Article

May Temperature Drives Cambial Resumption in the Boreal Black Spruce

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Abstract: The timings of the onset and ending of xylogenesis define the time window when environmental conditions are suitable for xylem formation. The relationship between the occurrence of xylem phenological events and the related climatic factors is critical to revealing how xylem formation responds to the changing climate. Given that temperature is the most important factor influencing growth in the boreal forest, we monitored air temperature and xylem phenology at five permanent plots of black spruce (*Picea mariana* (Mill.) BSP) along a latitudinal gradient of the boreal forest of Quebec, Canada. Microcores were collected weekly or biweekly from five to ten trees per site during the growing seasons from 2002 to 2019. We compared the relationships between air temperature and timings of the onset and termination of xylogenesis, testing the hypothesis that spring temperatures trigger the initiation of cambial activity. The onset of xylogenesis occurred from late May (DOY 149) to mid-June (DOY 163), and it terminated between late August (DOY 240) and late September (DOY 270). The spring phases of xylem phenology showed similar inter-annual variation among sites, while the variation in autumnal phases was less correlated among sites. The onset of xylogenesis was negatively correlated with the mean May temperature, and the correlations were consistent among sites, with r ranging from -0.61 to -0.77. The warmer May temperatures would advance cambial resumption, allowing the initial hypothesis that spring temperatures are a driving factor of xylogenesis to be accepted. With an increase of 1 °C in the mean May temperature, cambial resumption could be advanced by 2.7 days. Yet, no relationship between the termination of xylem phenology and monthly temperature was established, suggesting that other factors, possibly endogenous, could have affected the xylem phenology in autumn. Under warming conditions, we expect an advancement in the onset of xylogenesis, which may lengthen the growing season and potentially enhance cell production in black spruce.

Keywords: boreal forest; cambial activity; *Picea mariana*; temperature; xylogenesis

1. Introduction

The Earth's biosphere has undergone several climatic regimes. The rise in atmospheric CO_2 is one of the main factors causing changes in the global climate by instigating global warming. Global thermal changes in the atmosphere have brought about seasonal fluctuations all over the world [1] that directly affect the growth processes and productivity of plants [2]. Given the consistency in global seasonal fluctuations, the IPCC [3] is alarmed by the 1.5 °C mean annual increase in global temperature, while Plummer et al. [4] predict a 3 °C annual increase by 2050. There has been remarkable change in the mean global

temperature at a rate of 1 °C per year since 1900 [5], which greatly influences the eco-physiological mechanisms of plants. The study of forest biomes presents a wide view of climatic diversions that impact the natural composition of populations, altering their interactions and growth processes [6,7]. Despite experiencing harsh winters, boreal forests are the largest terrestrial carbon reservoir; they conserve moisture, which maintains plant metabolism and biodiversity in the forest [8]. Canada's boreal forest covers 1.3 billion acres, comprising the world's largest wetland reservoir, which provides a number of natural resources, one of which is biomass, which sequesters carbon in the form of wood.

Several studies indicate that wood formation in trees is a biological solution to the Earth's warming; by allocating carbon in their wood, trees ultimately reduce its content in the atmosphere [9]. This process involves the secondary growth of vascular tissues provoked by cambium cells [10]. Accordingly, as long as the temperature gain is maintained, a tree can continue its wood formation process. It has been observed that the period of activity is dependent on certain climatic factors, predominantly temperature [11,12]. The onset and duration of cambial activity hold great importance in the life of a tree for its longevity, wood quality, and volume attainment [13]. An overwhelming number of studies have stated that global climatic changes have altered the onset and duration of cambial activities in trees [14,15].

Temperature fluctuations affect cambial activity and the timings of cell division and cell enlargement [16]. In colder areas, the activity period (summer) is followed by a dormant period (arrival of the cold season), where both conditions, i.e., activity and dormancy, follow the day length and temperature [17,18]. Accordingly, the resumption of cambial cell division occurs from spring to summer in colder regions when trees receive maximum light and suitable temperatures [19]. The relationship between cambial activity and temperature can be seen to have a complex biological background when studied in view of geographical elements such as latitudinal gradients or slope. Latitudinal gradients affect temperature exposure in canopies [20], which, in turn, influences the photosynthetic ratio of trees [15,21].

The distribution of black spruce covers temperate and boreal ecotone regions where it forms different tree communities depending on their gradients, such as in the extreme north of Quebec, where there are black-spruce-dominated monospecific forests. In the current situation of atmospheric warming, there is a need to quantify tree growth, specifically the developing phases of wood formation, including cell division and enlargement, as well as the drivers of xylem phenology.

This study uses a long chronology of xylem phenology to analyze intra-annual wood formation at five permanent plots along a latitudinal gradient covering the eastern distribution of black spruce in Quebec, Canada. We test the climatic factors triggering the onset of xylogenesis in black spruce. This species exhibits different timings of cambial reactivation along the latitude, with an earlier onset occurring in the southern and warmer sites and a later onset in the northern and colder sites [5], mirroring the thermal gradient of spring temperatures across the study area. Accordingly, we test the hypothesis that the cambial reactivation in black spruce is triggered by spring temperatures.

2. Materials and Methods

2.1. Study Area and Tree Selection

This study was conducted at five permanent sites (Mirage (MIR), Camp Daniel (DAN), Mistassibi (MIS), Bernatchez (BER), and Simoncouche (SIM)) along a latitudinal gradient located between the 48th and 54th parallels in the boreal coniferous forest of Quebec, Canada (Figure 1). MIR, the northernmost site, was situated in the black spruce–lichen bioclimatic domain; while DAN and MIS were located in the black spruce–moss bioclimatic domain; and BER and SIM were in the balsam fir–white birch bioclimatic domain [22].
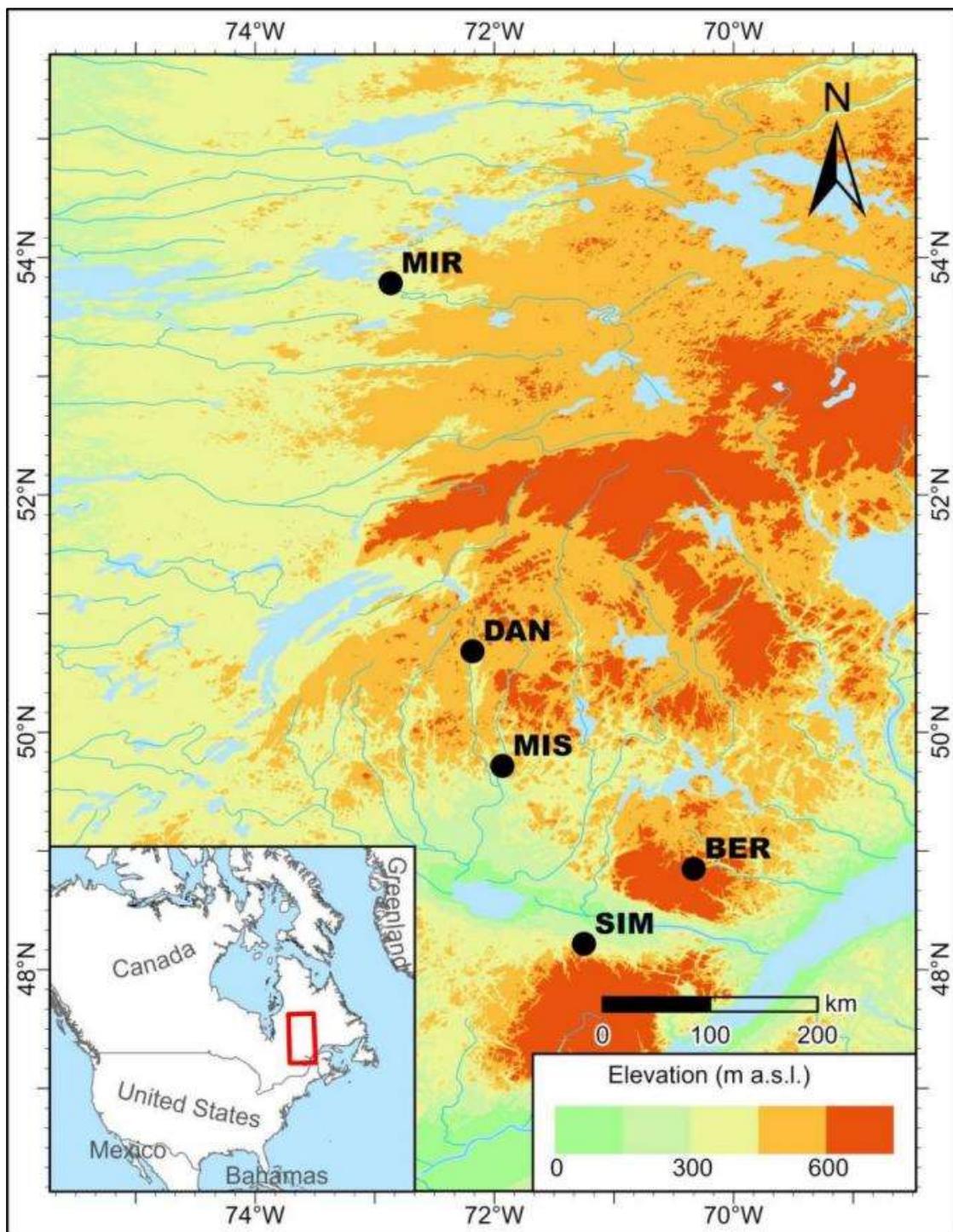
Figure 1. Locations of the five permanent sites in the boreal forest of Quebec, Canada.

The climate is typically boreal, with short, cool summers and long, cold winters. During the study period (2002–2019), mean annual temperatures across the study area ranged between −2.5 and 2.1 °C, with the northernmost (MIR) and southernmost (SIM) sites being the coldest and warmest, respectively. The total precipitation ranged from 817 mm (MIR) to 1162 mm (SIM) [23].

2.2. Microcore Sampling and Observation

Five to ten dominant or co-dominant even-aged black spruces were selected at each site (Table 1). Wood microcores were collected weekly or biweekly at breast height from April to October during 2002–2019, except for MIR, where sampling started in 2012. In total, 155 trees were used for sampling, with one tree sampled for 4 years on average. Microcores were extracted using surgical bone sampling needles until 2006 and Trephor from 2007 onward. The sampling followed a spiral trajectory on the stem, at least 5 cm apart, to avoid resin ducts induced by previous sampling [24].

Table 1. Information on sampled trees at the five permanent sites in the boreal forest of Quebec, Canada.

Site	Age (years)	DBH (cm)	Height (m)
MIR	111 ± 4	20.5 ± 1.1	12.6 ± 0.7
DAN	134 ± 3	22.0 ± 1.7	18.3 ± 1.3
MIS	113 ± 4	20.3 ± 1.6	18.2 ± 0.8
BER	133 ± 3	20.4 ± 1.8	16.8 ± 0.8
SIM	81 ± 2	20.9 ± 1.4	17.2 ± 0.8

The samples contained several previous tree rings, as well as developing layers of cambial zone and adjacent phloem [25]. After extraction, the microcores were preserved in Eppendorf microtubes with 50% ethanol in water at 5 °C. In the lab, the microcores were dehydrated in ethanol and D-limonene before being embedded in paraffin and cut into 10 μm thick slices using a rotary microtome. The transverse sections were stained with cresyl violet acetate (0.16% in water) and observed under visible and polarized light at magnifications of 400–500×.

The number of cells in the cambial zone, enlargement, wall thickening and lignification, as well as mature cells, was counted along three radial rows on each sample. In transverse sections, cambium and enlarging cells had thin primary walls that were not birefringent under polarized light. The radial diameter of an enlarging cell was at least twice that of a cambial cell. Given the arrangement of cellulose microfibrils, cells glistened under polarized light during the cell wall thickening and lignification phase [26]. Cells were found to be mature when the protoplast was lost, the tracheid lumen was empty, and the whole cell wall turned blue. In spring, wood formation was considered to have started when at least one radial file of enlarging cells was observed. In late summer, when no further cells were enlarging, cell production was considered complete. When no further cells were observed in the wall-thickening and lignification phase, wood formation was considered complete. The onset and termination of each phenological phase of xylem were assessed and calculated according to day of the year (DOY).

2.3. Weather Stations

At the beginning of sampling, an automatic meteorological station was installed in a forest gap at each permanent plot. The air temperature was observed at intervals of 15 min, and recorded as an hourly average using CR10X dataloggers (Campbell Scientific Corporation, Logan, UT, USA), which were then used to calculate the temperature series for the subsequent analyses.

2.4. Statistical Analyses

Correlations of annual temperatures and xylem phenology between sites were assessed by Pearson's correlations. Monthly mean air temperatures were used to represent the thermal conditions before and during wood formation and to calculate their relationships with the onset and ending of xylogenesis using Pearson's correlations. Linear regressions were used to assess the relationships between the monthly mean temperature before growth and at each phase of xylem phenology. Data analysis was conducted in SAS (SAS Institute Inc., Cary, NC, USA), and the final statistics were generated using JMP (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Air Temperatures at Study Sites

The annual temperatures were correlated across sites ($p < 0.01$), with correlation coefficients > 0.90, indicating that our study sites experienced similar inter-annual variation in temperature (Figure 2). The warmest years were 2006, 2010, and 2012. The coldest years during the study period were 2002, 2004, and 2019. The difference in temperature across sites was explained using latitude and altitude. On average, we recorded a difference of 4.6 °C between the warmest (SIM) and coldest (MIR) sites. BER, the highest elevation site, was on average 0.6 °C colder than MIS, which was situated at a higher latitude than BER. No significant trend in the annual temperature was observed during the study period ($p < 0.05$).
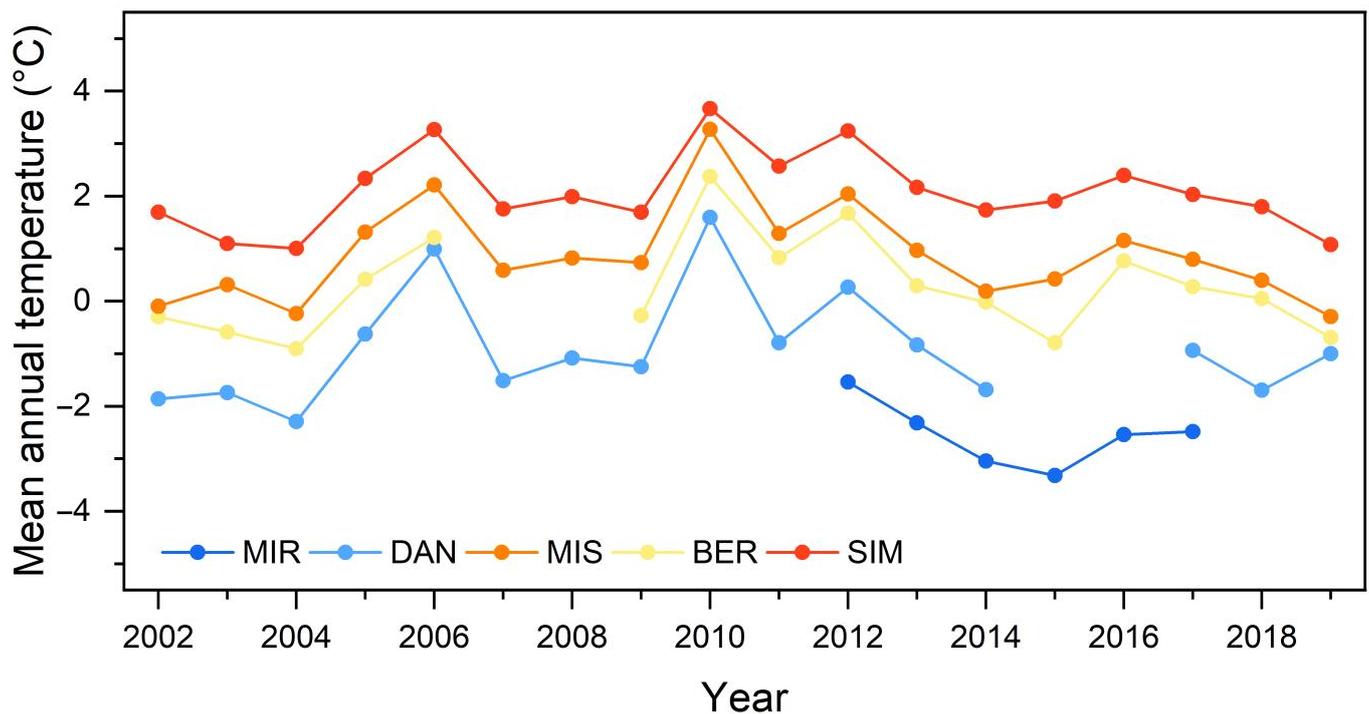

Figure 2. Mean annual temperature recorded at the five permanent sites in the boreal forest of Quebec, Canada.

3.2. Xylogenesis

On average, cell enlargement began earlier at the southernmost site (SIM), at the end of May (DOY 149), and later at the northernmost site (MIR), in mid-June (DOY 163) (Figure 3). The timings of the first enlarging cells at the other three sites ranged from DOY 154 at MIS to DOY 158 at BER. The onset of cell wall thickening and lignification and the appearance of the first mature cell followed a similar pattern to the onset of cell enlargement. The timings of the cell wall thickening and lignification started from mid- to late-June, from DOY 161 at SIM to DOY 175 at MIR. The first mature cell occurred in late June (DOY 174) at SIM and 15 days later at MIR.

The last enlarging cell occurred in late July (DOY 209) at MIS and 18 days later at SIM (Figure 3). Wood formation was terminated between late August (DOY 240) and late September (DOY 270), with MIR and SIM being the earliest and latest sites to complete xylogenesis, respectively.
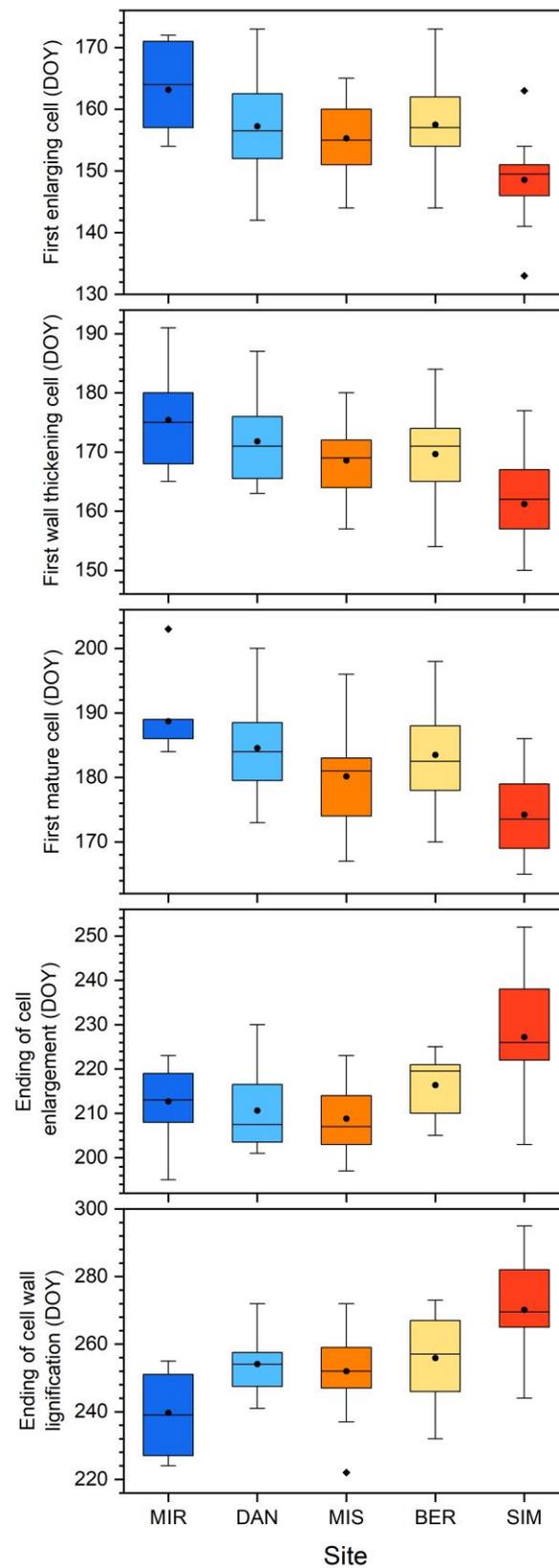
Figure 3. Xylem phenology of black spruce recorded during 2002–2019 at five permanent sites in the boreal forest of Quebec, Canada. The sites are listed at decreasing latitude. Lower and upper box limits represent the first and third quartiles, horizontal black lines represent median values, black dots represent mean values, whiskers represent 1.5× the interquartile range, and black diamonds represent outliers.

3.3. Correlations of Xylem Phenology between Sites

In spring, the timings of xylem phenology were synchronized across sites (Figure 4). The correlation coefficient indicated that the onset of cell enlargement was highly correlated ($p < 0.05$) between the five sites, with an r ranging from 0.57 to 0.92 (Figure 5). The onset of cell wall thickening and lignification and the first mature cell exhibited positive and significant correlations between sites ($p < 0.01$), with r ranging from 0.64 to 0.83 and from 0.67 to 0.85, respectively (Figure 5). The correlations with MIR were not significant, possibly because of the shorter time series.
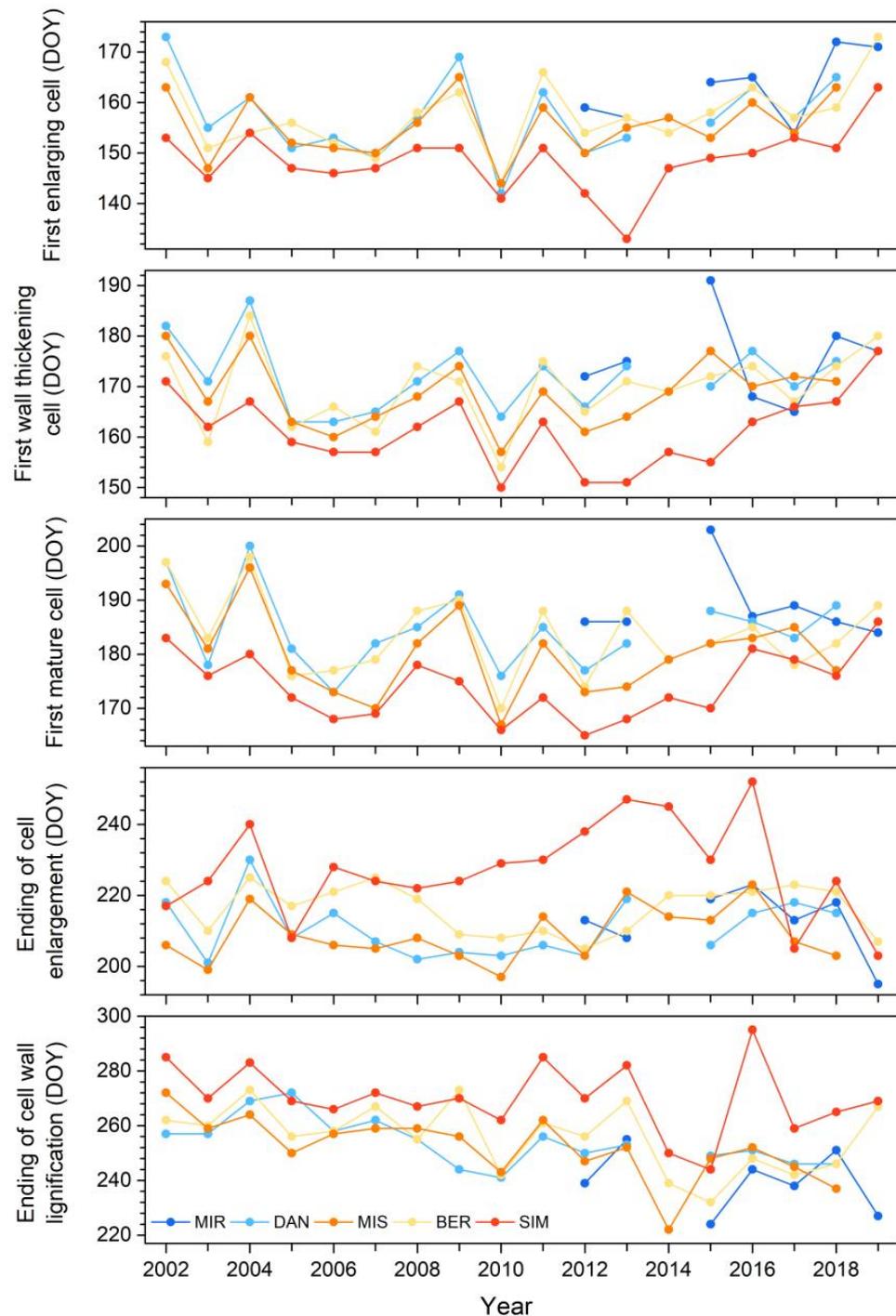

Figure 4. Timings of xylem phenology of black spruce recorded at the five permanent sites of the boreal forest of Quebec, Canada.
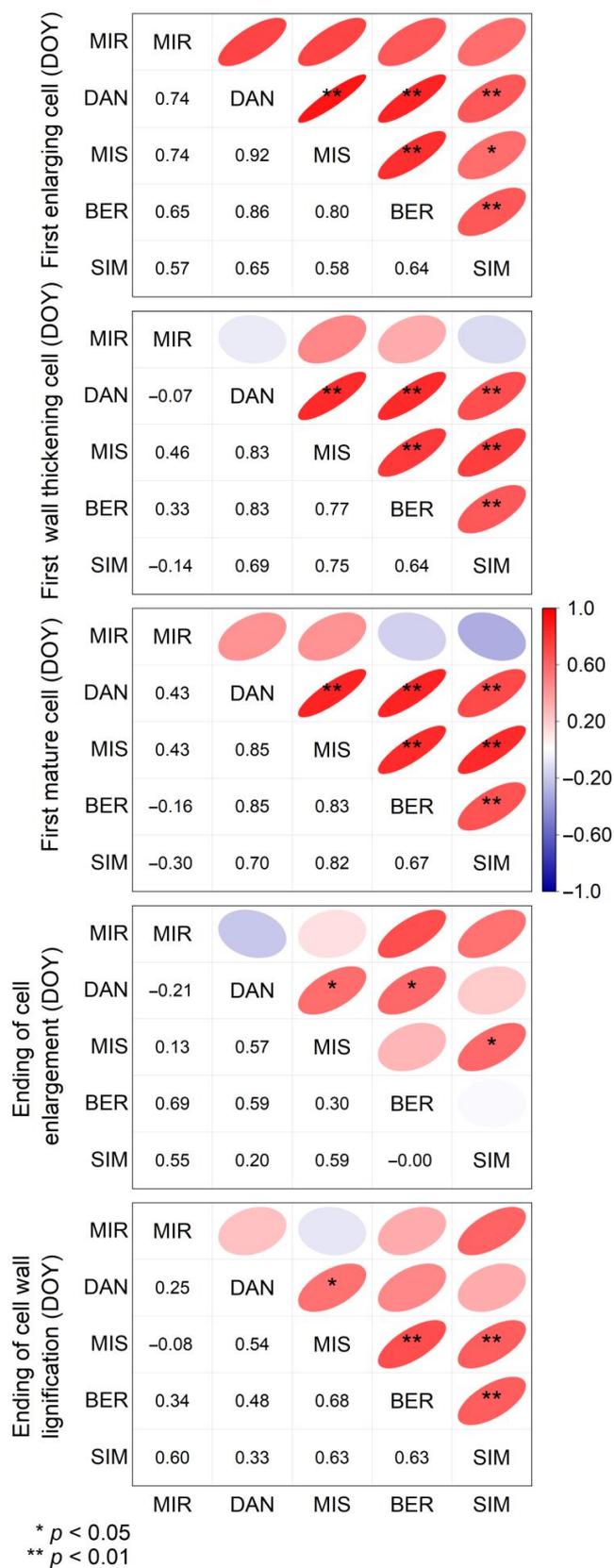
Figure 5. Correlation matrix for the xylem phenology of black spruce between five permanent sites in the boreal forest of Quebec, Canada. Pearson's *r* values are represented by both values and ellipse colors. Narrower ellipses represent high correlation, and the asterisks indicate significant correlation coefficients.

In autumn, the synchronisms in the phases of xylem phenology were lower (Figure 4). The termination of cell enlargement between DAN and MIS, DAN and BER, and MIS and SIM was significantly correlated ($p < 0.05$), with r ranging from 0.57 to 0.59. The other correlations for this phase were not significant ($p > 0.05$). The correlations for the end of cell wall thickening and lignification between DAN and MIS, MIS and BER, MIS and SIM, and BER and SIM were positive and significant ($p < 0.05$), with r ranging between 0.54 and 0.68 (Figure 5).

3.4. Relationships between Monthly Temperature and Xylem Phenology

We found high correlations between the onset of cambial activity and the mean May temperature ($p < 0.01$) at all sites except MIR, with r ranging from -0.61 to -0.77. Accordingly, the onset of cambial reactivation occurred earlier under warmer May temperatures (Figure 6). Although the temperatures of the previous months (January–April) had the same trends, the negative correlations with the onset of xylogenesis were not significant ($p > 0.05$).
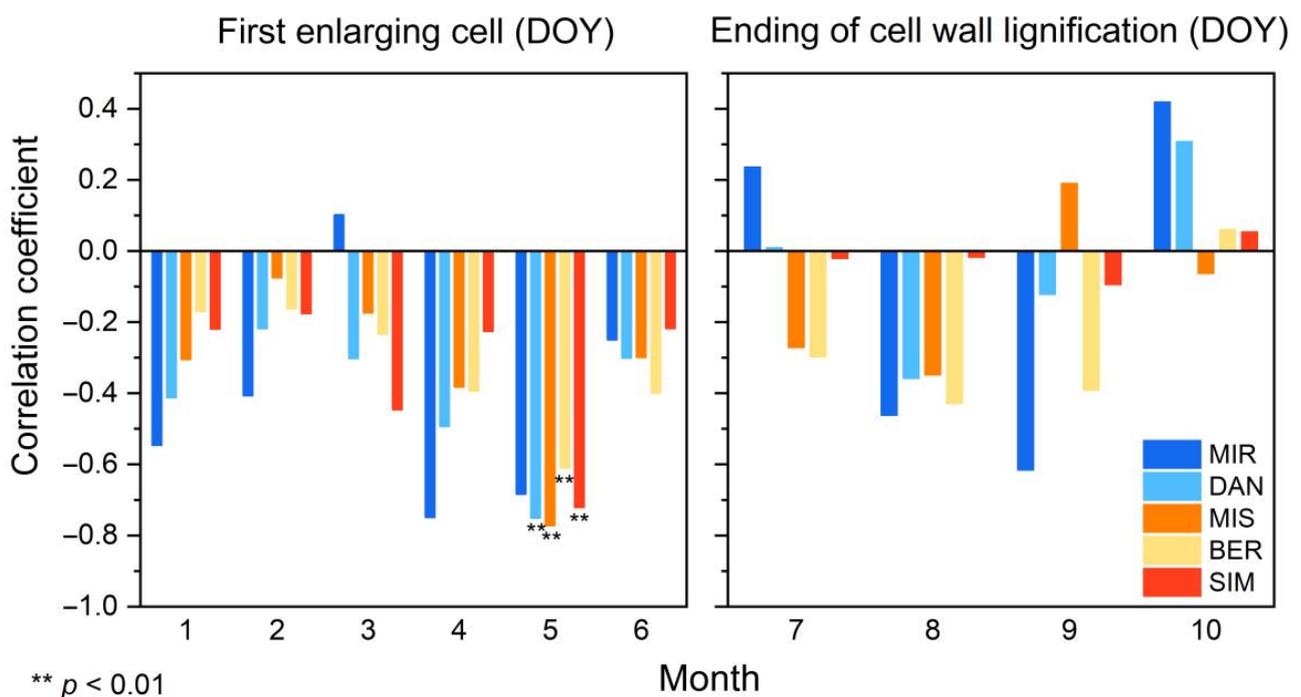

Figure 6. Correlations between the onset and ending of xylogenesis and monthly temperature at five permanent sites in the boreal forest of Quebec, Canada.

The correlations between the ending of xylogenesis and the monthly temperatures of July–October were not significant ($p > 0.05$), and no clear pattern was observed (Figure 6). Accordingly, the end of xylogenesis was not correlated with the air temperature of the summer.

The regressions between mean May temperatures and spring phases of xylem phenology were significantly positive ($p < 0.001$, Figure 7). The earlier onset of cell enlargement, cell wall thickening and lignification, as well as the earlier appearance of first mature cell were associated with the warmer mean May temperatures in the boreal forest of Quebec. With a 1 °C increase in May temperatures, we can expect an advancement of 2.7–3.1 days in the spring events. Furthermore, no significant relationship was detected between the mean May temperature and the autumnal phases of xylem phenology ($p > 0.05$, Figure 6), indicating that the variation of mean May temperature may not affect the termination of cell enlargement and cell wall thickening and lignification.
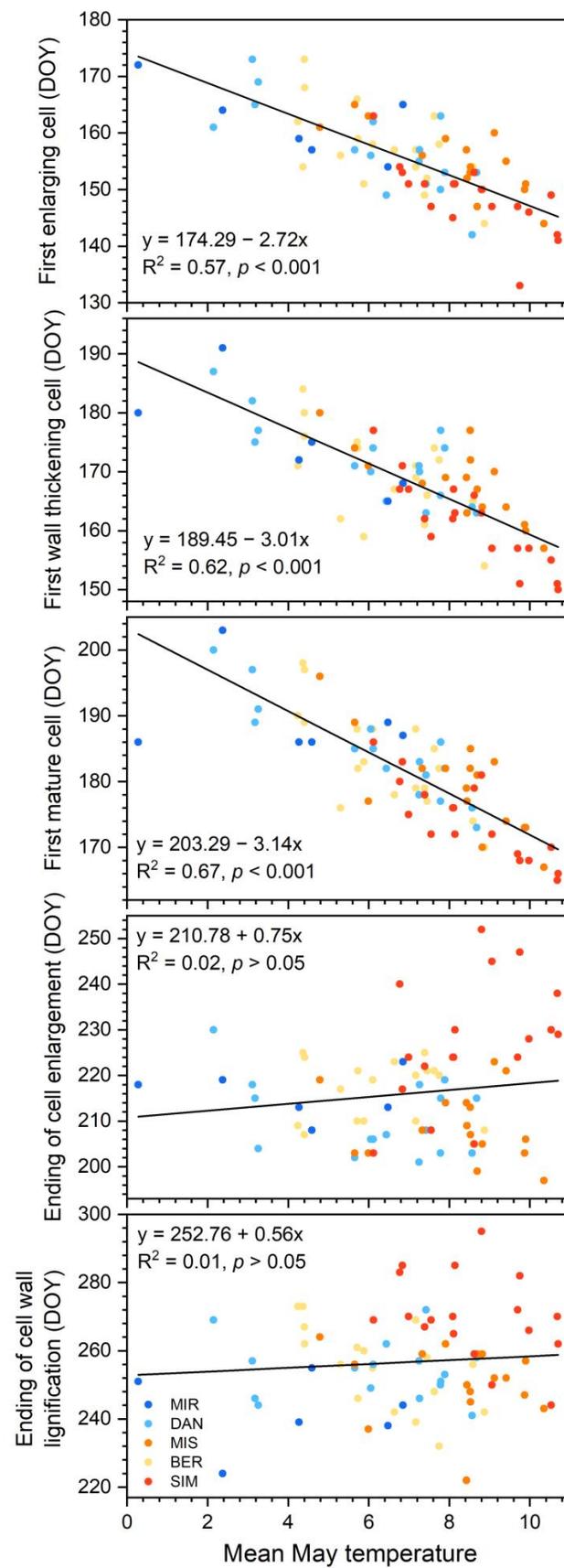
Figure 7. Relationships between the mean May temperature and xylem phenology at the five permanent sites in the boreal forest of Quebec, Canada.

4. Discussion

In this study, we compared an 18-year-long period of xylem phenology monitoring with air temperature measured at five permanent plots along a latitudinal gradient in the coniferous boreal forest of Quebec, Canada. This study found similar inter-annual variations in phenological events across sites, mainly in spring. Accordingly, the five sites experienced the common years with earlier or later onset of xylogenesis. Furthermore, we detected strong negative correlations between growth reactivation and the mean May temperature. Our results demonstrated that warmer temperatures in May can advance the onset of wood formation in black spruce, confirming the initial hypothesis that spring temperature drives the cambial resumption of black spruce.

4.1. Effect of Temperatures on the Onset of Xylem Phenology

The onset of xylem phenology played a critical role in affecting the quantity and quality of wood formation, thereby exhibiting the ability of cambium to capture the favorable environmental conditions after winter dormancy [15,25]. It has been demonstrated by numerous studies that the onset of xylem phenology in cold and temperate ecosystems is mainly triggered by temperature, according to either the accumulated heat sums or critical threshold temperatures [11,21,27–29], indicating that the initiation of cambial activity occurs when the cambium reaches an appropriate thermal condition. In a cold and arid region of the northeastern Tibetan Plateau, the warm spring could advance the cambial resumption of *Juniperus przewalskii* independently of the rain events that occur before the growing season [28,30]. Rossi et al. [25] proposed that spring temperatures (April and May) produced the best models to predict the timings of xylem phenology in conifers growing in the cold environment of the northern hemisphere. In line with these studies, our analyses revealed that, over the 18-year-long study period, the mean May temperature was the driving factor of the onset of xylogenesis in black spruce along a latitudinal gradient. In general, with an increase of 1 °C in the mean May temperature, the onset of xylogenesis could be advanced by 2.7 days. This result was lower than that found in the previous study within the same area, which predicted the onset of xylem phenology based on the mean annual temperature, as calculated for a shorter study period (7 years) [24]. The researchers detected that the onset of xylogenesis would be advanced by 4.3 days $°C^{-1}$. The difference between studies may result from the different time series or the new permanent plot (MIR) added in the northern part of the boreal forest.

In temperate and cold ecosystems, the cambium experiences two stages of dormancy in winter, namely, the rest and quiescent stages [31]. During the rest stage, which is mainly controlled by endogenous factors, the cambium is unable to reactivate even with sufficient IAA and favorable environmental conditions [15]. Correspondingly, our results showed no relationship between winter temperatures and the onset of xylem phenology. The cambium in the quiescent stage could be reactivated when exposed to the artificial heating of stems or natural warming [32,33]. Our study area was covered by snow from October to May, while the timings of cambial resumption in black spruce occurred from mid-May to late June; therefore, we propose that warmer temperatures before the growing season may result in an earlier snowmelt, allowing the earlier recovery of water uptake and transport through the roots and stem [34,35]. As such, May temperatures can directly influence the cambial resumption of black spruce.

Since the increasing temperatures in spring occurred earlier in the south, the thermal thresholds required for growth resumption were reached earlier than in the north [25,36]. Indeed, on average, the onset of cambial resumption at the southernmost site (SIM) was 14 days earlier than that at the northernmost site (MIR), mirroring the thermal gradient of sites in spring [37]. We did, however, find significant synchronism in the timings of cambium resumption across sites. All the sites exhibited an early onset of xylogenesis in 2010 as there was a warmer May temperature that year. During the colder Mays in 2002 and 2019, all sites showed a later initiation of cambial activity. Thus, we concluded that the

cambial resumption of black spruce across the latitudinal gradient had a similar response to May temperatures.

4.2. The Process of Xylogenesis

Based on causal modeling, Rossi et al. [36] suggested that the timing of the first enlarging cell could directly influence the timings of the first wall-thickening cell and the first mature cell. Consequently, the climatic factors affecting the onset of cell enlargement may also influence the successive timings of xylogenesis. In our study, the inter-annual variations among the spring phases of xylem phenology were similar. In addition, the timings of the first wall-thickening cell and the first mature cell were also highly correlated with the mean May temperature. The initiation of cell differentiation is related to the same pool of cells, namely, the first developing cells in xylogenesis, which could explain our findings [36].

In contrast with the spring phases, the inter-annual variation of the autumnal phases showed low or no correlations across sites, which could be related to the complexity of the process of xylem formation. The cessation of xylogenesis is affected by a series of interconnected physiological activities during the growing season [24], making the end of the growth period hard to predict. In some studies, water availability could affect the cessation of xylem phenology [28,38–40]. Although water availability is still crucial for xylem formation in the boreal forest [41], our study area was located in Quebec, a cold part of the continent that generally experiences snowmelt before the growing season as well as frequent and abundant precipitation throughout the growing season [24]. Hence, the effect of water availability was not detected on xylem phenology in this area [24,35]. Furthermore, in our study, we did not find significant relationships between the cessation of xylogenesis and temperatures before or during the growing season. Thus, the termination of xylem phenology in black spruce may be related to endogenous factors [42]. It has been demonstrated that wood formation in boreal forests may benefit from the warming-induced earlier onset of xylem phenology [43], potentially lengthening the growing season and providing more time for cambial activity. Consequently, more cells are produced, and in turn, the cessation of xylogenesis can be postponed. Therefore, the earlier onset of xylogenesis associated with a warmer spring may influence indirectly, rather than directly, the termination of xylem phenology [36,42].

5. Conclusions

Boreal forests experience a short period of xylem formation, resulting in a trade-off between avoiding harsh weather in the autumn and winter and growing under favorable environmental conditions during spring and summer. Based on the longest period of xylem phenology monitoring ever conducted in the boreal forest, this study investigated the relationships between temperature and xylem phenological phases to explore how temperature influences secondary growth reactivation. Our study confirmed that May temperatures played an important role in triggering the onset of xylem cell enlargement, in turn, influencing the subsequent phenological events in spring, i.e., secondary-wall thickening and the growth of the first mature cell. Although there was no correlation between temperature and the termination of xylogenesis, our study showed that warmer May temperatures would advance the occurrence of cambial resumption, prolonging favorable thermal conditions for cell division and differentiation and resulting in increased wood production, or more carbon sequestration in black spruce.

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