

VARIATION IN INTRA-ANNUAL WOOD FORMATION, AND FOLIAGE AND SHOOT DEVELOPMENT OF THREE MAJOR CANADIAN BOREAL TREE SPECIES¹

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- **Premise of the study:** In a warming climate, boreal trees may have adjusted their growth strategy (e.g., onset and coordination of growth among different organs such as stem, shoot, and foliage, within and among species) to cope with the extended growing seasons. A detailed investigation into growth of different organs during a growing season may help us assess the potential effects of climate change on tree growth in the boreal forest.
- **Methods:** The intra-annual growth of stem xylem, shoot tips, and foliage area of *Pinus banksiana*, *Populus tremuloides*, and *Betula papyrifera* was monitored in a boreal forest in Quebec, Canada during the growing season of 2007. Xylem formation was measured at weekly intervals, and shoot elongation and foliage expansion were measured three times per week from May to September. Growth indices for stem, shoot, and foliage were calculated and used to identify any climate–growth dependence.
- **Key results:** The time periods required for stem growth, branch extension, and foliage expansion differed among species. Of the three species, *P. banksiana* had the earliest budburst (20 May) yet the latest completion date of the foliage growth (2 August); *P. tremuloides* had the latest budburst (27 May) yet the earliest completion date of the foliage growth (10 July). Air temperature positively affected shoot extension growth of all three species. Precipitation positively influenced stem growth of the two broadleaf species, whereas growing season temperature positively impacted stem growth of *P. banksiana*.
- **Conclusion:** The results show that both the timing of growth processes and environmental dependences differ among co-occurring species, thereby leading to different adaptive capability of these boreal tree species to climate change.

Key words: *Betula papyrifera*; growth dynamics; intra-annual wood formation; meteorological factors; *Pinus banksiana*; *Populus tremuloides*; tree phenology.

Climate change might have important impacts on growth of trees and forests, as well as on forest productivity, by affecting the timing of tree phenological processes at mid and high latitudes of the northern hemisphere (IPCC, 2007). Climate controls the timing of tree growth by regulating the initiation and growth processes of tree organs (i.e., foliage, shoot, stem, and root) during a growing season. Because the timing of spring growth phases such as budburst, leaf-out, shoot extension, and flowering is primarily determined by the accumulated temperatures above a threshold value (Beaubien and Freeland, 2000), the spring phenology of trees has advanced as a result of warmer spring temperatures during recent decades (IPCC, 2007). Earlier budburst, flowering, and leaf unfolding in several species were detected from long phenological observation data.

For example, an 8-d earlier leafing out was observed in several European tree species (*Betula pubescens* Ehrh., *Prunus avium* L., *Sorbus aucuparia* L., and *Ribes alpinum* L.) from 1969 to 1998 (Chmielewski and Rötzer, 2001). In Canada, Beaubien and Freeland (2000), collecting data on the first flowering date of trembling aspen (*Populus tremuloides* Michx.), reported a 26-d shift to earlier blooming from 1900 to 1997. In addition, later leaf senescence and fall were also observed in Europe, but evidence for a delay of leaf senescence is more scattered (Menzel and Fabian, 1999). Khanduri et al. (2008) summarized delayed autumn events reported in previous studies and found an average delay of 1.4 d per decade in autumn events.

Empirical evidence on changes in the length of growing season is restricted to changes in budburst and leaf senescence. However, the growth pattern of twigs and stems and the timing of their growth have received much less attention. With climate warming, we assumed that the duration of shoot growth and wood formation is also longer during a growing season. This longer duration might affect wood properties and tree productivity. Also, the duration of growth defines the period where trees are the most vulnerable to extreme weather events (like drought and frost), insect attacks, and susceptibility to herbivores. There is some research on shoot elongation and bud set of trees (Junttila and Heide, 1981; Kanninen, 1985; Ozawa et al., 2000; Chuine et al., 2001). In many boreal trees, shoots are often preformed in the buds, but large components of new

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growth are also observed in some species (Kaya et al., 1994). The end of shoot growth seems to be largely influenced by day length (Kozłowski and Pallardy, 1997) and to some degree by temperature. Also, it is noteworthy that some conifers, such as Scots pine (*Pinus sylvestris* L.), in the subarctic terminate their shoot growth when day length is still at 24 h (F. Berninger, personal observation).

During recent years, an increasing number of studies have focused on intra-annual xylem formation (e.g., Tardif et al., 2001b; Deslauriers et al., 2003a, b; Rossi et al., 2006a, 2008; Ko Heinrichs et al., 2007; Thibeault-Martel et al., 2008; Huang et al., 2011). Some analyzed cambial activity and xylem formation and described the dynamics of xylem development and cell differentiation over time (Deslauriers et al., 2003a). Others investigated the endogenous (Nobuchi et al., 1995; Rossi et al., 2008) or exogenous factors controlling intra-annual xylem formation (Savidge, 1996; Deslauriers et al., 2003b, 2007; Rossi et al., 2006a, 2007). Rossi et al. (2009) first investigated needle and shoot phenology in combination with xylem development for three conifers [*Larix decidua* Mill., *Pinus cembra* L., and *Picea abies* (L.) Karst.] in Italy. They found secondary cell wall thickening of the first latewood cell occurred during the termination of needle and shoot lengthening, suggesting internal competition for resources. Aside from this study, no any other effort has been conducted to investigate the intra-annual stem growth in combination with the shoot and foliage growth together and compare growth processes of different tree organs among species. However, with potential climate warming, it is critical to understand the phenology of different organs like stem, shoot, and foliage and their coordination within and among species during a growing season because it may allow us to better assess which species would be more vulnerable to future climate change and how these species are coping with a warming climate. In addition, understanding the climate–growth relationships at a finer time scale (e.g., weekly scale) within a growing season may refine our knowledge of the climate–growth relationships at monthly and seasonal scales obtained from empirical tree-ring studies (Fritts, 1976). The boreal forest ecosystem is one of the most sensitive ecosystems to global climate change (IPCC, 2007) and is the most ideal ecosystem for monitoring any potential phenological changes in different organs of trees.

The current study aims to investigate the intra-annual xylem formation and foliage and shoot development of three economically and ecologically important boreal species in northwestern Quebec during the 2007 growing season. These are jack pine (*Pinus banksiana* Lamb.), a conifer, and trembling aspen and white birch (*Betula papyrifera* Marsh.), two broadleaf species. The specific purposes of the study were to (1) investigate the growth phenology of shoot, stem, and foliage of the three species during a growing season, (2) explore the potential relationships between growth of different organs and climatic variables. In the boreal forest, previous empirical studies showed that broadleaf species are usually limited by precipitation and coniferous species are affected by temperatures (Hofgaard et al., 1999; Tardif et al., 2001a, b; Ko Heinrichs et al., 2007; Huang et al., 2010). We hypothesized that intra-annual growth of stem, shoot, and foliage of different tree species under the same growing conditions are species-specific because of their different reactions to environmental factors such as climate. We also hypothesized that growing season temperature might be the most important factor for regulating growth of some conifers, whereas growing season precipitation might be critical for growth of broadleaf species.

MATERIALS AND METHODS

Study site and tree selection—The study area is part of the Lake Duparquet Teaching and Research Forest in northwestern Quebec, Canada (48°31'N, 79°25'W) (Harvey, 1999). This region is dominated by continental cold, dry air from the arctic in winter and by warm, moist air from the south in summer (Sheridan, 2002). Regional climate observations from 1971 to 2008 showed that mean annual temperature was around 0.7°C, with the warmest mean monthly temperature of 17.3°C in July and coldest mean monthly temperature of –17.9°C in January. The average annual total precipitation was around 889.8 mm, with 27.7% in the form of snow (Environment Canada, 2008). Under the influence of this climate, a vegetation transition zone where forest composition shifts from the broadleaf and coniferous mixed forests in the south to the coniferous dominated boreal forests in the north was observed in the region. The common tree species were trembling aspen, white birch, balsam poplar (*Populus balsamifera* L.), balsam fir [*Abies balsamea* (L.) Mill.], black spruce [*Picea mariana* (Mill.) B.S.P.], white spruce [*Picea glauca* (Moench) Voss.], eastern white cedar (*Thuja occidentalis* L.), and jack pine. Our study site was in a young jack pine plantation (planted in 1992) mixed with some natural stands of trembling aspen and white birch saplings. We selected this site because of the presence of all three species and the proximity to a microweather station, which allowed us to frequently access the site for monitoring tree phenology development. We believe that the phenological development of this mixed forest can be representative for the boreal forest in northwestern Quebec. Ten healthy trees per species were selected for the study (Table 1).

Field sampling—To monitor the cambial activity and xylem formation of these three species during the 2007 growing season, we took wood microcores (2.5 mm in diameter and 20–25 mm in length) weekly at 1 m above the ground in a spiral up the stem using the Trephor tool (University of Padua, Italy; Rossi et al., 2006b). The fieldwork started from 3 May to the end of September. To avoid any disturbance from injured wood (Forster et al., 2000), we kept at least 20–30 mm between adjacent sampling locations. The spiral sampling avoided extracting any sample right above any other sample location. As in another study (Huang et al., 2011), we did not observe any obvious loss of tree vigor when using our sampling approach in the study. In the field, each sampled microcore was stored immediately in a microtube with 50% aqueous ethanol and stored at 5°C to avoid tissue deterioration. In total, 630 samples were taken from these three species during 21 sampling weeks.

Budburst, shoot elongation, and needle/leaf enlargement were recorded from 3 May to 27 September. In the field, the timing of budburst (defined as 50% of buds open) was considered as the time of the onset of shoot elongation and foliage enlargement of the three species. For jack pine, two main branches per tree were chosen from the middle canopy, and the length of new shoot growth that developed from these two branches was measured three times per week. For trembling aspen and white birch, five main branches per tree were chosen from the middle canopy to measure the length of new branches and count the number of new leaves produced on them. They were also measured three times per week. These measurements collected in the middle canopy could properly represent the dynamics of shoot and foliage growth of the whole crown (Tang et al., 1999; Rossi et al., 2009). In addition, to avoid negative impacts of manual defoliation on the studied trees, six reference trees per species were randomly chosen in the same plot to measure the foliage (leaf/needle) area of new leaves produced during each visit day. Leaves from a new shoot chosen randomly from each reference tree were removed to measure the needle/leaf area each time using a scanner and the WinFOLIA software (Regent Instruments, Nepean, Ontario, Canada). Leaf/needle area averaged from the six reference trees was considered as foliage growth for the species on the visit day. In addition, tree height and diameter at breast height (DBH) were also measured for each studied tree. Increment cores were taken at DBH from each studied tree to determine the exact age.

TABLE 1. Mean diameter at breast height (DBH), mean height, and mean age, as well as the corresponding standard deviations of the studied tree species ($N = 10$).

Statistic	Jack pine	White birch	Trembling aspen
Mean DBH (cm)	10.2 ± 1.6	6.8 ± 1.9	8.3 ± 1.6
Mean height (m)	6.6 ± 1.0	7.5 ± 1.8	7.5 ± 0.9
Mean age (year)	14 ± 2	15 ± 2	17 ± 3

Climate data—The 2007 weather data were collected from the weather station at the Lake Duparquet Research Station, which is 2 km away from our study site.

Meteorological measurements were recorded hourly. Meteorological variables include daily maximum, minimum, mean air and soil (10 cm below-ground) temperature, growing degree-days (GDD) $>5^{\circ}\text{C}$, maximum and minimum relative humidity (RH), and precipitation. Daily maximum and minimum vapor pressure deficit (VPD) was calculated from daily minimum and maximum air temperature and RH according to Prenger and Ling (2001). According to the sampling intervals, such as weekly for stem and 2-d intervals for shoot and foliage, we calculated the corresponding meteorological variables.

Laboratory preparation—The collected wood microcores were prepared for microscopy as follows (Schweingruber, 1978; Deslauriers et al., 2003b). First, the cores were embedded in paraffin using dehydration with ethanol and D-limonene. Thereafter, both xylem and phloem were embedded in paraffin, and the microcores were then fixed on biocassettes (support) by means of paraffin blocks. Finally, transverse sections of 12–20 μm thick were cut with a rotary microtome (Leica RM2255, Leica Microsystems USA). To identify different phases of xylem cell development (i.e., radial cell enlargement, cell wall thickening and mature cell) and to count total cell numbers, we stained sections with cresyl fast violet (0.05% w/v) and safranin (1%, w/v). As a result, cell walls during the cell enlargement phase, cell wall thickening phase, and mature cell phase are pink, violet, and completely blue, respectively. All slices were photographed with a digital camera attached to the microscope. Each image was then analyzed by the software WinCELL (Régent Instruments, Nepean, Ontario, Canada), and three radial files (rows of cells) from each image were selected randomly to count the cell number. The vessels of the two broadleaf species during the counting were avoided (counts were of tracheids only).

Standardization—Ring width and cell number may generally vary to some extent along the circumference of a tree (Schmitt et al., 2004). Therefore, Vaganov (1990), Rossi (2003), and Thibeault-Martel et al. (2008) proposed standardizing cell numbers around the circumference. To this end, cell number produced during the previous 3 yr was counted on three parts of the sample. Mean number of cell rows produced during the year was divided by the average cell number during the past 3 yr in the sample to calculate the relative growth up to the sampling date. To convert this relative growth into absolute cell number, we then multiplied the relative growth by mean cell number of the whole tree (i.e., all samples combined) (Deslauriers et al., 2003a). The standardized cell number in each j -th sample and i -th 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 cell number counted, a_j is mean cell number of the previous rings for each j -sample, N is the number of j -samples, and a_m is mean cell number of the previous rings of all j -samples, a_i is mean cell number of the rings in i phase.

Fitting of a growth curve—Xylem cell formation, shoot extension, and foliage growth of individual tree were fit using the commonly used Gompertz sigmoidal growth function (Gompertz, 1825). The 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 like cotton hypocotyl (*Gossypium hirsutum* L.) elongation (Pegelow et al., 1977). All analyses were conducted using the SigmaPlot statistical package (version 10, Systat, San Jose, California, USA). The Gompertz function was described by Cheng and Gordon (2000) as $y = A \exp[-\exp(\beta - \kappa t)]$, 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 organ growth (xylem cell number, shoot length, foliage area), β is the x -axis placement parameter, and κ is the rate of change parameter. Through fitting of the Gompertz function, the critical points of intra-annual xylem, shoot and foliage development such as the onset date, the timing of maximum growth, the ending date, and growth rate were determined. Our approach to determine the onset and termination of xylem formation is similar to Rathgeber et al. (2011) who proposed to objectively to determine main phenological events occurring during wood formation (The onset of a given phase was defined as the date at which 50% of the observed radial files show at least one new cell in this phase,

while the termination of a given phase was defined as the date at which 50% of the observed radial files show at most one last new cell in this phase).

Growth indices—Inter-annual, as well as intra-annual growth of trees is well known not to follow exactly a growth curve but to vary according to climatic and ecological conditions. Climate effect on both intra- and inter-annual growth of trees has frequently been described by multiplicative models of expected growth and a climate modifier (Pietarinen et al., 1982). A simple method for this analysis, however, is to first remove the endogenous growth trend by fitting a growth curve and then analyze growth departure, calculated as dimensionless indices computed through a division of the observed by the expected growth (Fritts, 1976). We therefore used this approach to calculate growth indices for stem, shoot, and foliage for further climate analysis, as shown in Fig. 1. All measurements of cumulative organ growth (points in Fig. 1 [I]) were converted to weekly increments of cell growth (Fig. 1 [II]) by taking the vertical difference between two subsequent points. This difference is a “time derivative”: $\text{WRG} = \text{CG}_t - \text{CG}_{t-1}$, where WRG is weekly relative growth, CG is cumulative growth and subindices t and $t-1$ refer to the week in question and the previous week, respectively. The weekly growth index is calculated by dividing the measured weekly relative growth (mean of the 10 trees per species) by the estimated weekly relative growth from the Gompertz function (calculated from the differences of the estimated weekly increments of the function), as $\text{Weekly Index} = \text{WRG}_m / \text{WRG}_g$, where WRG_m is the measured weekly relative growth and WRG_g is the weekly relative growth estimated by the Gompertz function.

The resulting weekly dimensionless growth index (Fig. 1 p[III]) is free of any trend in time and the fluctuations of indices around mean values of 1 are assumed to reflect the expected environmental signal. For the shoot and foliage, a 2-d interval growth increment was calculated by taking the vertical difference between two subsequent points, and growth indices were also calculated as the procedure shown above for the stem.

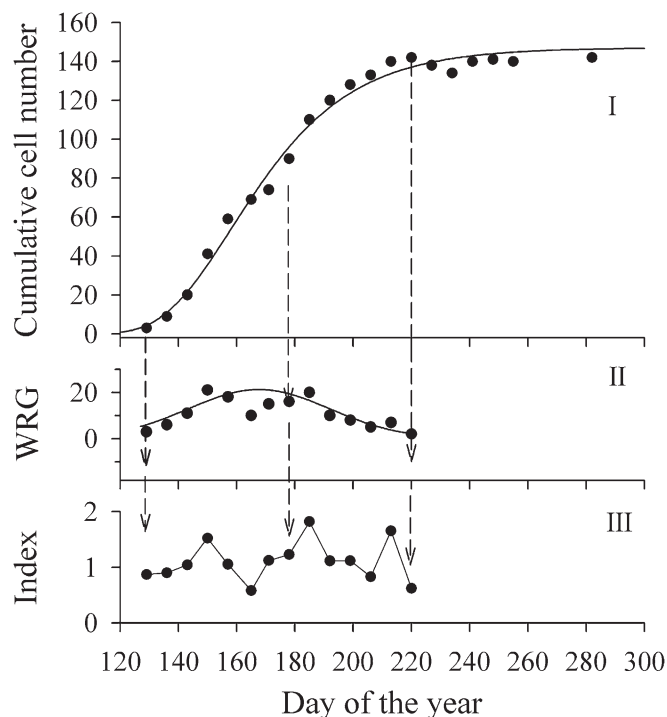


Fig. 1. Data measurement and transformation. In (I), the dots represent the weekly cumulative growth of cell production for a jack pine tree during the growth period for wood development. The solid line represents the Gompertz function fitted to this data. In (II), the dots are the weekly relative growth values (WRG), and the bell-shaped line represents the estimated WRG value derived from the Gompertz function. In (III), time series of the weekly index (WI) were calculated as the ratio between the measured and the estimated WRG.

Climate dependence and ANOVA—Mean growth indices of xylem cell formation, shoot extension, and foliage growth from all the trees per species were correlated with the corresponding meteorological variables (minimum, maximum, and mean air and soil temperatures, total precipitation, minimum and maximum VPD and RH, and GDD) to determine the potential growth limiting factors for different tree organs. The relationships between growth indices and meteorological factors in the previous time interval were also investigated. A one-way ANOVA was conducted to detect differences in the observed timing of onset, duration, and ending of xylogenesis, shoot and foliage growth and in the final total xylem cell number among species using SAS version 10 (SAS, Cary, North Carolina, USA).

RESULTS

Dynamics of intra-annual wood formation—The number of cambial cells and xylem cells of the three species in different stages was presented throughout the 2007 growing season in Fig. 2. Similar annual cambium dynamics were observed in the cambial zones of the three tree species (Fig. 2). In May, cell number in the cambial zone increased from 6–8 cells to 10–15 cells, indicating the onset of cambial activity. The increases in the number of cambial cells in jack pine were observed at the beginning of May, which was 2–3 wk earlier than trembling aspen and 3–4 wk earlier than white birch. Cambial cells of jack pine, trembling aspen, and white birch reached their maximum on 31 May, 14 June, and 21 June, respectively. Once annual cambial activity finished, the number of cambial cells decreased to the minimum value that corresponded to cell number of the dormant condition of the cambium (6–8 cambial cells). Termination of cambial activity of the three species occurred about mid August.

The three species showed the same dynamics of xylem cell differentiation, which is characterized by the delayed bell-shaped curves of enlarging and wall thickening cells, and an S-shaped curve of mature cells (Fig. 2). The onset of xylem cell enlargement of the three species, i.e., the beginning of xylem differentiation, started 1–2 wk later than the onset of cambial activity. The greatest rate of xylem cell enlargement of the three species was observed in June. The duration of xylem cells of all three species from cell enlargement phase to cell thickening phase was about 1 week. The duration from cell wall thickening phase to mature cell phase was 2 weeks for jack pine, and 1 week for both trembling aspen and white birch. The first mature xylem cell of jack pine, trembling aspen, and white birch was detected on 31 May, 7 June, and 14 June, respectively.

Weekly cumulative cell production was well fit by the Gompertz function (Fig. 3), as shown by high adjusted R^2 values for the three species in Table 2. The onset of xylem cell formation of jack pine, trembling aspen, and white birch, corresponding to the first xylem cell observed in cell enlargement phase, occurred on 7 May (± 3 d), 26 May (± 4 d), and 5 June (± 4 d), respectively. It was significantly different among the three species ($F_{2,27} = 264.16$, $P < 0.0001$). The ending date of xylem cell production of jack pine, trembling aspen, and white birch was on 9 August (± 4 d), 16 August (± 4 d), and 16 August (± 3 d), respectively. It was significantly different between jack pine and the two broadleaf species ($F_{2,27} = 15.84$, $P < 0.0001$). Both jack pine and trembling aspen terminated cell formation (i.e., xylem cell lignification was completed) on 13 September, which was 1 week later than for white birch. The duration of cell differentiation was between 98 and 126 d and was significantly different among the three species ($F_{2,27} = 75.52$, $P < 0.0001$). Jack pine had the longest wood-development growing season, and white birch had the shortest among the three

species. The total number of xylem cells produced for jack pine, trembling aspen, and white birch was 141 (± 47), 166 (± 23) and 152 (± 33), respectively (Fig. 2), and the ANOVA results showed no significant difference among them ($F_{2,27} = 0.93$, $P = 0.41$). The Gompertz function results showed that the average rate of cell production for jack pine, white birch and trembling aspen was 1.22, 1.81, and 1.97 cells per day, respectively (Table 2, Fig. 2).

Shoot and foliage growth and wood formation—Within a species, the onset of shoot elongation and foliage enlargement was different from the onset of xylem cell division (Fig. 4A). The onset of shoot elongation and foliage enlargement was detected on 20 May (± 3 d), 22 May (± 3 d), and 27 May (± 4 d) for jack pine, white birch, and trembling aspen, respectively. As a consequence, the onset of xylem cell division of jack pine and trembling aspen was, respectively, 13 d and 1 d earlier than its onset of shoot elongation and needle/leaf enlargement. However, the onset of stem xylem cell division of white birch was 14 d later than its onset of shoot elongation and leaf enlargement. Shoot elongation and needle enlargement of jack pine terminated on 28 June (± 4 d) and 2 August (± 3 d), respectively. Shoot elongation and leaf enlargement terminated, respectively, on 21 June (± 4 d) and 10 July (± 3 d) for trembling aspen and on 12 July (± 4 d) and 30 July (± 3 d) for white birch. The measured average final shoot length and foliage growth (needle area) for jack pine was 20.79 (± 3.78) cm and 0.55 (± 0.04) cm², respectively. The average final shoot length and foliage growth (leaf area) for white birch and trembling aspen were 84.63 (± 41.21) cm and 25.71 (± 5.90) cm², 35.74 (± 16.54) cm and 15.35 (± 1.43) cm², respectively. The three species showed the same order in the ending date of shoot elongation, leaf enlargement, and stem cell division, i.e., the ending of shoot elongation earlier than that of foliage enlargement, and the ending of foliage enlargement earlier than that of stem xylem cell division. Within the two broad-leaf species, the onset of shoot elongation and leaf enlargement of trembling aspen were 5 d later than that of white birch, whereas its ending date for shoot elongation and leaf enlargement was 21 d earlier than that of white birch. This timing indicates that the duration of shoot elongation and leaf enlargement of trembling aspen was shorter than that of white birch (Fig. 4B). For all three species, the duration of shoot elongation was shorter than that of stem cell division and leaf enlargement. The ANOVA results showed that among the three species, the onset, ending, and duration of foliage growth were significantly different ($F_{2,27} = 53.35$, $P < 0.0001$; $F_{2,27} = 117.84$, $P < 0.0001$; $F_{2,27} = 221.34$, $P < 0.0001$). The onset and duration of shoot growth also differed significantly ($F_{2,27} = 53.35$, $P < 0.0001$; $F_{2,27} = 88.32$, $P < 0.0001$). The ending of shoot growth in white birch differed significantly from that of the other two species ($F_{2,27} = 48.16$, $P < 0.0001$), but was not significantly different within the other two species ($F_{2,27} < 2.05$, $P > 0.05$).

In Fig. 3, the results showed similar growth pattern but delayed growth dynamics in shoot elongation, needle/leaf enlargement and stem xylem cell production in the three studied species during the growing period. Jack pine had a delayed S-shaped curve for stem and needle developments compared with an S-shaped curve for shoot development. White birch demonstrated a delayed S-shaped curve of stem growth in comparison with the S-shaped curves of shoot and leaf growth. Trembling aspen was found to have in turn the delayed S-shaped curves for shoot, leaf, and stem development.

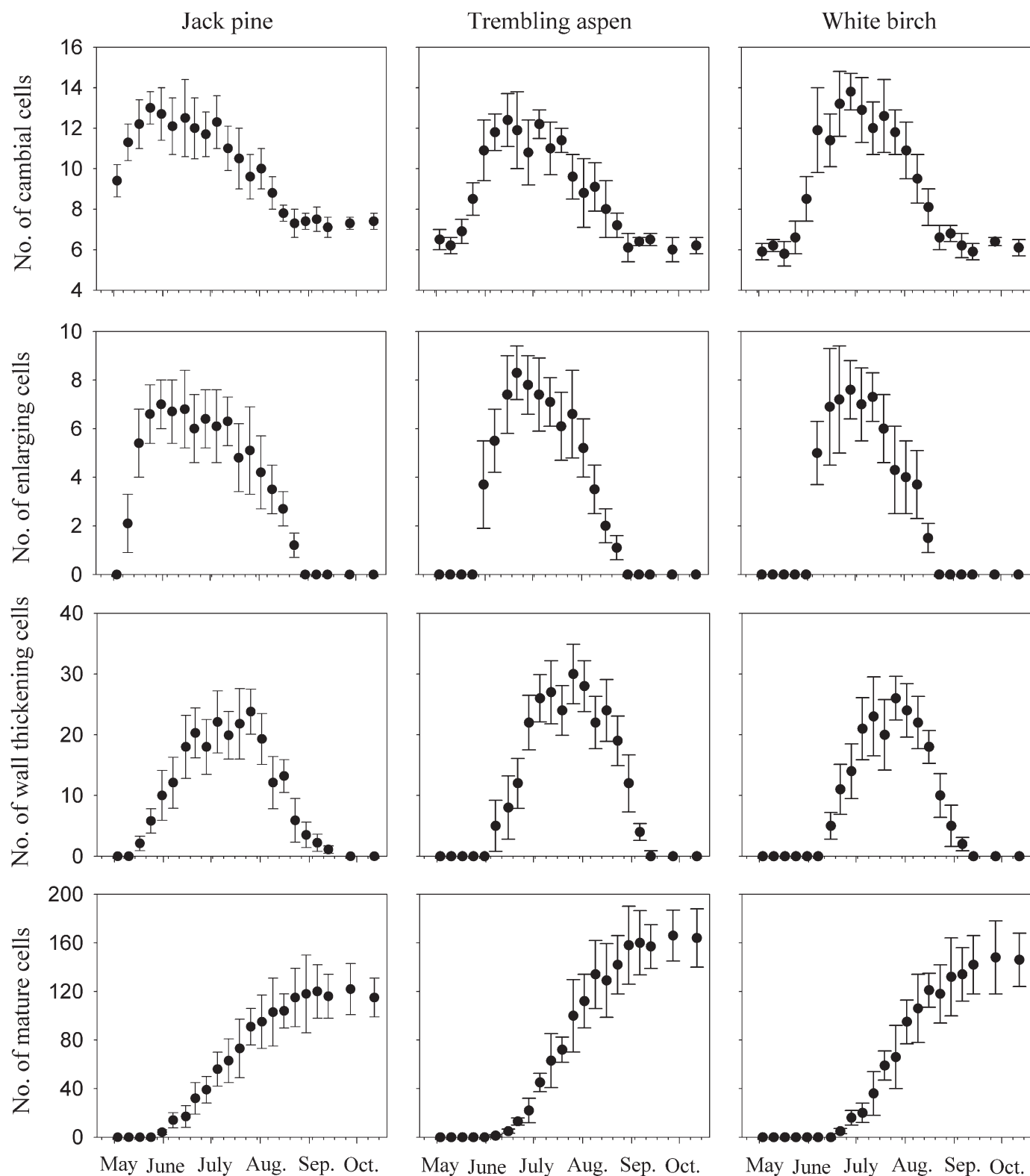


Fig. 2. Number of cells in the cambial zone, radial enlargement, secondary cell wall thickening, and mature cells in jack pine, trembling aspen, and white birch ($N = 10$) during the 2007 growing season. The dots represent mean number of cells; bars indicate standard deviations among trees.

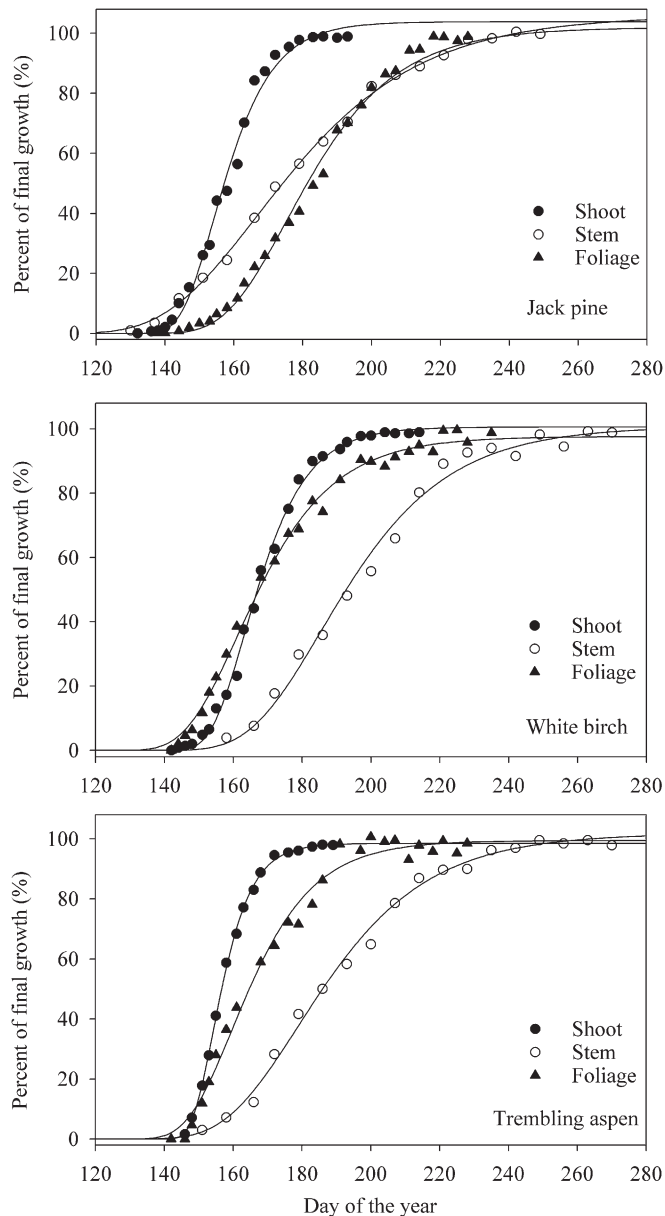


Fig. 3. Growth pattern of stem xylem cell formation, shoot elongation, and foliage enlargement and its Gompertz curve of the three species during the 2007 growing season.

Relationships between meteorological factors and intra-annual xylem formation, shoot and foliage development—Weekly growth index for stem showed no temporal trends and no heteroscedasticity over time for all the variables studied. As shown in Fig. 5A, correlation analysis results showed that weekly minimum and mean air temperatures ($R = 0.63$, $P = 0.01$; $R = 0.53$, $P = 0.04$; $N = 15$) and maximum, minimum, and mean soil temperatures ($R = 0.48$, $P = 0.07$; $R = 0.54$, $P = 0.04$; $R = 0.53$, $P = 0.04$; $N = 15$) were significantly positively correlated with weekly growth index of stem xylem cell production of jack pine. No significant correlation was found between weekly growth index of stem growth and other meteorological variables such as maximum air temperature ($R = 0.39$, $P = 0.15$), precipitation ($R = 0.14$, $P = 0.61$), maximum and minimum RH

($R = 0.23$, $P = 0.42$; $R = 0.38$, $P = 0.16$), maximum and minimum VPD ($R = 0.25$, $P = 0.40$; $R = 0.35$, $P = 0.19$), or GDD ($R = 0.48$, $P = 0.07$) (Fig. 5). Maximum, minimum, and mean soil temperatures were negatively correlated with weekly growth index of stem cell production of trembling aspen ($R = -0.56$, $P = 0.05$; $R = -0.59$, $P = 0.03$; $R = -0.58$, $P = 0.04$; $N = 13$). Precipitation was positively correlated with weekly growth index of stem xylem cell production of both trembling aspen ($R = 0.65$, $P = 0.02$, $N = 13$) and white birch ($R = 0.58$, $P = 0.04$, $N = 13$). No significant correlations were found between weekly growth index of stem xylem formation of the two broadleaf species and maximum, minimum, and mean air temperatures (aspen: $R = -0.43$, $P = 0.14$; $R = -0.37$, $P = 0.22$; $R = -0.42$, $P = 0.16$, $N = 13$; birch: $R = -0.30$, $P = 0.35$; $R = -0.53$, $P = 0.07$; $R = -0.40$, $P = 0.20$, $N = 13$), maximum and minimum RH (aspen: $R = -0.06$, $P = 0.85$; $R = 0.41$, $P = 0.16$; birch: $R = 0.26$, $P = 0.41$; $R = 0.44$, $P = 0.15$; $N = 13$), maximum and minimum VPD (aspen: $R = -0.24$, $P = 0.42$; $R = -0.34$, $P = 0.23$; birch: $R = -0.25$, $P = 0.42$; $R = -0.37$, $P = 0.22$; $N = 13$), or GDD (aspen: $R = -0.41$, $P = 0.17$; birch: $R = -0.35$, $P = 0.27$; $N = 13$), or meteorological data in the previous time interval (data not shown).

In Fig. 5, correlation analysis results showed that mean ($R = 0.51$, $P = 0.04$), minimum ($R = 0.61$, $P = 0.01$), and maximum air temperatures ($R = 0.53$, $P = 0.03$) were significantly correlated with growth index for shoot elongation of jack pine during the growth period. Maximum air temperature was positively correlated with growth index for shoot elongation of trembling aspen ($R = 0.60$, $P = 0.01$) and white birch ($R = 0.51$, $P = 0.04$). Correlation analysis results showed no significant correlation between growth index of foliage enlargement of the three species and the meteorological variables (Fig. 5). However, most of the meteorological variables were found to be positively, but nonsignificantly correlated with growth index of foliage enlargement except for negative correlation observed for maximum and minimum VPD (Fig. 5).

DISCUSSION

The study demonstrates that the coordination among budburst and the timing of foliage growth and diameter growth differs strongly among the three tree species as do the responses of tree growth to environmental factors. In boreal climates, the short periods of growth are the periods that trees are the most vulnerable to climate extremes, such as drought and frost during a growing season (e.g., Sakai and Larcher, 1987; Körner, 1999). Climate change might result in increased frequency and amplitude of extremes such as heat, drought, or extreme precipitation events (Huntington, 2004; IPCC, 2007). In this study, different meteorological factors were found to affect the intra-annual growth of tree species and of different tree organs. Difference in the timing of intra-annual growth for each species might cause different duration of growth for different organs among species.

Intra-annual growth pattern and dynamics—Since shoot and foliage development in trembling aspen starts later than its stem development, we concluded that the carbohydrates reserves in the previous growth year played an important role in producing its new xylem cells. This supports the well-known fact that the conditions of the previous year are of critical importance for radial growth of the current year (Hogg et al., 2005;

TABLE 2. Parameters of the Gompertz function fit to stem xylem cell formation (number), foliage area (cm²) and shoot length (cm) data of the three species.

Species	Organ	A	β	κ	γ	Adj. R^2	SE	F	df	P
Pine	Stem	141	6.45	0.039	1.22	0.93	2.16	1689.02	2, 19	<0.0001
	Needle	0.55	15.73	0.086	0.01	0.98	0.02	441.32	3, 16	<0.0001
	Shoot	20.79	8.98	0.11	5.73	0.99	0.92	435.47	3, 16	<0.0001
Aspen	Stem	166.2	8.39	0.047	1.97	0.94	4.79	1202.03	2, 17	<0.0001
	Leaves	15.35	12.12	0.076	0.29	0.98	0.64	954.72	2, 21	<0.0001
	Shoot	35.74	24.79	0.16	1.41	0.99	0.39	7800.66	2, 12	<0.0001
Birch	Stem	152	8.92	0.048	1.81	0.92	7.68	333.37	2, 15	<0.0001
	Leaves	25.71	10.53	0.065	0.42	0.99	0.64	2709.99	2, 23	<0.0001
	Shoot	84.63	9.95	0.101	2.13	0.99	1.68	4967.97	2, 21	<0.0001

Notes: F statistic, df = numerator, denominator degrees of freedom. SE = standard error of the estimate.

Huang et al., 2010) since a good portion of xylem growth in aspen precedes leaf extension. The shoot and foliage growth of white birch occurred earlier than its stem diameter, suggesting that the formation of early xylem cells might be triggered by photosynthesis in the newly formed leaves early in the growing season. This could explain why the diameter growth of white birch mostly depends on the conditions of the present year and not, as in many other hardwoods, on the weather conditions of the previous years (Tardif et al., 2001b; Huang et al., 2010). Trembling aspen and white birch are diffuse-porous species, which show little or no variation in size of the pores (vessels) within a growth ring. This is distinct from ring-porous species which show much larger size of the pores at the beginning of the growing season than those farther out in the ring (Lachaud, 1989; Čufar et al., 2008). Unlike many hardwoods, the foliage development of most pines is a slow process. Later onset of shoot and needle than stem growth observed in jack pine reflects that the carbohydrate reserves in the previous year and carbohydrates produced in the current early season by old needles might together stimulate new xylem cells formation during the early growing season (e.g., Kaipainen and Sofronova, 2004).

Altogether, our results showed that the coordination of different organs in a given tree is species-specific.

Among the three species, the duration of leaf enlargement for trembling aspen was shorter than that of the other two species. Since all aspen leaves were observed to emerge simultaneously after budbreak with a short duration of shoot elongation, subsequent tree growth during the growing season would seriously suffer if a late spring frost occurred after leaf emergence. On the contrary, white birch grows its leaves one by one successively after budbreak with a long duration of shoot elongation. Therefore, subsequent white birch growth will be less affected by spring extreme climates such as late spring frosts. Trembling aspen is a shade intolerant species (Burns and Honkala, 1990), and the short duration of its shoot elongation and leaf enlargement could help trees to occupy the upper canopy space and thus avoid the shade of other tree species. This short duration/fast growth also makes aspen trees less affected by interspecies competition during succession (Stadt et al., 2007). However, white birch is a more shade tolerant species than trembling aspen and the long duration and leaf development could allow trees to invade new habitats by expanding photosynthetic organs

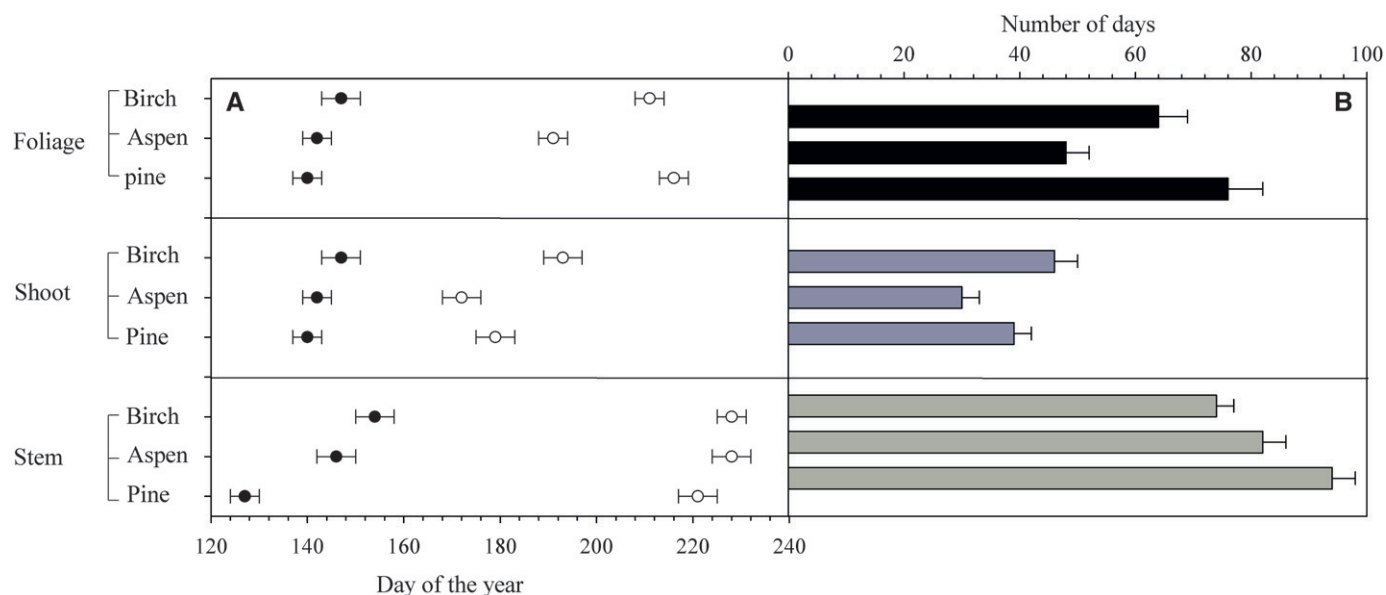


Fig. 4. (A) Onset date, ending date and (B) duration of the principal phenological events (i.e., stem xylem cell division [$N = 10$ per species], shoot elongation [$N = 20$ for jack pine; $N = 50$ per broadleaf species], foliage enlargement [$N = 120 \pm 20$ for jack pine; $N = 45 \pm 5$ per broadleaf species]) of the three species during the 2007 growing season. Solid cycles represent the onset date; open cycles represent the termination date. Bars correspond to the mean value of duration; error bars correspond to standard deviations among trees.

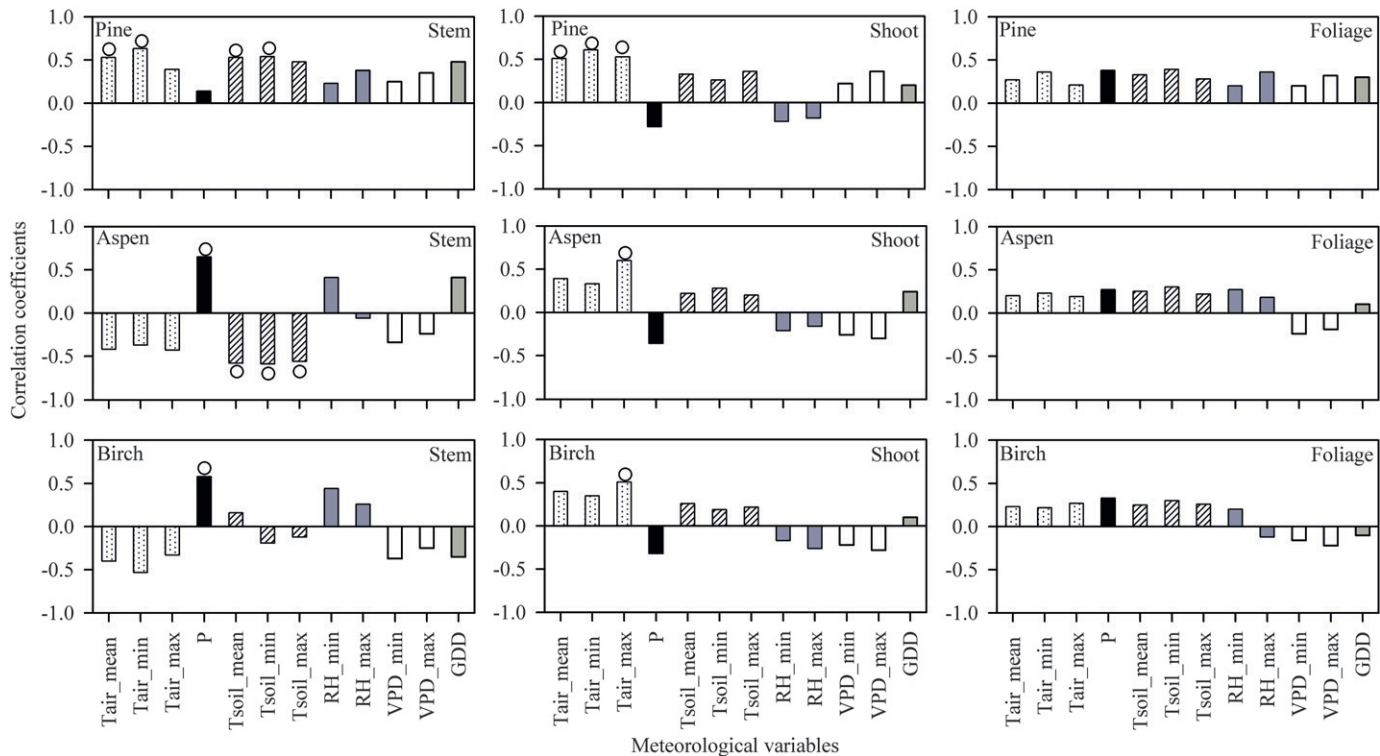


Fig. 5. Simple correlation coefficients (Pearson's correlation, $P < 0.05$) between the intra-annual stem xylem formation, shoot extension growth, foliage enlargement and the meteorological factors during the 2007 growing season. *Abbreviations:* T_{air} = air temperature, T_{soil} = soil temperature, P = precipitation, RH = relative humidity, VPD = vapor pressure deficit, and GDD = growing degree days above 5°C . Significant results ($P < 0.05$) are marked by open circles.

as widely as possible using the current year's products or by using newly formed leaves (Kikuzawa, 1983). Therefore, white birch could often coexist with trembling aspen during succession in the boreal forest. Jack pine is a typical postfire succession species and less affected by species competition from trembling aspen and white birch during succession. For all three species, we found that the shoot elongation was complete earlier than foliage enlargement and stem cell production. Trees attempt to reach maximum shoot length and tree height during a short time to occupy a favorable spatial position for photosynthesis.

A more rapid transition from wall thickening to mature cells in trembling aspen and white birch compared to jack pine demonstrates that broadleaf species had a faster xylem maturation rate than jack pine. This faster maturation rate might result from the higher photosynthesis rates of broadleaf species than that of jack pine. The ending of xylem cell production (mid-August) observed in the study are similar to Huang et al. (2011) and Vaganov et al. (2006), who also reported termination of cell production of tree species in about mid-August. Vaganov et al. (2006) described furthermore that variation in the start of cell division was larger than that in the end of the growing season. Vaganov et al. (1999) deduced that the date of the first cambial cell division depends on the estimated ending dates of constant snow cover and threshold values of air temperature as well as effective temperature sums. An earlier spring could result in a longer duration of cell production. In addition, the weekly minimum air temperature was about 11.2°C when new cell production of the three species ceased at our study site, indicating that the new cell production ceased at a much higher temperature than its necessary for the initiation in the spring, i.e., 5.3°C for

jack pine, $8.2\text{--}10.4^{\circ}\text{C}$ for trembling aspen and white birch. In addition, soil water content might not be the factor for explaining the termination of cell production because there was enough rainfall (730 mm, one seventh of annual total precipitation) falling in August in the study area. However, photoperiod was reported to act as a growth constraint or a limit after which the rate of tree-ring formation tends to decrease (Rossi et al., 2006b). Therefore, we infer that cell production ceases possibly also due to endogenous factors in addition to the photoperiod. When new xylem cell production ceases, the annual ring width reaches its final width because further wall thickening occurs in the inside of the cell wall and does not affect cell size. Therefore in the current growing season, annual ring width is primarily influenced by the meteorological factors during the cell production period, i.e., from mid-May to mid-August.

There were a number of statistically significant differences in the timing of growth between species. It was, however, impossible to say that one species was later or earlier than another, since growth between different plant organs was coordinated very differently in the species. Trembling aspen had the latest budburst, but the shortest duration for foliage development due to rapid foliage growth. Jack pine had the earliest budburst but the latest foliage growth. Compared to trembling aspen, white birch had an earlier budburst but later shoot extension and xylem growth. This shows that the periods when the trees are vulnerable to climate events differ vastly among the three species, indicating different adaptive capability to climate change.

Climate dependence—Intra-annual wood formation and growth of plant organs are controlled by both endogenous factors

(mostly due to hormonal regulation) and exogenous factors (e.g., climate). In this study, we first used an approach that is similar to the approach used in dendrochronology to successfully separate the endogenous growth curve and the exogenous environmental effects on growth. The resultant growth indices can separate a largely genetic and daylength-driven growth curve from the short-term climatic effects. We believe that this approach is superior to the approach of analyzing growth data without prerule of the mostly endogenous growth curve, which easily leads, in our opinion, to spurious correlations. For example, a warm spell will have a larger effect on growth when the cambium is well developed than during early spring, when there are few cambial cells.

Significantly positive correlations between weekly xylem cell growth index and air and soil temperatures observed for jack pine from 7 May to 9 August indicate that temperature was a dominant factor for positively controlling its cell production. Past studies in cold ecosystems found that tracheids mainly divide and enlarge during the warmest period of the growing season (Wang et al., 2002) because temperature has a strong effect on assimilate and phytohormone production in needles (Lachaud, 1989). But daily maximum growth rate occurred around the time of maximum day length, i.e., summer solstice (Rossi et al., 2006b; Gruber et al., 2009). Gruber et al. (2009) found that air and soil temperatures positively controlled xylem development of stone pine (*Pinus cembra* L.) in western Austria. Other studies also documented that temperature, especially night temperature (Richardson and Dinwoodie, 1960), is a critical factor for influencing radial cell enlargement. This positive temperature effect is also evidenced by many previous dendroclimatological studies of these boreal tree species. For example, a positive effect of temperature on radial growth of jack pine during the growing season was reported in western Quebec (Hofgaard et al., 1999; Tardif et al., 2001a; Huang et al., 2010). During the growing season, warmer soil temperature could favor root activity, thus transporting more water and nutrients for xylem cell growth. In agreement with Huang et al. (2011), we found that GDD was not the main factor for affecting xylem cell production.

The positive impact of air temperature on shoot elongation of jack pine during the growth period that was demonstrated in this study is consistent with Kanninen (1985). Through analysis of shoot elongation in *Pinus sylvestris* during the period of maximum elongation rate, the latter study documented that night temperature positively affected the shoot elongation rate more than day temperature. It is unlikely that the differences in the climate–growth relationships were an artifact of different temperatures during the periods when trees were growing since weekly average temperatures varied during June through August between 14°C and 20°C without much temporal trend. Positive but nonsignificant correlation between the needle area growth and temperature is in agreement with Junttila and Heide (1981), who reported that the needle length of *P. sylvestris* was significantly and positively associated with mean temperature of the growing season, especially June to August temperature in northern Fennoscandia. It is, however, noteworthy that our sites were much warmer than the sites of Junttila and Heide (1981) and that perhaps temperatures were less limiting for needle growth.

A positive effect of precipitation and a negative effect of air temperature on cell production of trembling aspen from 28 May to 16 August indicates that trembling aspen depended less on temperature than on water status of the trees. Since the soil was

moist during much of the period, we think that the growth might be limited by low daytime water potentials due to transpiration as suggested by Tardieu et al. (1999). Also, Schweingruber (1996) observed that there was a negative correlation between xylem formation of trembling aspen and air temperature. He further interpreted that the negative effect of high temperature could be due to temperature-caused water stress in trees, thus reducing photosynthetic production. Doley and Leyton (1968) showed that in vitro cell expansion and division of *Fraxinus* was sensitive to small changes in water potential. White birch was also shown to be water-limited during the cell production period from 4 June to 16 August. Our results together indicate that cell production of the two broadleaf species was water-limited during the cell production period in the growing season. The diameter growth of broadleaf species, even when growing in comparatively humid boreal forests, has been extensively reported to be water limited during the growing season (Tardif et al., 2001a, b; Hogg et al., 2005; Huang et al., 2010). We acknowledge that water and temperature limitations are climate and site dependent: trees growing on rocky outcrops may be mostly drought limited, and trees growing at low temperatures on a peatland at the treeline are probably always temperature limited. Our sites, were, however, quite representative for the region, and our results are similar to the results from elsewhere in the boreal zone (Tardif et al., 2001a; Huang et al., 2010, 2011). Statistical correlations for leaf elongation and climate were not statistically significant. We assume that this is due to a larger sampling error (our leaf area measurements were destructive and taken from different trees). In addition, our single growing-season data might limit us from fully exploring the relations between foliage growth and climate.

Conclusions—In the present study, we applied a new approach to study the effect of meteorological variables on intra-annual growth of trees. We demonstrated the use of the Gompertz function to model xylem cell formation and shoot and foliage growth, then calculated dimensionless growth indices through the commonly used detrending approach in dendrochronology to explore climate effect. Our results suggest that the coordination among stem, foliage, and shoot growth was species-specific. The different timings of phenological events suggest that trees will be sensitive to climate events during different time periods and will have different adaptive capability to climate change. More intra-annual phenological data collection at both spatial and temporal scales will be needed to clarify the coordination mechanism among different organs within a tree and among species under future climate change.

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