Xylogenesis in black spruce on two sites in the boreal forest of Quebec: the importance of temperature for the onset and duration of cell differentiation

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INTRODUCTION

The length of the growing season is one of the main determinants of tree production in forest ecosystems.
Several studies underlined the importance of temperature in both cambial reactivation and cell production and pointed out the existence of a temperature threshold above which growth occurred.
Climate warming is expected to influence the timing of cambial reactivation in the boreal forest, and thus cell differentiation and growth.
Moreover, recent studies suggested that a higher number of developing tracheids could prolong cell differentiation and lengthen the growing season.

AIMS:

To compare the growth patterns of cambium and xylem at two sites in the boreal forest
To understand how temperature affects the onset of xylogenesis
To define the causal links between timing, duration of xylogenesis and xylem cell production.

MATERIALS AND METHODS

The study compared cambial activity and cell differentiation in two sites (BER and SIM) characterized by different mean annual temperatures (0.5 and 2.2 °C, respectively) in the boreal forest of Quebec (eastern Canada).
Xylem growth was studied from April to October, from 2006 to 2009, collecting weekly wood samples (microcoring technique) on the stem in 6 black spruces (*Picea mariana*, (Mill.) BSP) from 2 even-aged mature stands.

Anatomical analyses of xylogenesis

After inclusion in paraffin, transverse sections (6-10 μm) were cut and stained with cresyl violet acetate to differentiate cambium and developing xylem cells (**Fig. 1**).
Four phenophases, computed in days of the year (DOY), were considered, including onset of both cell enlargement and wall thickening and lignification. Duration of xylogenesis was calculated as the difference between the onset of cell enlargement and the ending of cell wall thickening and lignification.

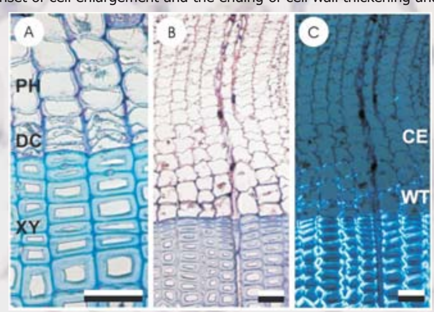


Fig. 1 Cross section of the outermost xylem (XY) showing dormant cambium (DC) and phloem (PH) collected at the beginning of April (**A**). Developing xylem collected in June, representing the maximum growth period, with cells in enlargement (CE) and in wall thickening (WT) observed under visible (**B**) and polarized (**C**) light. Scale bars = 20 μm

Onset, duration and ending of xylogenesis and xylem cell production were compared between sites and years using analysis of variance (ANOVA).

Temperature thresholds

Logistic regressions were used to calculate the temperature at which the probability of xylogenesis being active was 0.5. Temperature thresholds were calculated for minimum, mean and maximum daily air temperatures.

Causal models

Two causal models were used (Model 1 and Model 2) to assess the relationships between onset and ending of xylogenesis and cell production, pooling together trees across sites and years.

Model 1

$$V_1 \rightarrow V_2 \rightarrow V_3$$

Model 2

$$\begin{tikzcd} V_1 \arrow[r] \arrow[dr] & V_2 \arrow[d] \\ & V_3 \end{tikzcd}$$

where v were the independent measured variables given in **Table 1**, and the arrows described the interactions between v_1 and v_3 in the presence of possible interactions caused by v_2.

Table 1

	v_1	v_2	v_3
Hypothesis 1	Onset of xylogenesis	Ending of xylogenesis	Number of cells
Hypothesis 2	Onset of xylogenesis	Number of cells	Ending of xylogenesis

The following hypotheses were tested:
Hypothesis 1: onset and ending of xylogenesis (i.e. duration) affect xylem cell production
Hypothesis 2: number of xylem cells produced during growth affect the duration of xylogenesis

Simple (e.g. r_{v1v3}) and partial correlations ($r_{v1v3.v2}$) were performed between the three variables of the two models to verify each hypothesis. The assumptions and expectations reported in **Table 2** were checked in order to accept or refuse models and hypotheses.

Table 2

Assumptions for model applicability	Expectations: Both Models	Expectations: Model 1	Expectations: Model 2
r_{v1v2} signif. $\neq 0$	$r_{v1v2.v3}$ signif. $\neq 0$	$\lvert r_{v1v2} \rvert \geq \lvert r_{v1v3} \rvert$	r_{v1v3} signif. $\neq 0$*
r_{v2v3} signif. $\neq 0$*	$r_{v2v3.v1}$ signif. $\neq 0$	$\lvert r_{v2v3} \rvert \geq \lvert r_{v1v3} \rvert$	$r_{v1v3.v2}$ signif. $\neq 0$
		$r_{v1v3.v2}$ not signif.**	
		$\lvert r_{v1v2.v3} \rvert \leq \lvert r_{v1v2} \rvert$	
		$\lvert r_{v2v3.v1} \rvert \leq \lvert r_{v2v3} \rvert$	
		$r_{v1v2} \times r_{v2v3} \approx r_{v1v3}$	

* For model 2, model holds even if only one of these two simple correlations is not significant.
** The correlation is not necessarily significantly different from zero.

RESULTS

The onset of xylogenesis (**Table 3**) differed significantly between sites (ANOVA, F=13.71, p<0.01) and years (ANOVA, F=8.06, p<0.01).
The warmer site (SIM) showed an earlier onset of xylogenesis of 7.3 days on average, while 2009 (the colder year) was the year with the latest resumption of xylogenesis.

The ending of xylogenesis was similar between sites and years (**Table 3**), occuring at DOY 255 (12 September).

Overall, the duration of xylogenesis ranged 77-126 days, and was significantly different between years (ANOVA F=3.76, p<0.05) but not between sites (ANOVA F=2.58, p>0.05).

On average, trees in SIM (the warmer site) produced a higher number of cells along the tree ring.

Table 3

year	Xylogenesis: Onset (DOY) BER	Onset (DOY) SIM	Ending (DOY) BER	Ending (DOY) SIM	Duration (days) BER	Duration (days) SIM	Number of cells BER	Number of cells SIM
2006	152.0±2.6	145.7±3.1	254.7±8.5	256.3±9.3	102.7±9.3	110.7±8.0	22.3±3.3	25.9±7.9
2007	149.3±4.0	147.3±1.5	246.3±12.4	267.7±3.1	115.0±15.7	120.3±2.1	26.2±5.6	34.0±7.4
2008	159.7±3.1	149.3±6.5	255.0±8.7	255.0±10.1	95.3±11.4	105.7±16.6	18.6±5.8	28.9±17.2
2009	165.3±4.9	155.0±8.5	255.0±8.2	254.0±9.8	89.7±12.5	99.0±17.3	18.1±4.5	24.8±12.6

Temperature thresholds

Temperature thresholds for the onset of xylogenesis were similar between sites (**Table 4**) and years.

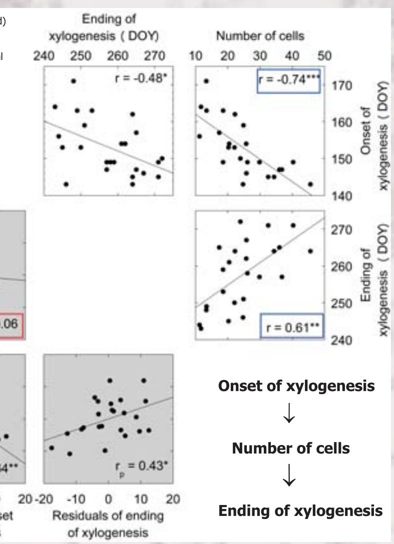
Table 4 – temperature (°C) at which the probability of xylogenesis being active is 0.5

	BER	SIM	ALL
T_{min}	3.9±1.2	4.9±1.1	4.4±1.2
T_{mean}	9.6±1.2	10.5±1.1	10.0±1.2
T_{max}	15.1±1.4	15.7±1.2	15.4±1.3

Causal models

A negative correlation between the onset of xylogenesis and the total number of xylem cells in the ring was found, while the total number of xylem cells was positively, correlated with the ending of xylogenesis (**Fig. 2**)
Thus, a higher number of cells was linked to an earlier onset and a later ending of xylogenesis.

Fig. 2 Simple (r, white background) and partial (r_p, gray background) correlations between onset and ending of xylogenesis and the total number of cells produced.
One, two and three asterisks correspond to a probability lower than 0.05, 0.01 and 0.001, respectively.



Although the expectations for both causal models were respected for Hypothesis 2, only Model 1 was accepted, according to the specific expectations of each model (**Table 2**). Therefore, the onset of xylogenesis influenced the number of cells, which in its turn, influenced the end of xylogenesis, but there was a lack of causal relationship between onset and ending of xylogenesis.

CONCLUSIONS

Temperature thresholds, similar between sites and years, were reached at different times in spring (2 weeks later in the colder site), depending on site and year.

The onset of xylogenesis differed between sites and years.

Trees having an earlier onset showed a longer duration of xylogenesis and produced a higher number of cells.

A higher number of cells delayed the ending of xylem maturation, so extending the duration of wood formation.

So the factors that determined the onset of xylogenesis (mainly temperature) indirectly affected the overall duration of wood formation.

MAIN ARTICLE
Lupi, C., Morin, H., Deslauriers, A. & Rossi, S. (2010) Xylem phenology and wood production: resolving the chicken-or-egg dilemma. **Plant, Cell & Environment**, 33, 1721-1730.

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Rossi S., Deslauriers A., Gričar J., Seo J.W., Rathgeber C.B.K., Anfodillo T., Morin H., Levanic T., Oven P. & Jalkanen R. (2008) Critical temperatures for xylogenesis in conifers of cold climates. **Global Ecology Biogeography**, 17, 696-707.
Thibeault-Martel M., Krause C., Morin H. & Rossi S. (2008) Cambial activity and intra-annual xylem formation in roots and stems of Abies balsamea and Picea mariana. **Annals of Botany**, 102, 667-674.

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