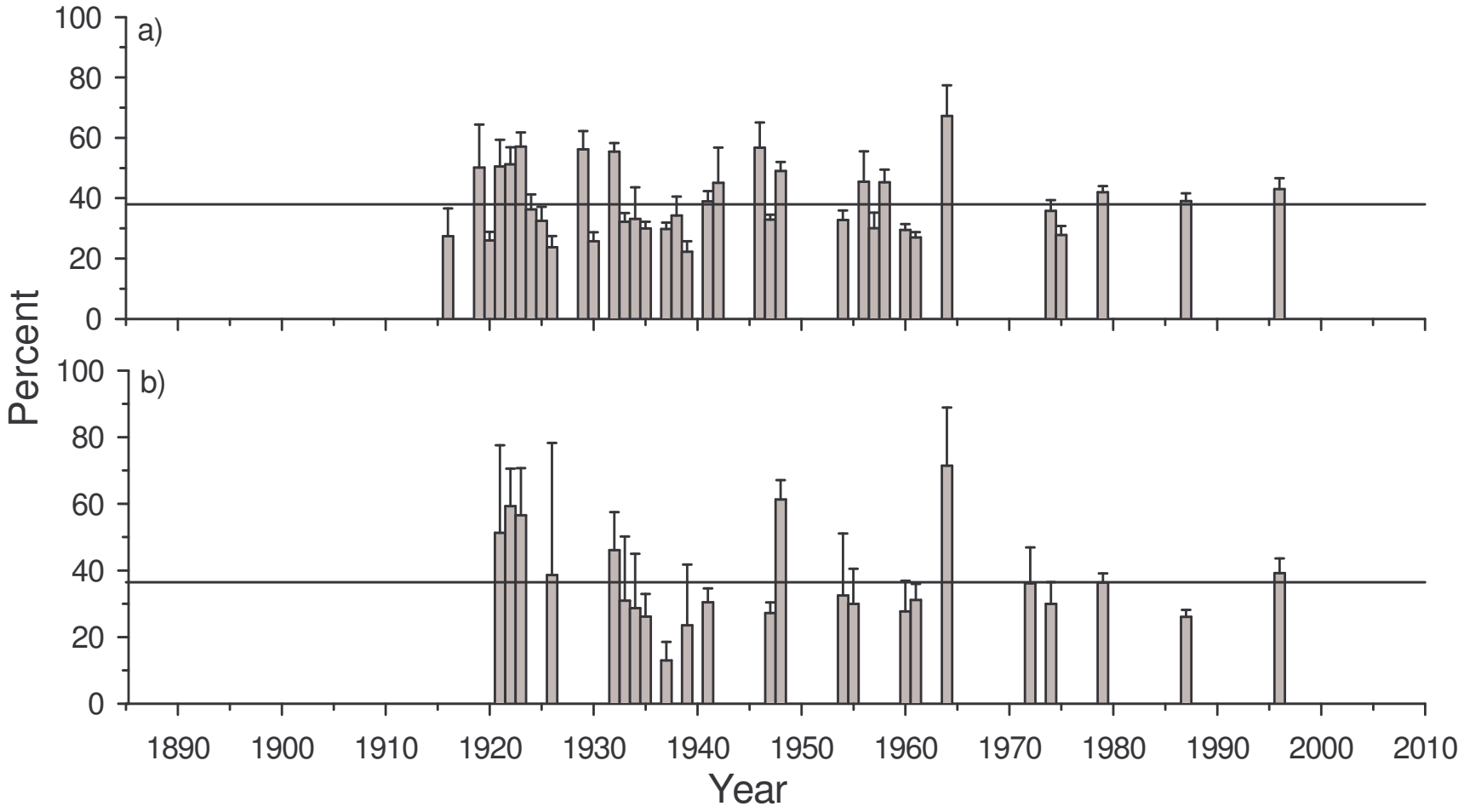

Figure 3: Density fluctuation position within the tree rings (percent of total ring width) for a) *Pinus banksiana* (n=5 sites) and b) *Picea mariana* (n=3 sites).All years for which density fluctuations represented 10% or greater of the total number of cores and at least three density fluctuations were present in any given year are shown. Bars represent means of all sites, error bars represent 95% confidence interval, and black lines represents overall means.

3.4 Tree Ring Chronologies

3.4.1 Common Interval Statistics

The descriptive statistics calculated from the residual chronologies for the period 1940-2001 for both *P. banksiana* and *P. mariana* (Table 3) indicate that earlywood (EW) represented a greater proportion of the growth ring than did latewood (LW). Both species also showed similar ring width (RW) values, indicating similar growth rates. In both species the highest mean sensitivity and standard deviation were observed in the latewood chronologies indicating greater year-to-year fluctuations. This tendancy can also be seen in Appendix H when comparing chronologies. The statistics related to the strength of the chronologies (common variation among trees) showed that the chronologies of *P. banksiana* shared more signals than those of *P. mariana*. This was indicated by stronger variance in the first principle component, a higher expressed population signal, and correlation among all radii compared to *P. mariana* and for all chronology types. The ring-width chronologies in both species had the strongest statistics when comparing all chronology types (Table 3).

3.4.2 Between and Within Species Correlation

The between-species analysis of chronology type indicated that earlywood, latewood, and ring width residual chronologies were significantly correlated in *P. banksiana* and *P. mariana* with the lowest correlation between respective chronologies being 0.635 (Table 4c). These results indicate that there is a common radial growth pattern between the two species. The within-species analysis of relationships among chronology types showed that in both species earlywood was more strongly correlated to

Table 3: Descriptive dendrochronological statistics for the *Pinus banksiana* (Pba, n=5 sites) and the *Picea mariana* (Pma, n=3 sites) tree ring residual chronologies of earlywood (EW), latewood (LW), and total ring width (RW) for the common period 1940-2001. Mean and standard deviation as well as range (in brackets) is presented.

Chronology type	EW	EW	LW	LW	RW	RW
Species	Pba	Pma	Pba	Pma	Pba	Pma
Mean ring width (mm)	1.01 ± 0.21	1.05 ± 0.29	0.35 ± 0.05	0.25 ± 0.04	1.36 ± 0.25	1.30 ± 0.32
	(0.81 - 1.31)	(0.80 - 1.36)	(0.30 - 0.42)	(0.22 - 0.29)	(1.11 - 1.73)	(1.02 - 1.65)
Mean sensitivity [a]	0.25 ± 0.03	0.25 ± 0.04	0.36 ± 0.05	0.30 ± 0.07	0.23 ± 0.03	0.22 ± 0.03
	(0.22 - 0.30)	(0.21 - 0.28)	(0.30 - 0.42)	(0.23 - 0.38)	(0.20 - 0.28)	(0.20 - 0.26)
Standard deviation	0.23 ± 0.03	0.23 ± 0.06	0.32 ± 0.04	0.40 ± 0.21	0.21 ± 0.03	0.21 ± 0.08
	(0.19 - 0.28)	(0.17 - 0.29)	(0.26 - 0.38)	(0.27 - 0.64)	(0.17 - 0.25)	(0.15 - 0.30)
First order	0.45 ± 0.05	0.39 ± 0.07	0.20 ± 0.08	0.10 ± 0.10	0.45 ± 0.06	0.35 ± 0.09
Autocorrelation [b]	(0.37 - 0.49)	(0.32 - 0.46)	(0.10 - 0.31)	(0.03 - 0.21)	(0.37 - 0.52)	(0.26 - 0.42)
Number of trees	18.40 ± 5.18	10.00 ± 7.81	18.40 ± 5.18	10.00 ± 7.81	18.40 ± 5.18	10.00 ± 7.81
	(14.00 - 27.00)	(1.00 - 15.00)	(14.00 - 27.00)	(1.00 - 15.00)	(14.00 - 27.00)	(1.00 - 15.00)
Number of radii	36.00 ± 10.39	18.33 ± 15.01	36.00 ± 10.39	18.33 ± 15.01	36.00 ± 10.39	18.33 ± 15.01
	(28.00 - 54.00)	(1.00 - 27.00)	(28.00 - 54.00)	(1.00 - 27.00)	(28.00 - 54.00)	(1.00 - 27.00)
Variance in the first	45.73 ± 3.82	40.65 ± 5.52	38.81 ± 4.97	22.09 ± 7.04	47.73 ± 4.21	41.44 ± 2.92
principle component (%)	(40.35 - 51.10)	(36.74 - 44.55)	(32.78 - 45.78)	(17.11 - 27.06)	(42.33 - 53.75)	(39.37 - 43.50)
Expressed population	0.91 ± 0.02	0.89 ± 0.02	0.87 ± 0.03	0.72 ± 0.10	0.91 ± 0.02	0.90 ± 0.01
signal [c]	(0.88 - 0.93)	(0.88 - 0.91)	(0.83 - 0.90)	(0.65 - 0.79)	(0.89 - 0.93)	(0.89 - 0.90)
Mean correlation among	0.43 ± 0.03	0.37 ± 0.06	0.35 ± 0.04	0.17 ± 0.07	0.45 ± 0.04	0.38 ± 0.03
all radii	(0.37 - 0.46)	(0.33 - 0.41)	(0.29 - 0.38)	(0.12 - 0.22)	(0.39 - 0.49)	(0.36 - 0.40)

[a] Mean sensitivity is the average difference between successive ring index values. This index ranges from 0 (no difference between successive ring widths) to 2 (every second ring missing) and larger values indicate the presence of considerable high-frequency variance (Fritts 1976).

[b] Calculated from the standard chronology.

[c] Expressed population signal statistic is an indicator of chronology reliability. It measures how well the chronology compares to the theoretical population chronology based on an infinite number of trees (Cook and Kairiustis 1990). The statistic ranges from 0.0 to 1.0, i.e. from no agreement to 1.0 for perfect agreement with the population chronology.

Table 4: Correlation coefficients for a) within-species analysis of *Pinus banksiana* (Pba) and *Picea mariana* (Pma) earlywood (EW), latewood (LW), and ring width (RW) residual chronologies, b) within-species lag analysis of *Pinus banksiana* (Pba) and *Picea mariana* (Pma) earlywood (EW), latewood (LW), and ring width (RW) residual chronologies (with a one year lag between residual chronologies and forward residual chronologies, EW f, LW f, PLW f, and RW f), and c) between-species analysis of *Pinus banksiana* (Pba) and *Picea mariana* (Pma) earlywood (EW), latewood (LW), and ring width (RW) residual chronologies. All values in bold are significant ($P \leq 0.050$).

a)	EW	LW	RW
	Pba		
Pba			
EW	**1.000**	**-**	**-**
LW	**0.314**	**1.000**	**-**
RW	**0.904**	**0.652**	**1.000**
	Pma		
Pma			
EW	**1.000**	-	**-**
LW	-0.056	**1.000**	**-**
RW	**0.929**	**0.269**	**1.000**

b)	EW f	LW f	RW f
	Pba		
Pba			
EW	-0.040	0.047	-0.121
LW	0.070	-0.055	-0.086
RW	0.021	0.012	-0.114
	Pma		
Pma			
EW	-0.144	0.167	-0.170
LW	0.041	0.074	-0.018
RW	-0.129	0.215	-0.158

c)	EW	LW	RW
	Pma		
Pba			
EW	**0.659**	0.011	**0.652**
LW	-0.022	**0.673**	**0.241**
RW	**0.525**	**0.280**	**0.635**

RW. In contrast with *P. mariana,* however, EW in *P. banksiana* was also correlated positively to LW (Table 4a). The within-species lag analysis showed that there was no significant relationship between residual and forward residual chronologies for any of the growth variables in either study species (Table 4b).

3.4.3 Tree Ring Chronology and Climate Association

The correlation functions between individual climate variables and both the EW and LW chronologies indicated that both chronology types have different associations to climate, whereas that of RW integrated both EW and LW signals and this was generally observed for each species (Figures 4 and 5). In *P. banksiana* EW was positively associated with overall precipitation in the summer of the year prior to ring formation (Figure 4a). In contrast, *P. mariana* showed only a positive correlation between EW and August total precipitation of the previous year as well as a stronger negative association between EW with June average temperature of the current year (Figure 5a). Drought was negatively associated with EW and summer (especially June and July) in the current year, while in *P. banksiana*, while in *P. mariana* it was important in July only (Figures 4a 5a)

There was also a negative association observed between LW and October and December total precipitation of the previous year (Figure 4b) in *P. banksiana*. During the year of ring formation, warm and dry spring conditions were positively associated with LW chronology in this species, and were most important during April and May (Figure 4b). There was also a significant association (0.226, P= 0.043) between LW chronology and maximum temperature in February. In contrast to *P. banksiana*, *P. mariana* did not show any correlation with spring average temperature or total precipitation (Figure 5).

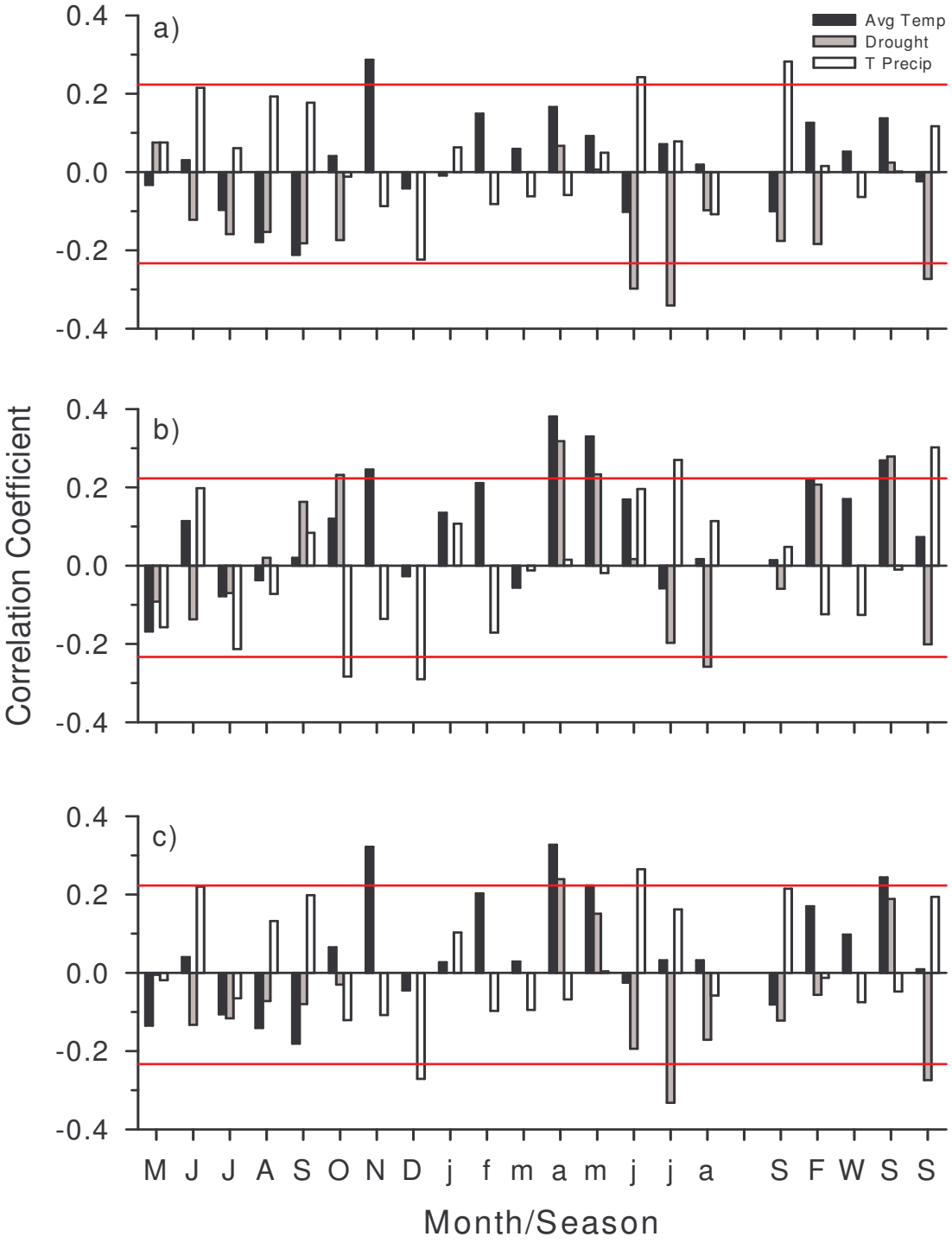

Figure 4: Correlation coefficients between *Pinus banksiana* a) earlywood, b) latewood, and c) total ring width residual chronologies and climate variables average temperature, drought code, and total precipitation. Red lines indicate upper and lower significance P $\leq$0.050. Months range from May previous (M) to current august (a) and seasons range from summer previous (S) to current summer (S).

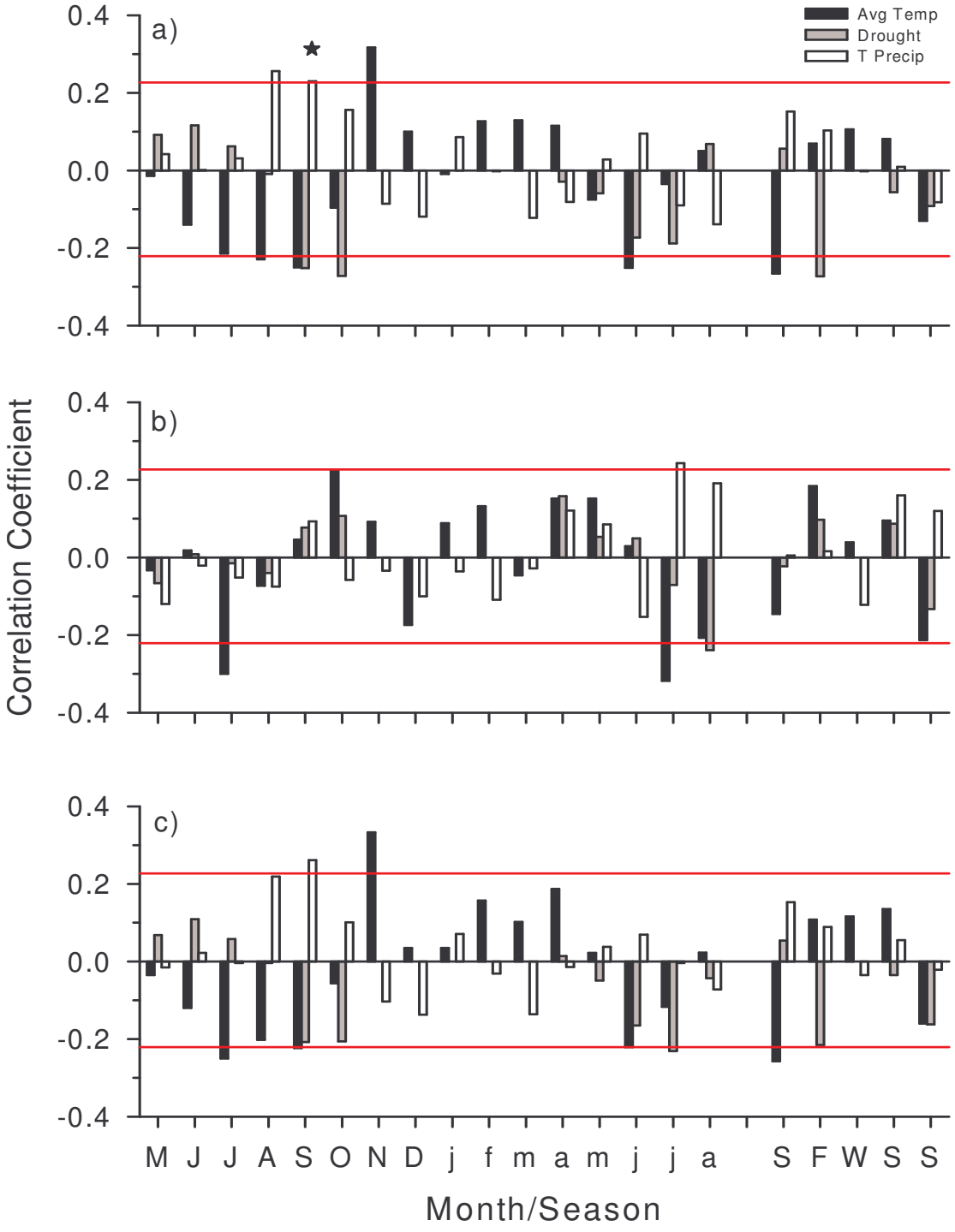

Figure 5: Correlation coefficients between *Picea mariana* a) earlywood, b) latewood, and c) total ring width residual chronologies and climate variables average temperature, drought code, and total precipitation. Red lines indicate upper and lower significance P $\leq$0.050. Months range from May previous (M) to current August (a) and seasons range from summer previous (S) to current summer (S). The starred value is not significant.

For *P. banksiana*, LW was positively correlated with summer drought in the previous year. During the summer of ring formation the negative effect of drought on radial growth was indicated by the significant correlation between LW and August drought in both *P. banksiana* and *P. mariana* (Figures 4b and 4c).

In *P. banksiana*, it was observed that there was a negative association between RW and December total precipitation of the previous year (Figure 4c). As with LW, RW was also associated with warm and dry spring conditions in the year of ring formation in this species (Figure 4c). *Picea mariana*, however, showed a positive association between RW and previous September total precipitation (Figures 5c). The negative effect of drought was most important for *P. mariana* RW in July of the current year, while for P. banksiana it was most important in July as well as summer (Figures 4c and 5c).

All chronologies in *P. banksiana* were positively affected by average temperature, and EW was negatively affected by previous September maximum temperature (-0.251, P= 0.025). In contrast, chronologies for *P. mariana* were negatively associated with previous summer and fall average temperatures. Common to both species was the positive relationship between warmer November temperatures in the year previous to growth and both EW and RW chronologies (Figures 4 and 5). There was also observed to be a positive association between LW in *P. mariana* and all chronologies in *P. banksiana* with June – July precipitation. In contrast to *P. banksiana* however, there was a stronger negative association in *P. mariana* between EW and RW chronologies with June, and LW with July average temperature.

4.0 Discussion

4.1 Density Fluctuation Abundance and Intensity

The results from the analysis of variance clearly showed that with increasing frequency, the DFs were more regionally represented (found in more sites), and a greater number of very distinctive DFs were observed. These results also helped to support the validity of the DF categories and frequency classes that were created. The physical differences found among density fluctuations agree with findings of Priya and Bhat (1998) who classified DFs in *T. grandis* into different types, based on their anatomy and location within the annual ring.

The observed frequency of DFs in the juvenile stage of the trees may be an indication that young trees are more sensitive to their environment and thus produce more DFs than older trees. This agrees with Copenheaver *et al.* (2006) who found that in *P. banksiana* juvenile trees were more prone to produce false rings than older trees. The same finding was observed in *P. sylvestris* by Rigling *et al.* (2001) and in *Pinus nigra* Arn. (Wimmer *et al.* 2000). In some tree species, multiple growth flushes may occur in a single year (Telewski and Lynch 1991), and may explain the juvenile effect in the two study species. These flushes produce multiple phases of elongation, are more common in younger trees than older trees, and have been found in *Pinus radiata* D. Don (Monteray pine) and *Pinus taeda* L. (loblolly pine) (Telewski and Lynch 1991). According to Kramer and Kozlowski (1960), trees rarely grow continuously during the entire year, resulting in recurrent flushes of shoot growth that may be caused by accumulation of an inhibitor or the deficiency of some substance essential for growth. Rudolph and Laidley (1990) suggested that the flushes are due to favorable moisture conditions in late summer,

and that they may or may not cause false rings in *P. banksiana*. There may be differences that exist between species in regards to the juvenile period (Wimmer 2000) that could explain the differential DF relative frequencies seen between *P. banksiana* and *P. mariana* in this youthful period of development. Further investigation such as inclusion of juvenile years in the ANOVA model as a covariable, could also allow to test whether or not the DFs occur under the same climatic conditions in the juvenile and mature periods, and would enable a better understanding of this phenomenon.

Results indicated that DF3s co-appeared almost exclusively with DF1s and DF2s, and that DF2s occurred alongside DF1s. It is possible that the distinctiveness of DFs and their pattern of appearance could be a measure of the regional intensity of the climatic conditions that occur in a particular year. Years in which DF3s are produced might represent worse growing conditions than years in which only DF1s are produced. This could be tested by comparing EW, LW and RW measurements in years with and without DFs with climate variables. Because all trees do not produce the exact same growth response to their environment (Fritts 1976), it was expected that *P. mariana* would not produce DFs. However, contrary to the hypothesis, *P. mariana* produced DFs, and in many of the same years as *P. banksiana*. This suggests that both species react to changes in their environment in a similar way. Differential anatomical features of DFs have also been described by Rigling *et al.* (2001) who found that the transition of the DFs varied from sharp to diffuse. This variation was attributed, among other causes, to differing triggering factors (such as temperature and precipitation), and the strength of the triggering factor. Kuo and McGinnes (1973) also found an association between the characteristics of the drought period and the structure of false rings. They showed that

severe droughts formed narrow false rings and that moderate droughts produced broader false rings. These studies have shown that differing degrees of drought can affect the physical characteristics of DFs. This characteristic of false rings would be interesting to measure in future study, and may be useful in determining intensity and/or length of unfavorable growing conditions such as drought Distinctiveness could potentially be better defined with image analysis programs such as WinDendro which gives intensity to the boundaries using grey pixel classification (Régent Instruments Inc. 2005). This data could then be assessed against climate data, giving a more quantitative analysis.

4.2 The Position of Density Fluctuations in Tree Rings

The position of the DF in the growth ring represents the point in the growing season when it was formed. This data could potentially be used to more accurately pinpoint timing of drought in the growing season. As there are physiological factors involved in tree growth as well as climatic factors, more in depth analyses and studies are required to investigate this possibility. One potential subject of study is early summer compared with late summer drought. Kuo and McGinnes (1973) found that the positions of false rings in *J. virginiana* were determined by the point in the growing season when droughts occurred. Late season droughts followed by ample rainfall usually resulted in false rings in the latewood zone, while early season droughts were correlated with false rings in the earlywood zone. De Micco *et al.* (2007) also suggested that DFs may provide information at the seasonal level. Campelo *et al.* (2007) categorized DFs based on their position within the rings and found that changes in climatic conditions at different times

of the growing season were associated with those DFs formed in different zones of the rings.

4.3 Density Fluctuation and Climate Relationships

Earlywood and latewood cells are produced in response to physiological and genetic control, and climatic factors (Larson 1960 Wimmer 2002). The synchrony of DF abundance and distribution among years in *P. banksiana* and *P. mariana* supports the idea that the trees are responding to regional climate in a similar fashion. It was found that formation of DFs was related to specific climatic variables in both species. Spring temperatures, particularly March, were significant in both species, showing that in years with cooler conditions at the start of the growing season, a higher frequency of DFs was observed. The effect of spring climate on DF production was also observed in terms of precipitation. Contrary to expectations, DF formation was related to increased levels of February, March, May, and spring snow in *P. banksiana* and with spring snow in *P. mariana*. Although February and March were not significant at the 95% confidence level in *P. mariana*, they would be considered significant at the 90% confidence level. Though a relationship with drought was expected, more spring snow as opposed to less resulted in the production of DFs. Density fluctuation formation was also directly related to February and March total precipitation in *P. banksiana* only. It is possible that cool springs with more snow represent a late start to the growing season and lead to more DFs being formed because of the shorter time available for latewood cell maturation. Wimmer et al. (200) observed that a wet April-dry May-wet June progression was most often correlated with DF formation in *P. nigra*. A similar result was found in this study with a

wet spring (more spring snow)-dry summer (increased drought) progression. A full understanding of this important spring climate signal requires further investigation.

During summer months, DF frequency was correlated with lower June and summer total precipitation in both species. It is probable that this reduction in precipitation was responsible for formation of cells with increased wall thickness and reduced tracheid diameter, which resumed with larger size and thinner walls in better conditions (Fritts 1976), as evidenced by the presence of numerous DFs. Rigling *et al.* (2002) also found a positive correlation between July and August precipitation and false ring formation on dry sites. The relationship with lower summer precipitation levels was emphasized by the Drought Code indices, whose R squared values were the highest among all climate variables. There was a significant increase in DF frequencies in years when droughts were more severe in July and summer in both study species. This relationship, along with a high abundance of DFs represented in a large proportion of sites, shows a more regional climate signal. Summer temperature does not appear to be as important a factor as precipitation in DF formation in either species, as July maximum temperature in *P. banksiana* was the only significant result observed. According to De Micco *et al.* (2007), DFs are usually formed by sudden drought events during the growing season. The cells that are produced have smaller lumina and thicker walls in comparison with normal cells formed before and after the stress. The formation of these types of cells can be explained by the limited cell expansion caused by a lack of water.

Other DF-climate associations include a relationship between precipitation and DF formation presented by Priya and Bhat (1998), who found that an unusually dry May followed by heavier rains in June was related to the production of false rings in *T.*

grandis, and that false rings were produced as a response to drought. Wimmer *et al.* (2000) found that a wet April with a dry May and a wet June was the most likely combination responsible for DF production. The association of DF frequency with dry periods throughout the growing season links these findings with results presented in this study. Density fluctuations were also found in *P. banksiana* by Copenheaver *et al.* (2006). The authors, however, found no correlation between temperature or precipitation and DF formation, and this study disagrees with the finding that external climate triggers are not important in the formation of DFs. The lack of correlation with climate presented by Copenheaver *et a*l. (2006) could perhaps be linked to problems or issues with dating and/or statistical procedures. There are many studies, however, that support the DF-climate relationships presented in this study. Glerum (1970) found that in *P. glauca* drought rings were produced in trees subjected to high level drought treatment. Rigling *et al.* (2001) found that temperature and precipitation changes were factors for false ring formation in *P. sylvestris*. Wimmer *et al.* (2000) found that precipitation was a factor in false ring formation and that false rings have the potential to be used for estimating climatic events due to their narrow window of formation in the year.

4.4 Between and Within Species Growth Relationships

As hypothesized, both species showed similar radial growth patterns, as indicated by the strong correlation between the residual chronologies for EW, LW, and RW of the two species. This was expected as both species were sampled from the same stands. Earlywood had a strong association with RW in both species, indicating that EW made up a larger portion of the growth rings than did LW.

4.5 Tree Ring Chronology and Climate Relationships

The correlation functions represent the separate relative effects of specific climatic factors on ring width (Fritts 1976). Variations in cell enlargement and differentiation that occur throughout the growing season are responsible for the numerous characteristics of the tree rings, as well as their general appearance (Fritts 1976). Differences were observed between and within the two study species in EW, LW, and RW growth and their relationships to climate variables. Tree growth has been found to be regulated by environmental and genetic factors, and is species specific (Wimmer 2002). The differential genetic makeup of *P. banksiana* and *P. mariana* could be at least partly responsible for the observed differences between species in terms of their response to climate variables. An important difference observed between the two species was that *P. banksiana* was more sensitive to precipitation and *P. mariana* was more sensitive to temperature. It was also observed that in *P. banksiana* EW width was positively associated with summer precipitation in the year prior to ring formation, and that LW and RW were positively associated with spring temperature in the current year. In *P. mariana* on the other hand, there was a strong association between all chronologies and either June or July temperatures in the current year, and no correlation with spring conditions. Since *P. banksiana* is more affected by spring climate, it may be able to take advantage of an earlier spring. Girardin and Tardif (2004) also found a positive growth response in conifers in Duck Mountain Provincial Forest, Manitoba, to warmer spring temperatures, specifically with higher April temperatures and *P. banksiana*. They also found a negative response to warmer June temperatures. Earlier growth resumption or start of photosynthesis in *P. banksiana* in spring, in comparison with *P. mariana*, would favor

the production of the larger LW and RW that were observed, as radial growth depends mainly on current photosynthesis (Kozlowski 1962). These larger rings could indicate more carbohydrate reserves present in the trees, which would then be less conductive to DF formation. This is also supported by the observation that more DFs were produced in *P.banksiana* in years with cool spring temperatures, which indicate a later start to the growing season. This is not absolute, however, as LW as measured in this study was partly due to the presence of DFs in the rings. Future analysis using true measurements of latewood could perhaps shed some light on this potential relationship.

Growth in both species was negatively affected by summer drought levels. Cell wall production and tree growth are highly dependant on carbohydrates synthesized from photosynthesis, which is temperature and water-stress sensitive (Kramer and Kozlowski 1960). Increased levels in drought would reduce the amount of photosynthesis carried out by trees and thus reduce carbohydrates, which could explain the reduced growth observed in both study species throughout the summer months.

Both species showed a positive association between radial growth and warmer fall (November) temperatures in the year previous to ring production. This is consistent with the findings of Stevenson and Tardif (2001) *Thuja occidentalis* L. (northern white cedar) trees in Manitoba. The authors suggested that it is possible that this association may regulate the accumulation of snow which was negatively correlated with radial growth. They also hypothesized that mild falls may facilitate longer growing seasons and an earlier resumption of photosynthesis in the spring by reducing the depth to which the soil is frozen. The influence of fall temperatures was also observed in *Larix laracina* (Du Roi) K. Koch. as well as *P. mariana* in the Churchill, Manitoba, area (Girardin *et al.*

2005), with a positive association between radial growth and a warmer previous October. All of these results help to illustrate that the climate signal may be far reaching and present in many tree species.

In terms of growth, climate, and DF formation, abundant summer (especially June) precipitation led to larger EW and LW growth in *P. banksiana*, thereby reducing the risk of DF formation. Warm spring temperatures also promoted larger LW and RW and fewer DFs. Summer drought in both study species promoted production of DFs as well as formation of smaller EW and RW, which was strongest in July.

5.0 Conclusions

The primary hypothesis of this study was confirmed, and a correlation between DF formation and climate was found. The study of DFs in *P. banksiana* and *P. mariana* has provided evidence that these two species were responding to the climate signals prior to and during the current growing season into their growth. The results also showed that the greater percentage of trees showing DFs, the more DF3s are observed, and thus the more regional the climate signal is. Contrary to the second hypothesis, both species demonstrated production of DFs and were associated with the same overall climatic signals. *Picea mariana* showed DFs in many of the same years and, more importantly, many of the same high DF frequency years as *P. banksiana*. Higher frequencies of DFs were formed in years with cooler springs and more spring snow, as well as in years with drier summers with a more severe drought rating. In support of the second hypothesis, *P. banksiana* and *P. mariana* showed similar radial growth patterns as indicated by the strong correlation observed between the same chronology types (EW, LW, and RW). Although July drought code and previous November average temperature were correlated with radial growth in both species, differences were observed in their responses to climate. In *P. banksiana,* warm and dry spring conditions and abundant summer precipitation were conductive to larger rings, while in *P. mariana* previous fall and current summer temperatures were most important. Density fluctuations in these two tree species in Nopiming Provincial Park have the potential to be used for future identification and analysis of past climatic events, due to their association with temperature and precipitation throughout the growing season. The juvenile effect, present in both species, needs to be taken into account in such reconstructions, perhaps through more complex

ANOVA testing. However, a better understanding of the juvenile effect's causes needs to be reached prior to attempts to utilize or eliminate the effect. Some aspects of DF formation, such as the juvenile effect and the distinctiveness of DFs and their possible relationship with severity of drought, require further study and investigation. The distinctiveness of DFs also poses an interesting topic for future research. Some studies, including this one, have already found anatomical differences in DFs, however, there is a need for quantification of such characteristics through methods such as isotope analysis or image analysis.

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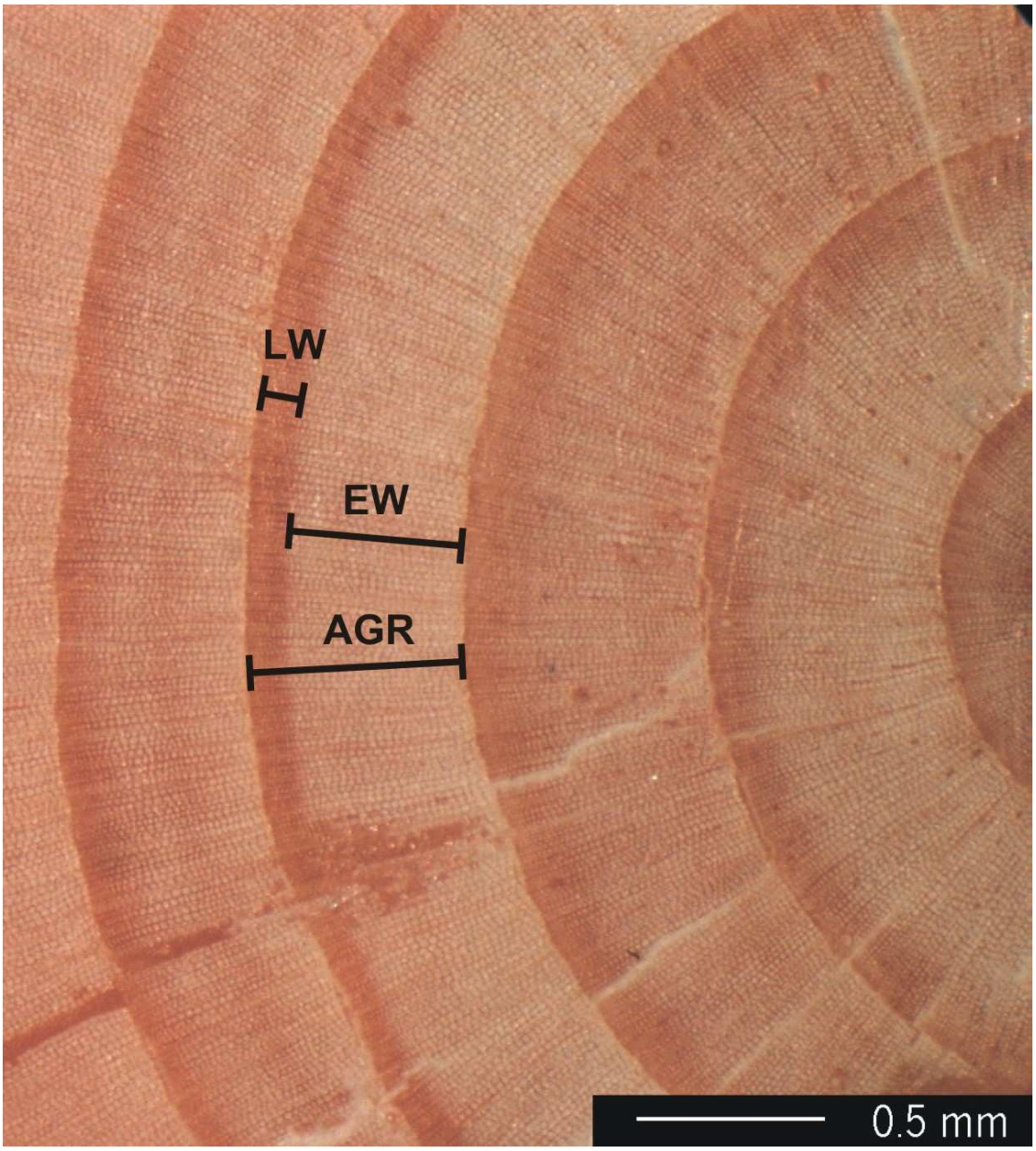
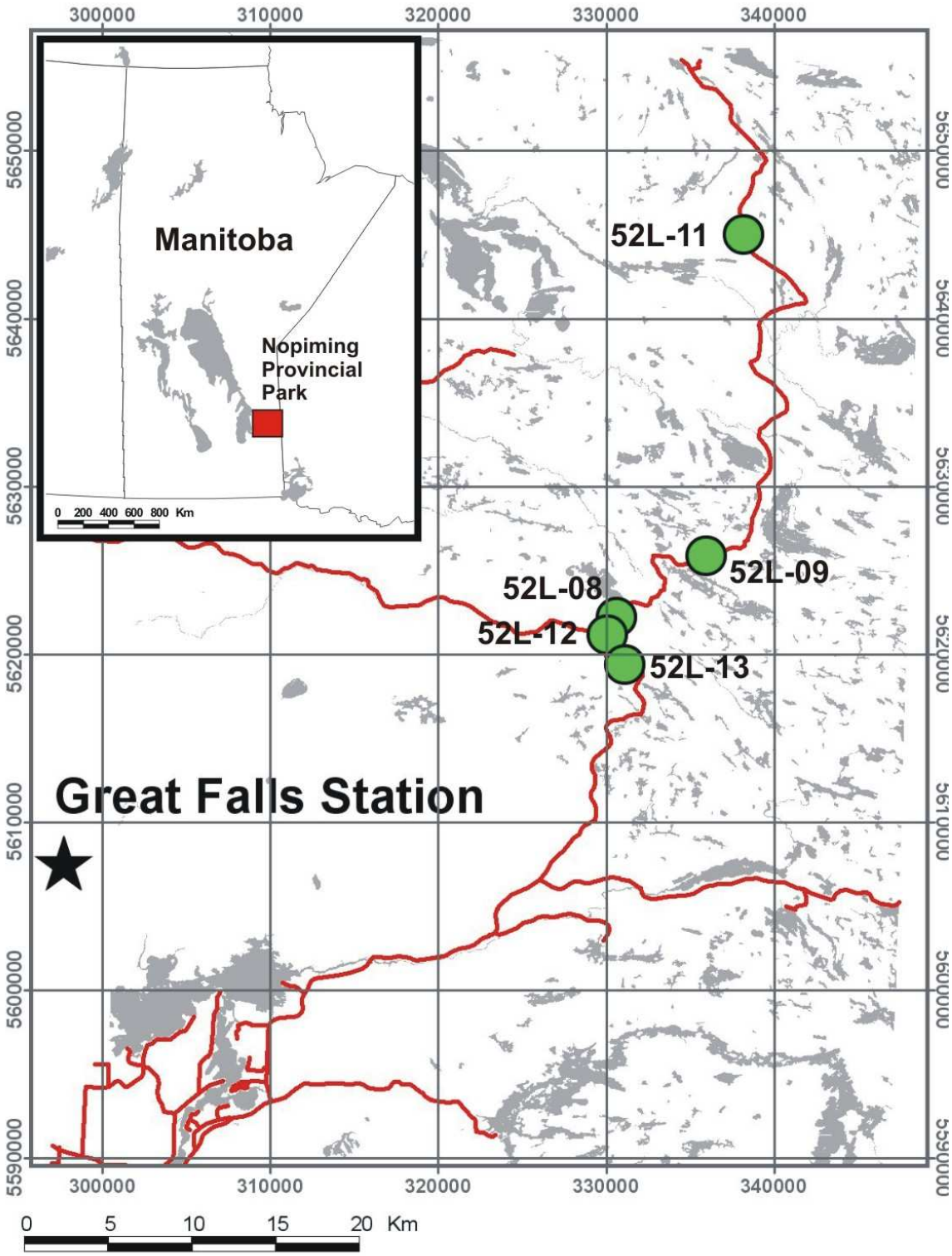
Appendices

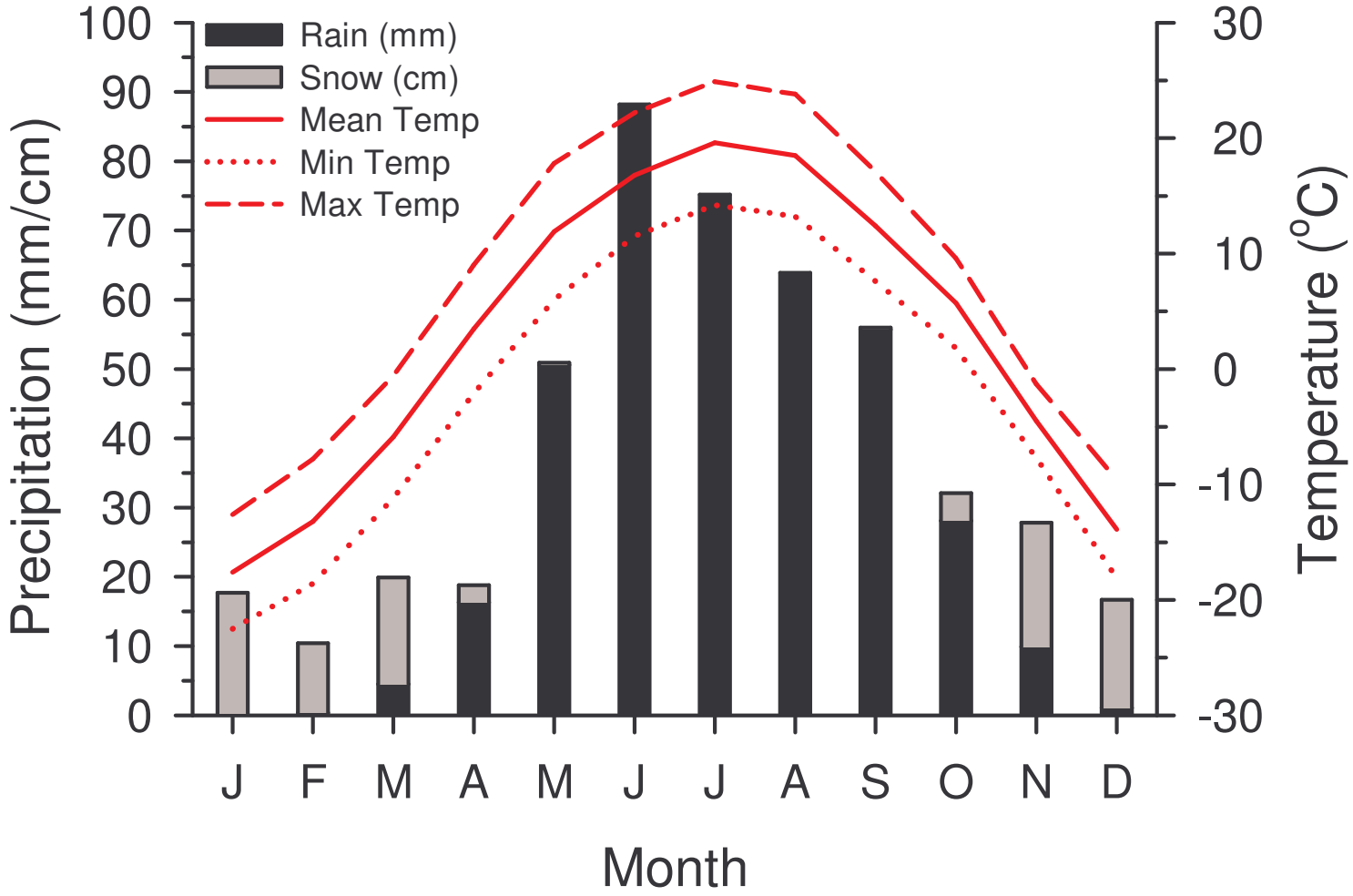
Appendix A: Picture of a *Pinus banksiana* Lamb. core, showing annual growth rings (AGR). The earlywood (EW) and latewood (LW) zones are indicated.



Appendix B: Location and surroundings of study area (Nopiming Provincial Park). The five sampling sites are indicated by green circles, and Great Falls Climate Station is indicated by the black star.



Appendix C: Climatic diagram for Great Falls, Manitoba. Monthly average temperature and precipitation data for the period 1971-2000 are presented

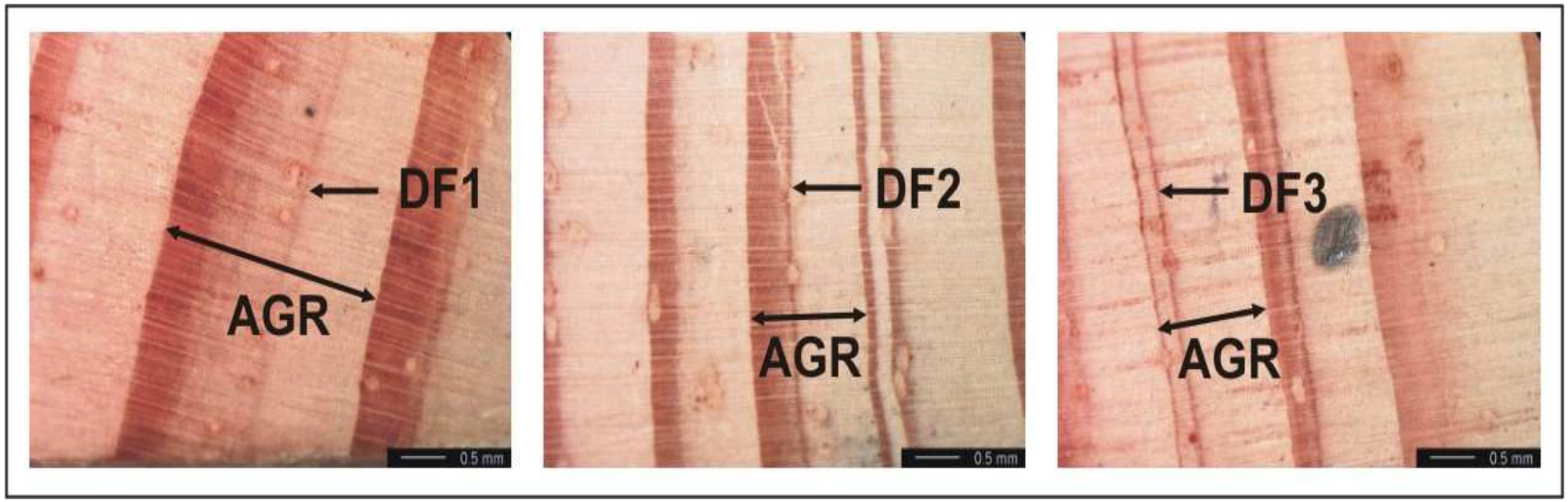


Appendix D: Characteristics of the five sites (52L-08, 09, 11, 12, and 13) sampled in Nopiming Provincial Park, Manitoba. Six species of trees are represented: *Abies balsamea* (Aba), *Betula papyrifera* (Bpa), *Pinus banksiana* (Pba), *Picea glauca* (Pgl), *Pinus mariana* (Pma), *and Populus tremuloides* (Ptr).

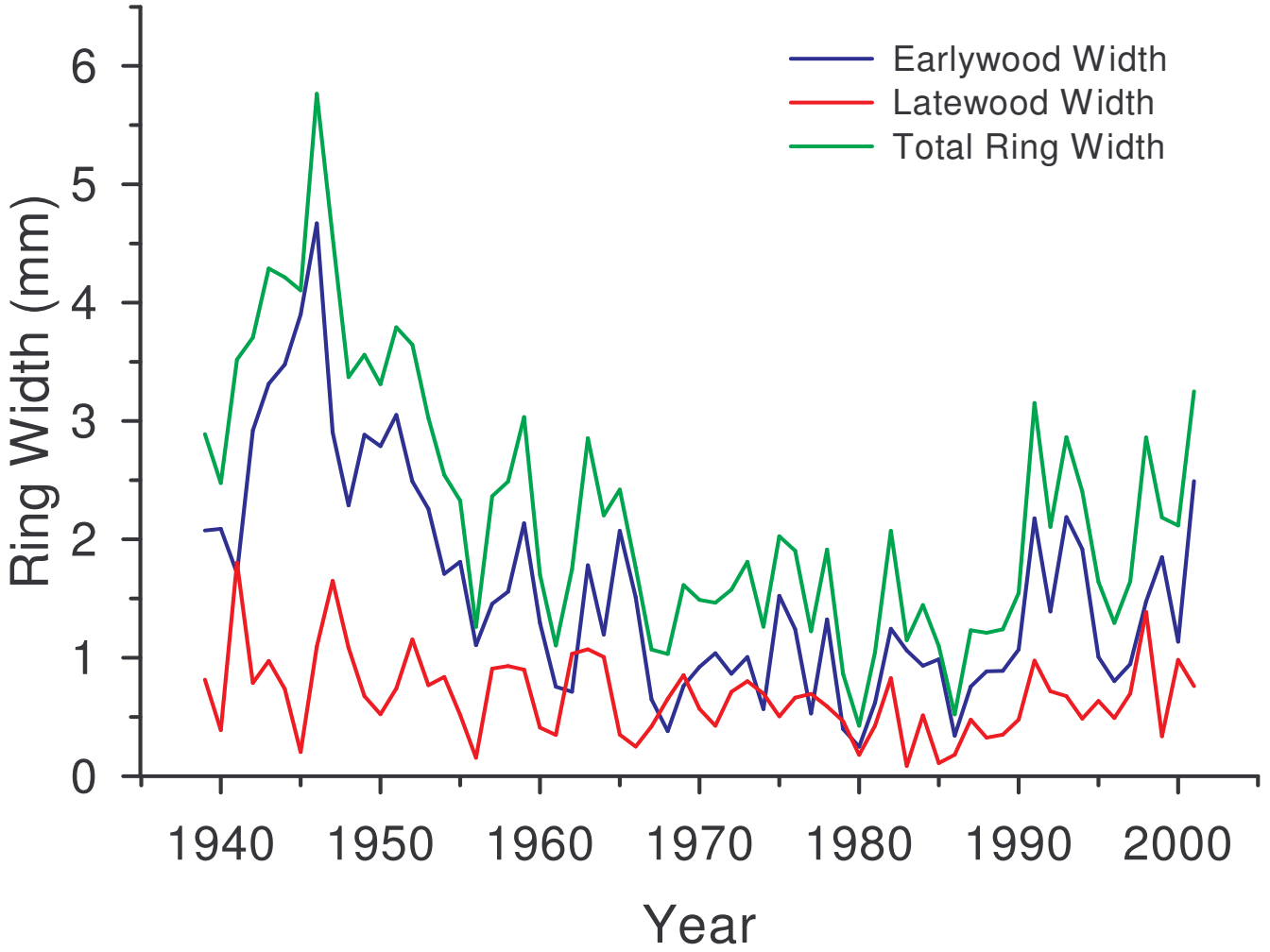
		52L-08	52L-09	52L-11	52L-12	52L-13
Species Density (trees/ha)	Aba	-	-	9	116	222
	Bpa	-	-	38	-	79
	Pba	422	741	235	422	365
	Pgl	-	-	-	42	48
	Pma	-	475	319	95	269
	Ptr	-	-	-	-	32
	Total	422	1216	601	675	1015
Species Basal Area (m^2/ha)	Aba	-	-	0.26	1.50	1.66
	Bpa	-	-	0.18	-	0.33
	Pba	11.50	18.40	8.07	12.13	15.50
	Pgl	-	-	-	0.17	1.07
	Pma	-	4.36	5.44	1.67	4.51
	Ptr	-	-	-	-	0.17
	Total	11.50	22.76	13.95	15.47	23.24
Dominant Trees	Species	Pba	Pba	Pba	Pba	Pma[a]
	Height (m)	8.43 ± 0.78	7.47 ± 0.70	8.78 ± 0.84	8.64 ± 0.99	10.27 ± 0.32
	DBH (cm)	24.0 ± 1.5	19.3 ± 2.6	26.9 ± 7.9	22.2 ± 2.1	25.1 ± 3.3
pH	LFH	4.87 ± 0.19	3.99 ± 0.26	4.35 ± 0.69	4.12 ± 0.18	4.61 ± 0.10
	A	5.35 ± 0.23	4.22 ± 0.38	4.75 ± 0.33	4.30 (n=1)	4.62 ± 0.11
	B	5.79 ± 0.38	-	4.69 (n=1)	-	-
Texture	Soil Pit #1	Fine sand	Rock	Loam	Rock	Gravel/ coarse sand
	Soil Pit #2	Fine sand	Sandy loam	Rock	Sandy loam	Sandy loam
	Soil Pit #3	Fine sand	Loam	Silt/clay loam	Rock	Organic

[a] At this site n=2 because one of the dominant trees was Pba (height 21.3 m, DBH 50 cm).

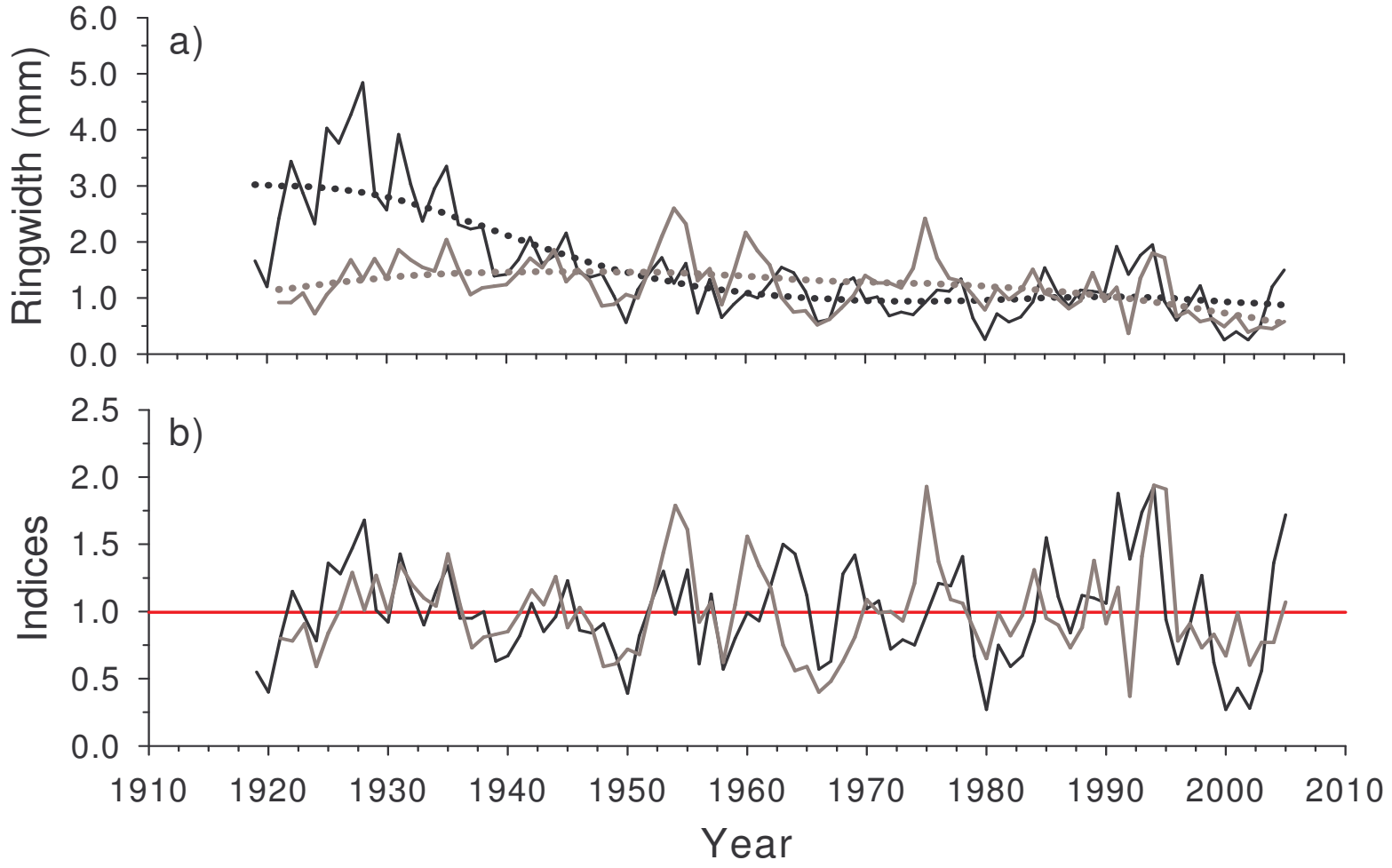
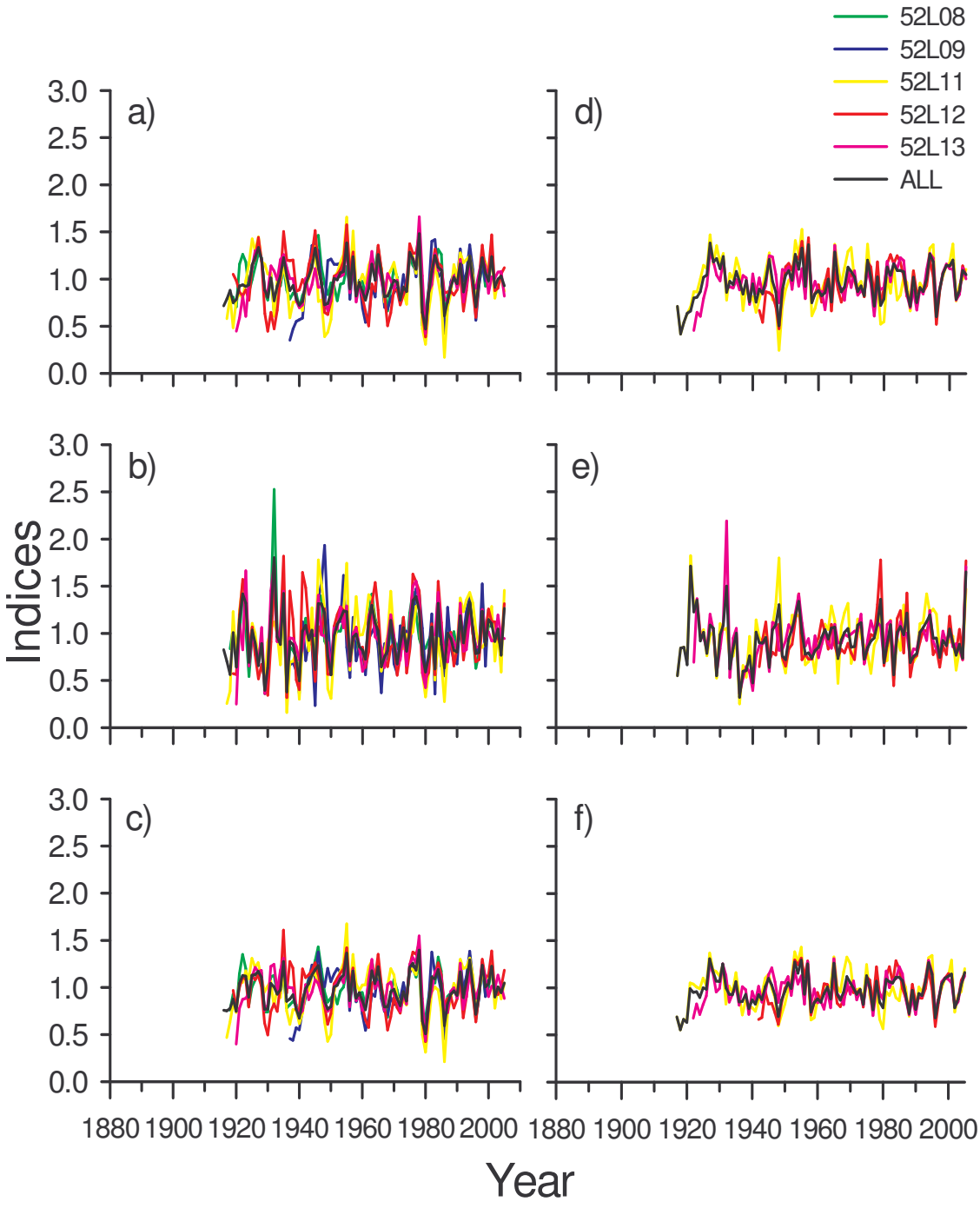
Appendix E: Illustration of the three density fluctuation categories in *Pinus banksiana* based on clarity and intensity. DF1s are hazy density fluctuations with low intensity, DF2s are moderately clear and intense density fluctuations, and DF3s are very clear and intense density fluctuations. Annual growth rings (AGR) are shown.



Appendix F: Measurements of earlywood, latewood, and total ring width for *Pinus banksiana* core 52L0902B, spanning the years 1939 to 2001.



Appendix G: An illustration of standardization. a) Total ring width measurements of *Pinus banksiana* core 52L1301B (solid black line) and *Picea mariana* core 52L1101B (solid grey line) showing the respective 50 year splines (dotted lines) fit to the measurement series. The ring width index for both cores is also shown (b). After standardization the tree ring indices have a mean of 1.0 (red line).



Appendix H: Standard a) earlywood, b) latewood, and c) ring width chronologies for *Pinus banksiana* (Pba, n=5 sites) and d) earlywood, e) latewood, and f) ring width chronologies for *Picea mariana* (Pma, n=3 sites). All chronologies presented have a minimum of 4 cores for any given year.