

## Influence of climate on seasonal patterns of stem increment of balsam fir in a boreal forest of Québec, Canada

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### ARTICLE INFO

#### Article history:

Received 31 October 2011

Received in revised form 22 March 2012

Accepted 17 April 2012

#### Keywords:

Growth

Balsam fir

Climate

Dendrometers

### ABSTRACT

It is important to develop a better understanding of the climatic factors controlling the growth of boreal forests. Dendrometer measurements were used to characterize inter-annual variation in seasonal patterns of stem diameter increment of balsam fir trees ( $n=3$ ) over seven growing seasons (2004–2010) in a boreal forest of Québec, Canada. For the period studied, cumulative seasonal growth ranged from 1.1 mm to 2.9 mm. Cumulative seasonal growth was a function of the timing of tree growth initiation and cessation along with the maximum growth rate observed throughout the growing season. The start and finish of diameter growth showed variations of 21 and 53 days, respectively, and duration of the growing season ranged from 38 to 107 days while maximum growth rates observed throughout a season ranged from  $36.0 \mu\text{m d}^{-1}$  to  $57.6 \mu\text{m d}^{-1}$ . Interestingly, similar cumulative annual growth can be achieved through very different seasonal growth patterns, depending on the inter-annual variation of the three factors mentioned above. Air temperature and photosynthetically active radiation appeared to regulate the initiation of tree growth with high photosynthetically active radiation and cool spring conditions delaying the start of growth. The maximum growth rate within a given season was related to snowpack depth and the timing of snowmelt. Deeper snowpack that melt earlier in spring was associated to higher maximum growth rates during the following season. Apart from exceptional climatic conditions that led to a very early growth cessation in 2006, the timing of growth cessation cannot be explained by climatic variables, suggesting that this phenological event is internally controlled by a physiological mechanism. Overall, the results indicate that the onset of growth as well as the maximum growth rate were regulated by climatic triggers. Consequently, changes in climate seasonality may have considerable effects on both seasonal pattern of growth and tree growth itself.

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### 1. Introduction

In Québec, Canada, balsam fir (*Abies balsamea* L. (Mill)) is the second most abundant tree species, representing approximately 15% of the available merchantable wood volume on public land (MRNF, 2009). To improve our knowledge of the growth–climate relationship for this economically important species, several studies have been undertaken over the last decade using different approaches at multiple scales. At the stand level, some studies have analyzed the control exerted by biophysical variables, including climate, on the growth and yield of boreal forest tree species (Ung et al., 2001). Others have examined how climate controls tree growth at the tree level using permanent sample plots or tree core measurement data (Goldblum and Rigg, 2005; Pokharel and Froese,

2009). The growth–climate relationship of balsam fir was also documented from day-to-day variations in stem diameter (Deslauriers et al., 2003b; Duchesne and Houle, 2011; Tardif et al., 2001) and by studying xylem formation and morphology at the cellular level (Deslauriers et al., 2003a; Deslauriers and Morin, 2005; Krause et al., 2010).

Modeling complex growth–climate relationships is an imposing challenge. Historically, classical dendroclimatic analysis, in which tree ring width measurements from wood samples were modeled from weather variables, was the most common technique to determine the effect of climate on tree growth (Fritts, 1976). However, the low temporal resolution (1-year measurements) of this technique limited its predictive power. For a given tree, growth rates may vary considerably from year-to-year due to climate fluctuations. However, contrasting climatic conditions can yield similar amounts of seasonal growth depending on the timing of the climatic events during the growing season. On a yearly basis, the same amount of growth can be achieved by a faster growth rate

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or by a longer growing period, which in turn results from earlier initiation of growth and/or later cessation of growth. Knowing how the climate is controlling the growth pattern within a growing season could lead to better comprehension of the growth–climate relationship.

In recent decades, innovative techniques such as dendrometers, micro-sampling and pinning have been developed to investigate the influence of climate on tree ring formation over a growing season (Deslauriers et al., 2007). Such approaches have permitted documentation of seasonal growth patterns with a relatively high level of precision. Some studies reported on the influence of climate on the pattern of tree ring formation for balsam fir trees (Deslauriers et al., 2003a,b; Deslauriers and Morin, 2005; Rossi et al., 2006, 2008; Tardif et al., 2001). Among these studies, Rossi et al. (2006) studied the timing of the maximum growth rate over six growing seasons for European and North American conifers, including balsam fir. To our knowledge, no other study reports on the inter-annual variability in the seasonal growth pattern of balsam fir tree over a prolonged period of time. The main objective of this study was to describe the inter-annual variation in the seasonal patterns of stem diameter increment of balsam fir trees growing in a boreal forest in Québec, Canada, over seven growing seasons. Secondly, we identified the most important climatic factors related to the seasonal growth pattern.

## 2. Materials and methods

### 2.1. Study site

The study site is located in Québec, Canada (47°19'41"N; 71°07'37"W; 771–864 m a.s.l.), 70 km north of Québec City. The canopy vegetation is mainly dominated by even-aged balsam fir with a small component of white spruce (*Picea glauca* (Moench) Voss) and paper birch (*Betula papyrifera* Marsh.). In 1999, a study plot (25 m × 50 m) was established in a mature stand to monitor nutrient fluxes and vegetation. Diameter at breast height (dbh) and basal area were 14.5 ± 3.7 cm (mean ± SE), and 18.6 m<sup>2</sup> ha<sup>-1</sup>, respectively, with balsam fir accounting for 88% of the basal area. The groundcover consists mainly of mosses and *Oxalis montana*, with small lichen patches. The vegetation rests on Precambrian charnockitic gneiss covered by sandy till, classified as Spodosols (Haplorthods) (Soil Survey Staff, 2010) or Orthic Humo-Ferric Podzol (Canadian Soil Survey Committee, 1992). The mean slope is 8%. Between 1999 and 2008, mean annual temperature and precipitation were 1.2 °C and 1355 mm, respectively. More details on site characteristics may be found in Duchesne and Houle (2008).

### 2.2. Dendrometric data

The microvariations in the stem diameters of three co-dominant balsam fir trees were measured at breast height (1.3 m above ground level) with automatic strain gauge dendrometers. Selected trees had similar stem diameter with well-developed crowns and no visible wounds on the trunk. The dendrometers (DEX70, Dynamax Inc., Houston, TX; accuracy over 20 °C range = 0.05 mm) are constructed of two aluminum bars attached to a flexible stainless steel band on which the strain gauge is attached (Link et al., 1998). As the stem diameter changes, differences in the relative tension experienced by the strain gauges are measured as a millivolt signal. Data are recorded every 30 min with a datalogger (CR10, Campbell Scientific, Logan, UT). Millivolt signals are converted to millimeter units after calibration. Each dendrometer was calibrated by altering the spacing of an internal micrometer and recording the millivolt signal following the procedure described in Link et al. (1998). Data were continuously acquired beginning in mid June 2003, but

we focused the subsequent analysis over seven growing seasons (May–September) from 2004 to 2010.

### 2.3. Seasonal growth pattern assessment

Among the various sigmoidal models available to describe growth patterns, the Gompertz equation is one of the most appropriate because of its flexibility and asymmetrical shape (Zeide, 1993). This equation has been used to describe tree growth patterns for entire lifespans (Aznar et al., 2007) as well as seasonal growth (Deslauriers et al., 2003a; Rossi et al., 2003, 2006). Even in absence of cell activity and stem growth, stem diameter expansion and contraction cycles are occurring due to day-to-day changes in plant water potential. Consequently, the precise identification of the moment to which instruments must be set to 0 is no simple task. For characterizing the complete seasonal growth pattern (May–September) and to avoid arbitrary choices in initial settings of instruments, a formulation of the Gompertz model that includes a fourth parameter indicative of the initial stem size at the beginning of the growing season was fitted to daily averaged raw measurement data:

$$Y = Y_0 + A \times \exp \left[ -\exp(\beta - \kappa \times t) \right]$$

where  $Y$  is the daily diameter measurements,  $Y_0$  is the lower asymptote,  $A$  is the upper asymptote,  $\beta$  is the  $x$ -axis placement parameter,  $\kappa$  is the rate of change parameter, and  $t$  is the time in days. Consequently,  $(A - Y_0)$  corresponds to the total seasonal growth while  $(Y_t - Y_{t-1})$  corresponds to the daily growth. We used the MODEL procedure with ordinary least squares method for parameter estimation (Gallant, 1987; SAS Institute, 2002). We first modeled seasonal growth pattern of individual trees ( $n = 3$ ) for each growing season ( $n = 7$ ) to assess inter-tree variability for a total of 21 models. For the subsequent analysis, we restricted our analysis to the average stem diameter variations for all trees to assess the impact of climate on the seasonal pattern of stem diameter increment. Timing of growth initiation and cessation was determined as the day of year (DOY) when modeled daily growth values go above and below 5  $\mu\text{m d}^{-1}$ , respectively.

### 2.4. Weather data

Soil temperature was measured using YSI series 400 thermistors (Cole-Parmer Canada, Montreal, Québec, Canada) installed at four locations within a distance of 30 m of the monitored trees. Weather parameters were measured in a clearing located approximately 600 m from the instrumented trees. Air temperature and relative humidity (HMP35CF, Campbell Scientific, Logan, UT) sensors were installed at a height of 3.3 m while a photosynthetically active radiation (PAR) sensor (LI190SB, Campbell Scientific, Logan, UT, light spectrum 400–700 nm) was installed at the top of a 14 m tower. Precipitation was measured by averaging the readings of two different pluviometers: a tipping bucket rain gauge (TE-525, Texas Electronics, Dallas, TX) and a precipitation gauge (35-1558, Fisher and Porter, Albany, NY). Measurements were made every 15 min and hourly averages were recorded by the data logger (CR-1000, Campbell Scientific, Inc.).

### 2.5. Influence of climate on the seasonal growth pattern

We investigated the relationships between a set of selected climatic variables and three parameters defining the seasonal growth pattern (growth initiation and cessation, and maximum growth rate) along with the cumulative seasonal growth. Weather variables were chosen based on the expected effect of weather on the regulation of seasonal tree growth pattern in a cold environment

**Table 1**  
Characterization of the average seasonal growth patterns for each year. Numbers in parentheses represent inter-tree variability ( $\pm 1$  SE).

Year	Seasonal growth (cm)	Timing of growth initiation (DOY)	Timing of growth cessation (DOY)	Growing season duration (days)	Maximum growth rate ( $\mu\text{m d}^{-1}$ )	Day of maximum growth (DOY)
2004	2.0 (0.1)	148(2.0)	224(5.3)	76(3.6)	47.6 (1.8)	173(1.2)
2005	2.0 (0.3)	137(2.8)	227(14.0)	90(15.9)	36.0 (3.5)	166(2.6)
2006	1.1 (0.1)	149(3.6)	187(7.4)	38(9.5)	49.1 (9.1)	161(2.2)
2007	2.9 (0.5)	133(3.3)	240(9.6)	107(9.8)	47.4 (7.1)	167(3.2)
2008	2.6 (0.4)	140(2.4)	227(9.7)	88(7.6)	54.3 (6.2)	167(4.3)
2009	2.3 (0.3)	146(0.7)	224(5.8)	77(6.4)	54.5 (2.2)	171(1.5)
2010	2.6 (0.4)	128(4.0)	212(17.1)	84(21.1)	57.6 (24.5)	154(2.0)

(ex: timing of snowmelt, soil thawing, air temperature threshold, etc.). The variables tested are listed in Table 3. All possible regression models with a maximum of two independent variables were tested with the RSQUARE procedure (SAS Institute, 2002) to determine the maximum amount of variance for each parameter defining the seasonal growth pattern that could be explained as a function of weather variables. The final models were selected based on Mallows's Cp-statistic (Mallows, 1973) and Akaike's information criteria (Akaike, 1973). Multicollinearity among weather variables of the selected models was tested using condition indexes and the variance inflation factor to verify that dependencies among variables did not affect the regression estimates (Belsey et al., 1980). We verified that no autoregressive structure remained in the error terms of the selected models with the AUTOREG procedure (SAS Institute, 2002).

### 3. Results

#### 3.1. Seasonal growth pattern

Observed and modeled seasonal diameters and associated growth rates are illustrated in Fig. 1. Nonlinear regressions explained between 94.5% and 99.5% of the variation in the seasonal diameter measurements. Seasonal growth ( $A - Y_0$ ) ranged from 1.1 mm in 2006 to 2.9 mm in 2007 (Table 1). The beginning of the growing season ranged from May 8 (DOY 128) in 2010 to May 29 (DOY 149) in 2006, while the end of the growing season ranged from July 6 (DOY 187) in 2006 to August 28 (DOY 240) in 2007. The length of the growing season ranged from 38 days in 2006 to 107 days in 2007, averaging 80 days. Maximum growth rate ranged from  $36.0 \mu\text{m d}^{-1}$  in 2005 to  $57.6 \mu\text{m d}^{-1}$  in 2010. Meanwhile, the timing of maximum growth ranged from June 3 (DOY 154) in 2010 to June 22 (DOY 173) in 2004. Inter-tree variability was much higher for the end of the growing season and the seasonal length as compared to other parameters defining the seasonal pattern of stem diameter increment. This was particularly true for the year 2010 which, in this case, was due to a very distinct growth pattern observed only for one of the three trees.

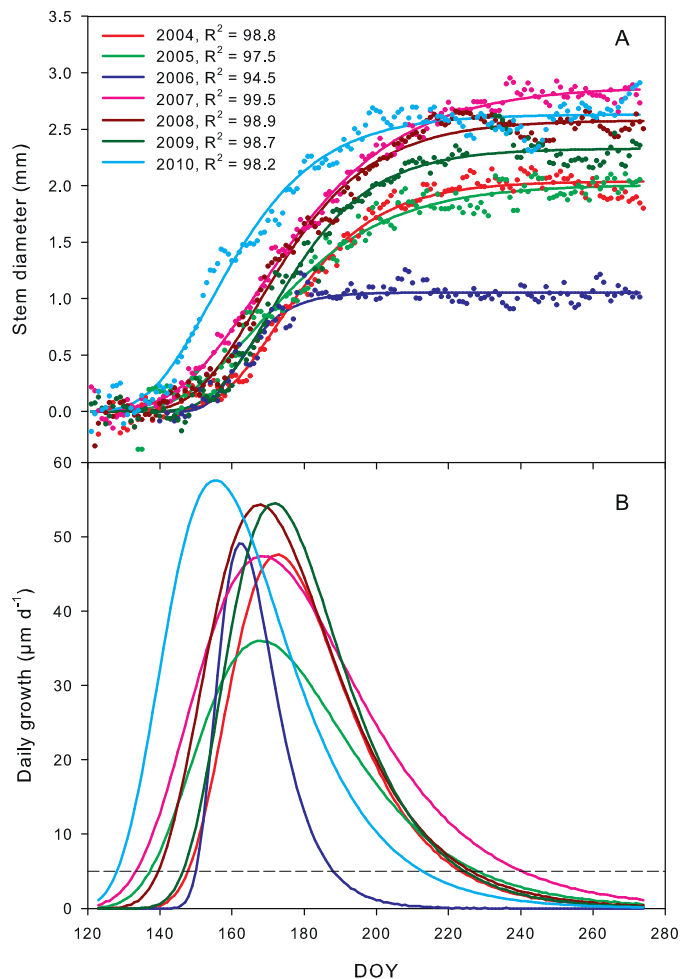
The timing of growth initiation, growth cessation, and the maximum growth rate value were not correlated ( $p \geq 0.17$ ). As expected, the variance associated with seasonal growth can be largely explained (>99.9%) by the timing of growth initiation and cessation in association with the maximum growth rate (Table 2, Fig. 2). The timing of growth initiation, maximum growth rate and moment of growth cessation explained 15.2%, 23.5% and 61.2% of the variance in seasonal growth, respectively.

#### 3.2. Impact of weather on the seasonal growth pattern

The relationships between the climatic variables and the parameters which define the seasonal growth pattern (timing of growth initiation and cessation and maximum growth rate) were investigated. These climatic variables were generally independent from each other with some exceptions. Maximum air temperature, total

degree-days, and maximum soil temperature were positively correlated ( $r \geq 0.78$ ,  $p \leq 0.038$ ). Maximum radiation was positively correlated to cumulative PAR ( $r = 0.82$ ,  $p = 0.024$ ), and cumulative precipitation was negatively correlated to the number of days without precipitations ( $r = -0.76$ ,  $p = 0.048$ ). Finally, the maximum snowpack height was positively correlated to the timing of snowmelt ( $r = 0.85$ ,  $p = 0.015$ ).

Climatic variables significantly explained a large part of the variance in the timing of growth initiation (94.8%), maximum daily growth rate (91.8%), and cumulative seasonal growth (98.1%) while 52.4% of the variance for the timing of growth cessation, marginally significant at  $p = 0.06$ , could be explained (Table 4, Fig. 3). The timing of the first DOY with average PAR  $> 500 \mu\text{mol s}^{-1} \text{m}^{-2}$  and the last DOY with air temperature below  $0^\circ\text{C}$ , respectively, explained 57.8%, and 37.0% of the variance



**Fig. 1.** Observed and modeled changes in stem diameters (A) and associated growth rates (B) of balsam fir trees over 7 growing seasons (May–September).

**Table 2**

Results of the multivariate regression analysis of cumulative seasonal growth in relation to the growing season parameters.

Variable	Coefficient	Std. error	T-statistic	Partial $R^2$	p-Value
Constant	-1.675	0.168	-9.97		0.002
Timing of growth initiation (DOY)	-0.028	0.0007	-37.9	0.152	<0.001
Timing of growth cessation (DOY)	0.027	0.0004	76.1	0.612	<0.001
Maximum growth rate ( $\mu\text{m d}^{-1}$ )	0.004	0.0001	47.2	0.235	<0.001
Total				0.999	<0.001

in the timing of growth initiation. The timing of growth cessation was partially explained by the timing of the peak in soil temperature (54.2%), but the correlation completely disappeared when data from 2006 were removed from the model. The maximum daily growth rate was best explained by the timing of snowmelt and the maximum snowpack height which explained 50.1% and 41.7% of the variance, respectively. Finally, the seasonal growth was largely explained by the first DOY with PAR  $> 500 \mu\text{mol s}^{-1} \text{m}^{-2}$  and the timing of the peak in soil temperature which explained 56.3% and 41.8% of the variance, respectively.

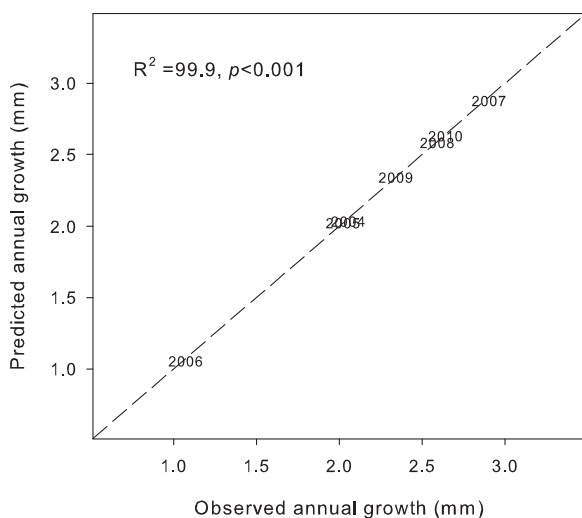
## 4. Discussion

### 4.1. Impact of weather on the seasonal growth parameters

Studies of stem diameter increment measured with dendrometers are characterized by a low number of observational years. As a result, statistical relationships with growth phases and climatic variables are often based on few observations and should be interpreted with caution. Moreover, many climatic variables can be correlated together, although the impact of co-linearity on the models arising from this study was assessed within our data set. With seven years of observation, the models are tentative and are not strictly interpreted in terms of causality.

#### 4.1.1. Growth initiation

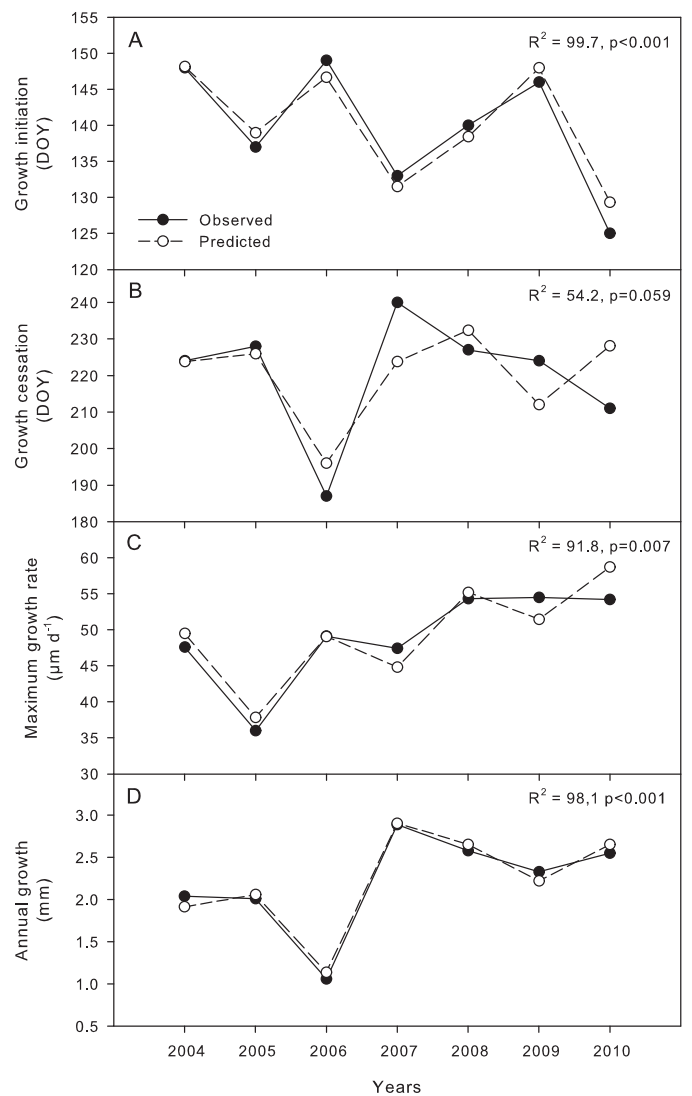
A 21-day range was observed in the initiation of growth (Table 1) from May 8 in 2010 to May 29 in 2006. Growth initiation was negatively related to the first DOY when PAR reach  $500 \mu\text{mol s}^{-1} \text{m}^{-2}$  and the last DOY with air temperature below  $0^\circ\text{C}$  (Table 4). Previous studies demonstrated that xylogenesis had a 0.5 probability of being active when air temperature reaches critical thresholds (Rossi et al., 2007, 2008), suggesting that a part of the unexplained variance is linked to factors other than temperature. Our data



**Fig. 2.** Observed and predicted seasonal growth from parameters defining the growing season (timing of growth initiation and cessation and maximum growth rate).

suggest that high PAR values during cold spring weather conditions seem to have delayed the initiation of tree growth (Table 3). For example, in 2006, PAR reached  $500 \mu\text{mol s}^{-1} \text{m}^{-2}$  on March 28 (DOY 87) while air temperature stayed below  $0^\circ\text{C}$  until May 8 (DOY 128). This resulted in a late initiation of growth (May 28). In contrast, in 2010, although the last DOY when air temperature got below  $0^\circ\text{C}$  (May 11) was similar to 2006, PAR reached  $500 \mu\text{mol s}^{-1} \text{m}^{-2}$  (April 20, DOY 110) much later than in 2006 which favored earlier growth initiation (May 8).

Although our data do not permit to conclude to a causal relationship between PAR and the beginning of tree growth, it is known that high PAR may favor winter desiccation and create large



**Fig. 3.** Observed and predicted value of (A) timing of growth initiation, (B) timing of growth cessation, (C) maximum daily growth rate, (D) annual growth. Note that when the year 2006 is removed from the regression, no significant model was obtained for growth cessation (panel B).



**Table 3**  
Selected climate parameters used to model seasonal growth patterns.

Climate parameter	Years						
	2004	2005	2006	2007	2008	2009	2010
<b>Air temperature</b>							
Last DOY with air temperature < 0 °C	125	135	128	116	122	105	131
Maximum temperature (°C)	19.3	23.2	21.8	20.9	19.3	20.4	23.7
DOY with the highest temperature	204	179	195	214	160	229	188
Total degree-days > 10 °C (°C)	358	540	474	421	417	397	537
<b>Soil temperature</b>							
First DOY with soil temperature > 1 °C	160	153	142	151	148	145	138
Maximum soil temperature (°C)	9.0	11.0	10.1	9.6	10.3	10.5	11.7
DOY with the highest soil temperature	243	245	217	243	251	232	247
<b>Photosynthetically active radiation (PAR)</b>							
First DOY with PAR > 500 $\mu\text{mol s}^{-1} \text{m}^{-2}$	88	91	87	123	106	110	110
Maximum PAR ( $\mu\text{mol s}^{-1} \text{m}^{-2}$ )	733	720	711	612	610	624	684
Cumulative PAR ( $\text{mmol s}^{-1} \text{m}^{-2}$ )	56	60	55	53	46	49	57
<b>Precipitation and snowmelt</b>							
Cumulative precipitation from May–September (mm)	604	520	436	393	533	481	444
Number of days without precipitation	72	74	81	86	64	70	83
Maximum snowpack height (cm)	77	102	139	85	149	106	80
DOY when snowmelt was complete	114	125	127	118	126	119	110

temperature fluctuation in needles. Winter desiccation occurs when plants lose water because of cuticular transpiration, but are unable to take up water that is frozen and unavailable in stems or soils (Friedland et al., 1984; Tranquillini, 1979). These losses increase in warm and windy conditions (Hadley and Smith, 1983). Needle heating due to high PAR values may also increase cuticular transpiration (Hadley and Amundson, 1992; Marchand and Chabot, 1978). Field and laboratory experiments demonstrated that winter needle mortality in natural red spruce stands is influenced by exposure to PAR and that desiccation can be initiated under controlled conditions by a strong light source in calm sub-freezing air (Hadley et al., 1991; Hadley and Amundson, 1992; Herrick and Friedland, 1991). In a chamber experiment, Hadley et al. (1991) reported that needle temperature of red spruce saplings may drop by 12 °C within 2.5 min after the light source has been turned off. It has been demonstrated that rapid temperature change in sun-exposed needles may cause freezing injury at temperature well above the threshold from injury by slow cooling (White and Weiser, 1964). Regardless of the exact mechanism, our results suggest that the occurrence of high PAR in early spring when soil water is frozen and soil moisture is relatively low may increase winter desiccation, delay stem rehydration or even cause winter injuries that may have detrimental impact on cambial activity, resulting in a later growth initiation.

**Table 4**  
Results of the multivariate regression analysis of the parameter defining the growing season ( $n = 7$ ) in relation to weather data.

Variables	Coefficient	Std. error	T-statistic	Partial R <sup>2</sup>	p-Value
<b>Growth initiation (DOY)</b>					
Constant	295.7	19.3	15.3		<0.001
First DOY with PAR > 500 $\mu\text{mol s}^{-1} \text{m}^{-2}$	-0.66	0.08	-8.2	57.8	0.001
Last DOY with air temperature < 0 °C	-0.72	0.11	-6.6	37.0	0.003
Total				94.8	0.003
<b>Growth cessation (DOY)</b>					
Constant	-35.8	105.5	-0.34		0.748
DOY with the highest soil temperature	1.06	0.44	2.43	54.2	0.059
Total				54.2	0.059
<b>Maximum daily growth (<math>\mu\text{m d}^{-1}</math>)</b>					
Constant	245.2	30.2	8.1		0.001
DOY when snowmelt was complete	-2.0	0.30	-6.6	50.1	0.003
Maximum snowpack height (m)	41.1	6.8	6.1	41.7	0.004
Total				91.8	0.007
<b>Seasonal growth (<math>\text{mm y}^{-1}</math>)</b>					
Constant	-7.6	0.869	-8.7		<0.001
First DOY with PAR > 500 $\mu\text{mol s}^{-1} \text{m}^{-2}$	0.028	0.003	8.6	56.3	<0.001
DOY with the highest soil temperature	0.029	0.003	7.4	41.8	0.002
Total				98.1	<0.001

#### 4.1.2. Growth cessation

Growth cessation ranged from July 6 in 2006 to August 28 in 2007. Among the three parameters defining the seasonal growth pattern, growth cessation explained the majority (61%) of the variance in the cumulative seasonal growth (Table 2). However, this parameter showed the higher inter-tree variability and was less well explained by the climatic variables. The correlation with the peak in soil temperature was largely influenced by the early growth cessation recorded in 2006 (Table 4). A previous study suggested that a heat stress episode, resulting from a combination of high temperature, high relative humidity, low precipitation and low wind velocities, may explain the exceptionally early growth cessation observed in 2006 at the same site (Duchesne and Houle, 2011). Such conditions resulted in an earlier peak in soil temperature for this specific year which was potentially responsible for the relationship found above. When 2006 data were removed, no significant relationship with climate was found suggesting that, with the exception of exceptional conditions such as those observed in 2006, the cessation of growth is not initiated by the climatic environment. The cessation of growth can be defined as the moment when all xylem cells have completed their differentiation and undergone apoptosis, or programmed cell death, to become functional sap transporters (Plomion et al., 2001). Therefore, the end of growth could be mostly determined by an earlier cell

differentiation phase rather than by climatic factors. For black spruce, the end of xylogenesis was dependent on the number of xylem cells produced earlier in the season (Lupi et al., 2010). Although, in cold environments, air temperature is a critical factor involved in the onset and ending of the growing period (Rossi et al., 2007, 2008), the critical temperatures associated with the termination of cambial activity exhibited a high range of variation among years and generally had a weak predicting power.

#### 4.1.3. Maximum growth rate

The timing of the maximum growth rate ranged from DOY 154 to DOY 173 (mean  $\pm$  95.0% C.I.:  $166 \pm 5.9$ , Table 1). These values were very close to those reported by Rossi et al. (2006) for balsam fir trees ( $168 \pm 5.5$ ) over the 1998–2004 period for a site located upper north of our study site. Conifers in cold environments generally synchronize maximum growth rate of tree-ring formation with day length. The maximum growth rate ranged from  $36.0 \mu\text{m d}^{-1}$  in 2005 to  $57.6 \mu\text{m d}^{-1}$  in 2010 (Table 1). It was principally related to the timing of snowmelt along with the maximum snowpack height, earlier snowmelt and deeper snowpack being associated with higher maximum growth rate. These two variables accounted for 91.8% of the variation in maximum growth rates over the study period. The timing of snowmelt has been identified as a controlling factor of the seasonal growth and tree-ring structure formation in northern latitudes (Kirdyanov et al., 2003; Vaganov et al., 1999). These authors suggested that a delayed snowmelt causes a delayed initiation of cambial activity and consequently, a reduction of the cumulative seasonal growth. Contrarily, others have suggested that delayed snowmelt may be beneficial for tree growth (Grippa et al., 2005). Later snowmelt may delay and reduce summer droughts at northern latitudes, because the water from the snowpack is released later in the season and also because later snowmelt coincides with cold spring temperatures with low evaporation. However, the high annual precipitation at our study site does not support the possibility that water could be a limiting factor. It has also been suggested that earlier snowmelt may expose the soil to freezing events that enhance fine root mortality and decrease subsequent vegetation productivity (Groffman et al., 2001).

#### 4.2. Inter-annual variability in seasonal growth pattern

Over the study period, cumulative seasonal growth exhibited an important variability ranging from 1.1 mm in 2006 to 2.9 mm in 2007 (Table 1). These two contrasting years correspond to the shortest (38 days) and longest (107 days) growing season lengths, respectively. The growing season began 16 days earlier in 2007 compared to 2006, but the large difference in the growing season length was mainly due to the fact that growth ceased 53 days earlier in 2006 than in 2007. Overall, the timing of growth cessation explained 61% of the variance in the cumulative seasonal growth over the study period (Table 2). Although spring climatic conditions are known to exert a control on the growing season length by determining the initiation of growth (Rossi et al., 2007, 2008), the ending of the growing season, which depends on the number of xylem cells produced and potentially on the associated climatic conditions, had the most important impact on cumulative seasonal growth in our study.

The results show that the same amount of cumulative seasonal growth can be achieved with very distinct seasonal growth patterns, as illustrated by the comparison of the years 2004 and 2005 (cumulative growth = 2 mm) and the years 2008 and 2010 (cumulative growth = 2.6 mm). In 2005, growth began 11 days earlier and ceased three days later compared to 2004, resulting in 14 more days of growth in 2005 (90 days) than in 2004 (76 days) (Fig. 1). However, the shorter growing season length in 2004 was offset by a higher growth rate, resulting in the same amount of

cumulative growth. For the years 2008 and 2010, similar growing season durations and maximum growth rates were observed. However, the growing season began 12 days earlier and ended 15 days earlier in 2010 compared to 2008. Such situations illustrate that the information “contained” in the ring width is limited. This may hinder the accurate prediction of the effect of climate on tree growth using a classic dendroclimatic approach, particularly in a context of global change where a larger variability in seasonality is expected. In fact, changes in seasonality have already been identified as a possible cause of the “divergence problem”, i.e. the tendency for trees present at temperature-limited northern sites to demonstrate a weaker growth response to mean temperature in recent decades, with the divergence being expressed as a loss in climate sensitivity and/or a divergence in trend (D’Arrigo et al., 2008).

#### 4.3. Impact of weather on cumulative seasonal growth

Variability in seasonal growth deduced from dendrometers was best explained by the timing associated with the earliest DOY when PAR reach  $500 \mu\text{mol s}^{-1} \text{m}^{-2}$  and the DOY with the highest soil temperature (Table 4). These two variables were also largely associated with the timing of growth initiation (DOY when PAR reach  $500 \mu\text{mol s}^{-1} \text{m}^{-2}$ ) and potentially growth cessation (DOY with the highest soil temperature), although climatic conditions in 2006 had a great influence on the relationship (see above). Over the seven year period, earlier peaks in PAR above  $500 \mu\text{mol s}^{-1} \text{m}^{-2}$  and in soil temperature were associated with lower cumulative growth. These variables appear to capture the variability associated with seasonal growth initiation and cessation which explain the major part (76%, Table 2) of the inter-annual variability in the cumulative seasonal growth.

## 5. Conclusion

Cumulative seasonal growth is determined by the timing of the initiation and cessation of tree growth as well as the maximum growth rate observed throughout the growing season. A number of climatic variables may affect these parameters and therefore determine the cumulative seasonal growth. At our site, and for the period studied, air temperature and PAR appeared to regulate tree growth initiation with a combination of high PAR and cool spring conditions delaying growth initiation. The maximum growth rate within a given season was related to snowpack depth and the timing of snowmelt. Deeper snowpack that melt earlier in spring was associated with higher maximum growth rates during the following season. Growth cessation was poorly related to climatic conditions, suggesting a physiological control. Rather, the timing of growth cessation could depend on the timing of the previous growth phases (i.e. production and differentiation of new xylem cells), which could in turn be affected by various climatic factors.

Our data also showed an important variability in the growth patterns between years. Interestingly, the same amount of cumulative growth can be achieved through very different growth patterns. In the field, elucidation of precise relationships between tree growth and climate is not a simple task because of the possible non-linear response of tree growth to climate and the strong interactive effects of climate parameters on tree growth (Pallardy and Kozłowski, 1979). In the future, control and field experiments should focus on the effect of climate on physiological processes such as leaf resistance, plant water relations, evapotranspiration and photosynthesis. Such information is a prerequisite for a better understanding of the growth–climate relationship and for accurate forecasting of the effect of climate change on tree growth.

## Acknowledgments

This research was supported by the Ministère des Ressources naturelles et de la Faune du Québec (MRNF), project number 0317 3065. We would like to thank Jean Gagné and Mario St-Germain for field assistance.

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