NOTE / NOTE

Xylem production in six tree species growing on an island in the boreal forest region of western Quebec, Canada

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Abstract: Xylem production was studied by repeatedly taking microcore samples from the stems of six tree species growing on the "réserve écologique des Vieux-Arbres", on Lake Duparquet, Québec, throughout the 1999 growing season. Species examined were paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), red pine (*Pinus resinosa* Ait.), and eastern white cedar (*Thuja occidentalis* L.). Onset of xylem cell production was observed in all species by 22 May 1999, and ended as early as mid-July and early August for white spruce and eastern white cedar, respectively. Xylem cell production in the remaining species ended between late August and mid-September. In general, the onset of latewood production ranged from the start of July to the first week of August. Typical sigmoidal curves were characteristic of ring width, number of cells, and number of earlywood cells over the growing season. Completion of the annual growth increment was quickest for white spruce and eastern white cedar, while it continued longest in both pine species. Numerous similarities in xylem production and tree ring formation over the course of the growing season were observed among the six species, suggesting that weather, along with photoperiod, plays a critical role in xylem production.

Key words: xylem production, tree ring formation, radial growth, boreal forest, image analysis.

Résumé : Les auteurs ont étudié la production de xylème, en prélevant de façon répétitive des microcarottes à partir de la tige de six espèces venant dans la « réserve écologique des Vieux-Arbres », sur le lac Duparquet, au Québec, tout au long de la saison de croissance en 1999. Ils ont examiné le bouleau à papier (*Betula papyrifera* Marsh.), l'épinette blanche (*Picea glauca* (Moench) Voss), l'épinette noire (*Picea mariana* Mill.) BSP), le pin gris (*Pinus banksiana* Lamb.), le pin rouge (*Pinus resinosa* Ait.), et le thuya blanc de l'Est (*Thuja occidentalis* L.). Chez toutes les espèces observées, le début de la production des cellules du xylème est survenue vers le 22 mai, en 1999, et s'est terminé aussi tôt que vers la mi-juillet début d'août, chez l'épinette blanche et le thuya, respectivement. Chez les autres espèces,, la production des cellules du xylème se termine entre la mi-août et la mi-septembre. En général, le début de la formation du bois final va du début de juillet à la première semaine d'août. Typiquement, on observe des courbes sigmoïdes pour la largeur des anneaux, les nombres de cellules, et les nombres de cellules du bois hâtif, au cours de la saison de croissance. L'achèvement de l'accroissement annuel est plus rapide chez l'épinette blanche et le thuya de l'Est, alors qu'elle se poursuit plus longuement chez les deux espèces de pins. On observe de nombreuses similarités dans la production du xylème et la formation des anneaux de croissance, au cours de la saison de croissance, parmi les six espèces, ce qui suggère que la lumière, avec la photopériode, joue un rôle critique dans la production du xylème.

Mots-clés : production de xylème, formation des anneaux de croissance, croissance radiale, forêt boréale, analyse d'images.

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Introduction

While dendrochronological investigations can be conducted using numerous techniques, 9 out of 10 studies have utilized only annual ring width variations for their purposes (Schweingruber 1996). In recent years however, detailed anatomical investigations of the production and development of xylem cells during the growing season have become more frequent. These fine-scaled studies aimed at a better understanding of the interrelationships between xylem cell production and (or) development and environmental factors for a given tree species (Antonova and Stasova 1993, 1997; Deslauriers et al. 2003b; Mäkinen et al. 2003; Schmitt et al. 2004; Deslauriers and Morin 2005; Rossi et al. 2006b). The knowledge of basic ring formation phases, such as the onset and cessation of xylem cell production as well as earlywood–latewood timing and duration, has been argued to improve assessment of the impact of climate on tree growth (Camarero et al. 1998; Gindl et al. 2000; Deslauriers et al. 2003b; Rossi et al. 2003; Schmitt et al. 2004; Deslauriers and Morin 2005). Greater detail on xylem cell production throughout the growing season can be used in forest-climate modelling, and fine-scale studies can be used to better calibrate response functions obtained from tree ring and climate.

Most studies of xylem cell production and (or) development in relation to climatic influences have been conducted on Eurasian species (Antonova and Stasova 1993, 1997; Antonova et al. 1995; Bäucker et al. 1998; Camarero et al. 1998; Abe and Nakai 1999; Gindl et al. 2000; Yasue et al. 2000; Oribe et al. 2001, 2003; Mäkinen et al. 2003; Rossi et al. 2003). Studies on multiple boreal species are very limited, and few boreal species of North America have been examined (Belyea et al. 1951; Fraser 1952; Forster et al. 2000; Wang et al. 2002; Deslauriers et al. 2003a; Rossi et al. 2003; Deslauriers and Morin 2005). For instance, two of the major boreal forest species of North America (black spruce (*Picea mariana* (Mill.) BSP), and jack pine (*Pinus banksiana* Lamb.)) lack description of their basic phenological and (or) anatomical characteristics (Deslauriers et al. 2003a).

Comparative information is missing on tree ring formation (onset and (or) cessation and production of xylem cells) among multiple boreal tree species. Knowledge of the range of variability in tree ring formation among species can be used to better calibrate radial growth – climate association models, and help decipher which species may benefit or not from climate change. The objective of this study was to document tree ring formation at weekly intervals within one growing season and evaluate its variability among six North American tree species in the boreal forest region — paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), black spruce, jack pine, red pine (*Pinus resinosa* Ait.), and eastern white cedar (*Thuja occidentalis* L.) — growing in the same location. The information gained from this study was also compared with that obtained from continuous band dendrometer readings (Tardif et al. 2001a) and the annually resolved radial growth – climate association (Tardif et al. 2001b) of the same species growing at the same site.

Materials and methods

Study area

The study site is on island 45 (48°27′18″N, 79°17′14″W) of the "réserve écologique des Vieux-Arbres", located on Lake Duparquet, Québec, approximately 700 km northwest of Montréal, Canada, and has been described in Bergeron and Brisson (1990) and Tardif et al. (2001a). The mean annual temperature at the LaSarre meteorological station, approximately 42 km to the north, for the reference period 1971–2000 was 0.7 °C (Environment Canada 2004). The average total annual precipitation for the region was 889.8 mm, of which snowfall represented 25.2% (Environment Canada 2004).

Data collection

In 1995, a detailed radial growth study was initiated at the study site using 40 trees from seven species and has been described in Tardif et al. (2001a, 2001b). Thirty-one of these same trees were used for the current study, each species having five representatives, except jack pine, which had six. Because of the lack of useable samples, balsam fir (*Abies balsamea* (L.) Mill.) was excluded from this study.

Microcore sampling of the 31 trees began in May 1999. A 2.5 mm diameter increment puncher developed by Forster et al. (2000) was used to extract each microcore sample (5–10 mm long) from each tree. Samples were taken between 82 and 146 cm above the ground level and at least 1 cm apart to minimize the chance of sampling trauma (scar) tissue produced by the tree as a result of prior sampling (Forster et al. 2000). The first sampling event was on 16 May 1999, the second was 6 d later, and followed consistently at 7-day intervals until the 17th week. Three more samples were taken between 19 September and 22 October 1999. A total of 20 samples, spanning 159 d, were extracted from each tree.

Environmental variables were recorded on site by means of three soil hydration sensors, one soil temperature sensor, one air temperature sensor, and one photosynthetically active radiation (PAR) sensor. More information on the equipment used can be found in Tardif et al. (2001a). Three automated meteorological stations were also in operation nearby, enabling validation of the meteorological data collected on site; Cetec (15 km to the north) and Sabrais (11 km west) were both mainland stations, and the third was on Heron island approximately 2 km northeast. The combined data from the nearby meteorological stations extended from April 2 to October 28, 1999. Meteorological data were recorded on site from May 20 to October 26, 1999. Data were unavailable from June 11–18, 1999, because of failure of the acquisition unit. On-site meteorological conditions were comparable to those of the nearby meteorological stations, and their regional representativeness was also corroborated by Tardif et al. (2001a, 2001b).

Laboratory processing techniques

All microcore samples were dried at air temperature and glued to wooden molding using waterproof epoxy, as the samples were soaked for 30 min in water before sectioning. The microcores were transversely sectioned with a rotary microtome to a thickness between 12 and 20 μm. The sec-

tions were then stained in a bath with a Safranin O solution (5% in water), then dehydrated and cleared with 50% ethanol, 95% ethanol, reagent alcohol, and a citrus-based clearing solvent, or D-limonene. A few drops of Permount® (Fisher Scientific Inc., Fairlawn, N.J.) were used to secure the cover slip. Each slide typically displayed five to eight sections. It should be noted that not all slides were of sufficient quality to be useable for image analysis, and therefore the entire 20 slides of any given tree were not represented in the analysis. A total of 516 slides (83%) were kept.

Images of each of the slides were acquired by means of a Polaroid digital microscope camera with a Nikon TV C-0.6× lens attached to a Nikon Eclipse E200 microscope (Jones et al. 2004; Sutton and Tardif 2005). The images were captured in .tiff format, in black and white, at a resolution of 1200 × 1600, using the 200× magnification, except for paper birch, which was examined at a magnification of 400× because of the smaller cell sizes. A green filter was used to maximize contrast between cell walls and lumen.

The onset of xylem cell production was visually estimated from the slides under the microscope. It should be noted that the use of an increment puncher has the potential to deform or compress the newest cells of the cambial zone (Forster et al. 2000), potentially resulting in a slight underestimation of the actual number of cells or ring width produced at a given time (A. Deslauriers, personal communication, 2005). A new tool for extracting microcores has been developed to overcome the problem of compression (Rossi et al. 2006*a*). It should also be noted that the accuracy of the onset of xylem cell production can be influenced by the time between sampling, which was 6 and 7 d in this case.

All images were analyzed using the program WinCELL Pro 2001 (Régent Instruments, Inc. 2001). Three radial files were randomly selected from the current year's (1999) growth ring. For paper birch, a species with diffuse porous wood, radial files with vessel elements were avoided to focus only on fibre formation. Ring width and number of cells produced were recorded on each of the three radial files. Other variables (tracheid or fibre diameter, lumen area, lumen diameter, cell wall thickness, average cell wall/lumen ratio, and earlywood–latewood classification) were established along a single radial file only, because of the time-consuming image processing involved. Automatic earlywood–latewood classification used the cell wall/lumen ratio, with a ratio >0.25 being considered latewood (Régent Instruments, Inc. 2001). This is equivalent to Denne's (1988) first interpretation of Mork's (1928) latewood definition ($2a \geq b$, where a is the double-wall thickness, and b is the lumen diameter). From these measurements, three variables describing tree ring formation were determined: ring width (mean of three radii/sample), number of cells (mean of three radii/sample), and number of earlywood cells (one radius/sample).

Data analysis

The dates for the onset of xylem cell production were compared among species using the nonparametric Kruskal–Wallis test (Sheskin 1997). If a significant difference was found, this was followed by the Mann–Whitney U test for pairwise comparisons (Sheskin 1997). Preliminary analyses were performed on the three tree ring formation variables,

and data from each individual tree were screened to identify and remove outliers. These variables were then standardized and transformed to relative values (0%–100%). This minimized variations related to tree age and size, allowing better comparison among species. These three variables were then modelled using the Gompertz function, a sigmoidal function that has been widely used to model xylem cell production during the course of a growing season (Camarero et al. 1998; Deslauriers et al. 2003*a*, 2003*b*; Mäkinen et al. 2003; Rossi et al. 2003, 2006*b*; Deslauriers and Morin 2005). The Gompertz function was fitted to the pooled data for each of these three variables of each tree species.

The Gompertz function is described by Cheng and Gordon (2000) as:

$$[1] \qquad y = a\exp\left(-e^{(\beta - \kappa t)}\right)$$

where y is the modeled value at time t of the variable under consideration, a is the upper asymptote, β is the x-axis placement parameter, and κ is the rate of change parameter, or more specifically, the "rate constant" described by Richards (1959) that controls the curve's distribution over time. The date of inflection (x_0), when rate of change in y is greatest, is at approximately 37% of y (Winsor 1932) and given by:

$$[2] \qquad x_0 = \beta/\kappa$$

Richards (1959) also provides a parameter that can easily be calculated from the previous coefficients: r is the weighted mean absolute rate of change in y (eq. 3) (Cheng and Gordon 2000).

$$[3] \qquad r = a\kappa/4$$

Furthermore, the onset of latewood production was determined as the point where the earlywood curve started diverging from the cell production curve as estimated by the Gompertz function. The end of xylem cell production was estimated as the date coinciding with 90% of the cell production asymptote, as in Jones et al. (2004). This was done to avoid the slight increase in the curves that continued until the end of sampling, and capture the point where the curves had effectively begun to level off. Additionally, the duration of xylem cell production was calculated as the date of the onset of cell production subtracted from the end of cell production.

Results and discussion

Onset of xylem production

The onset of xylem cell production was generally similar among the six study species (Fig. 1). Many trees had produced one or two cells by the first week of sampling (16 May), and all but three trees had begun xylem cell production by the second week (22 May). This suggests synchronous activation of xylem cell production. These similarities among species were observed despite inherent variability due to taxonomical differences, tree status (height, diameter)

Fig. 1. Meteorological variables recorded on site or nearby. (*a*) Air and soil temperatures recorded on site and air temperature recorded at a nearby meteorological station (Cetec). Also shown are the onset of xylem cell production (OCP, triangle) with standard deviation (horizontal bars), onset of latewood production (OLW, circle), and the end of cell production (date of 90% of cell production (ECP, square)). Species abbreviations are as follows: Bpa, paper birch; Pgl, white spruce; Pma, black spruce; Pba, jack pine; Pre, red pine; Toc, eastern white cedar. (*b*) Average soil hydration values transformed to 100% of maximum recorded on site, and rainfall amounts from nearby meteorological stations (Cetec and Sabrais stations).
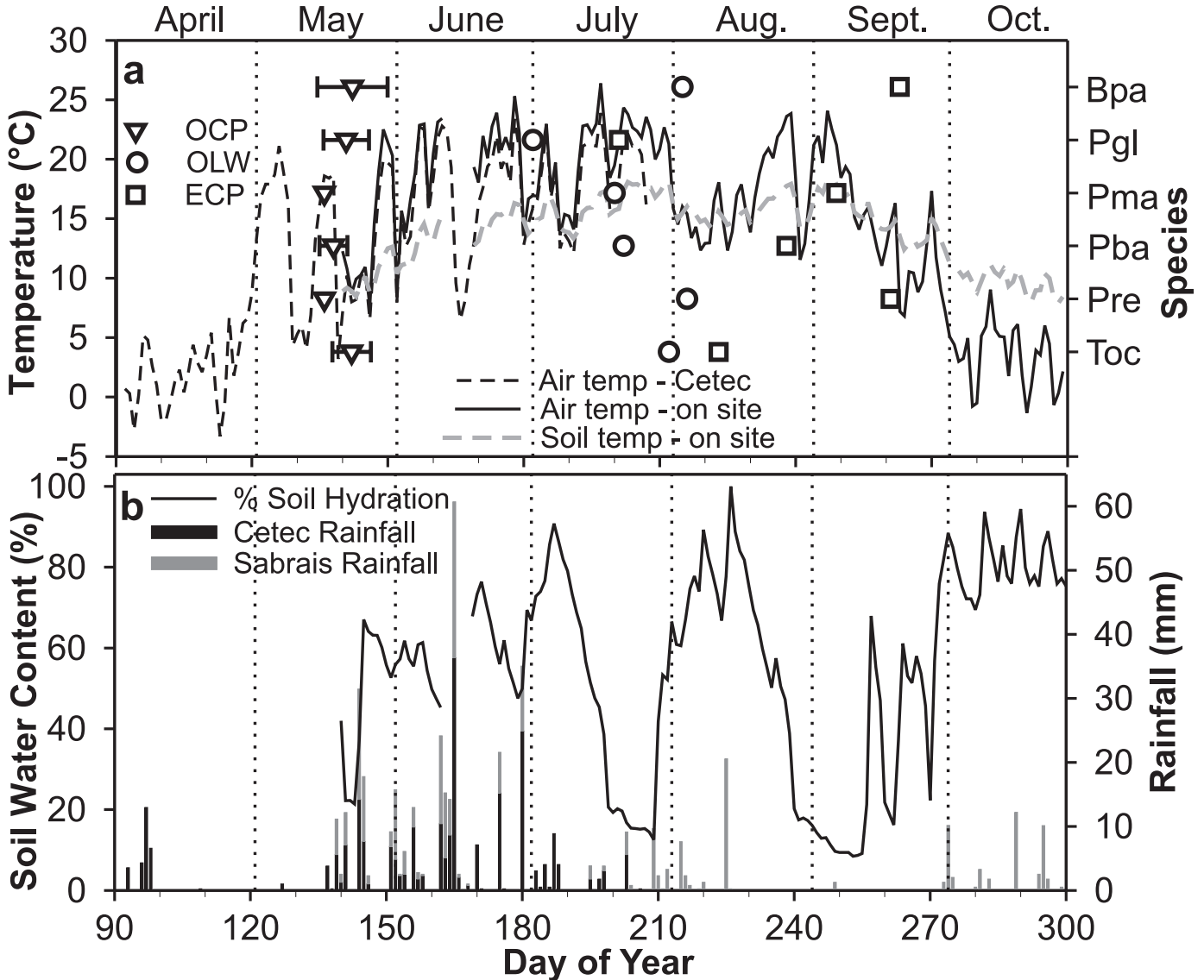
(Kozlowski and Peterson 1962), or sampling height (Fraser 1952; Bäucker et al. 1998). While we found both black spruce and red pine to begin cell production significantly earlier than eastern white cedar, this was only by 6 d. Tardif et al. (2001*a*) observed that conifers started daily radial increment earlier than paper birch; however, no significant difference was observed in the current study despite a single delayed paper birch. The overall dates of the onset of xylem cell production (mid- to late May) coincided with those estimated from automatic band dendrometers in 1997 for the same species and location (Tardif et al. 2001*a*). Similar dates for the onset of cell production were also noted in literature for paper birch, black spruce, red pine, and eastern white cedar (Fraser 1952; Ahlgren 1957; Forster et al. 2000).

Our results indicated that the onset of cell production was at a time while both soil and air temperatures were increasing on site (Fig. 1). These results also agree with Tardif et al. (2001*a*), who reported that the initiation of radial growth corresponded with a rapid increase in maximum soil and air temperatures. Typical spring conditions of fluctuating air temperatures combined with a lengthening photoperiod have been shown to promote bud burst, which precedes cambial reactivation and subsequent initiation of xylem cell production (Partanen et al. 1998). Vaganov et al. (1999) identified the timing of snowmelt, as well as sufficient soil and air temperatures, as the triggers for the onset of cambial activity. In the localized environment of the current study, these conditions appear to have been met at nearly the same time for all the species.

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Fig. 2. Gompertz function fitted to cumulative standardized ring width (RW), standardized number of cells (NC), and standardized number of earlywood cells (NEC). Vertical bars are standard deviation. NC subfigures show the onset of xylem cell production (circle, horizontal bars are standard deviation) and the end of cell production (square, date of 90% of cell production). Also in each NC subfigure, the onset of latewood production is displayed as the point where the NEC curve started diverging from the NC curve, as demonstrated by the horizontal broken line. NEC is expressed as a percentage of NC, and was determined along a single radial file compared with both RW and NC, which were measured on three radial files.
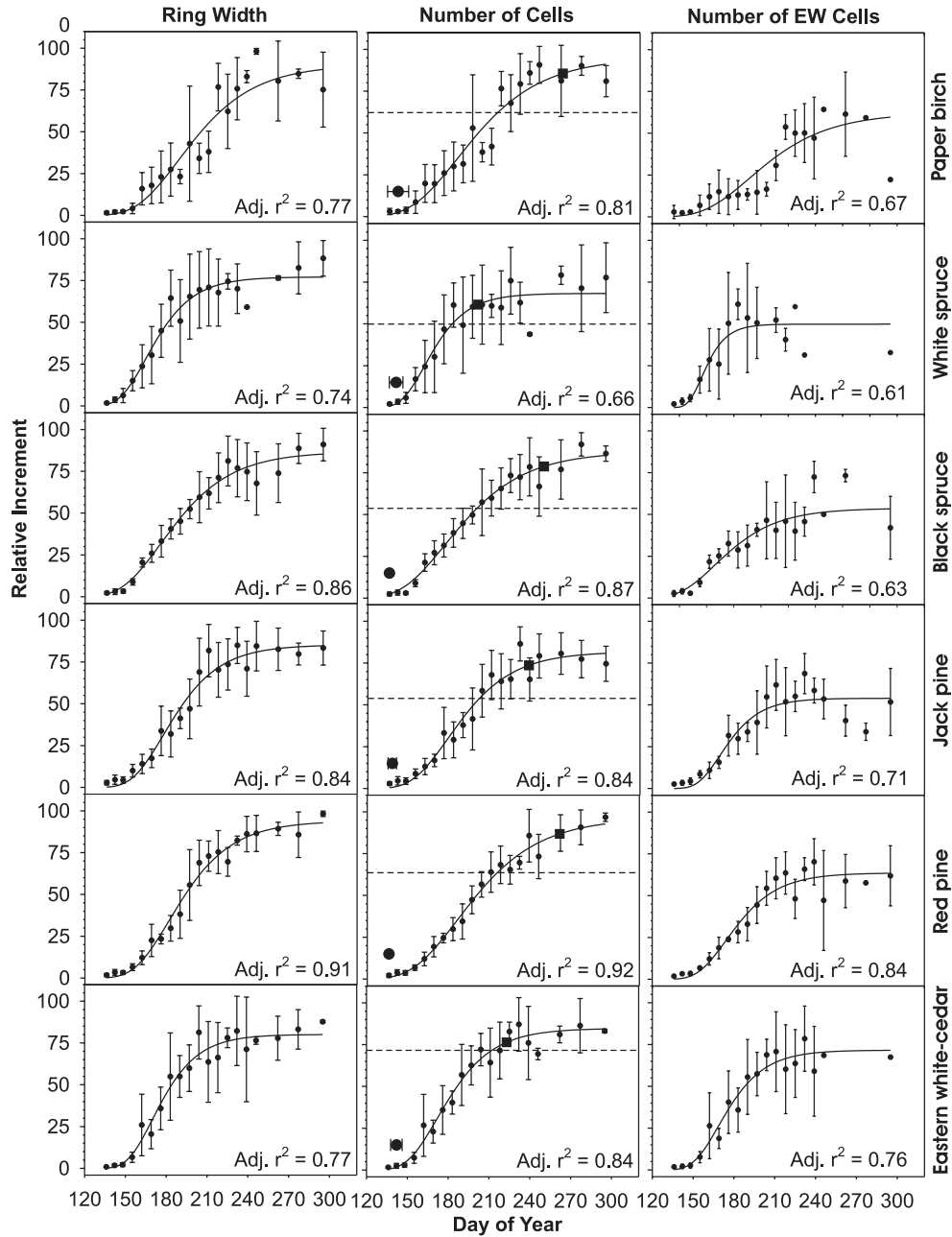
Ring formation and xylem cell production

Modeled ring width, number of cells, and number of earlywood cells for each species displayed a typical sigmoidal curve over the course of the growing season (Fig. 2). The Gompertz functions were all significant, with an adjusted coefficient of determination ranging from 0.61 to 0.92 ($P < 0.0001$). Little difference was observed between the Gompertz model fitted to relative ring width and relative number of cells produced (Fig. 2). Both have been shown to corre-

late well (Camarero et al. 1998), and unless otherwise indicated only the later will be presented.

The dates of greatest relative cell production for all of the species ranged from 11 June to 5 July and occurred at a time of little water deficit and after mean soil and air temperatures reached or exceeded 14 °C, and 20 °C, respectively (Fig. 1; Table 1). Tardif et al. (2001*a*) also found radial growth rates to peak as late as early July for these same species using band dendrometers. From May to mid-July, tem-

Table 1. Parameters for the Gompertz function fitted to the xylem cell production variables of six tree species in the boreal forest region of western Quebec, Canada.

Variables	Paper birch	White spruce	Black spruce	Jack pine	Red pine	Eastern white cedar
Ring width [a]						
a: asymptote (max. ring width (%))	90.2	77.1	86.7	85.2	93.9	80.1
β: x-axis placement parameter	6.11	8.54	6.09	7.73	7.13	9.15
κ: rate of change parameter	0.032	0.052	0.035	0.044	0.039	0.054
x_0: date of greatest growth	189 (8 July)	165 (14 June)	176 (25 June)	178 (27 June)	182 (1 July)	170 (19 June)
r: increment growth rate (% RW/d)	0.73	1.00	0.75	0.93	0.92	1.08
No. of cells [a]						
a: asymptote (max. no. of cells (%))	95.0	68.2	87.6	81.8	96.4	84.7
β: x-axis placement parameter	5.44	9.34	5.47	6.79	5.60	7.69
κ: rate of change parameter	0.029	0.058	0.031	0.038	0.030	0.045
x_0: date of greatest cell production	186 (5 July)	162 (11 June)	177 (26 June)	179 (28 June)	186 (5 July)	172 (21 June)
r: cell production rate (% cells/d)	0.69	0.98	0.68	0.78	0.72	0.95
No. of EW cells [b]						
a: asymptote (max. no. of EW cells (%))	62.2	49.9	53.7	53.9	63.6	71.6
β: x-axis placement parameter	5.79	15.45	6.45	10.32	8.32	9.00
κ: rate of change parameter	0.030	0.099	0.039	0.061	0.048	0.053

[a]Data were standardized as a percent of the maximum for ring width (RW) and number of cells and are therefore relative values.

[b]Number of earlywood (EW) cells was standardized against the total number of cells and are also relative values. Parameters x_0 and r are not presented for this variable.

perature has been shown to be the most important factor controlling cell production (Antonova and Stasova 1997; Deslauriers et al. 2003*a*; Mäkinen et al. 2003; Deslauriers and Morin 2005). This period coincides with most, if not all, of earlywood formation (Deslauriers et al. 2003*a*; Deslauriers and Morin 2005). Our results indicated that white spruce, followed by eastern white cedar, experienced the earliest dates of greatest relative xylem cell production (x_0), the fastest relative cell production rate (r), and the shortest duration of cell production compared with other species (Figs. 1 and 2; Table 1). Paper birch, black spruce, and red pine all responded similarly to each other. They had the lowest relative rates (r) and the longest duration of cell production, while jack pine was more intermediate in this respect (Figs. 1 and 2; Table 1). Rossi et al. (2006*b*) found that the timing of the maximum growth rates of numerous conifers (from both Europe and North America) corresponded with the summer solstice, when the photoperiod is longest. Similarly, we found the dates of the greatest relative cell production to overlap the summer solstice (21 June), with white spruce peaking 10 d prior and the remaining species on or shortly after this date (within 2 weeks). The peak in photoperiod may be a signal for the growth rate to decrease to successfully accomplish the growth and development of the entire tree ring prior to winter (Rossi et al. 2006*b*).

Paper birch registered the latest date (8 July) of greatest relative ring width growth (x_0), preceded by red pine 7 d earlier (Table 1). The date of greatest relative xylem cell production (x_0) for these two species occurred on 5 July, which again was the latest among the six species. In support of these results, paper birch was also found by Tardif et al. (2001*a*, 2001*b*) to be most dissimilar from the conifers in their annual radial growth – climate response and daily radial activity. Furthermore, the radial growth of paper birch responded most strongly to June precipitation (Tardif et al. 2001*b*), suggesting that greater dissimilarity between the conifers and paper birch may have resulted if the current study had not had a wet late May and June (Fig. 1).

Onset of latewood and cessation of xylem production

The onset of latewood production, based on the asymptote of the earlywood variable, was found to be generally similar among species (Figs. 1 and 2). White spruce began earliest (1 July), while for the remaining species, it occurred over a 2-week period ending 4 August. Both the time spent producing latewood and the latewood proportion were least for eastern white cedar, followed by white spruce, while the other species spent more time producing latewood, between one third and one half of the growing season (Figs. 1 and 2). Both white spruce and eastern white cedar are known to produce narrow latewood (Panshin and de Zeeuw 1970). Briand et al. (1993) also found that rapid growth in eastern white cedar resulted in as little as 10% latewood, but slow growth produced a greater proportion.

The end of xylem cell production was somewhat scattered among all the species, ranging from July 20th to September 20th (Figs. 1 and 2). White spruce and then eastern white cedar ended cell production first, around mid-July and early August, respectively. These two species demonstrated high relative cell production rates and a short season of radial growth. The production of xylem cells apparently decreased severely in both white spruce and eastern white cedar soon after the dry period of mid- to late July revealed by the soil hydration sensors (Fig. 1). Corresponding closely with our findings, Forster et al. (2000) found that the end of the growing season for eastern white cedar was mid-August, resulting in only 3 months of growth. In comparison, the growing season (duration of cell production) of white birch, black spruce, and red pine were longest, with that of jack pine being intermediate (Figs. 1 and 2). These species ended cell production over about 3 weeks from late August to mid-September.

Incorporation of these findings (e.g., growth rates, onset, cessation, and duration of xylem cell production and radial growth, earlywood–latewood relationships, the timing of greatest xylem cell production, and period of the major portion of tree ring formation) into process-based models could improve forecasts of the impact of climate change on forest growth. In a number of bio-climatic models, the period of radial growth is when carbon allocation to stem development is considered to occur, typically between the end of leaf out and the end of summer (Misson et al. 2004; Rathgeber et al. 2005). In some models, if data are lacking for parameter estimation, carbon storage and mobilization to stem growth is not represented, and carbon allocation is calculated simply as a fraction of net primary productivity determined on a yearly basis[2] (Hall et al. 2006). The results of this study could serve as inputs for development of allometric rules defining the carbon allocation to stem growth with respect to weather and photoperiod.

Conclusions

This study has demonstrated numerous similarities in the timing of xylem cell production among the five coniferous species, and to some degree, the one deciduous species examined. Our results suggest that any change in climate would have a relatively uniform qualitative influence on xylem cell production among the six species examined. A large proportion of cell production was shown to occur in June and July, and no strong quantitative differences were observed among species, which was corroborated by findings obtained from dendroclimatic analyses (Tardif et al. 2001b). It was noted that the timing of the greatest relative cell production corresponded well with the date of longest photoperiod (Rossi et al. 2006b). When comparing our results with those of other studies, some variability seems to be recurrent; however, given the varying optimal growing conditions in the boreal forest from year to year, flexibility in the growing process is a great advantage (Deslauriers et al. 2003a). Use of within-season microcore sampling complements standard dendrochronological (ring width) analysis, while proving somewhat redundant with band dendrometer readings. The latter method is less laborious than microcore sampling and processing, and therefore further study will focus on calibrating band dendrometers to actual cell production and development. Future studies should look at the timing of phenological events (e.g., bud burst, shoot elongation and cessation) in relation to cell production, developmental stages, and climatic conditions as well as multiple species at multiple sites. To increase the accuracy of recording the onset of xylem cell production in future studies, the sampling interval could be more frequent and begin sooner until the onset of cell production is confirmed.

Acknowledgments

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