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Variation in intra-annual radial growth (xylem formation) of *Picea mariana* (Pinaceae) along a latitudinal gradient in western Quebec, Canada[1]

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- *Premise of the study*: Climate warming might have resulted in altered initiation and termination dates of stem xylem growth in boreal stands. A systematic understanding of intra-annual xylem formation is thus needed for precise simulation of future growth in the context of sustainable forest management.
- *Methods*: A recently developed novel microsampling approach was employed over two growing seasons (2005–2006) to investigate the intra-annual stem xylem formation of *Picea mariana* at three sites along a latitudinal gradient (approximately 47.5–50°N) in western Quebec, Canada. The critical timings of xylem cell formation were determined and compared among sites/years. The relationships between xylem cell formation and meteorological variables were examined.
- *Key results*: From south to north, the onset of xylem cell production was detected on 20 May (SD ±3) at Angliers, 24 May (SD ±3) at Chicobi and 24 May (SD±4) at Muskuchii in 2005, and on 12 May (SD ±4) at Angliers, 14 May (SD ±3) at Chicobi and 20 May (SD ±3) at Muskuchii in 2006, respectively. Xylem cell production at each respective site terminated on 11 August (SD ±4), 7 August (SD ±3), and 7 August (SD ±4) in 2005, and on 8 August (SD ±4), 4 August (SD ±4), and 4 August (SD ±4) in 2006, respectively.
- *Conclusion*: Our study implies that despite the expected occurrence of earlier phenological development due to early spring climate warming, boreal trees like *P. mariana* might not be producing wider rings if cold temperatures occur later in the growing season in June to August. These results may challenge the view that boreal trees could be benefiting from spring warming to enhance growth.

Key words: boreal forest; climate change; Gompertz function; growing season; intra-annual xylem formation; *Picea mariana*; wood anatomy.

Climate warming has led to earlier springs and later autumns, thus prolonging the length of the growing season (IPCC, 2007). As a consequence, trees may have responded to this extended growing season through altered initiation and termination dates of phenological development and stem xylem growth. Phenological development is often easily monitored and has been well investigated (Menzel and Fabian, 1999; Zhou et al., 2001; Chuine et al., 2001; Menzel et al., 2006). For example, in Canada, Beaubien and Freeland (2000) collected data on the first flowering date of trembling aspen (*Populus tremuloides* Michx.) and found a 26-d shift to earlier blooming from 1900 to 1997. They also found an 8-d advancement in the first flowering date from 1936 to 1996 by analyzing the spring flowering index (mean of the first flowering dates of *P. tremuloides*, *Amelanchier alnefolia* Nutt., and *Prunus virginiana* L.).

In contrast, intra-annual stem xylem growth is less understood because cell production of the xylem is difficult to monitor during the growing season. Recently developed microsampling provides a feasible way to monitor the dynamic process of stem xylem formation from the first to last xylem cell during the growing season (Deslauriers et al., 2003a; Dufour and Morin, 2007; Ko Heinrichs et al., 2007; Rossi et al., 2007). The xylem tracheids are produced by the cambium, while the xylem cell number, their outer sizes, and the thickness of cell walls are limited by environmental factors such as climate (Richards, 1959; Antonova et al., 1995; Schmitt et al., 2004). Hence an intra-annual growth study allows us to refine our understanding of how meteorological factors regulate the formation of xylem from May to September. Deslauriers et al. (2008), based on an intra-annual investigation of *Pinus leucodermis* Ant. in southern Italy, found that hot climate conditions in 2003 resulted in an increased duration of xylogenesis by ca. 23 d in comparison to that of the subsequent year.

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L. Zhai et al. (unpublished manuscript) have used the microsampling approach to quantify the relationship of climate and intra-annual radial growth of three boreal tree species during the 2007 growing season in western Quebec. More xylem formed in trembling aspen and paper birch (*Betula papyrifera* Marsh.) with increased precipitation during the growing season, whereas more xylem formed with increased temperatures during the growing season for jack pine (*Pinus banksiana* Lamb.).

The effects of climate warming on tree growth become more significant at northern latitudes and high elevations, and the effects vary across species (Huang et al., 2010). Therefore, an investigation on intra-annual growth over a large latitudinal gradient may be able to detect a systematic change in the start and end dates of xylem formation during a growing season, thus assisting predictions of forest productivity. In the boreal forest, black spruce (*Picea mariana* Mill.) is one of the most widely distributed coniferous species and plays an important role in sustaining forest productivity (Harvey et al., 2002). Hence, under the framework of sustainable forest development, it is critical to improve our understanding of how intra-annual xylem formation of black spruce responds to a warming climate. Such knowledge in combination with other growth data will help us assess potential impacts of warming on growth and productivity of black spruce in the Canadian boreal forest.

In this study, the intra-annual xylem formation of black spruce was investigated along a latitudinal gradient from ca. 47.5° to 50°N in western Quebec during two growing seasons (2005 and 2006). The objectives of the study were (1) to determine the critical timings (the onset of xylem cell production, termination of new cell production of earlywood, and termination of new cell production of latewood) of xylem formation in black spruce growing along the latitudinal gradient during the two growing seasons; (2) to compare xylem formation at the three sites against meteorological conditions during the two growing seasons. Because higher growing-season temperatures were shown to increase the radial growth of black spruce over the same latitudinal gradient in western Quebec (Huang et al., 2010), we hypothesized that the northern black spruce stands may initiate xylem growth later than the southern stands and subsequently terminate xylem growth earlier than the southern stands.

MATERIALS AND METHODS

Study area—Our study area is located in western Quebec along a latitudinal gradient ranging from Angliers (ca. 47.5°N) in the south to Muskuchii (ca. 50°N) in the north (Fig. 1). The topography along the gradient is generally flat and uniform with low-elevation hills and rock outcrops (300–400 m a.s.l.). The region covers the climate transition zone, where the northern part is dominated by dry polar and moderate polar air masses during the winter, and the southern part is affected by moist maritime and moist tropical air masses during the summer (Sheridan, 2002). A climate gradient is also present in the studied latitudinal gradient, as described in Huang et al. (2010). Under the influence of this climate gradient, a vegetation transition zone covers the boreal forest of western Quebec from 48° to 50°N (Hofgaard et al., 1999; Bergeron et al., 2004). The common boreal tree species including trembling aspen, paper birch, black spruce, and jack pine occur across the gradient, but their abundance changes from south to north, i.e., increased abundance of conifers and decreased abundance of broadleaf species (Gauthier et al., 2000).

Climate data—At each of three selected mesic sites between 47.5° and 50°N, including Angliers (47°32.60′N, 79°13.60′N), Collines Chicobi (49°16.96′N, 78°19.11′W), and Collines Muskuchii (49°56.75′N, 78°42.88′N) (Fig. 1), a microweather station was installed (at 3 m height) to monitor the hourly meteorological conditions during the years of 2005 and 2006. A soil temperature sensor was installed to measure the hourly soil temperatures at a soil depth of 10 cm. In total, the measured meteorological parameters used to explore the relations with xylem formation in the study include hourly maximum, mean, and minimum air temperatures; hourly precipitation; hourly maximum, mean, and minimum soil temperatures 10 cm below the soil surface. Because the three meteorological stations did not work well to measure daily weather conditions through the entire two growing seasons (daily temperatures and precipitation data available only until August 2006), we compared the monitored weather data of each site with data obtained from the nearby climate stations and found they matched well (Fig. 2). Therefore, daily weather data from the stations Angliers, Lac Berry, and Matagami were correspondingly used with the three study sites along the south–north gradient (Fig. 2). The hourly weather data were calculated to obtain weekly and monthly mean climate variables such as weekly and monthly air and soil temperatures, as well as growing degree days (GDD, a measure of heat accumulation to estimate the growth and development of plants and insects during the growing season, ≥5°C) before the onset date of the xylem formation and from May to August.

Field sampling—Five healthy black spruce trees per site were chosen as our monitored trees. The selected stands at Angliers are dense and grow on a moist slope, co-occurring with jack pine stands. Their mean age as of 2006 was 65 yr (range: 59–71 yr), and mean DBH was 17.65 cm (SD ±2.32 cm). The selected stands at Collines Chicobi grow on a flat and fertile soil, co-occurring with jack pine, trembling aspen, and paper birch stands (Hamel et al., 2004). Their mean age as of 2006 was 50 yr (range: 44–56 yr) and mean DBH was 23.45 cm (SD ±4.24 cm). The selected stands at Collines Muskuchii also grow on a flat and fertile soil, co-occurring with jack pine, white birch, and balsam fir stands. Their mean age as of 2006 was 98 yr (range: 84–112 yr) and mean DBH was 25.25 cm (SD ±2.35 cm). Sampling was conducted throughout two growing seasons, from May to September in 2005 and 2006. To monitor cambial activity and xylem growth (Forster et al., 2000) during a growing season, we sampled microcores (2.5 mm in diameter and 20–25 mm in length) weekly from each tree stem at 1–1.3 m DBH using a Trephor tool (University of Padua, Italy, Rossi et al., 2006b). Based on the weekly data, the daily resolution of xylem growth was interpolated through a Gompertz curve (see later section). To avoid any disturbance from injury wood (Forster et al., 2000), we maintained at least 20–30 mm between adjacent sampling locations on the stem during the same sampling year. For the subsequent sampling year, a different location on the stem was sampled to avoid any disturbance from the previous sampling year. We did not observe any obvious loss of tree vigor when using our sampling approach during the two growing seasons. Each microcore was stored immediately in a microtube with 50% ethanol and stored at 5°C to avoid tissue deterioration.

Laboratory data preparation—In the laboratory, the microcores were prepared according to the following steps (Schweingruber, 1978; Deslauriers et al., 2003b): (1) each microcore was fixed in paraffin with an angle of 45–60°; (2) 12–20 μm thick cross sections were cut from each microcore using a rotating microtome (Leica RM 2245); (3) all cross sections were stained with safranin (1% w/v in water) and permanently fixed to the slides. Each prepared section was further used to measure a series of cell variables for final analysis. The analytical procedures were as follows (1) five radial files per section were randomly (resin ducts avoided) chosen; (2) cell number along each of the selected five radial files was obtained using an image analysis system and the software WinCELL (Régent Instruments, Nepean, Ontario, Canada). In total, an experienced technician spent 6 months in the laboratory obtaining the data.

Standardization—Due to eccentric growth, tree ring-width varies greatly along the circumference of each tree stem. Correspondingly, cell number of each prepared section also varies among different samples and trees (Schmitt et al., 2004). Therefore, a procedure called "Standardization" (Vaganov, 1990) was used to obtain a series of unbiased cell numbers. Standardization has often been used in previous wood anatomical studies (Deslauriers et al., 2003a; Rossi et al., 2006a). The unbiased number is calculated through the following steps as reported by Rossi (2003): (1) the number of cells in the three previous years was counted on each of five radial files per sample; in our case, cell numbers in 2002–2004, and 2003–2005 were counted for standardization of cell measurements in 2005, and 2006, respectively; (2) a ratio was obtained for each sample by dividing mean cell number of the sample by mean cell number of all samples per tree; (3) the number of xylem cells in each xylem formation phase (i.e., cell enlargement, cell wall thickening, and mature cell, see Deslauriers et al., 2003a) was then multiplied by the ratio to standardize the measured data according to

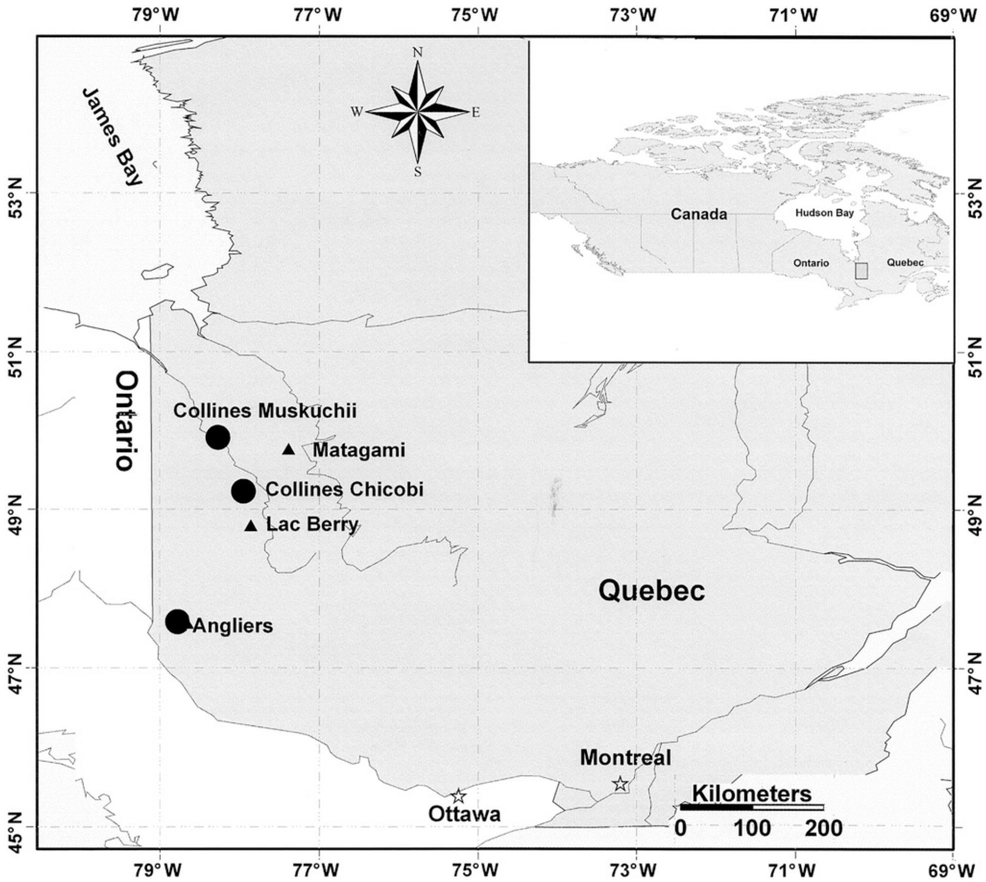

Fig. 1. Map of the three study sites at Angliers, Collines Chicobi, and Collines Mushuchii (solid circles) and the corresponding nearby climate data sites Angliers, Lac Berry, and Matagami (solid triangles) along the latitudinal gradient in western Quebec.

the sample's relative position on the stem (Deslauriers et al., 2003a, b). According to the relative position of the sample, the standardized number of cells in each *j*-sample and *i*-phase (nc_{ij}) was calculated as $nc_{ij} = n_{ij}\,(a_m/a_i)$ with

$$a_m = \frac{\sum_{j-1}^{N} a_j}{N},$$

where n_{ij} is the number of cells counted, a_j is the mean cell number of the previous rings for each *j*-sample, N is the number of *j*-samples, and a_m is the mean cell number of the previous rings of all *j*-samples.

Curve fitting through the Gompertz function—To appropriately describe the growth curve of the xylem formation during a growing season, we used the Gompertz function to fit the raw measurements of each xylem-growth time series. This function has been previously used to describe intra-annual diameter growth of trees (Deslauriers et al., 2003a; Rossi et al., 2006b) and other intra-annual growth processes, e.g., cotton hypocotyl elongation (Pegelow et al., 1977). The Gompertz function was described by Cheng and Gordon (2000) as

$$y = A \exp\left[-\exp^{(\beta-\kappa t)}\right]$$

in which y is the cumulative sum of growth, t is time computed as day of the year, A is the upper asymptote of the total number of xylem cells, β is the *x*-axis placement parameter, and κ is the rate of change parameter.

Through fitting the Gompertz function, the critical points of intra-annual xylem development such as the onset date of xylem cell formation, termination date of xylem earlywood cell production, and termination date of xylem latewood new cell production were determined. The curve fitting was done by the software SigmaPlot version 10 (Systat Software, Chicago, Illinois, USA). To test for differences among sites and between the two growing seasons, we compared the identified critical dates using ANOVAs with the software SAS version 10 (SAS, Cary, North Carolina, USA). From the estimated constants, the weighted mean absolute rate of cell production (r) was calculated according to Richards (1959) as $r = A\kappa/[2(v + 2)]$, where the parameter v was set at 0.0001, because the Gompertz function is a special case of the Richards function when $v = 0$ (Deslauriers et al., 2003a, b).

Growth relations to climate—Cell variables including weekly cell increment, the onset date of xylem cell production, termination date of production of new earlywood cells, and termination date of production of new latewood cells were compared with climate (the meteorological variables) for the two growing seasons of 2005 and 2006 and among the three sites over the latitudinal gradient. Climate data here include growing degree days (GDD ≥5°C) before the onset date of xylem cell production, mean weekly air and soil temperatures prior to the onset date of xylem cell production, GDD (≥5°C) from May to August, and monthly mean temperatures.

RESULTS

Climate data—As shown in Fig. 3, climate data during the two growing seasons showed that across the three sites, monthly temperatures from June to August in the year of 2005 were higher than those in the year of 2006. However, May temperatures in 2005 were lower than those in 2006. Along the gradient, temperatures at the southern site Angliers were warmer than those of the other two northern sites. July temperatures in 2005 and 2006 were 20.27° and 19.36°C, respectively,

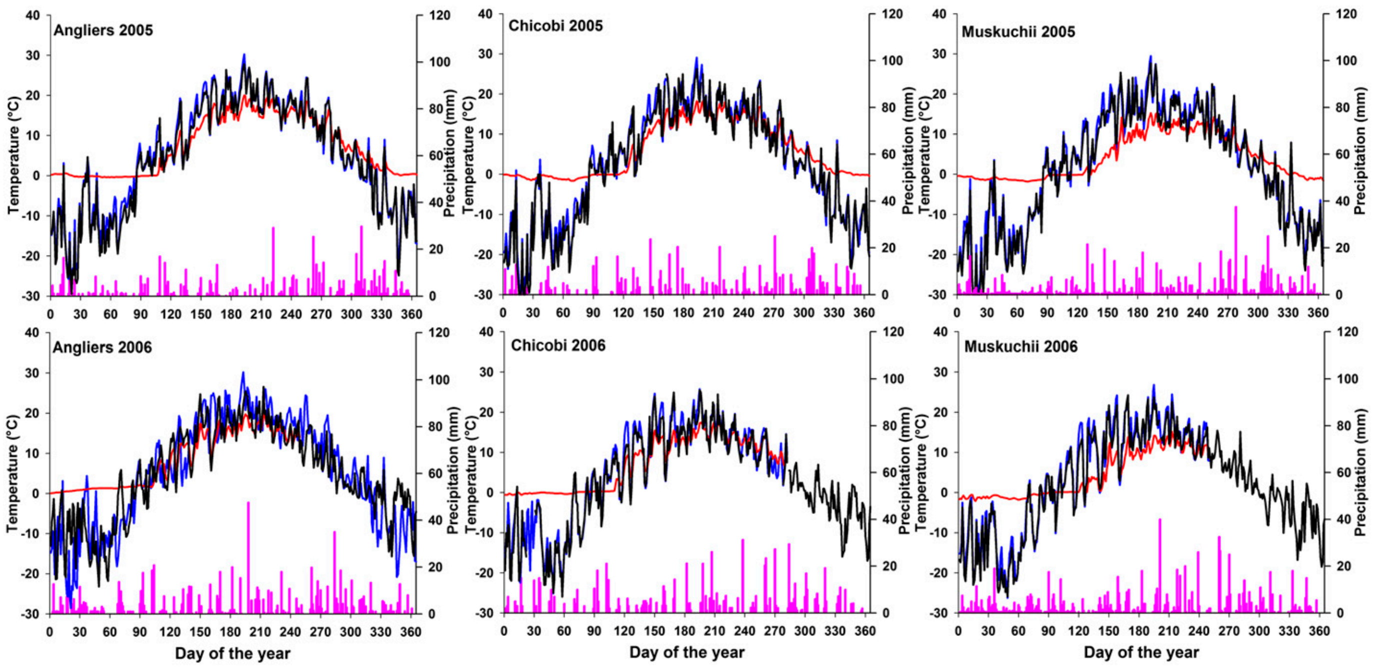

Fig. 2. Daily mean temperatures obtained by our weather stations (blue curves) and the daily mean temperatures (black curves) and total precipitation (pink vertical bars) obtained from nearby climate stations along the latitudinal gradient in western Quebec during 2005 and 2006 growing seasons. Red curves represent the daily soil temperatures monitored by our weather stations.

at Angliers, whereas they were 17.49° and 17.37°C, respectively, at Collines Chicobi, and 17.33° and 16.94°C, respectively, at Collines Muskuchii. As listed in Table 1, growing degree days (≥5°C) from May to August in 2005 were higher than those in 2006 for the three sites. However, growing degree days (≥5°C) at the onset date of the first xylem cell production in 2005 were generally lower than those in 2006. Weekly mean air temperatures prior to the onset date of the first xylem cell production across the three sites during the two growing seasons varied from 7.8° to 11.8°C. Weekly mean soil temperatures prior to the onset date of the first xylem cell production across the three sites during the two growing seasons varied from 4.3° to 7.1°C. Within a site, weekly mean air and soil temperatures prior to the onset date of the first xylem cell production in 2005 were lower than those in 2006.

Gompertz curve fit—The Gompertz curves corresponded well to the weekly cell number increment of the stem xylem (Fig. 4), (lowest adjusted $R^2 = 0.97$, $P < 0.0001$) (Table 2). The parameters of the Gompertz curves showed that the maximum cell number (A) ranged from 44.01 in 2006 to 55.17 in 2005 at Collines Muskuchii (Table 2). Generally, across the three sites, more total xylem cells were counted in 2005 than in 2006, indicating that a higher rate of cell production occurred in 2005 than in 2006 (Table 3). Along the gradient, stands at the southern Angliers site produced fewer weekly cells than did stands at the other two northern sites. Stands at the Collines Chicobi and Collines Muskuchii sites produced a similar number of cells during each week over both growing seasons. In general, stands produced more earlywood cells than latewood cells during a growing season among all sites (Table 3). Interestingly, stands produced a higher ratio of latewood cells to total cells in 2006 compared to that in 2005, especially when we considered stands at northern sites.

Critical dates during xylem formation—As listed in Table 1, the onset date of xylem cell production was on 20 May (SD ±3)

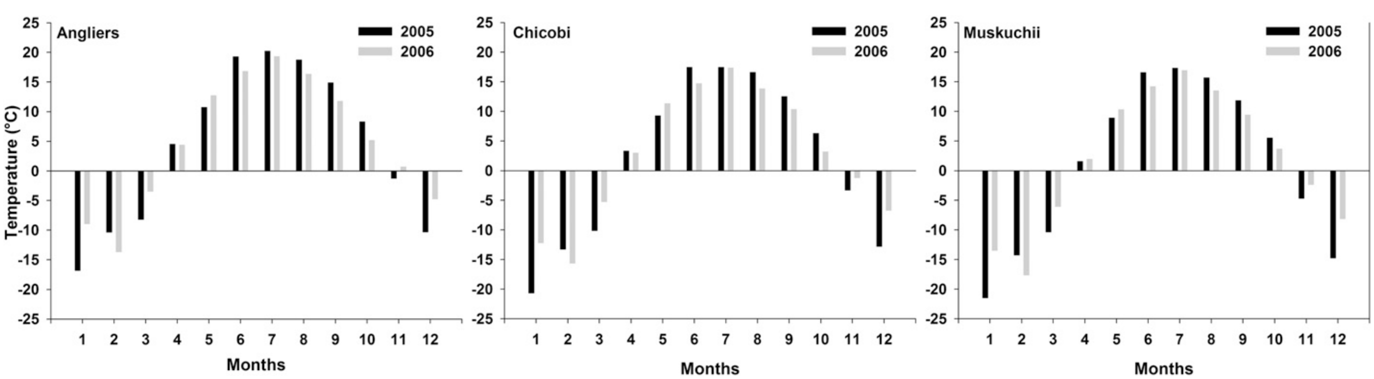

Fig. 3. Monthly mean temperatures at the three study sites in western Quebec along the latitudinal gradient in 2005 and 2006.

TABLE 1. Onset date of the first xylem cell, growing degree days (GDD ≥5°C) at onset date of the first xylem cell production, mean air temperatures during the week before xylem cell onset date (Tmean), mean soil temperatures (10 cm belowground) during the week prior to the onset of xylem cell formation (Tsoil), and termination date of new earlywood production (EW), termination date of latewood cell production, and GDD from May to August at the three sites in western Quebec during 2005 and 2006 growing seasons.

Sites	Year	Onset (±SD)	GDD (°C) at onset	Tmean	Tsoil	EW ending date	Termination date (±SD)	May–August GDD (°C)
Angliers (southernmost)	2005	20 May (3)	106.6	7.8	5.5	7 July (3)	11 August (4)	1547
	2006	12 May (4)	130.1	10.8	6.6	30 June (4)	8 August (4)	1447
Chicobi	2005	24 May (3)	101	9.4	6.4	9 July (4)	7 August (3)	1301
	2006	14 May (3)	114	11.8	7.1	5 July (3)	4 August (4)	1196
Muskuchii (northernmost)	2005	24 May (4)	77.9	8.9	4.3	9 July (4)	7 August (4)	1210
	2006	20 May (3)	147.2	11.3	5.3	5 July (3)	4 August (4)	1137

at Angliers, 24 May (SD ±3) at Collines Chicobi, and 24 May (SD ±4) at Collines Muskuchii in 2005, and on 12 May (SD ±4) at Angliers, 14 May (SD ±3) at Collines Chicobi and 20 May (SD ±3) at Collines Muskuchii in 2006, respectively. Correspondingly, the termination date of latewood cell production was on 11 August (SD ±4) at Angliers, 7 August (SD ±3) at Collines Chicobi and 7 August (SD ±4) at Collines Muskuchii in 2005, and on 8 August (SD ±4) at Angliers, 4 August (SD ±4) at Collines Chicobi and Collines Muskuchii in 2006, respectively. Overall, the onset date of xylem cell production, termination date of the earlywood production, and termination of xylem latewood production in 2005 were generally later than in 2006 at each site. Across the three sites, the onset of xylem cell production and termination date of earlywood cell production

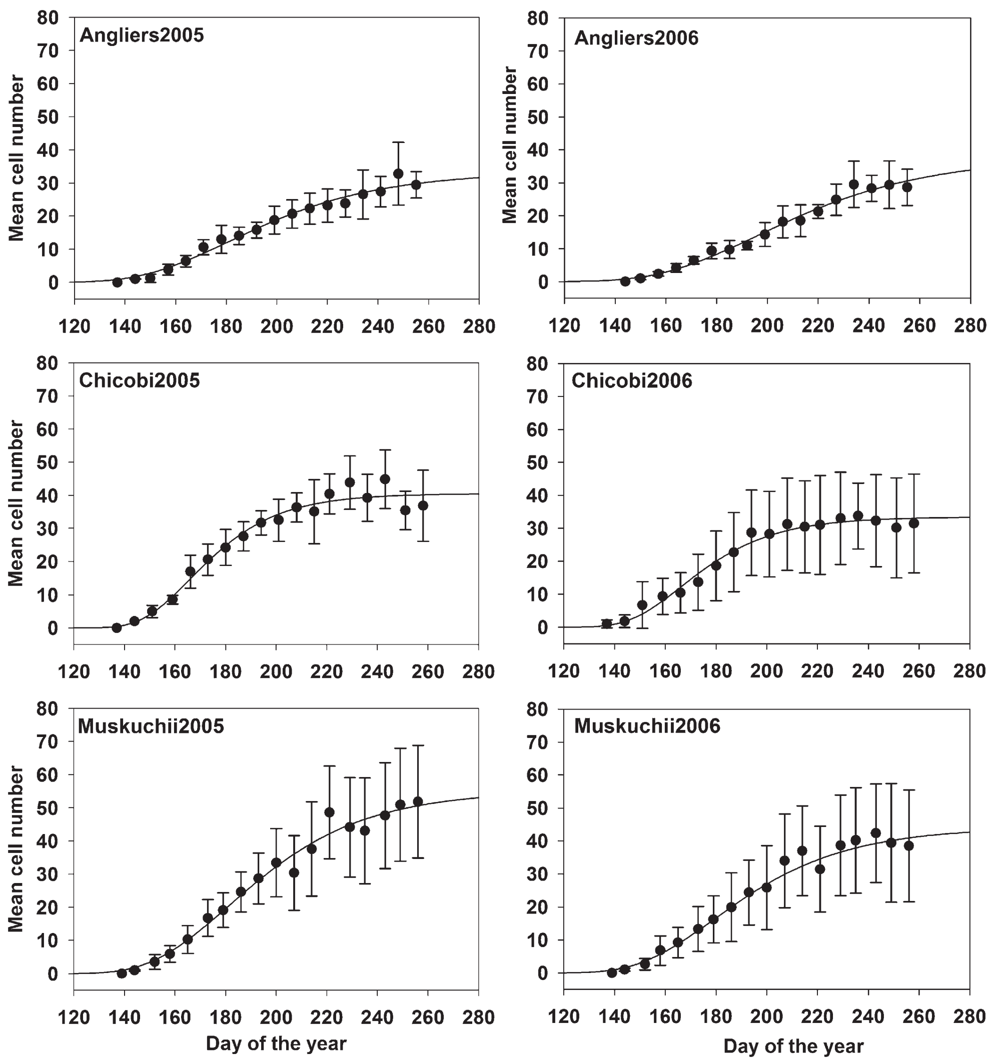

Fig. 4. Gompertz curve fit to mean total of xylem cells from May to September at the three sites in western Quebec during 2005 and 2006 growing seasons. Error bars indicate the standard deviations (SD).

TABLE 2. Parameters of the Gompertz curve fit on the weekly number of stem xylem cells in black spruce at three sites in western Quebec during the 2005 and 2006 growing seasons.

Sites	Year	A	β	κ	r	Adj. R^2	SE	F_{df}	P
Angliers	2005	33.39	5.32	0.029	0.24	0.98	1.53	$337.9183_{2/16}$	<0.0001
	2006	37.87	5.12	0.026	0.25	0.98	1.39	$457.7875_{2/16}$	<0.0001
Chicobi	2005	40.51	8.59	0.052	0.53	0.97	2.67	$254.6720_{2/17}$	<0.0001
	2006	33.37	8.12	0.049	0.41	0.98	1.75	$371.9401_{2/17}$	<0.0001
Muskuchii	2005	55.17	5.95	0.033	0.46	0.98	2.65	$399.8026_{2/17}$	<0.0001
	2006	44.01	6.09	0.034	0.37	0.98	1.83	$543.9217_{2/17}$	<0.0001

Notes: A = upper asymptote of the total number of xylem cells, β = x-axis placement parameter, κ = rate of change parameter; r = mean rate of cell production, Adj. R^2 = adjusted R^2; SE: standard error of the estimate; F statistic, df = numerator/denominator degrees of freedom.

at Angliers were both 1 week earlier than those at the two northern sites during the two growing seasons. However, the termination of xylem cell production at Angliers was later than that observed at the two northern sites. No difference in the onset date of xylem cell production, termination date of the earlywood production, and termination date of xylem latewood production was observed at the two northern sites during the two growing seasons, except for the onset date of xylem cell production in 2006. Overall, as shown in Fig. 5, it is clear that the duration of xylem cell production at Angliers was the longest among the three sites over the two growing seasons. The duration of xylem cell production at Collines Chicobi and Collines Muskuchii was similar over the 2 years. Within a site, the period of formation of earlywood was longer than that of latewood. Moreover, the period of latewood formation at the two northern sites was shorter than that at the southern Angliers site. ANOVAs results showed no significant difference among sites ($F_{2,\,18}$ = 0.003, P = 0.997) and between years ($F_{1,\,18}$ = 0.073, P = 0.792).

DISCUSSION

Earlywood growth and climate—The onset date of xylem cell production of black spruce ranged from mid-May to the end of May during the two growing seasons. These results agreed with recent intra-annual tree-ring studies from western Quebec (Tardif et al., 2001; Ko Heinrichs et al., 2007; L. Zhai et al., unpublished manuscript). For instance, Ko Heinrichs et al. (2007) observed that the onset of xylem cell formation of several boreal species ranged from mid-May to 22 May at Lac Duparquet, western Quebec. L. Zhai et al. (unpublished manuscript) reported an onset of xylem cell formation on 7 May for jack pine, 28 May for trembling aspen, and 5 June for paper birch at Lac Dances from northwestern Quebec. Similar dates for the onset of xylem cell formation of boreal tree species such as paper birch, black spruce, and red pine (*Pinus resinosa* Sol. ex Aiton) have also been documented (Fraser, 1952; Ahlgren, 1957; Forster et al., 2000). It is generally believed that the onset of xylem formation is controlled by photoperiod, temperatures, and water availability (Hänninen, 1995; Leinonen et al., 1997) as well as auxin production (Wang et al., 1997). In our study area, water availability in May is rarely found to limit black spruce growth because of sufficient winter snow and spring rainfall (Huang et al., 2010). Threshold temperatures have been reported to trigger the onset of xylem cell production across the boreal forest. A physiological threshold temperature of >5°C (Jarvis et al., 1989; Körner, 1998; Schmitt et al., 2004) could be responsible for stimulating the onset of xylem growth in May from the study region. In this study, mean air temperatures during the week before the onset of xylem cell production ranged from 7.8° to 9.4°C in 2005 and from 10.8° to 11.8°C in 2006 across the three sites, respectively. Mean soil temperatures during the week before the onset of xylem cell production ranged from 4.3° to 6.4°C in 2005 and from 5.3° to 7.1°C in 2006 across the sites (Table 3). In the same region, Ko Heinrichs et al. (2007) also reported that the onset of xylem cell production was at a time that coincided with rising air and soil temperatures. L. Zhai et al. (unpublished manuscript) observed that the onset of xylem cell production was at 5.3°C for jack pine, and ca. 8.2°–10.4°C for both trembling aspen and paper birch in the

TABLE 3. Earlywood (EW) cell number, latewood (LW) cell number, total cell number, and the ratio between either earlywood or latewood, and the total cell number at three sites in western Quebec during two growing seasons.

Sites	Year	Number of cells: Earlywood	Number of cells: Latewood	Total	EW/Total (%)	LW/Total (%)
Angliers	2005	18.8	7.76	26.56	70.8	29.2
	2006	10.96	10.32	21.28	51.5	48.5
Chicobi	2005	31.72	8.72	40.44	78.4	21.6
	2006	22.72	8.52	31.24	72.7	27.3
Muskuchii	2005	28.72	18.92	48.64	59	41
	2006	19.88	14.12	34	58.5	41.5

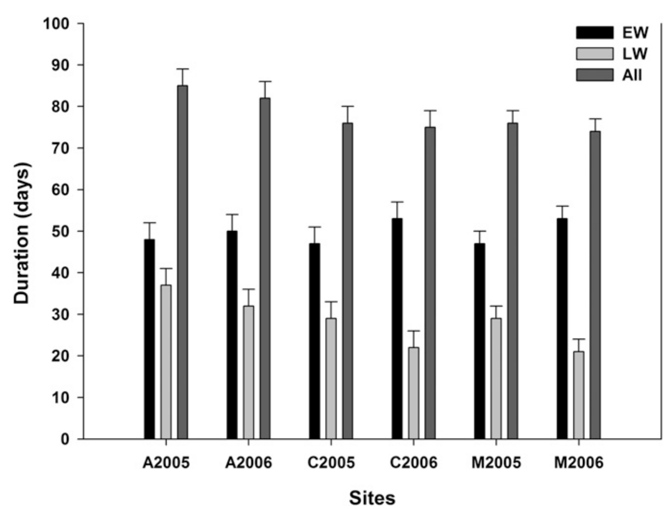

Fig. 5. Period of formation of earlywood (EW), latewood (LW), and all xylem cells (All) at Angliers (A), Collines Chicobi (C), and Collines Muskuchii (M) in western Quebec during 2005 and 2006 growing seasons. Error bars indicate the standard deviations (SD).

mixed boreal forest of northwestern Quebec. Schmitt et al. (2004) documented that, at tree line, growth occurred when the daily temperatures was above 5°C. Rossi et al. (2007) reported that xylogenesis was active when the mean daily air temperatures was 5.6°–8.5°C. Growing degree days (GDD) of ≥5°C were reported to be a major climate factor for controlling trembling aspen productivity at the spatial scale in western Quebec (Lapointe-Garant et al., 2010). Across the three sites along the gradient, however, GDD at the onset of xylem cell production was found to vary considerably across the three sites and two growing seasons, ranging from 77.9° to 147.2°C. This variation indicates that GDD could play a less important role in triggering the onset of xylem cell production than in controlling forest productivity in the studied gradient. An earlier onset of xylem cell production of black spruce in 2006 compared to 2005 across the three sites may be directly attributed to the positive effect of warmer May temperatures in 2006 on cell production. Deslauriers et al. (2003a) also observed an earlier onset of cell production in balsam fir in a warmer 1999 than in either 1998 or 2000 in northeastern Quebec. In the eastern Italian Alps, Rossi et al. (2007) also reported the earliest initiation of cambial activity for the studied tree species [*Larix deciduas* Mill., *Pinus cembra* L., and *Picea abies* (L.) Karst] in 2003 due to warmer April and May temperatures in 2003 compared to either 2002 or 2004. Along the south–north gradient, an earlier initiation of the xylem formation of black spruce at the southern Angliers site than that at the two northern sites in the two growing seasons might be due to an earlier warm spring in the south, thereby triggering an earlier onset of phenological development and xylem growth of the trees in the south. The small difference in the onset of xylem formation in the two northern sites in our study could be attributed to a similar climate dominance (cold and dry climate from the arctic in winter [Sheridan, 2002]) at these two nearby sites or similar local site conditions. A later termination of earlywood production in 2005 than in 2006 across the three sites suggests that warmer June and July temperatures in 2005 might have resulted in longer production of earlywood. As a result, a higher percentage of earlywood cells was observed in 2005 across the three sites. Deslauriers et al. (2003a) also observed that the duration of earlywood formation of balsam fir was ca. 6–7 wk in the normal years 1998 and 2000, but was ca. 9–10 wk in the warmer year 1999. Wang et al. (2002) documented that black spruce stands produced more earlywood cells at tree line in northern Quebec in warmer years as well. Along the gradient, a higher percentage of earlywood cells produced by trees at the two southern sites than that at the northern Collines Muskuchii site also indicates that warmer climate in the south may be favorable for production of more earlywood cells.

Latewood growth and climate—Overall, the onset of latewood cell production of black spruce, i.e., the termination date of earlywood cell production, ranged from the end of June to early July across the three sites. The results are consistent with Deslauriers et al. (2003a) who reported that the earlywood–latewood transition for balsam fir occurred from 2 July to 19 July in northeastern Quebec. Across the three sites, our studied black spruce trees ceased producing new xylem latewood cells during the first half of August. L. Zhai et al. (unpublished manuscript) also found that the end of new cell production of jack pine, trembling aspen, and white birch was on 9, 16, and 16 August, respectively, in northwestern Quebec. Vaganov et al. (2006) documented that at high latitude, new cell production of tree species usually ceased in mid-August. Therefore, the duration of the latewood xylem new cell production was ca. 3–5 weeks across the three sites during the two growing seasons. Deslauriers et al. (2003a) also observed that the duration of latewood cell production for balsam fir was ca. 3–5 weeks in northeastern Quebec. After the termination of new latewood cell production, however, lignin deposition in latewood cells (i.e., lignification) persisted from the end of August to mid-September. Our results are consistent with the previous intra-annual tree-ring studies that also found lignification until the end of August to mid- or late September (Deslauriers et al., 2003a; L. Zhai et al., unpublished manuscript). A higher ratio of latewood cells to the total xylem cells produced in 2006 than in 2005 across the three sites might be due to colder July and August temperatures in 2006 than in 2005. Cold summer temperatures in 2006 resulted in an earlier start of latewood cell production (i.e., termination of the xylem earlywood cell production) and earlier termination of latewood production across three sites, thereby producing fewer total cells in the colder year. Consequently, higher ratios of latewood cells to the total cells were observed in the narrow annual growth increment of 2006 compared to the wider annual growth increment of 2005. Wang et al. (2002) also observed fewer xylem cells and high latewood density of black spruce in cold years than in hotter years at the tree line of the boreal forest in Quebec. An earlier termination of latewood production for the northern trees than the southern trees during each of the two growing seasons might also be ascribed to the limiting effect of colder summer temperatures on cell growth in the north than in the south. This supports our hypothesis that trees terminate cell production earlier in the north than in the south due to an earlier arrival of cold temperatures in the north. Past studies also found that August temperatures were strongly correlated with the maximum tree-ring wood density (D'Arrigo et al., 1992; Schweingruber et al., 1993). Overall, the duration of xylem cell production for the southern trees was found to be about 1 week longer than that of the northern trees across the sites. Trees growing during the warm May of 2006 started xylem cell production earlier than those growing in cold May of 2005, indicating that May temperatures are critical for the onset of xylem formation. However, cold June to August temperatures in 2006 resulted in an earlier termination of earlywood cell production and of latewood cell production, suggesting that June to August temperatures played a particularly important role in regulating cell production processes.

Conclusions—Sustainable forest management requires tree growth information both at inter- and intra-annual time scales to simulate future growth precisely. The recently developed microsampling procedure provides a feasible way to monitor intra-annual growth dynamics during a growing season. In this study, the dynamics of intra-annual xylem formation of black spruce were investigated along a latitudinal gradient from ca. 47.5° to 50°N during the two growing seasons 2005 and 2006 in western Quebec. From south to north, the onset and termination of xylem cell production were detected over the gradient. Compared to 2005, warmer May temperatures in 2006 were found to trigger the earlier onset of xylem cell formation of that year. However, cold June to August temperatures in 2006 might have resulted in an earlier termination of the earlywood and latewood cell production of that year. Consequently, higher ratios of the latewood cells to the total xylem cells in 2006 were observed across the three sites in comparison with 2005. Our study may imply that despite the expected occurrence of earlier phenological development due to early spring climate warming, boreal trees might not be producing a wider ring-width if cold temperatures occur later in the growing season in June to August. These results may challenge the view that growth of boreal trees might be enhanced by spring warming. Therefore, the results of finer-scale intra-annual studies should be integrated into future tree-growth simulation models. In addition, with different warming amplitudes across successive seasons, a warm summer might result in greater growth of the northern black spruce stands compared to southern stands, which could lead to low wood density in northern stands. However, a cold summer might lead to more latewood relative to earlywood production, thus increasing wood density in the southern stands. Future intra-annual growth studies will be needed to expand intra-annual growth databases, which will further improve our capability of modeling growth and productivity of black spruce stands in the eastern Canadian boreal forest.

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