

1 Original article

2 **DURATION OF XYLOGENESIS IN BLACK SPRUCE LENGTHENED BETWEEN 1950**  
3 **AND 2010**

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10 **Running title:** trends in cambium phenology

11

## ABSTRACT

*Background and Aims* Reconstructions have identified the 20<sup>th</sup> century as uniquely warm in the last 1000 years. Changes in phenology of the primary meristems converged toward increases in length of the growing season. Has the phenology of secondary meristem changed during the last century, and to what extent?

*Methods* Timings of wood formation in black spruce [*Picea mariana* (Mill.) B.S.P.] were monitored for nine years on a weekly time-scale at four sites in the boreal forest of Quebec, Canada. Models for assessing xylem phenology were defined and applied to reconstruct onset, ending and duration of xylogenesis between 1950 and 2010 using thermal thresholds on chronologies of maximum and minimum temperatures.

*Key Results* All sites exhibited increasing trends of both annual and May-September temperatures, with the greatest changes observed at the higher latitudes. Phenological events in spring were more affected than those occurring in autumn, with cambial resumptions occurring 0.5-0.8 days decade<sup>-1</sup> earlier. Duration of xylogenesis has significantly lengthened since 1950, although the models supplied wide ranges of variations, between 0.07 and 1.5 days decade<sup>-1</sup>, respectively.

*Conclusions* The estimated changes in past cambial phenology demonstrated the marked effects of the recent increase in temperature on the phenological traits of secondary meristems. In the long run, the advancement of cambial activity could modify the short time window for growth of the boreal species and dramatically affect the dynamics and productivity of trees in these temperature-limited ecosystems.

33 **Keywords:** boreal forest, cell differentiation, *Picea mariana*, threshold temperature, wood  
34 formation, xylogenesis

35

37 Hemispheric-scale reconstructions of surface temperature fluctuations over the last millennium  
38 have identified the 20<sup>th</sup> century as uniquely warm (cf. Hughes, 2002). Although an increase in the  
39 global temperature of between 1.4 and 5.8 °C is expected during the period 1990-2100, the  
40 greater increases are predicted to occur at the higher latitudes of the northern hemisphere (IPCC,  
41 2007). For the boreal forest of North-Eastern Canada, climatic models predict increases in  
42 temperature of up to 3 °C over the next 50 years, with the largest increases occurring in winter  
43 and spring, when plant growth resumes (Plummer *et al.*, 2006). In cold ecosystems, the growing  
44 season is strictly defined by the harsh winter temperatures (Rossi *et al.*, 2008b, 2011b). Such  
45 climate modifications could thus severely affect the growth timings and dynamics of the boreal  
46 species, with consequent changes in productivity of biotopes that have obvious ecological  
47 importance and economic potential.

48 The interest in the cold forests of high altitude and latitude is linked to various causes such as the  
49 short growing season and high sensitivity of the species to climate changes (Körner, 2003a).  
50 Plants of these ecosystems are assumed to be good indicators of changes in their environment  
51 (Pisaric *et al.*, 2003). With the current changes in temperature, possible variations in phenology –  
52 the study of the timings of recurring seasonal biological events – have acquired particular  
53 importance worldwide. According to Forrest and Miller-Rushing (2010), interest has been  
54 focused on documenting the recurrent appearance of the first flower blossoms or bud bursts in  
55 spring, the dates of animal migration, or timings of the first frost-damaged leaves in autumn. The  
56 longest monitoring periods in plants are concentrated in the botanical gardens of temperate  
57 Europe and concern the effects of such changes on the growth dynamics of the primary

58 meristems (buds, leaves and flowers). There is no historical documentation on the phenology of  
59 the secondary meristem, the cambium, because it is not a macroscopically perceptible  
60 phenomenon like leaf development or flower maturation. Cambial activity occurs beneath the  
61 bark and, in high-latitude forests, produces a number of xylem cells that increases the stem  
62 diameter annually by one tree ring, which integrates the effects of climatic events occurring  
63 during the season when the cambium was active (Frankenstein *et al.*, 2005). Tree rings have thus  
64 been used as a tool to explore the long-term growth reactions to historical climate variations  
65 (Huang *et al.*, 2010). However, to our knowledge, retrospective studies concerning  
66 reconstructions of cambium phenology are still lacking due to the very recent identification and  
67 application of the standard procedures of analysis (Rossi *et al.*, 2006a, 2006b; Seo *et al.*, 2008;  
68 Gričar *et al.*, 2009).

69 Analyses on the variations in the concentrations of CO<sub>2</sub> in the atmosphere showed that the  
70 biospheric activity increased remarkably as a result of warming surface air (Myneni *et al.*, 1997).  
71 This implies that even small changes in global temperature may be reflected by disproportionate  
72 responses at regional level that can markedly influence all biological processes, in particular  
73 those concerning growth. Although several endogenous variables can influence the dynamics of  
74 xylem formation (Marion *et al.*, 2007; Rossi *et al.*, 2008a; Rathgeber *et al.*, 2011, Anfodillo *et*  
75 *al.*, 2012), temperature remains the main driving factor in cold environments. A local overheating  
76 in spring can reactivate cambium, inducing the conversion of starch reserves into sucrose for the  
77 activation of cell division and production of secondary xylem (Begum *et al.*, 2007; Gričar *et al.*,  
78 2007). Deslauriers *et al.* (2008) observed that the higher temperatures occurring in spring 2003  
79 led to earlier onsets of division and differentiation of xylem cells. The onset of xylogenesis  
80 influences the number of cells produced by the cambium which, in turn, influences the ending of

81 cell differentiation (Lupi *et al.*, 2010; Rossi *et al.*, 2012). Several studies in cold environments  
82 demonstrated that a certain temperature, in the form of heat sum or thermal threshold, is  
83 necessary to enable the cambium to divide (Rossi *et al.*, 2008b; Seo *et al.*, 2008; Swidrak *et al.*,  
84 2011). Rossi *et al.* (2011b) simulated several warming scenarios to predict changes in xylem  
85 phenology. The model predicted longer duration of xylem growth at higher temperatures, with  
86 increases of 8-11 days/°C because of an earlier onset and later ending of growth. Twenty-five  
87 percent longer durations of xylogenesis were predicted with an increase of 3 °C in the mean  
88 annual temperature (Rossi *et al.*, 2011b).

89 Although substantial increases in temperature were observed during the last 100 years, with the  
90 mean surface temperature rising by 0.7 °C at global scale and by 0.5-1.5 °C across North  
91 America since the late 19<sup>th</sup> century (Zhang *et al.*, 2000; IPCC, 2007), the rate of warming over  
92 the last 50 years (0.13 °C decade<sup>-1</sup>) is almost double that over the last 100 years (IPCC 2007). For  
93 the northern regions of North America, McKenney *et al.* (2006) estimated increases attaining  
94 0.26 °C decade<sup>-1</sup> in the second half of the 20<sup>th</sup> century. The question is if and to what extent the  
95 modifications in air temperature during this period have affected cambial phenology. The model  
96 developed by Rossi *et al.* (2011b) simulated a potential xylem phenology under a possible and  
97 simplified climate warming, represented by a uniform increase in air temperature. However, no  
98 information was provided about changes in the timings of cambial growth occurring in the past.  
99 Moreover, there is evidence of divergent effects of climate change on the seasonal temperatures,  
100 with spring having the greater warming (Zhang *et al.*, 2000). Improvements in the precision of  
101 the models of cambial growth are thus expected to produce results consistent with the more  
102 realistic climatic scenarios.

103 This paper aimed to reconstruct timings of cambium phenology over the last 60 years in Quebec,  
104 Canada. This was done by (i) collecting and analyzing a dataset of cambium phenology and wood  
105 formation in black spruce [*Picea mariana* (Mill.) B.S.P.] based on a weekly monitoring for 9  
106 years in four permanent sites at different latitudes and altitudes, (ii) defining and validating a  
107 phenological model of xylem based on the air temperature measured in the sites, and (iii)  
108 applying the phenological model on the chronologies of air temperature generated for the period  
109 1950-2004 by the ANUSPLIN model (McKenney *et al.*, 2006). The effects of climate change on  
110 plants have mainly been demonstrated by changes in the phenology of primary meristems, which  
111 have revealed marked increases in length of the growing season (Menzel, 2000; Zhou *et al.*,  
112 2001; Sparks and Menzel, 2002; Badeck *et al.*, 2004). Thus, according to the results provided on  
113 primary meristems, the hypothesis that duration of xylogenesis has lengthened since 1950 was  
114 tested by the model.

115

116

## MATERIALS AND METHODS

### 117 **Study area and xylem sampling**

118 The study was conducted on black spruce in the Saguenay-Lac-Saint-Jean area, in the boreal  
119 forest of Quebec, Canada. Four sites [Simoncouche (abbreviated as SIM), Bernatchez (BER),  
120 Mistassibi (MIS) and Camp Daniel (DAN)] were identified in mature even-aged stands at  
121 different altitudes and latitudes to obtain as wide as possible a range in the dynamics of tree  
122 growth (Table 1). Details on site characteristics were provided by Rossi *et al.* (2011b).

123 In each site, tree-ring formation was studied from April to October during 2002-2010 in 5 (2002-  
124 2005) and 10 (2006-2010) trees. Wood microcores were collected weekly following a spiral  
125 trajectory on the stem from 30 cm below to 30 cm above breast height (1.3 m) using surgical  
126 bone sampling needles in 2002-2006 and Trephor in 2007-2010 (Rossi *et al.*, 2006a). Samples  
127 usually contained the previous 4-5 tree rings and the developing annual layer with the cambial  
128 zone and adjacent phloem. Samplings were always taken at least 5 cm apart to avoid getting resin  
129 ducts on adjacent cores.

130 The microcores were stored in ethanol solution (10% in water) at 5 °C to avoid tissue  
131 deterioration. Microcores were dehydrated with immersions in ethanol and D-limonene and  
132 embedded in paraffin (Rossi *et al.*, 2006a). Transverse sections of 6-10 µm thickness were cut  
133 from the samples with a rotary microtome, stained with cresyl violet acetate (0.16% in water) and  
134 examined within 10–25 minutes under visible and polarized light at magnifications of 400–500×  
135 to differentiate the developing and mature xylem cells. Occasionally, distorted rows of cells



136 prevented a adequate analysis of the sample. In these cases, the sections were gently stressed on  
137 the slide with thin needles to better observe all cells of the developing tree ring.

### 138 **Microscopic observations**

139 In each sample, the radial number of cells in the cambial zone, radial enlargement phase, cell wall  
140 thickening phase, and mature cells were counted along three radial rows. In cross section,  
141 cambial cells were characterized by thin cell walls and small radial diameters (Rossi *et al.*,  
142 2006b). The dormant cambium was composed of 3-5 closely-spaced cells. At the onset of  
143 cambial activity, the cambial zone began to widen rapidly as the number of cells increased,  
144 revealing that cell division had started. During cell enlargement, the tracheids were composed of  
145 a protoplast still enclosed in the thin primary wall but with radial diameter at least twice that of a  
146 cambial cell. Observations under polarized light discriminated between enlarging and cell wall  
147 thickening tracheids (Thibeault-Martel *et al.*, 2008). Because of the arrangement of cellulose  
148 microfibrils, the developing secondary walls were birefringent when observed under polarized  
149 light. Instead, no glistening was observed in enlargement zones, where the cells were still  
150 composed of just primary wall (Abe *et al.*, 1997). Lignification was detected with cresyl violet  
151 acetate by a color change from violet to blue. The color change over the whole cell wall revealed  
152 the end of lignification and the tracheid reaching maturity (Gričar *et al.*, 2005).

153 The cell number in the 3 rows was averaged for each tree and used to assess onset and ending of  
154 xylogenesis. In spring, when at least one tangential row of cells was observed in the enlargement,  
155 xylem formation was considered to have begun. In late summer, when no further cell was  
156 observed in wall thickening and lignification, xylem formation was considered complete. The

157 duration of xylogenesis was assessed as the number of days occurring between onset and ending  
158 of xylogenesis and was calculated as the average among trees for each studied site and year.

### 159 **Datasets of air temperature**

160 Two datasets of air temperature were used in this study and consisted of time series (i) measured  
161 in the four sites and (ii) estimated by a climatic model. Measured and estimated temperatures  
162 were used for the definition and application of the phenological model, respectively. For the first  
163 dataset, a standard weather station was installed in 2001 in a forest gap on each site. Air  
164 temperature data were collected at 3 m above ground level every 15 minutes and recorded as  
165 averages every hour by means of CR10X dataloggers (Campbell Scientific Corporation, Canada).  
166 Maximum and minimum values were later calculated from the 24 measurements per day. The  
167 second dataset consisted of air temperatures generated at a daily resolution for the period 1950-  
168 2004 by the ANUSPLIN model of the Canadian Forestry Service. This model used a multi-  
169 variate non-parametric surface and point fitting approach to estimate the time series of maximum  
170 and minimum temperature corresponding to the location of each site according to the algorithm  
171 described by McKenney *et al.* (2006). To verify the consistency of the modeled time series, linear  
172 regressions were performed between the measured and estimated temperatures for the  
173 overlapping years (2002-2004).

### 174 **Definition and validation of the phenological model**

175 The model consisted in applying thermal thresholds for estimating xylem phenology using  
176 logistic regressions to calculate the probability of xylem growth being active at a given measured  
177 daily temperature. According to Rossi *et al.* (2011b), binary responses were coded as non-active

178 (value zero) or active (value 1) growth, and temperature thresholds were calculated when the  
179 probability of xylem growth being active was 0.5. For each site and year, the model was fitted  
180 with minimum and maximum temperature series and results from each site were compared by  
181 analysis of variance (ANOVA) and Tukey's test. None of the 72 estimated functions was  
182 excluded because of lack of fit. Model validation was performed according to Legendre and  
183 Legendre (1998) by comparing the observations with the predicted values calculated using the  
184 estimated temperatures. A classification table was produced in the form of a contingency table,  
185 which for each day compared the observed active or non-active xylem growth to that predicted by  
186 the model.

#### 187 **Application of the phenological model**

188 A quadratic logistic regression was applied on the time series of daily temperatures generated by  
189 the ANUSPLIN model, with binary responses coded as 0-1 if temperatures were lower or higher  
190 than the threshold, respectively. The two solutions of the quadratic regression corresponded to  
191 the days of the year when the probability of temperature being higher than the threshold was 0.5,  
192 and included the period of xylem growth (Rossi *et al.*, 2011b). The phenological model was  
193 iteratively applied to the temperature series of each site to estimate changes in the timings of  
194 xylem growth. The resulting time series, which consisted of the dates of onset and ending of  
195 xylogenesis from 1950 to 2010, were tested for the presence of autocorrelation until the fourth  
196 order (McKenney *et al.*, 2006). Since no autocorrelation was observed for the onset of  
197 xylogenesis and the errors were only occasionally serially correlated at the second and third order  
198 for ending and duration of xylogenesis, the long-term trends were analyzed by Analysis of  
199 Covariance (ANCOVA).

## RESULTS

201

### 202 **Observed and modeled temperatures**

203 The region has a typical boreal climate with cold winters and cool summers (Table 1). The mean  
204 annual temperature in the four study sites varied between -0.9 and 2.0 °C while May-September  
205 temperature was 11.0-13.3 °C. The sites are characterized by long winters with temperatures  
206 close to or below zero, with the coldest generally being measured in January and reaching -47.1  
207 °C in DAN in 2009. The summers are short with absolute temperatures exceeding 30 °C in all  
208 sites (Table 1). The warmest maximum temperatures were observed in 2002 in all sites. The  
209 temperature patterns were synchronous across the four study sites, with the coldest being DAN  
210 and BER, those located at the highest latitude and altitude, respectively. SIM was the warmest  
211 site both for annual and May-September temperatures (Supplementary data Fig. S1). The hottest  
212 year was 2010, which globally showed the highest annual temperatures, although high May-  
213 September maximum temperatures were also observed during 2005. The lowest maximum and  
214 minimum temperatures were detected in 2004.

215 The regressions indicated correlations between measured and modeled temperatures with R  
216 square varying between 0.56 and 0.94 (Supplementary data Table S1). The stronger relationships  
217 were found for the annual maximum temperature, which on average showed an R square of 0.93.  
218 SIM exhibited the lowest R square while DAN and MIS were the sites with the higher R square  
219 for both the annual and May-September temperature. Overall, statistics confirmed that modeled  
220 data could represent the temperatures occurring in the four study sites during 1950-2001.

221 The positive slopes of the regressions performed on the temperature series for the period 1950-  
222 2010 indicated an increasing trend of both annual and May-September temperatures, although all  
223 models showed  $p > 0.05$  (Fig. 1). The highest slopes were observed for maximum temperatures of  
224 May-September with increases of 0.04-0.28 °C decade<sup>-1</sup>. Overall, lower slopes were estimated for  
225 annual temperature than for May-September temperature except for the minimum temperature in  
226 DAN and MIS. A clear pattern of change in the slopes with latitude was noticeable, with the  
227 greater increases in maximum temperature being observed at the higher latitudes, although this  
228 pattern was less obvious for minimum temperature.

229 The deviation from the 60-years average was calculated for the temperature series  
230 (Supplementary data Fig. S2). The 1960s were characterized by below-average values of both  
231 minimum and maximum temperatures of May-September. However, a similar pattern was not  
232 detected for the annual temperature. From 1970 to 1998, values were located around the average.  
233 After those years, both annual and May-September temperatures were clearly above the historical  
234 average, with the greater deviations for the maximum temperature of May-September.

### 235 **Model definition and validation**

236 At the four sites, xylem growth lasted between 80 and 133 days, with SIM having the longest  
237 duration (Fig. 2). Overall, the onset of xylem growth occurred from mid-May to mid-June (DOY  
238 139-166), covering a range of c.a. one month. Later onsets of xylogenesis were detected in 2002  
239 and 2009 and at the highest altitude and latitude, in BER and DAN, respectively. The ending of  
240 xylem growth differed by more than one month between the end of August in BER, MIS and  
241 DAN, and the beginning of October in SIM.

242 On average, the logistic regressions assessed the temperature thresholds at 4.4 and 15.5 °C for  
243 minimum and maximum temperature, respectively (Table 2). For a temperature above the  
244 calculated thresholds, xylem growth was more likely to be active than non-active. Although MIS  
245 had slightly higher values compared with the other sites, no significant difference was detected  
246 by ANOVA for either minimum or maximum temperature ( $P>0.05$ , Table 2).

247 The results generated by the logistic regressions were verified by forecasting the presence or  
248 absence of xylem growth in the study sites and comparing results by means of a contingency  
249 table (Table 3). Overall, observations showed that xylem growth was active during about one  
250 third of the year and not active during 72.3% of the year. For minimum and maximum  
251 temperatures, 94.9 and 95.0% of the predictions were confirmed by observations, respectively,  
252 confirming that the model with both temperatures produced reliable estimations of the thresholds  
253 and suitably predicted timings of the phenological phases of xylem. On average, not active and  
254 active xylem growth was correctly predicted for 69.0 and 25.9% of days, respectively, while the  
255 predictions were not confirmed for only 1.5–3.1% of days.

## 256 **Model application**

257 The model generated using the threshold temperatures was used for estimating chronologies of  
258 cambium phenology (onset, ending and duration of xylogenesis) for the period 1950-2010 (Fig.  
259 3). Long-term trends of all series were tested using ANCOVA, which calculated models with R  
260 square ranging between 0.36 and 0.60 and significance  $p<0.0001$  (Table 4). Predictions of the  
261 models using both minimum and maximum temperatures showed significant negative trends in  
262 all sites ( $p<0.05$ ), revealing an earlier onset of xylogenesis that was estimated by the slope of the  
263 regression at 0.5-0.8 days decade<sup>-1</sup>. Significant slopes for the ending of xylogenesis were detected

264 only with the model using minimum temperatures, which indicated a delay of 0.7 days decade<sup>-1</sup>  
265 (Table 4). Longer durations of xylogenesis were predicted for the period 1950-2010, with the  
266 higher (1.5 days decade<sup>-1</sup>) and lower (0.07 days decade<sup>-1</sup>) increases estimated by the model using  
267 minimum and maximum temperatures, respectively. Significant differences among sites were  
268 found for all phenological models ( $P < 0.0001$ , Table 4), with SIM having earlier onsets, later  
269 endings and longer durations of xylogenesis over all chronologies (Fig. 3). Differences in  
270 cambial phenology among BER, MIS and DAN were less marked. No significant interaction  
271 year $\times$ site was observed by ANCOVA ( $p > 0.05$ , Table 4).

272

## DISCUSSION

273  
274 Compared with the primary meristems such as leaves and buds, analyses on the phenology of the  
275 secondary meristem have only been emerging in the last decade. At the time of writing, the  
276 chronologies of cambial phenology deriving from direct observations are spatially and temporally  
277 fragmented (Rossi *et al.*, 2008b; Moser *et al.*, 2010; Rathgeber *et al.*, 2011; Swidrak *et al.*, 2011),  
278 which prevents the understanding of long-term responses of the cambium to environmental  
279 changes and any interpretation of the trends over time (Sparks and Menzel, 2002). This paper  
280 thus aimed to reconstruct timings of cambium phenology of black spruce over the last 60 years to  
281 test the hypothesis that duration of xylogenesis has lengthened since 1950. In the boreal forest,  
282 wood formation is restricted within 3-4 months by thermal limits that characterize the change  
283 between favourable and unfavourable periods for growth. In spring, cambial reactivation occurs  
284 from mid-May to mid-June, when the temperatures allow snow to melt and soil to warm up  
285 (Rossi *et al.*, 2011a). Mature xylem is observed in September, when all cells have concluded  
286 differentiation, which corresponds to nighttime temperatures of 4-5 °C, and maximum  
287 temperatures reaching 15-16 °C. For the first time, long-term chronologies of cambial phenology  
288 are provided, which allows investigation of the impact of past increases in temperature on wood  
289 formation. The dynamics and periods of xylem growth and their eventual changes over time are  
290 of particular interest for the global carbon budget as they define the period of main biomass  
291 accumulation in wood, during which trees act as an important sink of the carbon sequestered  
292 from the atmosphere. An extending period of tree growth associated with warmer temperature  
293 could allow cambial cells to divide more vigorously and longer, thus producing wider tree rings  
294 and greater amounts of wood.



295 **Trends of temperature and phenology**

296 The chronologies generated by the ANUSPLIN model (McKenney *et al.*, 2006) for the four study  
297 sites exhibited increasing trends of both annual and May-September temperatures between 1950  
298 and 2010. In some cases, the modeled climatic data were only partially correlated with  
299 measurements, and this may be explained by the remote location of the sites and by the scarcity  
300 of nearby weather stations used for the climatic modeling. The greatest changes were observed  
301 for maximum temperature at the higher latitudes, attaining increases of up to  $0.28\text{ }^{\circ}\text{C decade}^{-1}$  in  
302 DAN, the most northern site. For a similar period (1950-1998), Zhang *et al.* (2000) estimated that  
303 the higher increases in temperature for this region occurred in summer, with values ranging  
304 between  $1.0$  and  $1.5\text{ }^{\circ}\text{C}$ . Plummer *et al.* (2006) showed different trends for Quebec, with  
305 temperature rising by up to  $6\text{ }^{\circ}\text{C}$  in all seasons except in early spring, before the observed onset  
306 of xylogenesis. Our temperature chronologies exhibited a higher warming than the estimations of  
307 Zhang *et al.* (2000) and were more conservative than those of Plummer *et al.* (2006).

308 Changes in phenology of the primary meristems represents one of the best-documented effects of  
309 climate change on plants, with results converging toward increases in length of the growing  
310 season (Zhou *et al.*, 2001; Sparks and Menzel, 2002; Badeck *et al.*, 2004). In Canada, Beaubien  
311 and Freeland (2000) reported that the first flowering date of aspen poplar showed a marked trend  
312 of earlier flowering with an advance of 26 days over the period 1900-1997. For the northern  
313 hemisphere, Schwartz *et al.* (2006) estimated that during 1955-2002 the dates of first leaf and  
314 first bloom have been  $1.2$  and  $1.0\text{ days decade}^{-1}$  earlier. Greater advances of  $2.1\text{ days decade}^{-1}$   
315 were calculated between 1951 and 1996 for leaf unfolding in Europe (Menzel, 2000). Despite  
316 similar lengths of the study periods, the results vary widely, which could be explained by the

317 complex origin (observations or estimations) and nature (leaf or flower buds) of the datasets and  
318 species over the broad spatial scales of analysis. Moreover, a high heterogeneity in change of  
319 temperature has been observed across North America, with lower effects of warming occurring in  
320 the eastern part of the continent, where this work was carried out (Schwartz *et al.*, 2006). Overall,  
321 the hypothesis that duration of xylogenesis has lengthened over the last 60 years has been  
322 confirmed, although the estimated increasing trends of cambial phenology exhibited lower slopes  
323 than those observed in the primary meristems.

#### 324 **Does phenological cascade prevent estimating the end of xylogenesis?**

325 In Europe, the beginning of the growing season has advanced by 2.7 days decade<sup>-1</sup> in the last 30  
326 years, while its ending showed smaller annual variations and has occurred just 1 day decade<sup>-1</sup>  
327 later (Chmielewski and Rötzer, 2001). Sparks and Menzel (2002) definitely confirmed that earlier  
328 events were more variable and changed faster than later events. This was consistent with our  
329 results, which showed more marked changes in the spring onset than in late-summer ending of  
330 xylogenesis, and contrasting slopes and significances were observed over the study period from  
331 the trends of ending of xylogenesis. During development, the cambial derivatives (i.e. the cells  
332 produced by cambial division) alter both morphologically and physiologically, progressively  
333 assuming definite features. In other words, cells differentiate into the specific elements of the  
334 stem tissues, represented by the phases of enlargement, wall thickening and lignification.  
335 Investigations into xylem phenology and climate-growth relationships have focused mainly on  
336 the onset of the growth process, i.e. onset of xylem production or differentiation, while the end of  
337 growth still remains partly or completely unexplored (Gričar *et al.*, 2007; Rossi *et al.*, 2007; Seo  
338 *et al.*, 2008; Turcotte *et al.*, 2009). According to our findings, this could essentially be due to a

339 greater number of significant responses being obtained between onset of growth and climate  
340 rather than a mere lack of interest in the final phases of the growth process (Hänninen and  
341 Tanino, 2011).

342 In cold environments, cell production is closely related to xylem phenology (Lupi *et al.*, 2010;  
343 Rossi *et al.*, 2012). The date of onset of xylogenesis affects the number of cells produced by the  
344 cambium which, in turn, influences the ending of cell differentiation. As a result, earlier cambial  
345 resumptions lengthen the period available for cell division in the secondary meristem, increasing  
346 the growth potential during the year (Gričar *et al.*, 2005; Deslauriers *et al.*, 2008). In conifers,  
347 wider tree rings (i.e. with higher amount of cells) require a longer period for differentiating and  
348 maturing the tracheids, which delays the ending of wood formation. Thus, any environmental  
349 factor affecting the resumption of growth in spring could indirectly influence the production and  
350 temporal dynamics of cell differentiation by affecting all successive phenological phases of  
351 xylem (Rossi *et al.*, 2006b). The hypothesis of an indirect effect of environment on the chain of  
352 phenological events in the xylem provides valuable cues for identifying the relative importance of  
353 the factors affecting timings and dynamics of xylem growth, and makes the relationships between  
354 the temperatures occurring in late-summer and the date of ending of xylem growth more  
355 complex.

### 356 **Model and thermal predictors of xylogenesis**

357 Several methods have been applied to investigate plant growth and its changes over time.  
358 Definitions of the growing season differ according to plant species, and are calculated in different  
359 ways, either directly (bud or cambial phenology), or indirectly (thermal sums, days with air and  
360 soil temperatures above certain thresholds, freezing days) (Nizinski and Saugier, 1988; Körner

361 and Paulsen, 2004; Schwartz *et al.*, 2006; Seo *et al.*, 2008). In our reconstruction of past cambial  
362 phenology, the applied temperature thresholds were not defined a priori. They were instead  
363 statistically assessed on a wide dataset of observations collected weekly from four permanent  
364 plots over nine years, by defining a binary response of presence or absence of growth, and  
365 modeling the logistic response probability according to a vector of explanatory variable, either  
366 minimum or maximum temperature. The resulting temperature thresholds have the advantage of  
367 being objectively assessed and statistically validated, and are as close as possible to the biological  
368 limits of the growth process in the stem. However, the definition of the model assumed a linear  
369 response of cambial phenology to temperature, which is expected to occur only for narrow  
370 thermal ranges.

371 In this study, the minimum and maximum temperature thresholds allowing xylogenesis ranged  
372 between 4-5 °C and 15-16 °C, respectively, which confirm previous findings from other conifer  
373 species of cold climates (Rossi *et al.*, 2008b; Swidrak *et al.*, 2011) but contrast with the  
374 hypothesis of a cumulated effect of temperatures for cambial resumption (i.e. heat sums, Seo *et*  
375 *al.*, 2008; Swidrak *et al.*, 2011). Cambium is a sink for carbohydrates, and its activity requires a  
376 continuous supply of energy in the form of sucrose which, for the first cells to be formed, is  
377 extracted from the storage tissues or produced by photosynthesis (Oribe *et al.*, 2003; Deslauriers  
378 *et al.*, 2009). During cell maturation, trees assign a large amount of carbon obtained from  
379 photosynthesis to the deposition of cellulose microfibrils in order to provide the developing cells  
380 with secondary walls. The thresholds estimated in this paper could represent the critical  
381 temperatures limiting the demand for photo-assimilates by the metabolic processes involved in  
382 cell growth. Moreover, as xylogenesis is the most important net accumulation of biomass in  
383 forest ecosystems, knowledge about the climatic factors on the verges of the growing season is

384 crucial to determine the time window during which the carbon sequestered by the atmosphere is  
385 permanently stocked in trees.

386 The models using maximum and minimum temperature produced similar results in terms of onset  
387 of xylogenesis, but calculated different endings, and hence different durations of xylogenesis for  
388 the last 60 years (Table 4). Both models provided equally reliable estimations of xylem  
389 phenology, which prevented a definitive choice of the most suitable model. Unlike  
390 photosynthesis that is able to maintain high assimilation rates even at temperatures below 5 °C,  
391 xylem formation necessitates large amounts of available sucrose to be allocated in the growing  
392 tissues to complete growth, which is a temperature-limited process (Körner, 2003a; Deslauriers *et*  
393 *al.*, 2009). Cell doubling time remains quite constant at temperatures of 10–25 °C, but triples  
394 when temperatures fall from 10 to 5 °C, and cell division stops at 1–2 °C (Körner, 2003b).  
395 Moreover, comparing the daily growth responses of conifers to maximum and minimum  
396 temperatures, the better results were observed with the latter (Deslauriers and Morin, 2005; Wei  
397 *et al.*, 2007, Rossi *et al.*, 2008b). However, the effects of the two variables have still not been  
398 experimentally and definitively disentangled, and which temperature mostly controls the length  
399 of the growing period remains an unresolved question.

400

## CONCLUSIONS

401  
402 This paper used the phenological model developed by Rossi *et al.* (2011b) and weekly  
403 observations performed for 9 years in four permanent sites in Quebec, Canada to reconstruct the  
404 timings of cambium phenology over the last 60 years. All sites exhibited increasing trends of  
405 both annual and May-September temperatures, with the greatest changes occurring for maximum  
406 temperature at the higher latitudes. Accordingly, earlier cambial resumptions by 0.5-0.8 days  
407 decade<sup>-1</sup> were estimated, while significant delays for the ending of xylogenesis were calculated  
408 only with the model using minimum temperatures. Phenological events in spring were confirmed  
409 to be more variable and changing faster than those occurring in autumn. Results confirmed the  
410 initial hypothesis that duration of xylogenesis has lengthened since 1950. However, contrasting  
411 extents were observed, ranging between 0.07 and 1.5 days decade<sup>-1</sup>, calculated with the model  
412 based on maximum and minimum temperatures, respectively. To our knowledge, this is the first  
413 time that past cambial phenology has been modeled and reconstructed.

414 Consistent with the findings reported for leaf and flower buds, changes in cambial phenology  
415 showed increasing trends in length of the growing season, demonstrating the effects of the recent  
416 global warming on secondary meristems of trees. If the observed trend is maintained unaltered in  
417 the long run, the demonstrated advancement of cambial activity could dramatically modify the  
418 short time window for growth of the boreal species and markedly affect cell production of the  
419 secondary meristem. The findings of this work revealed that long-term increases in temperature  
420 can substantially extend wood formation and, consequently, the dynamics and productivity of  
421 cold ecosystems, by removing the thermal constraints to the activity of carbon sinks in trees.

422 However, evidence of these trends in forest ecosystem productivity requires to be confirmed by  
423 further specific investigations.

424

425

## ACKNOWLEDGEMENTS

426 This work was funded by Consortium de Recherche sur la Forêt Boréale Commerciale and Fonds  
427 de Recherche sur la Nature et les Technologies du Québec. The authors thank B. Dufour, G.  
428 Dumont-Frenette, F. Gionest, C. Lupi, S. Pedneault, P.-Y. Plourde, G. Savard, C. Soucy and M.  
429 Thibeault-Martel for technical support. Special thanks are extended to D. McKenney, K.  
430 Lawrence and P. Papadopol for sharing their dataset with the temperature chronologies, to J.  
431 Pedlar for his recommendations on data analysis, and to A. Garside for checking the English text.

432



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556

## FIGURE LEGENDS

557 **Fig. 1** Temperatures during 1950-2010 in the four sampling sites (graphics with different scales).

558 Gray lines correspond to linear regression analyses

559 **Fig. 2:** Cambial phenology in black spruce during 2002-2010 in the boreal forest of Quebec,

560 Canada.

561 **Fig. 3** Estimation of cambial phenology from period 1950-2010 (onset, ending and duration of

562 xylogenesis). Lines correspond to regression analyses performed by ANCOVA

563

**Table 1:** Location of the four study sites listed in decreasing latitude and climatic characteristics measured during the period 2002-2010.

Site	Latitude	Longitude	Altitude (m a.s.l.)	Mean temperature		Absolute annual temperature	
				Annual (°C)	May-September (°C)	Maximum (°C)	Minimum (°C)
DAN	50°41' N	72°11' W	487	-0.9	11.0	34.2	-47.1
MIS	49°43' N	71°56' W	342	1.0	12.7	35.1	-42.4
BER	48°51' N	70°20' W	611	0.3	11.4	33.1	-39.8
SIM	48°13' N	71°15' W	338	2.0	13.3	35.7	-39.7



**Table 2:** ANOVA comparisons performed among the threshold temperatures occurring when the probability of xylem growth in black spruce being active was 0.5. The thresholds were estimated on a dataset of cambial phenology collected during 2002-2010 in the boreal forest of Quebec, Canada.

Threshold temperature (°C)	SIM	BER	MIS	DAN	<i>F</i> -value	<i>P</i>
Minimum	4.2±1.0	4.0±1.9	5.4±1.3	4.0±1.3	2.68	0.06
Maximum	15.1±0.7	15.2±1.4	16.3±1.4	15.4±1.4	1.64	0.19

**Table 3:** Proportions of observed and predicted days with non-active (first and second row) or active (third and fourth row) xylem growth in black spruce. Predictions were obtained using the minimum and maximum temperatures estimated during 2002–2010 in the boreal forest of Quebec, Canada. The first and fourth rows correspond to the days correctly predicted by the model.

Observed xylogenesis	Predicted xylogenesis	Model using minimum temperatures (%)	Model using maximum temperatures (%)
No	No	69.2	68.8
No	Yes	3.1	3.5
Yes	No	2.0	1.5
Yes	Yes	25.7	26.2

**Table 4:** ANCOVA models comparing the chronologies of cambial phenology (onset, ending and duration of xylogenesis) of black spruce predicted for 1950-2010 using thresholds of minimum and maximum temperature. One, two and three asterisks indicate statistically significant differences at  $p < 0.05$ ,  $p < 0.001$  and  $p < 0.0001$ , respectively.

Xylogenesis	Temperature	Source	Regressors		Statistics		Coefficients	
			Type I SS	F-value	F-value	R square	Intercept	Slope ( $10^1$ )
Onset	Minimum	Year	219.9	5.6*				
		Site	6000.0	51.1***	22.9***	0.40	307.9	-0.8
		Year×site	64.2	0.5				
	Maximum	Year	713.5	14.3**				
		Site	5852.0	39.1***	19.1***	0.36	237.5	-0.5
		Year×site	100.8	0.6				
Ending	Minimum	Year	627.0	15.3**				
		Site	60303.2	49.0***	23.6***	0.41	125.3	0.7
		Year×site	125.8	1.0				
	Maximum	Year	36.8	0.9				
		Site	8754.5	74.1***	32.3***	0.48	351.9	-0.4
		Year×site	116.4	0.9				
Duration	Minimum	Year	1589.6	21.4***				
		Site	23747.7	106.7***	49.3***	0.59	-182.6	1.5
		Year×site	308.2	1.3				
	Maximum	Year	1074.9	13.0**				
		Site	28846.8	116.6***	52.5***	0.60	114.4	0.07
		Year×site	409.3	1.6				

Figure 1

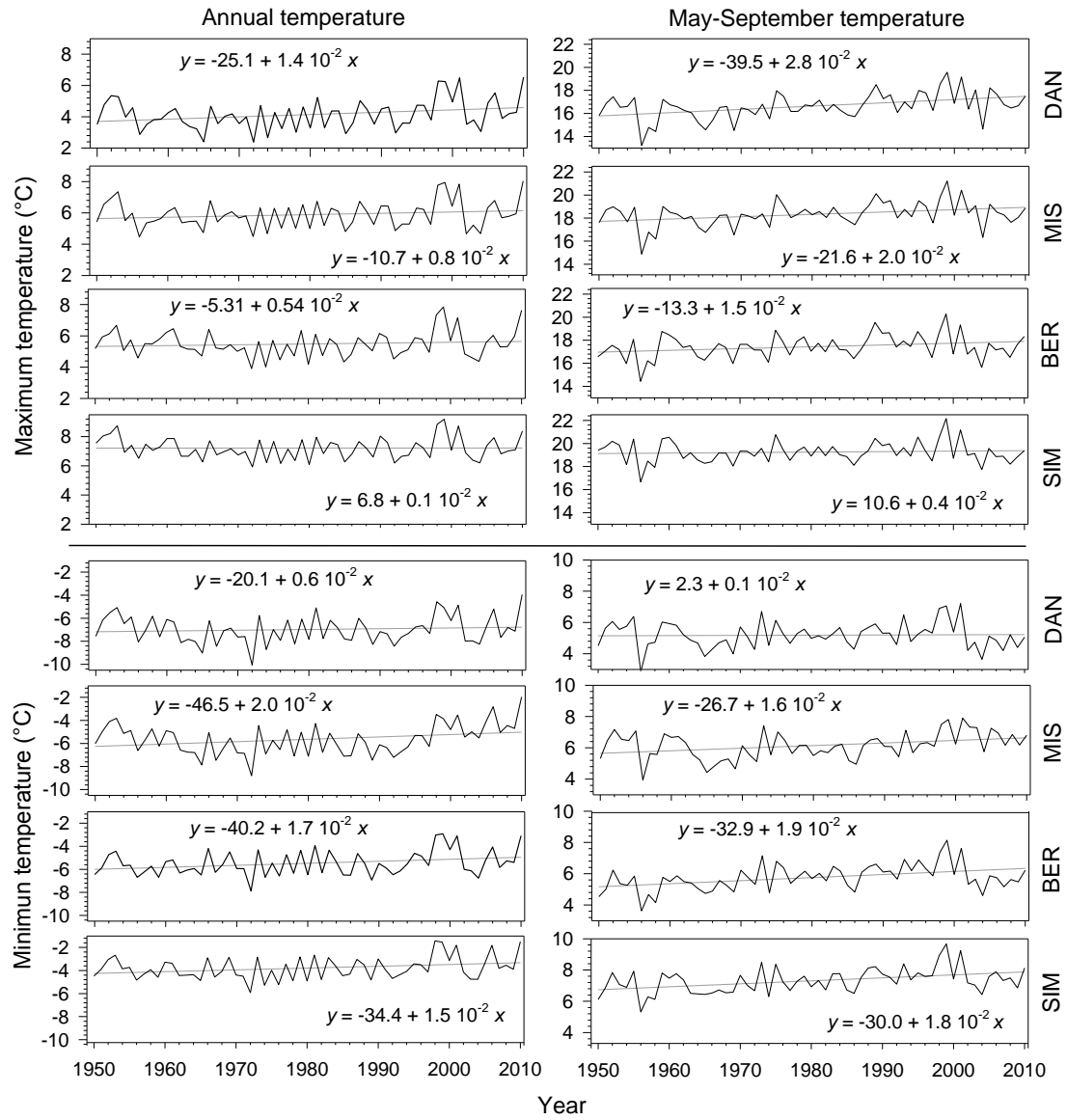


Figure 2

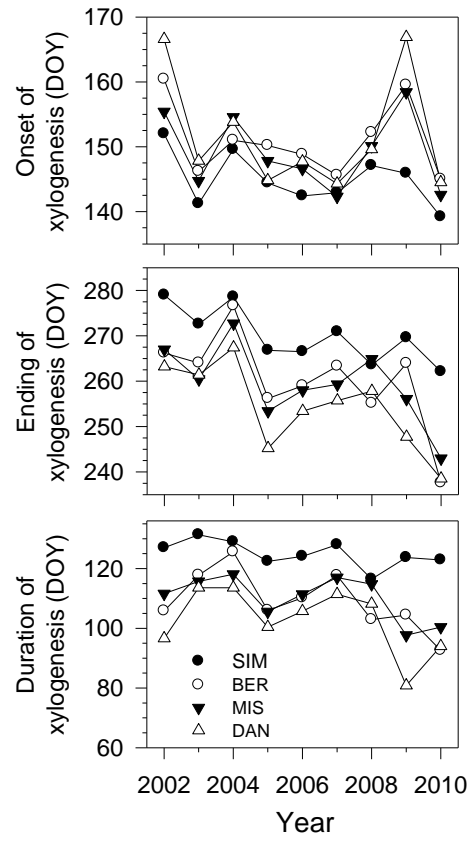
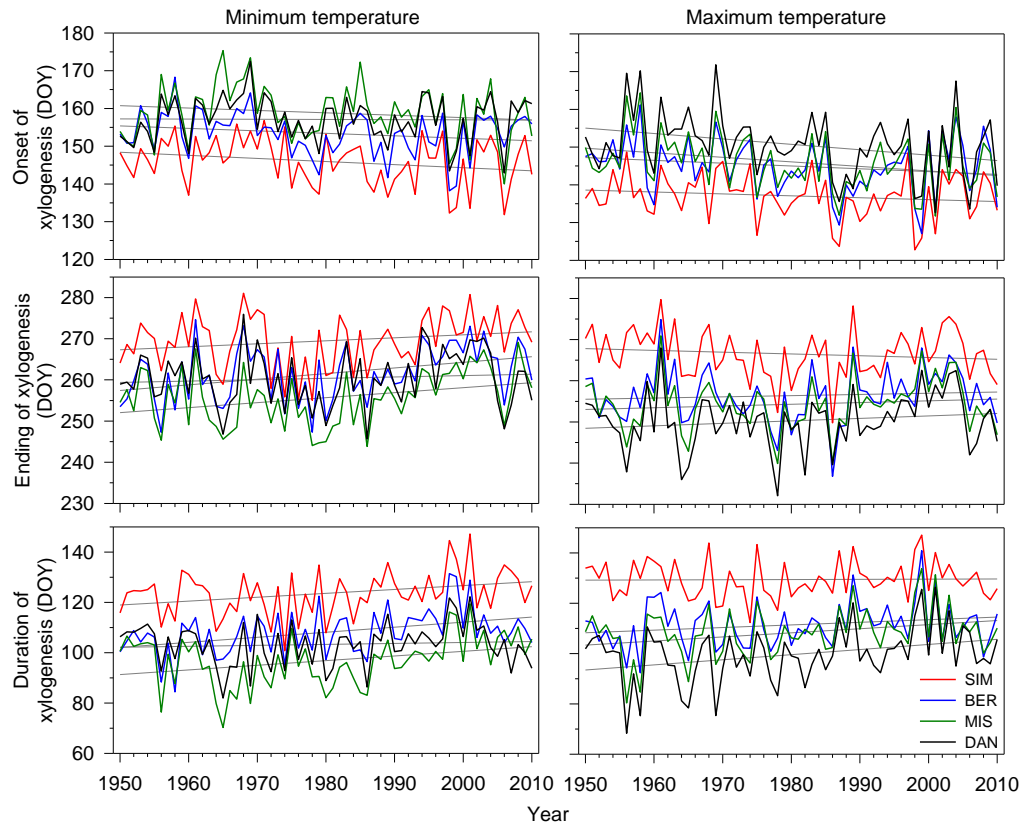
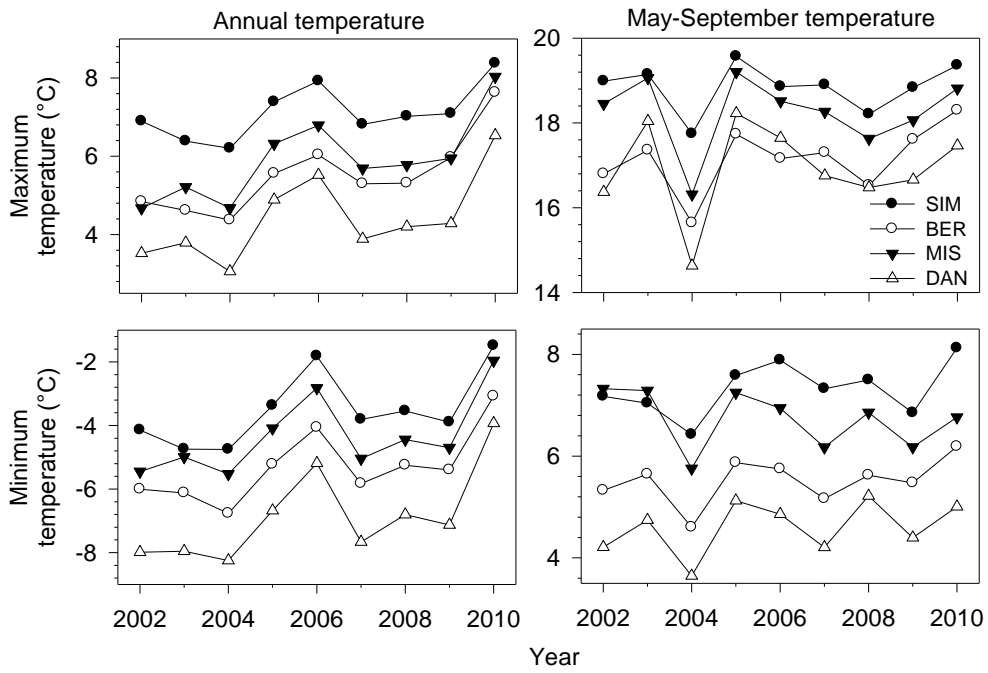


Figure 3



## SUPPLEMENTARY DATA

**Fig. S1:** Variation of the maximum and minimum temperature expressed as annual means and as the May-September period in the four sampling site (graphics with different scale).



**Table S1:** Relationships in the form of linear regressions between measured and estimated temperatures in the four study sites for the overlapping years 2002-2004. All models were significant at  $p < 0.0001$ .

Temperature	Site	Annual			May-September		
		Intercept	Slope	R square	Intercept	Slope	R square
Minimum	DAN	0.80	0.95	0.87	2.22	0.82	0.62
	MIS	-0.35	0.96	0.87	1.66	0.76	0.57
	BER	0.93	0.90	0.86	2.37	0.77	0.60
	SIM	0.82	0.90	0.86	2.95	0.73	0.56
Maximum	DAN	0.96	0.97	0.93	4.02	0.82	0.72
	MIS	0.87	0.99	0.94	3.76	0.85	0.71
	BER	0.81	0.97	0.93	3.82	0.81	0.69
	SIM	0.52	0.98	0.92	4.52	0.79	0.67



**Fig. S2:** Deviation from average of the period 1950-2010 in the form of difference between the actual temperature and historical mean.

