AN ANALYSIS OF THE DAILY RADIAL ACTIVITY OF 7 BOREAL TREE SPECIES, NORTHWESTERN QUEBEC

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Abstract. In the 'Des Vieux Arbres' ecological reserve situated within northwestern Québec, 40 band dendrometers were installed on 7 of the major boreal tree species. The late Spring–early Summer daily radial activity registered in 1997 was related to daily weather variables. For each tree species, the daily mean i) cumulative radial increment and ii) radial activity indexed series obtained by first-difference standardization were analyzed. The results indicate the existence of strong similarities among the 7 species. All showed strong synchronous fluctuations in radius during late winter and early spring. This period ended with a short but sharp increase in radial increments that marked the passage of water into the stem. This initial swelling, less obvious in *Pinus* species was followed by a prolonged period of little change in radial activity. Meteorological data indicated that air temperature was positively related to stem swelling during the late winter–early spring period. Both air and soil temperatures became negatively related to radial expansion once the passage of water has occurred in the stem. Starting in early June, all species registered a sustained increase in radial increments possibly associated with active cell division. After this, radial expansion was negatively related to air temperature and positively to rainfall.

Keywords: band dendrometers, boreal forest, late winter–early summer, meteorological factors, stem increment, shrinkage and swelling

1. Introduction

About 50 years ago, Belyea *et al.* (1951) stated that our knowledge concerning the course of seasonal growth of forest trees in Canada was very inadequate. Today, data related to the seasonal growth behaviour of the major tree species in Canada are still lacking. In recent decades, no studies were published on the seasonal cambial activity of tree species in the Canadian boreal forest. Most of the research on the evolution of seasonal radial growth in trees has been carried from the 1920s to the 1960s. In Ontario, important investigations were conducted by the Forest Insect Laboratory in Sault Ste. Marie and the Petawawa Forest Experimental Station Chalk River on some of major tree species of the region (Belyea *et al.*, 1951; Fraser, 1952, 1954, 1956, 1958). Few studies have also been recently published for North America (Lodewick, 1925; Daubenmire and Deters, 1947;

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Daubenmire, 1949, 1950; Jackson, 1952; Turner, 1956; McClurkin, 1958; Bormann and Kozlowski, 1962; Kozlowski and Winget, 1964; Zahner *et al.*, 1964; Winget and Kozlowski, 1964, 1965; Braekke and Kozlowski, 1975; Pereira and Kozlowski, 1976; Conner *et al.*, 1981; Robertson, 1992).

To monitor the seasonal course of changes in cambial activity, two methods have traditionally been used (Chalk and Phil, 1930; Bannan, 1955). The first approach has relied on the use of multiple sampling and histological analysis of wood samples whereas the second approach has focused on the use of growth curves obtained by either dendrometers or dendrographs. Today, automated dendrometers allow for continuous measuring of cambial activity in trees at time scales ranging from seconds to days. Two basic types of dendrometer (either manual or automated) have been used to monitor the seasonal course of cambial activity (Bormann and Kozlowski, 1962; Kramer and Kozlowski, 1979). The first type, the band dendrometer, measures the changes in the tree circumference whereas the second type, the point dendrometer, measure the changes at a single point (radius) on the tree (see MacDougal, 1921; Reineke, 1932; Daubenmire, 1945; Belyea *et al.*, 1951; Fritts and Fritts, 1955; Phipps and Gilbert, 1960; Bormann and Kozlowski, 1962).

Both band and point dendrometers have their advantages and disadvantages. Band dendrometers, if no errors related to slack in the bands occur (Keeland and Sharitz, 1993), are believed to provide a better estimation of the average radial growth because they summarize the growth of all radii. In contrast, measurements obtained by point dendrometers were reported to differ significantly with location (height and exposition) on a tree (Bormann and Kozlowski, 1962). Point dendrometers allow however to better estimate the variations within a tree (Kozlowski and Winget, 1964). Despite these drawbacks, the main disadvantage of both dendrometers lies in the difficulty to interpret the results obtained. Dendrometer measurements do not permit to distinguish between xylem, phloem and periderm increment and these are also confounded with the overall swelling and shrinkage of the stem (Fraser, 1956; Kozlowski and Winget, 1964). Histological analyses despite being time consuming and prone to errors resulting from interrupted and repeated sampling of different radii allow to better establish the duration of cambial growth (Fraser, 1956). Given both the advantages and disadvantages of each of these methods, it has long been recognized that dendrometers and histological analyses should be used in conjunction (Buckhout, 1907; Pearson, 1924; Lodewick, 1925; Chalk and Phil, 1930; Fraser, 1952, 1956, 1958; Zahner *et al.*, 1964).

In this initial research project, the daily radial activity of 7 of the major tree species of the Eastern Canadian boreal forest was monitored using automated band dendrometers. The 7 species studied were white birch (*Betula papyrifera* Marsh.), balsam fir (*Abies balsamea* (L.) Mill.), white cedar (*Thuja occidentalis* L.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) B.S.P.), jack pine (*Pinus banksiana* Lamb.) and red pine (*Pinus resinosa* Ait.). The main goal of this study was to better understand how the daily radial activity of these tree species was controlled by daily weather variations. More precisely, three objectives were put forward i) to compare the seasonal course of the radial activity among the 7 species, ii) to assess the beginning of the active radial growth season for these species and iii) to compare the course of the daily radial activity with daily environmental data.

2. Methods

2.1. STUDY SITES

The study site is located approximately 700 km north of Montreal and lies within the ‘Des Vieux Arbres’ insular ecological reserve situated on Lake Duparquet in northwestern Québec. Lake Duparquet (48°28′N, 79°17′W) is a large uncontrolled body of water with an area of about 25 km^2. About 170 islands are distributed on the lake ranging from a few square meters to about 0.7 km^2. This region located in the Canadian Shield (Wiken, 1986) is also part of the Northern Clay Belt of Québec and Ontario, which resulted from the maximum extension of postglacial Lakes Barlow and Ojibway (Vincent and Hardy, 1977).

Lake Duparquet is at the southwestern limit of Quebec’s boreal forest (Rowe, 1972) where surrounding late successional stands are dominated by balsam fir and white birch (Bergeron and Bouchard, 1984). Specifically the forest of the ecological reserve is located on an island of Lake Duparquet. The island covers an area of 1.4 ha and has an undulating topography with a maximum elevation of 14 m over the summer water level of Lake Duparquet. The island’s surface alternates between exposed bedrock and till underlying a thin organic layer. Open areas are mainly colonized by jack pine and red pine while white birch, spruce and balsam fir characterized the close canopy part of the island. For a period dating to ca. 1800 AD there was evidence of fires in 1799, 1849, 1881, 1901, and 1914. There was a large variation in fire severity in which several patches were left unburned (Bergeron and Brisson, 1990).

The climate of the region is continental with cold winters and warm summers. The closest meteorological station to our study site is located about 42 km north at La Sarre. The mean annual temperature for the period 1961–1990 is 0.8 °C (Environment Canada, 1993). A cold arctic air mass dominates the region during the winter with the mean temperature of January being –17.9 °C. The mean July temperature is 16.8 °C. The total annual precipitation for the region is 856.6 mm; snowfalls represent 25.2% of the total annual precipitation (Environment Canada, 1993).

2.2. DENDROMETER MEASUREMENT PROTOCOL

On the ‘Des Vieux Arbres’ ecological reserve, 40 automatic band dendrometers were installed during the late summer of 1995 on individual trees from 7 of the major tree species of the Eastern Canadian boreal forest. Specifically band dendromet-

TABLE I

Mensurational characteristics of sample tree by species. Standard deviations are given in parentheses

Species (number of sample trees)	Mean year of establishment	Mean DBH (cm)	Mean height (m)	Mean height to live crown base (cm)	Mean sapwood width (mm)
Abies balsamea	1940	15.1	12.0	164.6	34.2
(n = 5)	(35.2)	(1.4)	(1.5)	(29.9)	(17.7)
Betula papyrifera	1898	13.5	11.9	248.7	56.1
(n = 5)	(25.5)	(3.6)	(3.1)	(9.1)	(10.5)
Pinus banksiana	1907	21.9	12.2	202.6	31.8
(n = 7)	(54.6)	(11.7)	(7.4)	(128.4)	(19.7)
Picea glauca	1891	24.1	16.4	156.7	40.2
(n = 5)	(28.6)	(4.2)	(2.1)	(35.0)	(17.6)
Picea mariana	1933	12.5	10.5	110.0	14.1
(n = 5)	(11.2)	(3.5)	(1.4)	(38.5)	(3.0)
Pinus resinosa	1902	27.7	15.0	235.6	60.9
(n = 8)	(56.1)	(14.1)	(8.1)	(123.2)	(26.6)
Thuja occidentalis	1922	16.3	8.8	183.4	16.2
(n = 5)	(11.3)	(5.9)	(2.4)	(51.6)	(2.7)

ers were installed on 5 *Betula papyrifera*, 5 *Abies balsamea*, 5 *Thuja occidentalis*, 5 *Picea glauca*, 5 *Picea mariana*, 7 *Pinus banksiana* and 8 *Pinus resinosa* trees. The general mensurational characteristics of the trees are summarized in Table I. The oldest and youngest mean establishment date were, respectively, 1891 and 1940 with both *B. papyrifera* and *P. glauca* trees being among the oldest, and both *P. mariana* and *A. balsamea* trees being among the youngest. Mean diameter at breast height (DBH) ranged from 12.5 to 27.7 cm and mean tree height from 8.8 to 16.4 m (Table I). The largest trees (DBH and height) were *P. glauca* and *P. resinosa*. The mean height to the crown base ranged between 110.0 to 235.6 cm and the mean sapwood width ranged from 14.1 to 60.9 mm.

The microvariations in the stem circumference were measured at breast height with automatic band dendrometers. These work by converting a change in band length (tree circumference) into an electrical signal using a linear variable differential transformer (LVDT) (AEC, Agricultural Electronics Corporation, 1995). These sensors ‘continuously’ record stem circumference variations and the LVDT outputs are recorded into a data logger (AEC, 1995). The dendrometers have a resolution of 3.5 to 3.9 micrometers of change in band length per millivolt of change in electrical output. The band of Invar 36 surrounding the trunk has a thermal expansion-contraction factor of 1.26 micrometer/meter/°C which makes the effect of temperature negligible on the measurements. For a tree with a circumference of one meter, a ten-degree increase in temperature would make the band increases in length by 12.6 micrometers (AEC, 1995). The data were therefore not corrected for thermal expansion. We believed, as also stressed by Winget and Kozlowski (1965), that the thermal effect on bands was not important in relation to the actual changes in stem size.

To monitor the environmental variables, 2 soil hydration sensors, 1 soil temperature sensor (±50 °C), 1 air temperature sensor (±50 °C) and 1 photosynthetically active radiation (PAR) sensor were installed on the site. Hydration records, given in microfarad units, were transformed in % hydration using a reference value in early spring, i.e. at the time soil hydration was maximum. Data from the 2 sensors were then averaged to produce a site hydration variable. Both the air temperature and the hydration readings were further checked against air temperature and rainfall data obtained from 2 nearby automated meteorological stations. These were located at Rapide-Danseur and Heron Island, approximately 15 km north and 2 km northeast, respectively, from the ‘Des Vieux Arbres’ ecological reserve.

The automatic system (dendrometers and environmental sensors) used in this study operates all year long and is powered by solar collectors (AEC, 1995). The system includes four driver modules, each connected to 10 dendrometers. The outputs from these modules are feed into a central control and acquisition unit. The environmental sensors feed directly into this unit. Data were recorded each 15 min from approximately mid-May to mid-October and every hour during the rest of the year. In 1995, data were collected starting at the end of the month of August and they were mainly used to assess the operating status of the system. In 1996, the system ceased to operate for a brief interval in June at a critical time, i.e. at the time of the onset of the active growing season. Because of this discontinuity in the data, the 1996 data will not be examined here. In this study, only data from the period starting March 1, 1997 to July 10, 1997 will be presented and analyzed. In July 1997, the system was again shutdown after a lightning hit the site.

2.3. CHRONOLOGICAL DEVELOPMENT

To eliminate the effect of diurnal temperature and moisture fluctuations on stem circumference changes, we averaged the circumference measurements on a daily basis. We have averaged for each day the 24 readings obtained from 12 A.M. to 11 P.M.. In studies using manual dendrometers, measurements were usually made in the early morning to minimize the influence of stem shrinkage during the day (Daubenmire and Deters, 1947; Daubenmire, 1949; Ahlgren, 1957; Turner, 1956; Winget and Kozlowski, 1965; Conner and Day, 1992; Robertson, 1992). Before averaging the data, they were carefully screened to remove aberrant measurements. We refer to the momentary activities of birds and other organisms (spiders, squirrels, woodpeckers, etc.) that interfered with the normal layout of the band or the dendrometer itself. These erratic data were detected i) by directly plotting the circumference data overtime; ii) by comparing suspect data measurements with similar data within species and iii) by comparing plots of the minimum and maximum daily measurements. Data from dendrometers showing a malfunction were also deleted. Our data illustrated strong similarities among individual trees within each species (see Figure 1a for *P. mariana*). Daubenmire and Deters (1947) also observed that changes in radial growth for different specimens of the same species closely corresponded.

To ease comparison, March 1 was arbitrarily set to zero (0) value for all band dendrometers. All daily circumference increments were transformed to radial increment using the (radius = circumference/2π) formula (Figure 1a). To minimize the effect of age, vigour, and competition between trees, the radial increment curves were transformed into percentage (Figure 1b, Daubenmire and Deters, 1947; Jackson, 1952). Others have preferably converted diameter changes into basal area (cm^2 yr^{-1}) to reduce the variability of growth increments among trees of different ages (Winget and Kozlowski, 1965; Conner and Day, 1992). For each of the 7 tree species, 2 parameters were studied (1) the mean cumulative daily radial increment curve, calculated using each tree percentage curve (Figure 1c); and (2) the mean daily radial activity indexed curve, calculated using the difference between the mean value of two consecutive days (Figure 1d; Bormann and Kozlowski, 1962; Cohen *et al.*, 1997). Thus, the mean daily radial activity indexed curves were constructed by applying first-order differencing to the mean daily cumulative radial increment curve. Differencing constitutes a special type of filtering that is particularly useful for removing an intrinsic growth trend (Chatfield, 1989).

2.4. STATISTICAL ANALYSIS

In previous studies aimed at analyzing the relationships between daily cumulative radial increment and meteorological data, few details have been given on data transformation prior to statistical analysis (see Fritts, 1958; McClurkin, 1958; Braekke and Kozlowski, 1975; Conner and Day, 1992; Robertson, 1992; Cohen *et al.*, 1997). Seasonal trends in cumulative radial increment and temperature data are however significant. In some studies, the number of days from the beginning of the measurement elevated to simple, square and cubic power were included as independent variables in multiple regression analysis as a way to eliminate the trend in the cumulative radial increment curve. Numerous studies solely relied on graphical comparison of the cumulative radial increment with meteorological data (see Lodewick, 1925; Friesner and Walden, 1946; Turner, 1956; Ahlgren, 1957).

A closer look at Figure 1d revealed that the mean daily radial activity indexed curve has unstable mean and variance with time. For example, the early portion showed more variability compared to the later portion of the curve. Preliminary analysis also showed that correlation's signs were shifting with time when meteor-

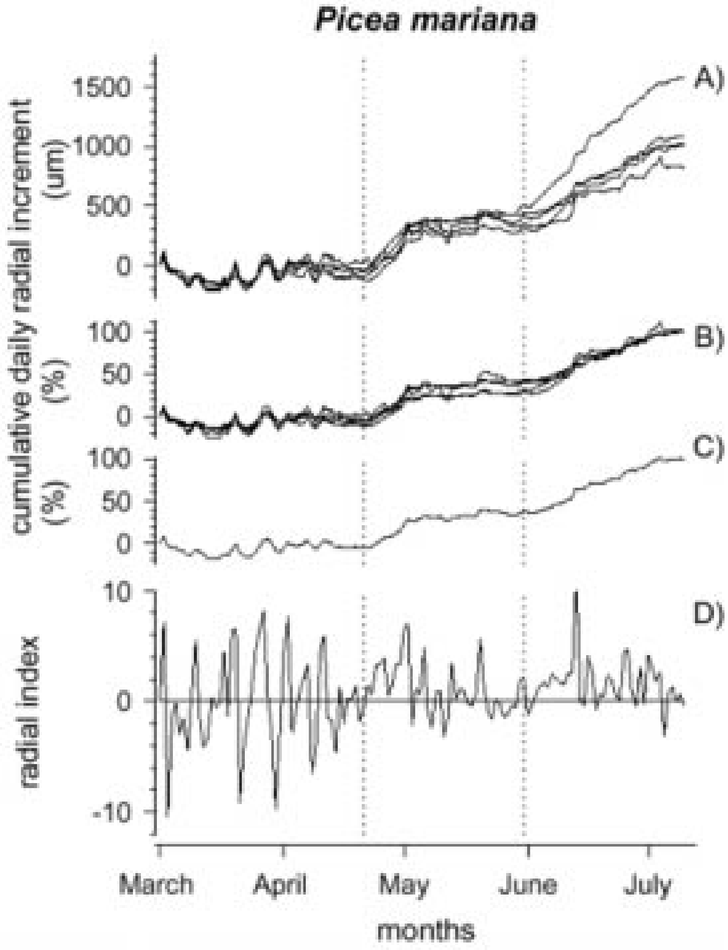

Figure 1. Daily radial increment curves for the 5 *Picea mariana* trees. A) cumulative daily radial increment in micrometer, B) cumulative daily radial increment in percentage, C) mean cumulative daily radial increment in percentage and D) mean daily radial activity indexed curve obtained by first-difference standardization. The timespan covered is from March 1 to July 10. Vertical dotted lines indicate from the left to the right the three phases of radial activity discussed in the text 1) March 1 to April 20, 2) April 21 to May 30 and 3) May 31 to July 10.

ological variables like air temperature were correlated with the mean daily radial activity indexed curve (not presented). The fact that some meteorological variables presented inverted correlations in different portions of the season precluded the use of the entire time series as a dependant variable. This phenomenon is well illustrated in the response of annual tree-ring series to climate factors; temperature may be positively correlated to radial growth in the early growth season and negatively as the season progress.

In this study, both the mean daily cumulative radial increment and the mean daily radial activity indexed curves were initially analyzed graphically. To transform as little as possible the 7 species' mean daily radial activity indexed curves; these were divided into three discrete periods. The three following periods i) March 1 to April 20, ii) April 21 to May 30 and iii) May 31 to July 10 were used. For each period, nonparametric Kendall's Tau correlation coefficients were calculated to assess the relationship between the species' mean daily radial activity and meteorological variables. These variables were hydration (%), minimum-maximum-average soil and air temperatures (°C), total photosynthetic active radiation (PAR, micro mols m^2 sec^{-1}), number of hr per day with PAR, and precipitation (mm). Except precipitation and PAR, the first-order differences for these variables were also used as variables in the correlation analyses. The resulting three matrices of correlation were then joined and submitted to a principal component analysis (PCA) using solely the significant Kendall's coefficients ($p < 0.05$). Positive and negative coefficients with the same variables were divided into two categories. Only meteorological factors with more than two occurrences were maintained in the final PCA analysis. The PCA was calculated on a covariance matrix using program CANOCO VER 3.1 (ter Braak, 1990, 1994).

3. Results

3.1. GROWTH CURVES

The course of the changes in the mean daily cumulative radial increment from late winter to early summer showed strong similarities among the 7 tree species (Figure 2). A principal component analysis revealed that 95% of the variance was held in common by the 7 species (not presented). Three main periods of stem fluctuations can be observed in all species. First, a synchronous period of instability characterized by strong episode of swelling and shrinking of the stem can be observed from day 1 (March 1) to about day 51 (April 20). These fluctuations in radius were registered from late winter to early spring. Around April 20, this initial period of instability ended with a short and sudden swelling of the stem that was observed in all species. Swelling was however less pronounced in *B. papyrifera* and *P. resinosa*. This initial extended increase in stem radius that lasted to the first week of May was immediately followed by a period of stability characterized by practically no radius increment. This stable period was particularly noticeable in *A. balsamea*, *B. papyrifera* and *P. banksiana* (Figure 2). At the end of May–early June, a third period (Day 92 to Day 132), characterized by a steep and continuous increase in mean cumulative daily radial increment was again observed in all species. This trend continued until the beginning of July. The onset of this trend was however delayed in *B. papyrifera*. The slope of the cumulative curve during this period suggested that the 7 tree species had a similar growth rate (Figure 2).

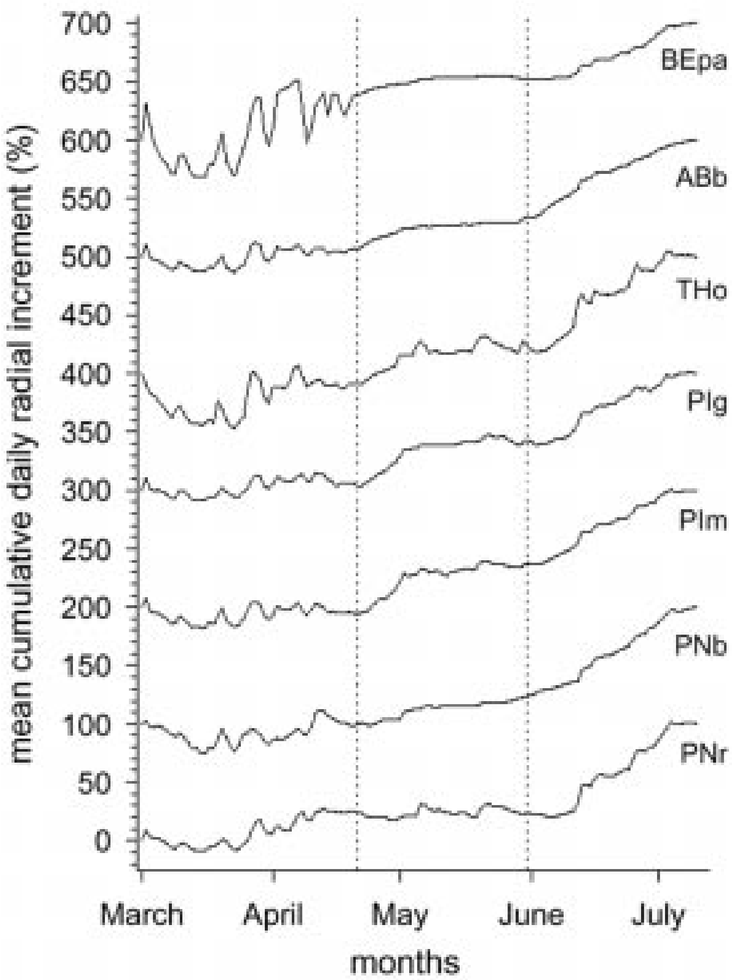

Figure 2. Mean cumulative daily radial increment for each tree species. BEpa: *Betula papyrifera*, ABb: Abies balsamea, THo: *Thuja occidentalis*; PIg: *Picea glauca*, PIm: *Picea mariana*, PNb: *Pinus banksiana*, and PNr: *Pinus resinosa*. The species-specific abbreviations follow Day (1967). Each species' curve was adjusted by adding a constant (100) to facilitate comparison. The timespan covered is from March 1 to July 10. Vertical dotted lines indicate from the left to the right the three phases of radial activity discussed in the text 1) March 1 to April 20, 2) April 21 to May 30 and 3) May 31 to July 10.

The mean daily radial activity indexed curves for the 7 species also highlight the strong similarities between them (Figure 3). A principal component analysis revealed that 71% of the variance was held in common by the 7 species (not presented). The three previously depicted periods can again be easily observed. Strong day to day variations in radius characterized the late winter to early spring period. Again this was particularly noticed in *B. papyrifera*, *A. balsamea* and *T. occidentalis*. The initial swelling period can also be determined by the continuous

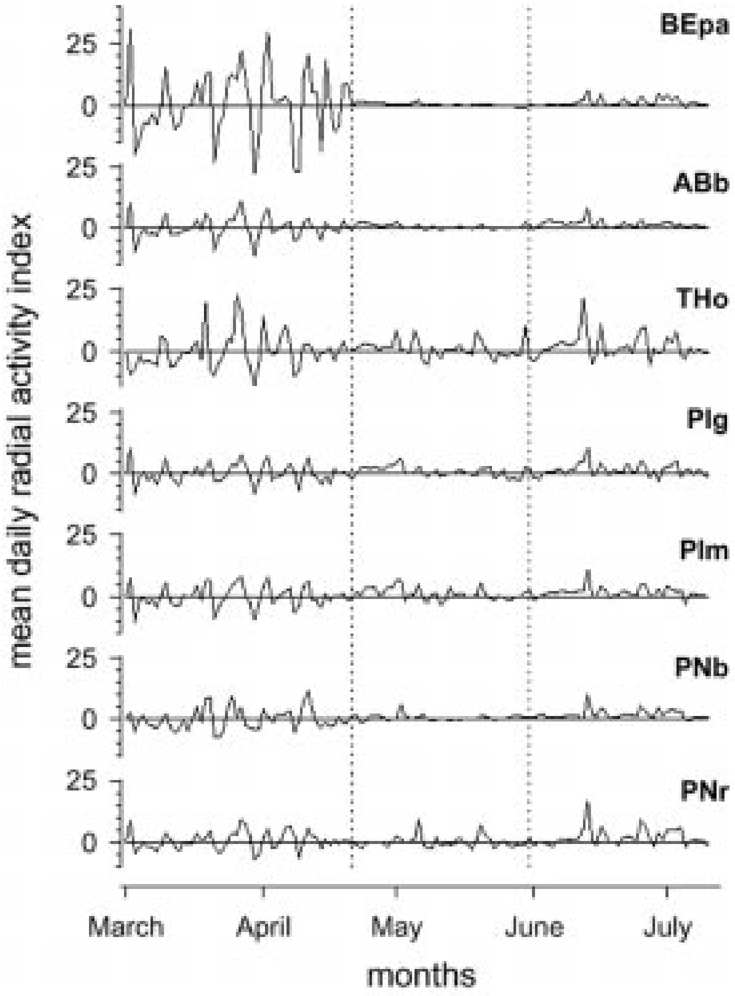

Figure 3. Mean daily radial activity indexed curve for each tree species. BEpa: *Betula papyrifera*, ABb: Abies balsamea, THo: *Thuja occidentalis*; PIg: *Picea glauca*, PIm: *Picea mariana*, PNb: *Pinus banksiana*, and PNr: *Pinus resinosa*. The timespan covered is from March 1 to July 10. Vertical dotted lines indicate from the left to the right the three phases of radial activity discussed in the text 1) March 1 to April 20, 2) April 21 to May 30 and 3) May 31 to July 10.

positive mean daily radial activity index recorded near the end of April. In May, the day to day variation in radius was minimum in *B. papyrifera*, *A. balsamea* and *P. banksiana*. In late May–early June, all species presented an increase in their indexed curve (continuous values above zero) and day to day change in growth again became more important (Figure 3).

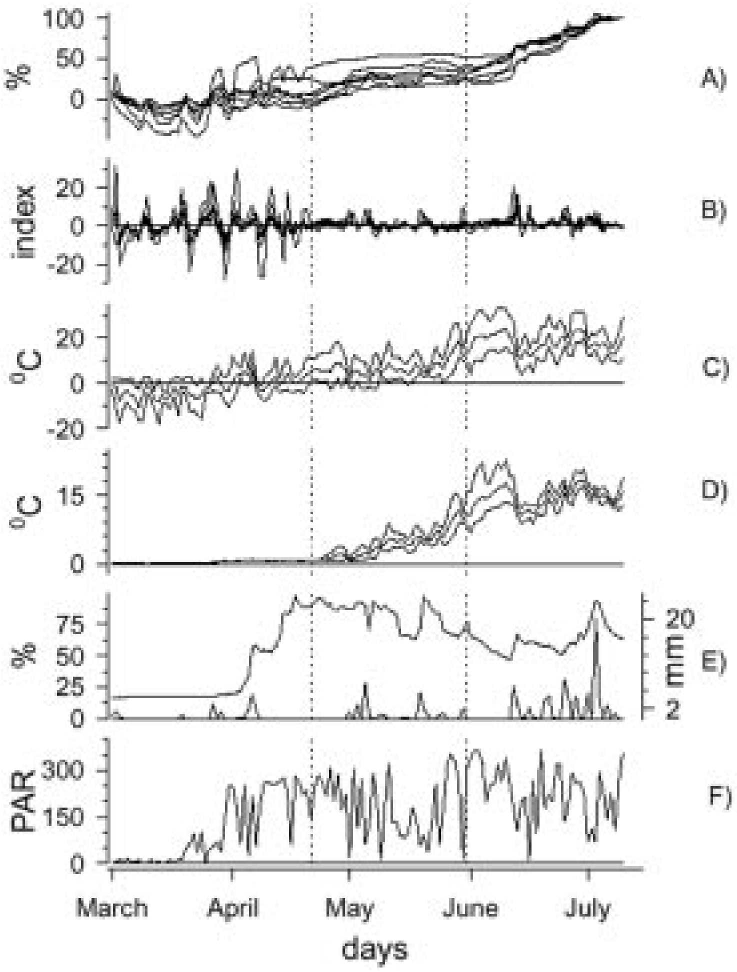

Figure 4. Comparison of the mean daily radial activity curves with selected meteorological factors. A) Species' mean cumulative daily radial increment curves, B) Species' mean daily radial activity indexed curves, C) minimum-mean-maximum air temperature, D) minimum-mean-maximum soil temperature, E) soil hydration and rainfall, and F) total daily photosynthetically active radiation. The timespan covered is from March 1 to July 10. Vertical dotted lines indicate from the left to the right the three phases of radial activity discussed in the text 1) March 1 to April 20, 2) April 21 to May 30 and 3) May 31 to July 10.

3.2. RELATIONSHIPS WITH METEOROLOGICAL DATA

The graphical comparison of both the mean daily cumulative radial increment and mean daily radial activity index of the 7 species with meteorological data showed that the strong variations observed from March 1 to April 20 were occurring at a time when minimum air temperature was below freezing (Figure 4). Soil temperatures during that time were also near the freezing point. This is consistent with soil hydration remaining low until the first week of April. In 1997, snowmelt and soil rehydration apparently occurred in early April. The initial period of continuous swelling in radius occurred when soil hydration was maximum and soil temperatures (especially maximum soil temperature) were beginning to warm. The late May–early June general period of increasing stem radius was initiated or coincided by a brief interval of warmer soil and air temperatures. For example, minimum, mean and maximum air temperature, respectively, exceeded 10, 15 and 25 °C (Figure 4c). Intense rainfalls also coincided with the onset of this trend despite soil hydration being reduced. During that period, tree radius was increasing despite a steady decline in soil hydration (Figure 4).

To better highlight which were the main meteorological factors associated with the daily radial fluctuations recorded in the species' mean daily radial activity indexed curves, principal component analysis was used (see Statistical analysis and Figure 5). Both the first and second principal components explained, respectively, 42 and 32% of the variation in the initial matrix. The ordination diagram showed a clear separation among the three time periods analyzed and the 7 tree species themselves (Figures 5a, b). From March 1 to April 20 (period 1), increases in the species' mean daily radial activity indexed curves were mainly associated with both minimum and mean air temperatures (Figure 5). The first-order differencing of these two variables were also positively associated with radial expansion. During that period, swelling of the stem was mainly controlled by warm minimum air temperature. Few differences were recorded between the species for that period (Figure 5b) and no other meteorological factors were related to radial fluctuations.

During the second depicted period that lasted from about April 21 to May 30, variation in soil temperatures became more important in controlling the fluctuations observed in the mean daily radial activity indexed curves (Figure 5a). Minimum, maximum and mean soil temperature as well as both maximum and average air temperatures showed to be negatively correlated to radial swelling. Soil hydration had however a positive effect on daily radial swelling. The first-order differencing for these variables were however not correlated with radial expansion. These correlations thus need to be interpreted with caution because they may simply reflect opposite trends in the series. First-order difference in both mean soil and minimum air temperatures were however negatively correlated with daily radial expansion. *B. papyrifera* and to a lesser extend *P. glauca* were more sensible to both hydration and soil temperature. *P. banksiana* did not show any significant relations to the other species; no correlation between the species' radial expansion and the meteorological data were included in the PCA. Only a slight positive correlation with number of hours with PAR (Kendall Tau = 0.279, p = 0.0196, n = 40) was observed for *P. banksiana*. Conifer species and particularly *T. occidentalis* showed to be negatively affected by both maximum soil and mean air temperature during this period (Figure 5).

During the third period (May 31 to July 10), another set of meteorological variables became highly important in controlling radial expansion. Precipitation,

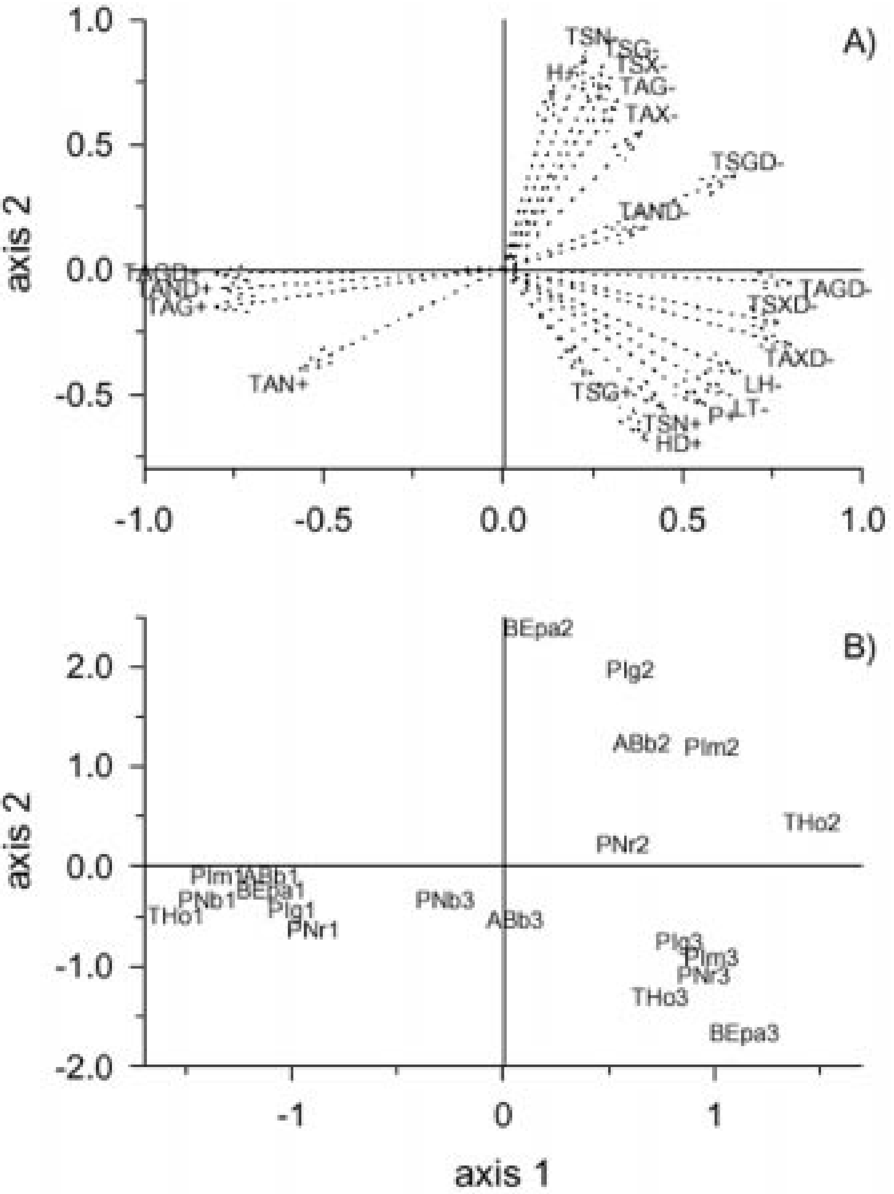

Figure 5. Principal component analysis of the Kendall's coefficient between each species mean daily radial activity indexed curve and meteorological factors. A) position of the descriptors along the first two axes of the PCA. Legend: TAG (Average air temperature), TAN (Minimum air temperature), TAX (Maximum air temperature), TSG (Average soil temperature), TSN (Minimum soil temperature), TSX (Maximum soil temperature), LT (Total photosynthetic active radiation), LH (number of hr per day with PAR), P (Precipitation) and H (Hydration). The letter 'D' appearing after a variable's abbreviation refers to the first-order differences of that variable. The plus and minus signs also refers to the positive or negative influence of each variable. B) position of the 7 species along the first two axes of the PCA. Legend: BEpa: *Betula papyrifera*, ABb: Abies balsamea, THo: *Thuja occidentalis*; PIg: *Picea glauca*, PIm: *Picea mariana*, PNb: *Pinus banksiana*, and PNr: *Pinus resinosa*. The number appearing after a species abbreviation refers to the different period analyzed 1): March 1 to April 20; 2) April 21 to May 30 and 3) May 31 to July 10.

first difference in hydration as well as both minimum and mean soil temperatures were positively associated with radial expansion. Total daily PAR and number of hours with PAR were negatively related to radial expansion. Again, *B. papyrifera* responded more strongly to rainfall, soil temperature and PAR than other species. Compared to the second period, all 7 tree species were also less spread in the ordination diagram and showed to be affected in a more similar way by weather (Figure 5b). Inspection of the Kendall's Tau coefficient also revealed that both *B. banksiana* and *A. balsamea* had fewer significant correlations with weather variables during this last period and this explain their position toward the center of the ordination diagram (Figure 5b).

4. Discussion

4.1. INITATION OF RADICAL GROWTH

The dendrometer measurements alone cannot be used to precisely determinate the date of the onset of the xylem formation in our 7 tree species. As stated earlier, dendrometers do not allow to differentiate between the meristematic activities resulting from the vascular cambium and/or the phellogen. They also do not permit to distinguish between the xylem and the phloem differentiation from the vascular cambium. The records obtained represent the total shrinking-swelling and deposition of new xylem, phloem and periderm (Belyea *et al.*, 1951; Fraser, 1952; Kramer and Kozlowski, 1979).

Growth initiation in the early spring may thus be readily confused with rehydration of internal tissues before the beginning of cambial growth. Our data indicated that the earliest sustained radial expansion (ca. April 20) was the result of stem swelling. According to Freni (1956 in Kozlowski and Winget, 1964) the onset of turgidity in the cambium of *Abies* and *Pinus* preceded that of cambial activity by several weeks. Kozlowski and Peterson (1962) reported the same for *P. resinosa*. Fraser (1956) who used both dendrometers and histological analyses reported that a swelling period was invariably found before any wood cells were laid down. It was also observed that phloem differentiation in *P. banksiana*, *P. resinosa*, *A. balsamea* and *P. mariana* predated that of the xylem by up to six weeks (Alfieri and Evert, 1968, 1973).

Despite these limitations, it was recognized that the 'grand period' of radial growth (wood deposition) in trees coincided with the given general upward trend found in the cumulative growth increment (Pearson, 1924; Belyea *et al.*, 1951; Fraser, 1956). Belyea *et al.* (1951) described three distinct phases in the cumulative radial increment for some of the boreal tree species of Canada. In early mid-May, an initial period of swelling that lasted at least a week was observed. This period was followed by active cell division indicating the 'grand period' of growth. A third period characterized by the cessation of increments accompanied by dehydration of the cells and preparation of the cambial for its winter rest was also observed (Belyea *et al.*, 1951). Except for the later third period that we could not document, our results also indicate a similar progression in the mean cumulative radial increment for all 7 tree species. An initial swelling of the stem was however observed to occur prior to the month of May that is in mid-April.

Earlier studies have attempted to identify which factors were controlling the onset of radial growth. In early spring, water availability does not constitute a limiting factor to radial growth and as hypothesized by others (Hansen and Brenke, 1926; Friesner and Walden, 1946; Turner, 1956; Ahlgren, 1957; Fraser, 1958), temperature was probably the main determinant factor for the initiation of radial growth in all species. Our data suggest that the 'grand period' of growth also coincided with or followed a sudden increase in both soil and air maximum temperature in early June. Reimer (1952 in Fritts, 1958) reported that the initiation of radial growth in *A. saccharum* was also determined by soil and air temperature. Fraser (1956) observed that late warming of soil may delay radial growth. According to Daubenmire (1949) however day length would be more important than temperature in explaining the resumption of radial growth in spring.

4.2. DAILY RADIUS ACTIVITY

Strong similarities in the mean cumulative radial increments were observed among the 7 tree species. Three particular phases were observed from March to July 1997. In late winter - early spring, all species presented strong day to day variations (shrinkage and swelling) in stem radius. These occurred at a time when the soil was frozen. These stem fluctuations occurred during the dormant season and were significantly correlated with both minimum and mean air temperatures. Rapid stem contraction and expansion were observed to be frequent during the dormant season and these were also associated with large temperature fluctuations (Buckhout, 1907; Friesner and Walden, 1946; Daubenmire, 1950; Ahlgren, 1957; Winget and Kozlowski, 1964). Those of Small and Monk (1959) who observed that winter stem contractions in *Fraxinus americana* were maximum during cold morning whereas stem expansion was greatest around mid-day, i.e. when temperature was warmest also supported our findings.

During this first period, *B. papyrifera* showed to register the most important fluctuations in stem radius. The species also recorded the most radial expansion by mid-April. *B. papyrifera* like *Acer saccharum* was reported by Johnson (1944) to be a heavy producer of sap during the spring. Sap flow production in *B. papyrifera* was reported to be driven by root pressure whereas stem pressure occurs in *A. saccharum* (Kramer and Kozlowski, 1979). In *A. saccharum*, sap flow is known to occur when freezing nights are followed by warm days and the process stops when temperature continuously remained above freezing. In contrast, the root-pressure-generated flow increases as soil warms and ceases with increased transpiration related to leaves expansion (Kramer and Kozlowski, 1979). Our results suggest that sap flow production in *B. papyrifera* could be also driven by stem pressure in addition to root pressure. They also indicated that daily fluctuations in radius were greatest when both minimum and maximum air temperatures were, respectively, below and above freezing. In *B. papyrifera*, no increases in stem radius were related to increasing soil temperature.

In most species, a synchronous and short period of stem expansion was observed around April 20. This first period of rapid initial expansion of the stem apparently coincided with the passage of water in the stem. It corresponded with the initial warming of the soil and occurred at a time when hydration values were maximum. This short event marked the beginning of a period characterized by week fluctuations and no important increase in stem radius. This period lasted until the end of the month of May. During that period, soil hydration values were positively related to radial expansion. Warm soil temperatures and high maximum air temperature became the main factors controlling radial fluctuations.

In their study, Daubenmire and Deters (1947) reported that evergreen conifers were more prone to abrupt changes in stem diameters than deciduous species during the dormant season. They argued that the persistent leaves of conifers made them more susceptible to transpiration during vigourous winter and thus to stem shrinkage. Their softer wood also would make them more sensitive to turgor pressure changes. Our data suggested that *B. papyrifera* was more sensitive to the negative effect of soil temperatures and to the positive effect of high soil hydration than conifer species. Result from the PCA indicated that during the month of May, conifer species like *T. occidentalis* were more sensitive to the negative effect of daily differences in mean air and maximum soil temperatures. This may indicate a higher transpiration rate in conifers.

The onset of the active production of xylem was identified to be the ‘grand period’ of radial expansion observed in late May–early June. This phase also probably coincided with shoot growth and leaf expansion. All 7 species showed this period to coincide strongly. Preliminary analysis for the 1999 growing season showed that the production of secondary cambium started in late May–early June for all 7 species (Lambert, unpublished data). Similar results were obtained by Daubenmire and Deters (1947). In a two-year study, evergreen and deciduous species all began their ‘grand period’ of growth at a similar time despite their ecological and taxonomic distinction (Daubenmire and Deters, 1947). Jackson (1952) observed that the start of the growing radial season was however variable across species. The positive trend observed in the mean cumulative daily radial increment lasted until early July where radial growth rates began to decrease. During the ‘grand period’ of growth, air temperature and PAR were negatively associated with radius expansion whereas both minimum soil temperature and rainfall gained in importance.

It is well documented that tree stems shrink during the day and that they swell during the night (Pearson, 1924; Braekke and Kozlowski, 1975; Pereira and Kozlowski, 1976; Kramer and Kozlowski, 1979; Cohen *et al.*, 1997). During day-time, an internal water deficit develops in trees because more water is loss in transpiration than is replaced by absorption through the roots. During the night both transpiration and absorption are low; but the rate of absorption exceeds that of transpiration (Kozlowski and Winget, 1964; Kramer and Kozlowski, 1979). It was reported that cold soil temperature may affect radial growth by reducing water uptake by roots (Kramer and Kozlowski, 1979). The positive effect of warmer soil temperature during the night may indicate increasing stem rehydration and a beneficial role in maintaining internal water balance. During the ‘grand period’ of growth, rainfalls also had a direct effect on radial expansion and contributed to reduce internal water stress. Braekke and Kozlowski (1975) also observed in *B. papyrifera* and *P. resinosa* that each rainfall was followed by a marked stem swelling. A significant portion of the increase in radius following a rainfall was reported to reflect stem hydration (Ahlgren, 1957; Kozlowski and Winget, 1964; Braekke and Kozlowski, 1975).

The negative effect of daily difference in both soil and air maximum temperatures as well as total PAR further indicate the negative effect of transpiration on radial expansion. Pereira and Kozlowski (1976) observed that stem shrinkage in both *A. balsamea* and *P. resinosa* was similar and that it depended on environmental factors affecting transpiration and the past history of the plant. Diurnal change in stems were correlated to temperature and vapour pressure deficit as well as to foliage water potential. Fritts (1958) observed that variations in both maximum air temperature and soil moisture were the most influential variables affecting the daily radial growth of beech (*Fagus grandifolia*). Cohen *et al*. (1997) observed that maximum daily stem shrinkage was minimum on cloudy and rainy days, i.e. when transpiration rates were low. They observed that water loss through transpiration was related to increasing solar radiation. Fritts (1958) also observed that more sunshine increased transpiration and water loss from the tree, causing the cell to be less turgid and thus cell enlargement to be less.

5. Conclusion

In conclusion, this study showed that band dendrometers can provide useful information regarding the relationships between daily fluctuations in radial increment and meteorological factors. From late winter to early summer, three general phases in radial activities were observed. In each of these, radial activity responded to different meteorological variables. The strong relationship to soil temperature was not anticipated as well as the strong similarities among the 7 species. *B. papyrifera* appeared however to be more sensitive than the other species to water stress in the early growing season. This species usually neglected in dendroclimatic analysis because of the diffuse character of its wood and the presence of numerous missing-incomplete rings may however reveal itself a good indicator of dry years.

To better estimate the onset date of the active radial growth of our 7 tree species, future studies should involve collecting information on the phenological development of these trees (time of swelling of the buds, flowering, shoot growth, leaves development etc.). Incorporating histological analyses during growing seasons would also allow to better calibrate the dendrometer measurements. The possibility to collect data during a complete year would definitely help provide a better picture of the differences between species as water stress becomes more significant as the growing season progress. An analysis of the radial increment of each tree should also be conducted to better assess the importance of factors like age, diameter, height and soil depth. Comparison using standard dendroclimatic methods may also provide interesting information by comparing both the daily and annual response to meteorological variables.

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