

UNIVERSITÉ DU QUÉBEC À CHICOUTIMI

**ESTIMATION DE LA XYLOGÉNÈSE CHEZ L'ÉPINETTE NOIRE
ENTRE 1950 ET 2010**

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RÉSUMÉ

Selon les reconstitutions des variations de température à la surface de la terre, le 20^e siècle s'est démarqué par des températures particulièrement chaudes dans le contexte des dernières mille années. De plus, la vitesse du réchauffement est plus élevée dans les écosystèmes nordiques. Les changements dans la phénologie des méristèmes primaires des feuilles et des fleurs représentent les effets les mieux documentés du changement climatique chez les plantes, avec des résultats convergents dans le monde entier vers des événements anticipés au printemps et décalés à l'automne menant donc vers une augmentation de la durée de la saison de croissance. Cependant, les tendances historiques de la phénologie, quant à la croissance des méristèmes secondaires (cambium), n'ont pas de registres à long terme. La dynamique de la formation du bois chez l'épinette noire [*Picea mariana* (Mill.) BSP] a été suivie pendant les neuf dernières années sur une échelle de temps hebdomadaire dans quatre sites situés à différentes latitudes (entre le 48^e et le 51^e parallèle) et altitudes dans la forêt boréale du Québec, au Canada. Les modèles d'évaluation de la phénologie du xylème ont été définis et appliqués pour reconstituer le début, la fin et la durée de la xylogénèse pendant la période de 1950 à 2010 en utilisant des seuils thermiques appliqués sur des séries historiques de températures maximales et minimales. Tous les sites ont affiché une tendance croissante en ce qui concerne les températures annuelles et la période mai-septembre. Les plus grands changements de température ont été observés pour la température maximale à des latitudes élevées. Les événements phénologiques du printemps ont été plus touchés que ceux qui se produisent en automne, avec un début anticipé de l'activité cambiale de cinq à huit jours par 100 ans et des retards pour la fin de la xylogénèse statistiquement significatifs calculés uniquement avec le modèle utilisant la température minimale. Les changements estimés dans la phénologie cambiale démontrent les effets marqués de la récente augmentation de la température sur la période de la croissance et de la dynamique des méristèmes secondaires des arbres.

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Premièrement, je remercie Annie Deslauriers, ma directrice de recherche, de m'avoir accueillie comme son étudiante et de m'avoir appuyée tout au long de ce travail. Je tiens également à remercier mon co-directeur Sergio Rossi pour sa présence et son soutien dans les bons comme dans les moins bons moments, en particulier avec les statistiques. À Hubert Morin et Patrick Fonti pour leurs commentaires et corrections.

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Quand je suis arrivée au Canada, la première chose qui m'a marquée, ce sont les journées particulièrement froides. Au début, cela n'a pas été facile, mais j'ai découvert que les gens étaient sympathiques et j'ai commencé à me faire des amis avec lesquels, même les jours les plus froids, j'ai passé de beaux moments chaleureux.

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STRUCTURE DU MÉMOIRE

Le mémoire comprend trois chapitres. Le premier est une introduction générale et une présentation détaillée des aspects de l'analyse cellulaire et des outils statistiques. Le deuxième chapitre est sous forme d'article scientifique rédigé en anglais où les résultats et la discussion de la recherche sont présentés. Le troisième est une conclusion générale qui comprend les contributions, le résumé des principaux résultats et les perspectives de la recherche.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1.Introduction générale

Tous les êtres vivants sont directement influencés par les fluctuations de l'environnement dans lequel ils se trouvent. La phénologie, de la racine grecque *phainomai*, qui veut dire « apparaître », étudie les relations des facteurs environnementaux et des phénomènes biologiques périodiques (Forrest *et al.*, 2010). La température est un facteur important qui influence le développement des organismes, donc sa phénologie. Actuellement, un des changements importants est l'augmentation de la température moyenne mondiale à la surface de la terre de 0.5 à 1 °C depuis la fin du XIX^e siècle (IPCC, 2002). Les projections indiquent un réchauffement d'environ 0.2 °C par décennie (IPCC, 2007). La plus grande augmentation des températures a eu lieu à des latitudes moyennes et élevées dans l'hémisphère nord (IPCC, 2007) et on prévoit que la température moyenne mondiale de la surface de la terre augmentera de 1.4 à 5.5 °C pendant la période de 1990 à 2100 (IPCC, 2001).

La température est connue pour être un des facteurs principaux qui affecte le début de la croissance radiale des arbres (Oribé *et al.*, 2001; Rossi *et al.*, 2006b; Begun *et al.*, 2007) et la différenciation cellulaire (Rossi *et al.*, 2007) et donc, la phénologie du cambium dans la tige. Selon le travail de Begun *et al.* (2007), un réchauffement localisé de la tige au printemps peut réactiver le cambium en induisant la conversion des réserves en amidon vers du saccharose afin de promouvoir la division des cellules du cambium et la différenciation du xylème secondaire. Plusieurs études réalisés dans les environnements froids ont aussi démontré qu'un certain seuil thermique dans la température moyenne de l'air, entre 8-9 °C, est nécessaire afin d'activer la croissance du cambium (Rossi *et al.*, 2008).

Au Québec, les modèles climatiques prévoient une augmentation de température de 3 °C au cours des cinquante prochaines années; les hausses les plus importantes se produisant en hiver et au printemps (Plummer *et al.*, 2006; Williamson *et al.*, 2009) lorsque les arbres commencent leur croissance. Face aux changements climatiques, les variations possibles de

productivité forestière ont acquis une importance particulière. En effet, au Canada, 60% des revenus proviennent de l'exploitation de la forêt boréale (Burton, 2003).

Le bois occupe le cinquième rang d'importance dans le commerce mondial. Il est utilisé pour fournir du carburant, des fibres et du bois de construction (Plomion *et al.*, 2001). De grandes quantités de bois sont utilisées comme carburant, pour l'extraction des fibres et pour la construction (Plomion *et al.*, 2001, Chaffey, 2002). En plus, le développement des cellules du bois représente l'un des plus important réservoir de CO₂ atmosphérique (Plomion *et al.*, 2001). Dans le but de mesurer et de prévoir les effets des changements climatiques, une compréhension de la phénologie et de la dynamique de croissance des arbres en milieu boréal est nécessaire.

1.1.1. Sites d'étude

L'étude a été réalisée sur l'épinette noire [*Picea mariana* (Mill.) B.S.P.]. Depuis 2001, quatre pessières noires pures ont été identifiées comme sites d'étude dans la région du Saguenay-Lac-Saint-Jean, dans la forêt boréale du Québec, Canada (figure 1.1). La région a une topographie légèrement vallonnée avec des collines atteignant entre 500 et 700 m d'altitude. Le climat est continental avec des étés courts et frais et des hivers longs et froids (tableau 1.1, Rossi *et al.*, 2010). Ces peuplements d'épinettes noires sont équiens et matures et se trouvent à différentes altitudes et latitudes. Les quatre sites ont été choisis afin d'obtenir un gradient dans la dynamique de la croissance des arbres (tableau 1.2). Les lieux sélectionnés n'ont pas subi, autant que possible, l'impact humain afin de s'assurer que les arbres se sont développés sous l'influence des perturbations naturelles seulement.

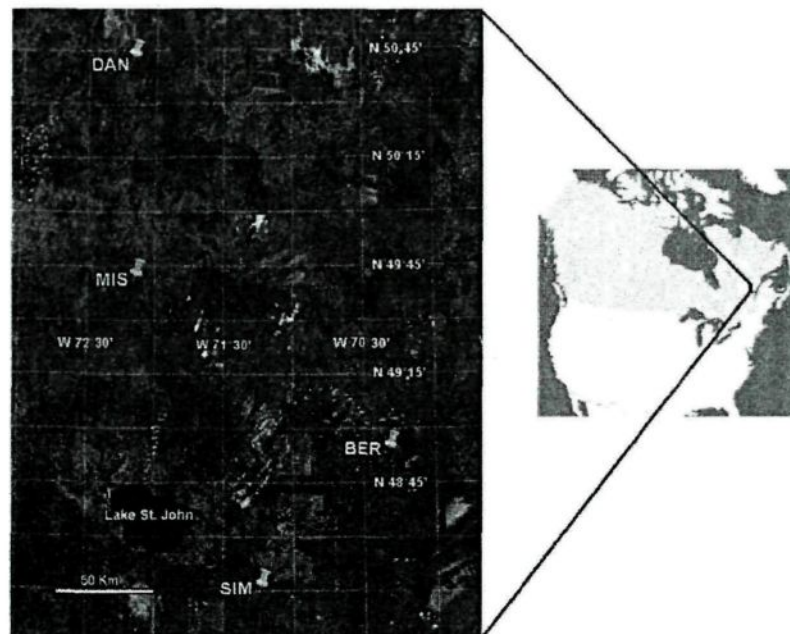


Figure 1.1. Localisation géographique des sites d'étude

Tableau 1.1. Caractéristiques climatiques de la période 2002-2010

ID	TEMPÉRATURE MOYENNE		TEMPÉRATURE ABSOLUE ANNUELLE	
	ANNUELLE (°C)	MAI-SEPTEMBRE (°C)	MAXIMALE (°C)	MINIMALE (°C)
BER	0.3	11.4	33.1	-39.8
SIM	2.0	13.3	35.7	-39.7
MIS	1.0	12.7	35.1	-42.4
DAN	-0.9	11.0	34.2	-47.1

Tableau 1.2. Localisation des quatre sites d'étude

ID	SITE	LATITUDE	LONGITUDE	ALTITUDE (mASL)
SIM	Simoncouche	48°13' 46.4"N	71°15' 08.5"W	338
BER	Bernatchez	48°51' 57.3"N	70°20' 29.8"W	611
MIS	Mistassibi	49°43' 54.6"N	71°56' 52.6"W	342
DAN	Camp Daniel	50°41' 45.7"N	72°11' 00.3"W	487

1.1.2. Structure de la méthodologie

Le présent travail a été effectué en trois étapes (figure 1.2). La première étape est celle de l'analyse de la température. Celle-ci se travaille avec deux bases de données indépendantes pour construire une seule base de données continue et journalière de température de 1950 à 2010. Pour la deuxième étape, on travaille avec une base de données cellulaire hebdomadaire de la période de 2002 à 2010 obtenue pendant la saison de croissance. L'objectif de l'analyse de la base de données cellulaire est de comprendre les mécanismes de la formation du bois et de déterminer le seuil de température. Durant la saison de la formation du bois, le suivi de la croissance nous permet de connaître le début, la fin et la durée de la xylogénèse (la phénologie). Pour ce qui est de la troisième étape, on utilise la base de données de température continue et le seuil de température pour faire l'estimation de la phénologie de la période de 1950 à 2010.

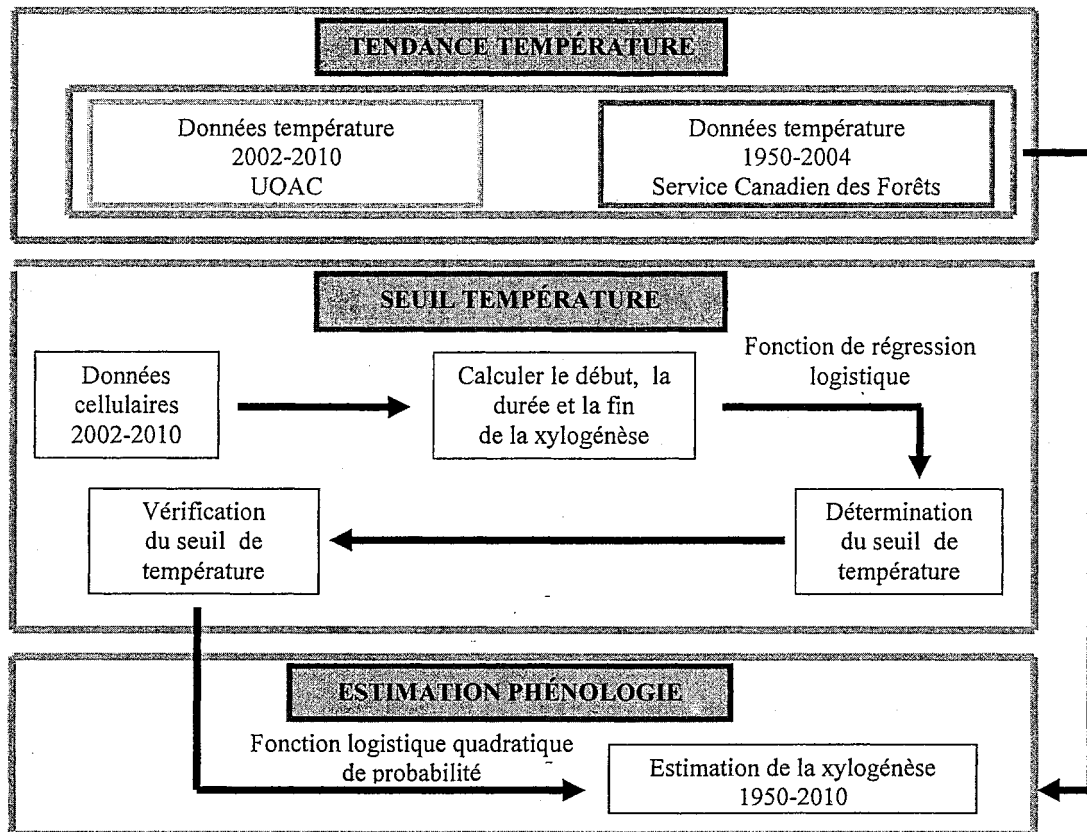


Figure 1.2. Schéma de la structure de la recherche. La première étape est identifiée en bleue, la deuxième en vert et la troisième en orange.

1.1.2.1. Données météorologiques

Dans cette étude, deux bases de données de température journalière ont été utilisées et se composent (1) d'une base de données de la station météo standard située dans chaque site d'étude sur la période de 2002 à 2010 et (2) d'une base de données d'estimation de la température de 1950 à 2004, pour chaque site, obtenues auprès du Service canadien des forêts (McKenney *et al.*, 2007). Pour la première base de données, l'ensemble des données de température mesurée est prise dans chaque site d'échantillonnage de 2002 à 2010, la température de l'air a été contrôlée toutes les 15 minutes et, par la suite, la moyenne horaire est calculée. Les températures minimales et maximales ont été enregistrées chaque heure dans un enregistreur de données CR10X (Campbell Scientific, Canada).

La deuxième base de données est composée de températures quotidiennes estimées de 1950 à 2004 modélisée par le Service canadien des forêts à travers le modèle ANUSPLIN (Hutchinson, 1995; Price *et al.*, 2000; McKenney *et al.*, 2006), de l'analyse du paysage et du Laboratoire d'Applications Service canadien des forêts, en Ontario. ANUSPLIN est un progiciel d'ajustement de surface non paramétrique multivarié permettant d'élaborer des modèles du climat à une échelle spatiale continue. Pour cette étude, l'estimation ponctuelle, correspondant à l'emplacement de chaque site d'étude, a été utilisée pour générer les températures minimale et maximale journalières.

Pour relier les deux bases de données et obtenir une série de température continue et journalière de 1950 à 2010, la vérification de la consistance des séries chronologiques de températures estimées et mesurées a été effectuée par des régressions linéaires entre les trois ans de données de température qui se chevauchent soit de 2002 à 2004.

Deux types de température ont été considérés dans ce travail afin d'obtenir une approche à l'estimation de la phénologie de *Picea mariana*, les températures minimale et maximale. Trois raisons ont été considérées pour fonctionner uniquement avec ces deux températures. Le premier, calculer la moyenne entre les températures maximale et minimale a été jugé inutile, compte tenu du fait qu'il ne fournit pas d'information supplémentaire, parce que la température moyenne provient d'un calcul arithmétique et n'est pas directement lié avec les processus biologiques qui sont considérés (Körner, 1998). Deuxièmement, la base de données de températures modélisées qui sera utilisé à l'avenir pour l'estimation de la phénologie de 1950-2001 est seulement disponible dans ces deux températures. Troisièmement, les températures extrêmes sont autant de facteurs critiques à l'égard d'une meilleure compréhension du passé et du potentiel de changement global futur (Bonsal *et al.* 2001).

1.1.2.2. Phénologie de 2002 à 2010

Préparation de micro-carottes et observations microscopiques

La phénologie du cambium a été étudiée à l'aide d'analyses intra-annuelles effectuées sur des micro-carottes de bois. L'obtention des échantillons (micro-carottes) a été réalisée sur les épinettes noires dominantes ou co-dominantes de 120 à 140 ans, en suivant une trajectoire en spirale sur la tige de 30 cm en dessous et de 30 cm au-dessus à hauteur de poitrine (1.3 m) à l'aide d'aiguilles chirurgicales pour le prélèvement osseux dans la période de 2002 à 2006 et à l'aide du Trephor dans la période de 2007 à 2010. Le Trephor permet la récolte de plusieurs micro-carottes de bois sur un même arbre à différents moments durant la saison de croissance, avec un dommage minimal sur l'arbre échantillonné (Rossi *et al.*, 2006a). Cinq arbres ont été échantillonnés de 2002 à 2005 et dix arbres de 2006 à 2010. La taille de l'échantillon a été augmentée pendant la période 2006-2010 pour améliorer la précision et la représentativité des résultats. La micro-carotte de bois est extraite à toutes les semaines à partir du début mai jusqu'en octobre. L'échantillonnage a été effectué hebdomadairement, parce que dans une période plus grande, il est possible de perdre la résolution. D'un autre côté, un échantillonnage dans une période plus courte implique un investissement majeur de temps et d'argent. Une interpolation a été nécessaire pour estimer les valeurs quotidiennes et pour passer d'une résolution hebdomadaire à une résolution journalière. De 21 à 26 micro-carottes ont été collectées annuellement sur chaque arbre, selon le site et par an. La récolte a été effectuée pour les années de 2002 à 2010. Dans ce mémoire, j'ai participé à la récolte et à l'analyse des micro-carottes des années 2009 et 2010. Les données des années 2002 à 2005 relèvent du travail de Dufour et Morin (2007) et les données de 2006 à 2009, de Lupi *et al.* (2010). La surveillance du développement de la xylogénèse se fait par le comptage du nombre de cellules cambiales, en phase d'élargissement, en phase de lignification et celles qui ont complétées leur maturation et, avec toutes ces informations, une base de données cellulaires est développée (figure 1.3, Abe *et al.*, 1997; Antonova et Stasova, 1997; Thibeault-Martel *et al.*, 2008). La base de données cellulaire est utilisée pour connaître le début, la fin et la durée de la xylogénèse de la période de 2002 à 2010. Le début de la xylogénèse a été défini comme le jour de l'année

(jour julien) lorsque le nombre moyen de cellules en phase d'élargissement est égal ou supérieur à 1. La fin de la xylogénèse a été définie comme le jour lorsque le nombre de cellules en phase de lignification est inférieur ou égal à 1.

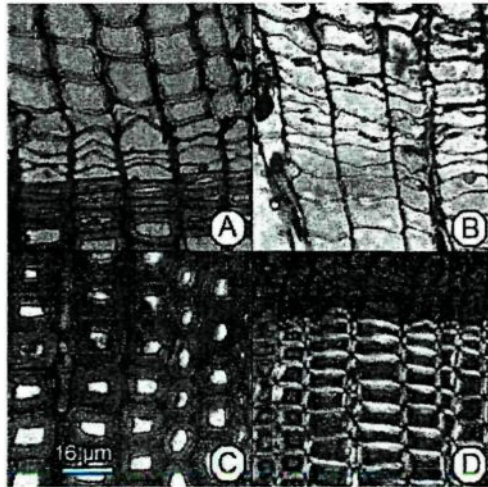


Figure 1.3. A) Cellules cambiales, B) Cellules en phase d'élargissement, C) Cellules en phase de lignification et D) Cellules matures

1.1.2.3. Aperçu des outils statistiques utilisés

Estimation du seuil de température

Avec une base de données continue de l'observation des stades de développement cellulaire et les températures de l'air de 2002 à 2010, on peut élaborer un modèle de reconstruction de la phénologie de la xylogénèse pour la période de 1950 à 2010. Ce modèle a été ensuite validé à l'aide des données observées dans quatre sites d'échantillonnage.

Premièrement, le seuil de température représente la température à laquelle il y a une probabilité de 50% d'avoir activité cambiale. Le seuil de température a été calculé en utilisant la fonction de probabilité logistique (figure 1.4, Legendre et Legendre, 1998; Rossi *et al.*, 2007; Deslauriers *et al.*, 2008). Ces seuils ont été calculés pour chaque année, site et arbre où la surveillance de la croissance cellulaire a été réalisée (2002-2010).

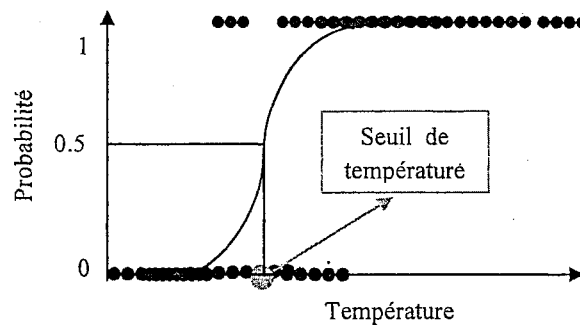


Figure1.4. Graphique explicatif de la fonction de régression logistique et du seuil de température

Estimation phénologie 1950-2010

Dans une deuxième étape, la fonction logistique quadratique de probabilité (Coudun et Gégout, 2006, Rossi *et al.*, 2011), basée sur la limite thermique de croissance calculée ci-dessus, a été utilisée pour estimer le début, la fin et la durée de la xylogénèse à partir des températures maximale et minimale journalières pour la période de 1950 à 2010 (figure 1.5).

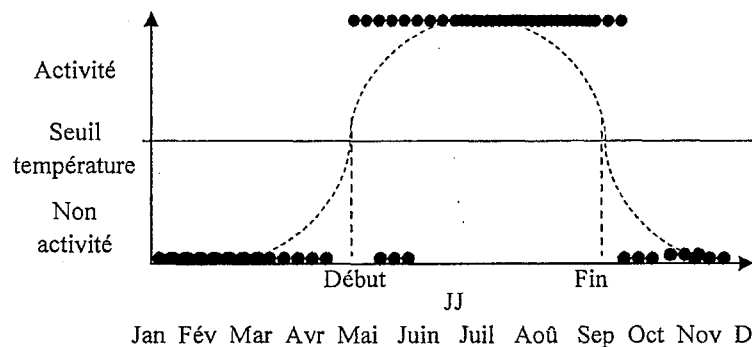


Figure1.5. Graphique représentatif de la fonction logistique quadratique de probabilité
Estimation de la xylogénèse de la période de 1950 à 2010 (line pointillée)

1.1.3. Objectifs et hypothèse

Les objectifs du mémoire sont : (1) Modéliser le début, la fin et la durée de la xylogénèse des soixante dernières années et (2) à partir de la modélisation, vérifier si le début et la durée de la saison de croissance ont été modifiés avec le temps. Ces objectifs seront abordés dans l'article scientifique contenu dans ce mémoire de maîtrise.

Notre hypothèse est : Une augmentation de température a été observée au cours des cent dernières années (IPCC, 2001). Comme le début de la saison de croissance dépend de la température (Rossi *et al.*, 2007; Deslauriers *et al.*, 2008), le début de la saison de croissance pourrait être avancé et la durée augmentée (Rossi *et al.*, 2011).

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CHAPITRE II

DURATION OF XYLOGENESIS IN BLACK SPRUCE LENGTHENED BETWEEN 1950 AND 2010

Jacqueline Boulouf Lugo, Annie Deslauriers, Sergio Rossi

Soumis à la revue scientifique.

2.1. DURATION OF XYLOGENESIS IN BLACK SPRUCE LENGTHENED BETWEEN 1950 AND 2010

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Running title: lengthening of xylogenesis

2.1.1.1. Summary

- Reconstructions have identified the 20th 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. Did the phenology of secondary meristem have changed during the last century, and at which extent?
- Timings of wood formation in *Picea mariana* (Mill.) B.S.P. were monitored for nine years on a weekly time-scale in 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.
- 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⁻¹ 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⁻¹, respectively.

- 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 trees.

Keywords: boreal forest, cell differentiation, global warming, *Picea mariana*, temperature, xylogenesis.

2.2. Introduction

Hemispheric-scale reconstructions of surface temperature fluctuations over the last millennium have identified the 20th century as uniquely warm in the context of the last 1000 years (cf. Hughes, 2002). Although an increase in the global temperature of between 1.4 and 5.5 °C is expected during the period 1990-2100, the greater increases are predicted to occur at the higher latitudes of the northern hemisphere (IPCC, 2001). For the boreal forest of North-Eastern Canada, climatic models predict increases in temperature up to 3 °C over the next 50 years, with the largest increases occurring in winter and spring, when plant growth resumes. In cold ecosystems, the season allowed for growth is strictly defined by the harsh winter temperatures (Rossi *et al.*, 2008b, 2011b). Thus, such modifications could severely affect the growth timings and dynamics of the boreal species, with consequent changes in productivity of biotopes that have obvious ecological importance and economic potential.

Recent interest in the forests of high altitude and latitude is linked to various causes such as the short growing season, high sensitivity of the species to climate changes and the possibility that plants of these environments are good indicator of changes in progress (Pisarcic *et al.*, 2003). Because of these current changes in temperature, possible variations in phenology – the study of the timings of recurring seasonal biological events – have acquired particular importance worldwide. According to Forrest & Miller-Rushing (2010), interest has been focused on documenting the recurrent appearance of first flower blossoms or bud bursts in spring, the dates of animal migration, or timings of the first frost-damaged

leaves in autumn. The longest monitoring periods in plants are concentrated in the botanical gardens of temperate Europe and concern the effects of such changes on the growth dynamics of the primary meristems, those producing buds, leaves and flowers. The phenology of the secondary meristem, which is represented by the cambium of trees, has no historical documentation because it is not a perceptible phenomenon like leaf development or flower maturation. Cambial activity occurs beneath the bark and, in high-latitude forests, produces a number of xylem cells that increases the stem diameter annually by one tree ring, which integrates the effects of climatic events occurring during the season when cambium was active (Frankenstein *et al.*, 2005). Thus, tree rings have been used as a tool to explore the long-term growth reactions to historical climate variations (Huang *et al.*, 2010), but, to our knowledge, retrospective analyses on the phenological phases of cambium are still lacking due to the very recent identification and application of the standard procedures of analysis (Rossi *et al.*, 2006a, 2006b; Marion & Gričar, 2007; Gričar *et al.*, 2009).

Analyses on the variations in the concentrations of CO₂ in the atmosphere showed that the biospheric activity increased remarkably as a result of warming surface air (Myneni *et al.*, 1997). This implies that even small changes in global temperature may be reflected by disproportionate responses at regional level, and accompanied by positive feedbacks which can markedly influence all biological processes, and in particular those concerning growth. Although several endogenous variables such as species, age, and vitality can influence the dynamics of xylem formation (Marion *et al.*, 2007; Rossi *et al.*, 2008a; Rathgeber *et al.*, 2011), temperature remains the main driving factor in cold environments. A local heating in spring can reactivate cambium, inducing the conversion of sucrose into starch reserves for

the activation of cell division and production of secondary xylem (Begun *et al.*, 2007; Gričar *et al.*, 2007). Deslauriers *et al.* (2008) observed that the higher temperatures occurring in spring 2003 led to earlier onsets of division and differentiation of xylem cells. The onset of xylogenesis influences the number of cells produced by cambium which, in turn, influences the ending of cell differentiation (Lupi *et al.*, 2010). Several studies in cold environments demonstrated that a temperature between 8-9 °C is necessary to enable cambium to divide (Rossi *et al.*, 2008b). Rossi *et al.* (2011b) simulated a warming scenario to predict changes in onset, ending and duration of xylogenesis. The model predicted longer duration of xylem growth at higher temperatures, with increases of 8-11 days/°C because of an earlier onset and later ending of growth. Twenty-five percent longer durations of xylogenesis were predicted with an increase of 3 °C in the mean annual temperature (Rossi *et al.*, 2011b).

Although the model developed by Rossi *et al.* (2011b) simulated xylem phenology under a future climate warming, no information was supplied about changes in the timings of cambial growth in the past. The greater increases in temperature were observed during the last 100 years, with the mean surface temperature rising by 0.7 °C at global scale and by 0.5-1.5 °C across North America since the late nineteenth century (Zhang *et al.*, 2000; IPCC, 2007). The rate of warming over the last 50 years (0.13 °C decade⁻¹) is almost double that over the last 100 years (IPCC, 2007), and for the northern regions of North America, McKenney *et al.* (2006) estimated greater increases attaining 0.26 °C decade⁻¹ in the second half of the century. The question is if and to what extent cambial phenology changed during this period. This paper aimed to reconstruct timings of cambium phenology

over the last 60 years in Quebec, Canada. This was done by (i) collecting and analyzing a dataset of cambium phenology and wood formation in black spruce [*Picea mariana* (Mill.) B.S.P.] based on a weekly monitoring during 9 years in four permanent sites at different latitudes and altitudes in Quebec, Canada, (ii) defining and validating a phenological model of xylem based on the air temperature measured in the sites, and (iii) applying the phenological model on the chronologies of air temperature generated for the period 1950-2004 by the ANUSPLIN model (McKenney *et al.*, 2006).

2.3. Materials and methods

Study area and xylem sampling

The study was conducted on black spruce in the Saguenay-Lac-Saint-Jean area, in the boreal forest of Quebec, Canada. The region has a gently rolling topography with hills reaching 500-700 m a.s.l. on thick and undifferentiated glacial till deposits. Four sites [Simoncouche (abbreviated as SIM), Bernatchez (BER), Mistassibi (MIS) and Camp Daniel (DAN)] were identified in mature even-aged black spruce stands at different altitudes and latitudes to obtain as wide as possible a range in the dynamics of tree growth and to select stands where the absence of evidence of human impact assured that trees had developed under the influence of natural disturbances only (figure 2.1; Table 2.1). In each site, the dominant or codominant 120-140-year-old trees with upright stems and similar growth rates were chosen (Dufour et Morin, 2007).

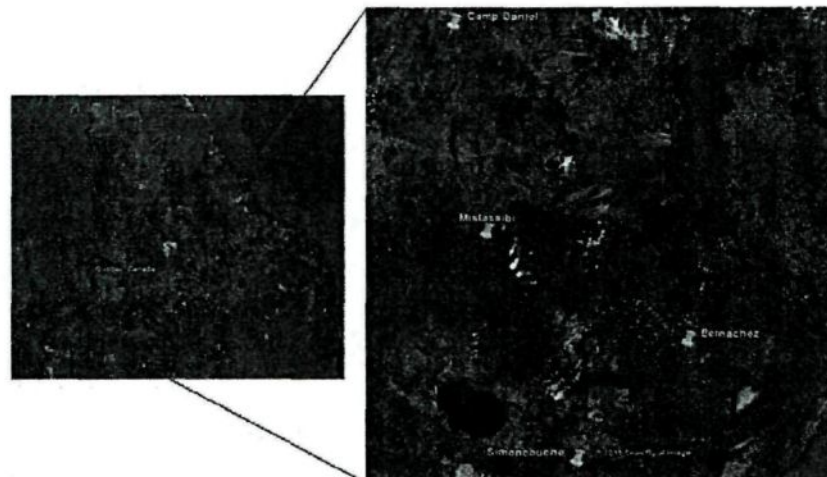


Figure 2.1. Location of the four study sites in the forest of Quebec, Canada

Table 2.1. Location and climatic characteristics measured during the period 2002-2010 of the four study sites listed at increasing latitudes

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

In each site, tree-ring formation was studied from April to October during 2002-2010 in 5 (2002-2005) and 10 (2006-2010) trees. The sample size was increased during 2006-2010 to improve accuracy and representativeness of the results. Wood microcores were collected weekly following a spiral trajectory on the stem from 30 cm below to 30 cm above breast height (1.3 m) using surgical bone sampling needles in 2002-2006 and Trephor in 2007-2010 (Dufour et Morin, 2007; Rossi *et al.*, 2006a). From 21 to 26 microcores were collected annually from each tree, depending on the site and year. The very small wounds inflicted by the thin piercing tubes of the tools and the consequently narrow areas of traumatized tissues around the sampling points [within a circumference of about 1 cm around the hole (Forster *et al.*, 2000)] allowed repeated samplings by microcore extraction. Samples usually contained the previous 4 or 5 tree rings and the developing annual layer with the cambial zone and adjacent phloem. Samplings were performed on the same tree for not more than 4-5 years and wood samples were always taken at least 5 cm apart to avoid getting resin ducts on adjacent cores. A disturbance reaction of the xylem to the wound spreading to adjacent samples only occurred occasionally.

The microcores were placed in Eppendorf microtubes with an ethanol solution (10% in water) and stored at 5 °C to avoid tissue deterioration. Microcores were oriented by marking the transverse side with a pencil under a stereo-microscope at magnifications of 10-20×, dehydrated with successive immersions in ethanol and D-limonene and embedded in paraffin (Rossi *et al.*, 2006a). Transverse sections of 6-10 µm thickness were cut from the samples with a rotary microtome. The sections were stained with cresyl violet acetate (0.16% in water) and examined within 10-25 minutes under visible and polarized light at magnifications of 400–500× to differentiate the developing and mature xylem cells.

Microscopic observations

In each sample, the radial number of cells in the cambial zone, radial enlargement phase, cell wall thickening phase, and mature cells were counted along three radial rows. Rows with cells with large tangential sizes were selected, to ensure that only cells cut at their middle longitudinal part were considered. In cross section, cambial cells were characterized by thin cell walls and small radial diameters (Antonova & Stasova, 1997; Rossi *et al.*, 2006b). The dormant cambium was composed of 3-5 closely-spaced cells. At the onset of cambial activity, the cambial zone began to widen rapidly (within a week) as the number of cells increased, revealing that cell division had started. During cell enlargement, the tracheids were composed of a protoplast still enclosed in the thin primary wall but with radial diameter at least twice that of a cambial cell. Deformed rows of tracheids were frequently observed in this phase, due to the enlargement process occurring despite strong compression between xylem tissues and bark. Observations under polarized light discriminated between enlarging and cell wall thickening tracheids (Thibeault-Martel *et al.*, 2008). Because of the arrangement of cellulose microfibrils, the developing secondary walls shone when observed under polarized light. Instead, no glistening was observed in enlargement zones where the cells were still composed of just primary wall (Abe *et al.*, 1997). The progress of cell wall lignification was detected with cresyl violet acetate reacting with the lignin (Rossi *et al.*, 2006b). Lignification was shown by a colour change from violet to blue. The color change over the whole cell wall revealed the end of lignification and the tracheid reaching maturity (Gričar *et al.*, 2005).

The cell number in the 3 rows was averaged for each sample and used to assess onset and ending of xylogenesis. In spring, when at least one horizontal row of cells was observed in the radial enlargement phase, xylem formation was considered to have begun. In late summer, when no further cell was observed in wall thickening and lignification phase, xylem formation was considered complete. The duration of xylogenesis was assessed as the number of days occurring between onset and ending of xylogenesis and was calculated as the average among trees for each studied site and year.

Datasets of air temperature

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

performed between the measured and estimated temperatures for the overlapping years (2002-2004).

Definition and validation of the phenological model

Logistic regressions [LOGISTIC procedure in SAS 9.2 (SAS Institute Inc., Cary, NC)] were used to calculate the probability of xylem growth being active at a given measured temperature where binary responses were coded as non-active (value zero) or active (value 1). The logistic regression took the general form:

$$\text{Logit}(\pi_t) = \ln\left(\frac{\pi_t}{1-\pi_t}\right) = \beta_0 + \beta_1 t_d$$

where π_t was the probability of xylem growth being active for a given temperature t , t_d was the temperature measured on a given day d by the weather stations, and β_0 and β_1 were intercept and slope of the logit regression respectively (Rossi *et al.*, 2011b). Temperature thresholds (t) were calculated when the probability of xylem growth being active was 0.5, i.e. when $\text{Logit}(\pi_t)=0$ and then when $t=-\beta_0/\beta_1$. Therefore, for a temperature above t , xylem growth was more likely to be active than non-active. Fitting verification included χ^2 of the likelihood ratio, Wald's χ^2 for regression parameter and goodness of fit, Hosmer-Lemeshow \hat{C} for eventual lack of fit (Quinn & Keough, 2002). For each site and year, the model was fitted with minimum and maximum temperature series and results from each site were compared by analysis of variance (ANOVA) and Tukey's test. None of the 72 (4 sites \times 9 years \times 2 temperatures) estimated functions was excluded because of lack of fit. Model validation was performed by comparing the observations

(active and non-active xylem growth) with the predicted values calculated using the estimated temperatures (Legendre & Legendre, 1998).

Application of the phenological model

A quadratic logistic regression was applied on the time series of estimated temperatures to calculate the probability of a day experiencing a temperature higher than the average threshold previously estimated by the phenological model. Model application required a quadratic function because of the typical bell-shaped annual pattern of the temperatures (Rossi *et al.*, 2011b). The binary responses were coded as 0-1 if temperatures were lower or higher than the threshold, respectively, and the quadratic fitted logistic regression took the form:

$$\text{Logit}(\pi_d) = \ln\left(\frac{\pi_d}{1-\pi_d}\right) = \beta_0 + \beta_1 d_t + \beta_2 d_t^2$$

where π_d was the probability of a day d experiencing minimum or maximum temperatures higher than the threshold t , d_t was the day of the year with a measured temperature t , and β_0 , β_1 and β_2 were the function coefficients. $\text{Logit}(\pi_d)=0$ corresponded to the days of the year (d) when the probability of temperature being higher than the threshold t was 0.5 and included two distinct solutions:

$$d_{1,2} = \frac{-\beta_1 \pm \sqrt{\beta_1^2 - 4\beta_0\beta_2}}{2\beta_2}$$

Therefore, for the days of the year comprised between d_1 and d_2 , the temperature was more likely to be higher than the threshold t , and xylem growth to be active. The phenological model was iteratively applied to the temperature series generated by the climatic model for the four sites to estimate changes in the timings of xylem growth. The resulting time series were tested for the presence of autocorrelation until the fourth order using AUTOREG procedure in SAS (McKenney *et al.*, 2006). Since no autocorrelation was observed for the onset of xylogenesis and the errors were serially correlated only occasionally at the second and third order for ending and duration of xylogenesis, the long-term trends were analyzed by Analysis of Covariance (ANCOVA).

2.4. Results

Observed and modeled temperatures

The region has a typical boreal climate with cold winters and cool summers (Table 2.1). The mean annual temperature in the four study sites varied between -0.9 and 2.0 °C while May-September temperature was 11.0-13.3 °C. The sites are characterized by long winters with temperatures close to or below zero, with the coldest generally being measured in January and reaching -47.1°C in DAN in 2009. The summers are short with absolute temperatures exceeding 30 °C in all sites (Table 2.1). The warmest maximum temperatures were observed in all sites in 2002. The temperature patterns were synchronous across the four study sites, with the coldest ones being DAN and BER, those located at the highest latitude and altitude, respectively. SIM was the warmest site both for annual and May-September temperatures (Fig. 2.2). The hottest year was 2010, which globally showed the highest annual temperatures, although high May-September maximum temperatures were also observed during 2005. The lowest maximum and minimum temperatures were detected in 2004.

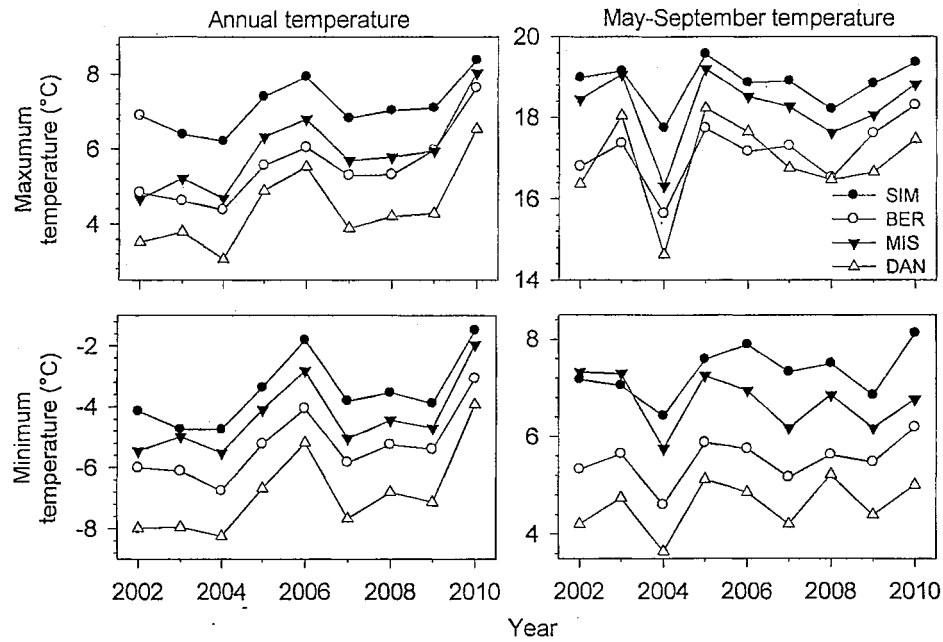


Figure 2.2. Variation of the maximum and minimum temperature expressed as annual means and as the May-September period in the four sampling site (graphics with different scale).

The regressions indicated satisfying correlations between measured and modeled temperatures with R^2 varying between 0.56 and 0.94 (Table 2.2). The stronger relationships were found for the annual maximum temperature, which on average showed an R^2 of 0.93. SIM exhibited the lowest R^2 while DAN and MIS were the sites with the higher R^2 for both the annual and May-September temperature. Overall, statistics confirmed that modeled data could suitably represent the temperatures occurring in the four study sites during 1950-2001.

Table 2.2. 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 ²	Intercept	Slope	R ²
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

The positive slopes of the regressions performed on the temperature series for the period 1950-2010 indicated an increasing trend of both annual and May-September temperatures, although all models showed $p > 0.05$ (Fig. 2.3). The highest slopes were observed for maximum temperatures of May-September with increases of 0.04-0.28 °C decade⁻¹. Overall, lower slopes were estimated for annual temperature than for May-September temperature except for the minimum temperature in DAN and MIS (Fig. 2.2). Although it was not statistically significant, a clear pattern of change of the slopes with latitude was noticeable, where the greater increases in maximum temperature

were observed at the higher latitudes, although this pattern was less obvious for minimum temperature.

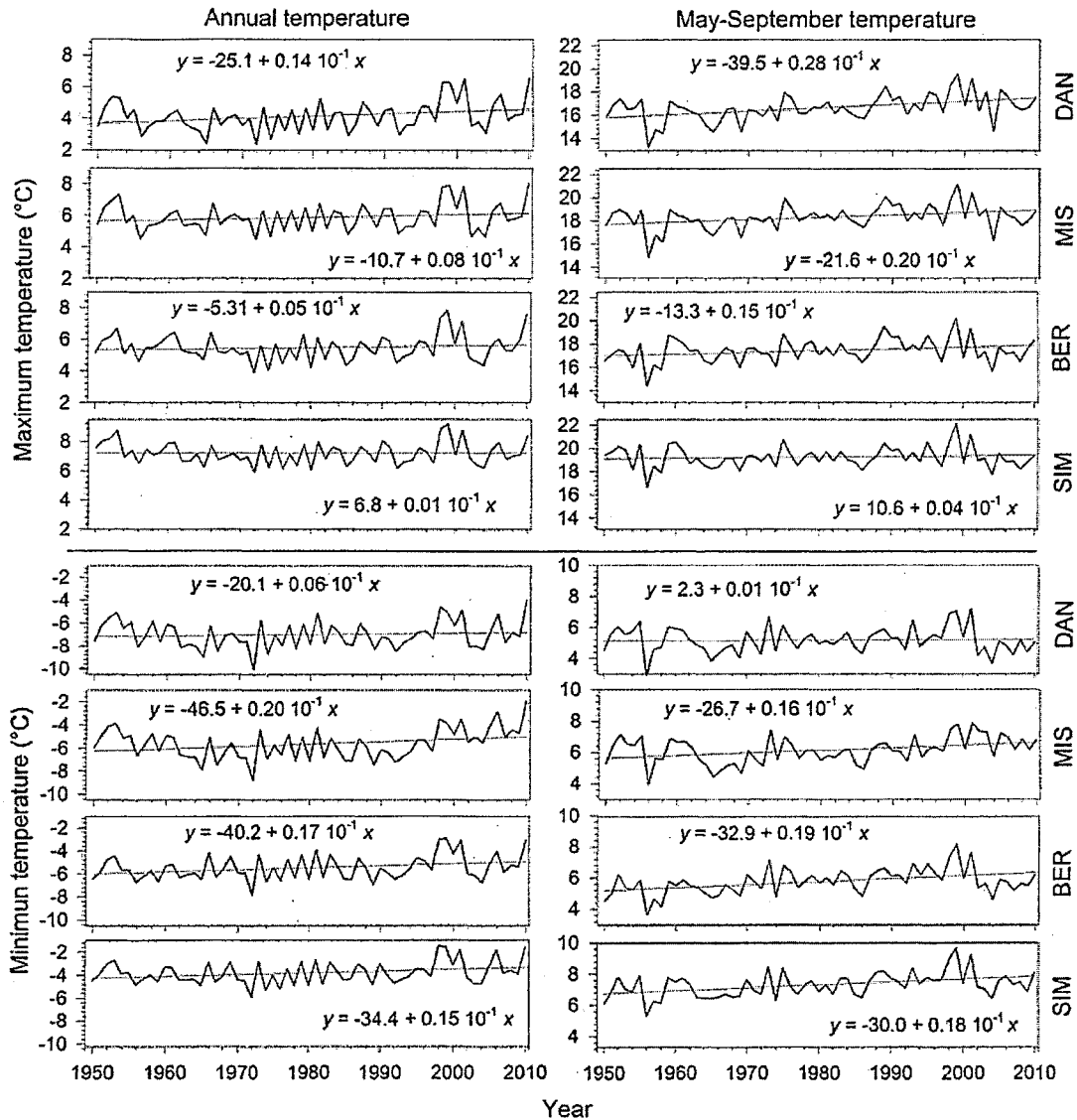


Figure 2.3. Mean of temperatures during 1950-2010 in the four sampling sites, incorporating the estimated temperatures (1950-2001) and in situ temperatures (2002-2010) for the four sampling sites (graphics with different scale). Lines correspond to linear regression analyses.

The deviation from the 60-years average was calculated for the temperature series (supporting information, Fig. 2.4). The 1960s were characterized by below-average values of both minimum and maximum temperatures of May-September. However, a similar pattern was not detected for the annual temperature. From 1970 to 1998, values alternately below and above the average were observed. After those years, both annual and May-September temperatures were clearly above the historical average, with the greater deviations for the maximum temperature of May-September.

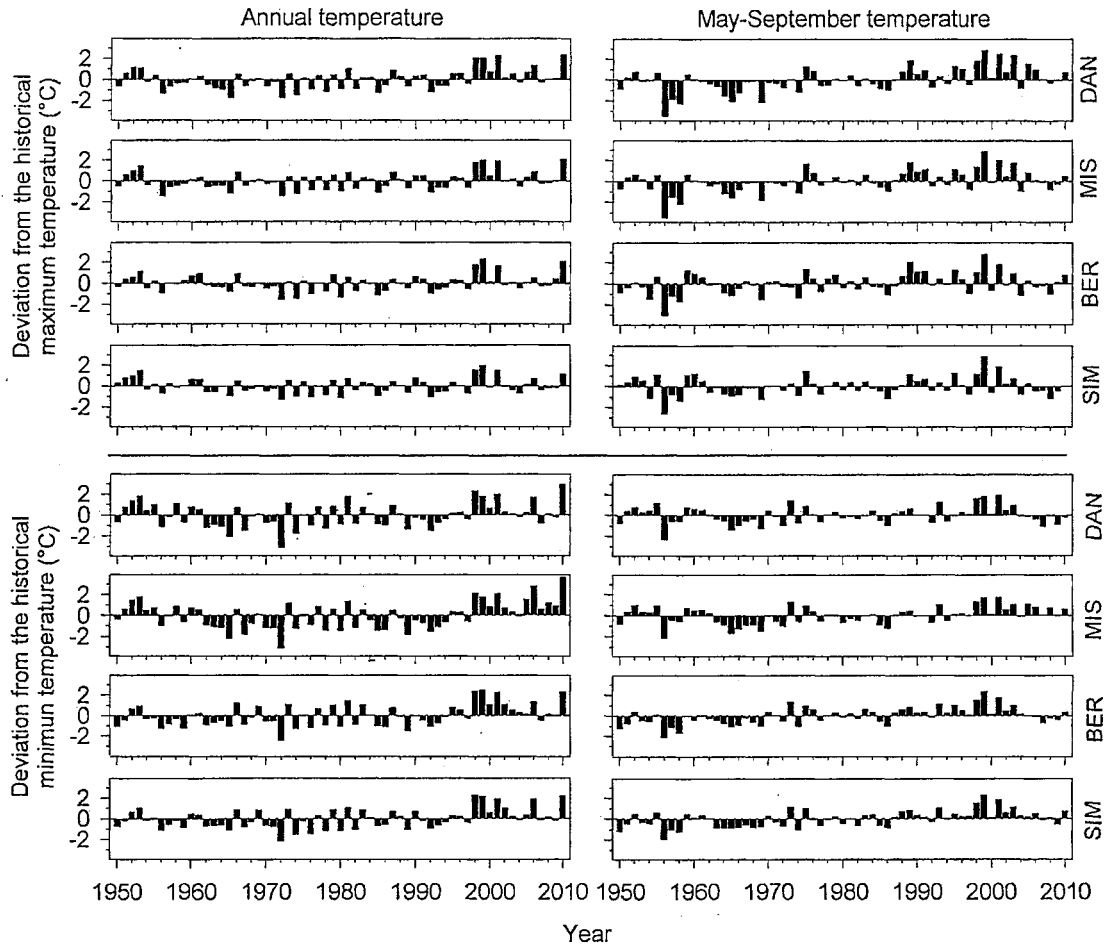


Figure 2.4. Deviation from average of the period 1950-2010 in the form of difference between the actual temperature and historical mean (last sixty years).

Model definition and validation

In the four sites, xylem growth lasted between 80 and 133 days, with SIM being the site with the longest duration (supporting information, Fig. 2.5). Overall, the onset of xylem growth occurred

from mid-May to mid-June (DOY 139-166), covering a range of c.a. one month. Later onsets of xylogenesis were detected in 2002 and 2009 and at the highest altitude and latitude, in BER and DAN, respectively. The ending of xylem growth differed by more than one month between the end of August in BER, MIS and DAN, and the beginning of October in SIM.

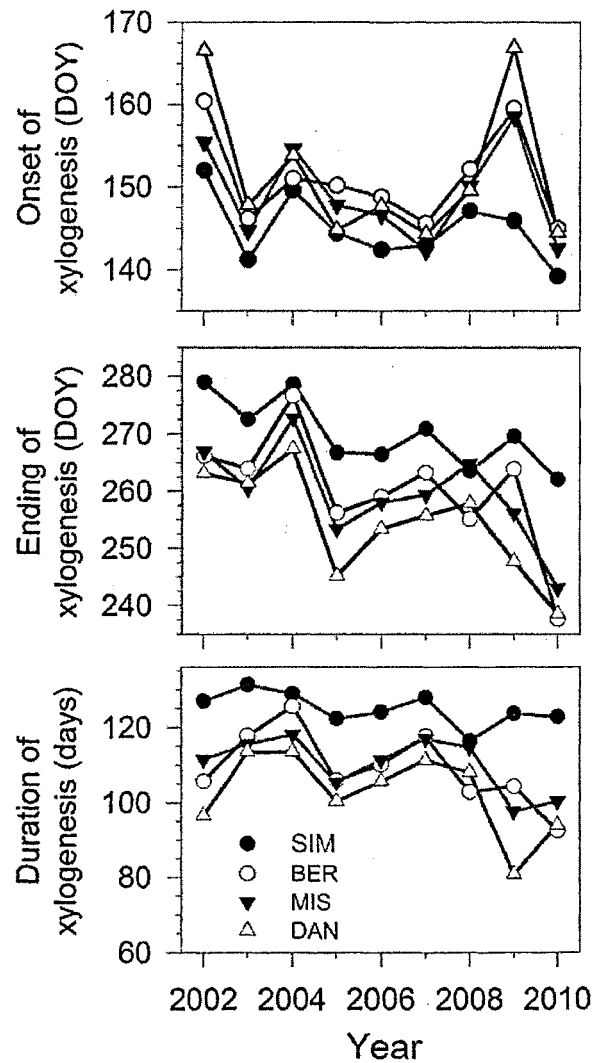


Figure 2.5. Average of the onset and ending in DOY (day of year) and duration in number of days (days) of xylem growth in black spruce during 2002-2010 in the boreal forest of Quebec, Canada.

On average, the logistic regressions assessed the temperature thresholds at 4.4 and 15.5 °C for minimum and maximum temperature, respectively (Table 2.3). For a temperature above the calculated thresholds, xylem growth was more likely to be active than non-active. Although MIS had slightly higher values compared with the other sites, no significant difference was detected by ANOVA for either minimum or maximum temperature ($P>0.05$, Table 2.3).

Table 2.3. 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	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

The results generated by the logistic regressions were verified by forecasting the presence or absence of xylem growth in the study sites (Table 2.4). Overall, observations showed that xylem growth in black spruce was active during about one third of the year and not active during 72.3% of the year. For minimum and maximum temperatures, 94.9 and 95.0% of the predictions were confirmed by observations, respectively, confirming that the model with both temperatures produced reliable estimations of the thresholds and suitably predicted timings of the phenological phases of xylem. On average, not active and active xylem growth was correctly predicted for 69.0

and 25.9% of the days, respectively, while the predictions were not confirmed only in 1.5–3.1% of days.

Table 2.4. 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

Model application

The model generated using the threshold temperatures was used for estimating chronologies of cambium phenology (onset, ending and duration of xylogenesis) for the period 1950-2010 (Fig. 2.5). Long term trends of all series were tested using ANCOVA, which calculated models with R^2 ranging between 0.36 and 0.60 and significances $p < 0.0001$ (Table 2.5). Predictions of the models using both minimum and maximum temperatures showed significant negative trends in all sites ($p < 0.05$), revealing an earlier onset of xylogenesis that was estimated by the slope of the regression at 0.5-0.8 days decade⁻¹. Significant slopes for the ending of xylogenesis were detected

only with the model using minimum temperatures, which indicated a delay of 0.7 days decade⁻¹ (Table 2.5). Longer durations of xylogenesis were predicted for the period 1950-2010, with the higher (1.5 days decade⁻¹) and lower (0.07 days decade⁻¹) increases estimated by the model using minimum and maximum temperatures, respectively. Significant differences among sites were found for all phenological models ($P < 0.0001$, Table 2.5), with SIM being the site with earlier onsets, later endings and longer durations of xylogenesis over all chronologies (Fig. 2.6). Differences in cambial phenology among BER, MIS and DAN were less marked. No significant interaction year×site was observed by ANCOVA ($p > 0.05$, Table 2.5).

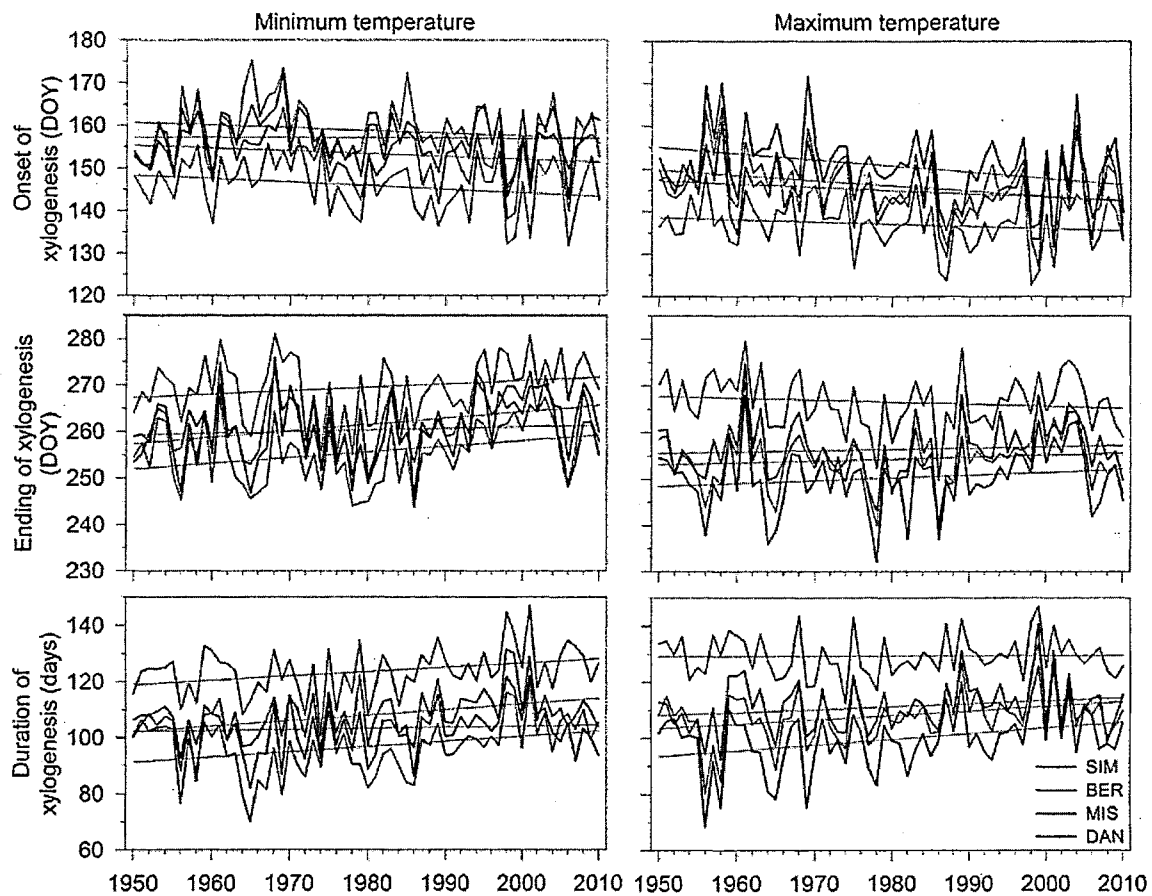


Figure 2.6. Estimation of cambial phenology from period 1950-2010 (onset, ending and duration of xylogenesis). Lines correspond to regression analyses performed by ANCOVA.

Table 2.5. 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 ²	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				

2.5. Discussion

Compared with the primary meristems such as leaves and buds, analyses on the phenology of the secondary meristem have only been emerging in the last decade. At the time of writing, the available chronologies of cambial phenology deriving from direct observations are spatially and temporally fragmented (Rossi *et al.*, 2008b; Moser *et al.*, 2010; Rathgeber *et al.*, 2011; Swidrak *et al.*, 2011), which prevents any interpretation of the trends over time (Sparks & Menzel, 2002). This paper thus aimed to reconstruct timings of cambium phenology of black spruce over the last 60 years in Quebec, Canada. In the boreal forest, wood formation is restricted to within 3-4 months by thermal limits that characterize the change between favourable and unfavourable periods for growth. In spring, cambial reactivation occurs from mid-May to mid-June, when the temperatures allow snow to melt and soil to warm up (Rossi *et al.*, 2011a). Mature xylem is observed in September, when all cells have concluded differentiation, which correspond to nighttime temperatures of 4-5 °C, and maximum temperatures reaching 15-16 °C. Ninety-five percent of the daily predictions of cambium phenology using the model with threshold temperatures were confirmed by observations, demonstrating that, in cold climates, temperature is the key signal for estimating stem growth with a very satisfactory reliability.

Trends of temperature and phenology

The chronologies generated by the ANUSPLIN model (McKenney *et al.*, 2006) for the four study sites exhibited increasing trends of both annual and May-September temperatures between 1950 and 2010. The greatest changes were observed for the maximum temperature at the higher latitudes, attaining increases up to 0.28 °C decade⁻¹ in DAN, the northern site. For a similar

period (1950-1998), Zhang *et al.* (2000) estimated that the higher increases in temperature for this region occurred in summer, with values ranging between 1.0 and 1.5 °C. Plummer *et al.* (2006) showed different trends for Quebec, with temperature rising by up to 6 °C in all seasons except in early spring, before the observed onset of xylogenesis. Our temperature chronologies exhibited a higher warming than the estimations by Zhang *et al.* (2000) and were more conservative than those by Plummer *et al.* (2006).

According to the change in temperature, reconstruction of cambium phenology showed earlier onset of xylogenesis in the last 60 years, estimated at 0.5-0.8 days decade⁻¹. Significant delays of 0.7 days decade⁻¹ in the ending of xylogenesis were estimated only with the model using minimum temperatures, while no significant slope was observed in trends using maximum temperatures. Changes in phenology of the primary meristems represents one of the best-documented effects of climate change on plants, with results converging toward increases in length of the growing season (Zhou *et al.* 2001; Sparks & Menzel, 2002; Badeck *et al.*, 2004). In Canada, Beaubien & Freeland (2000) reported that the first flowering date of aspen poplar showed a marked trend of earlier flowering with an advance of 26 days over the period 1900-1997. For the northern hemisphere, Schwartz *et al.* (2006) estimated that during 1955-2002 the dates of first leaf and first bloom have been earlier by 1.2 and 1.0 days decade⁻¹. Greater advances of 2.1 days decade⁻¹ were calculated between 1951 and 1996 for leaf unfolding in Europe (Menzel, 2000). Despite similar lengths of the study periods, the results vary widely, which could be explained by the complex origin (observations or estimations) and nature (leaf or flower buds) of the datasets and species over the broad spatial scales of analysis. Moreover, a high heterogeneity in change of temperature has been observed across North America, with lower

effects of warming occurring in the eastern part of the continent, where this work was carried out (Schwartz *et al.*, 2006). Nevertheless, in general the estimated increasing trends of cambial phenology exhibited lower slopes than those observed in primary meristems.

Does phenological cascade prevent estimating the end of xylogenesis?

In the last 30 years in Europe, the beginning of the growing season has advanced by 2.7 days decade⁻¹, while its ending showed smaller annual variations and has occurred just 1 day decade⁻¹ later (Chmielewski & Rötzer, 2001). Sparks & Menzel (2002) definitely confirmed that earlier events were more variable and changed faster than later events. This was consistent with our results, which showed more marked changes in the spring onset than in late-summer ending of xylogenesis, and contrasting slopes and significances were observed from the trends of ending of xylogenesis over the study period. During development, the cambial derivatives (i.e. the cells produced by cambial division) alter both morphologically and physiologically, progressively assuming definite features. In other words, cells differentiate into the specific elements of the stem tissues, represented by the phases of enlargement, wall thickening and lignification. Investigations on xylem phenology and climate-growth relationships have focused mainly on the onset of the growth process, i.e. onset of xylem production or differentiation, while the end of growth still remains partly or completely unexplored (Gričar *et al.*, 2007; Rossi *et al.*, 2007; Seo *et al.*, 2008; Turcotte *et al.*, 2009). This could be essentially due to a greater number of significant responses being obtained between onset of growth and climate rather than a mere lack of interest in the final phases of the growth process (Hänninen & Tanino, 2011). Photoperiod seems to play an important role in bud set of Norway spruce via the *FT*-like genes (Gyllenstrand

et al., 2007). However, although primary and secondary meristems share some common regulatory mechanisms (Matte Risopatron *et al.*, 2010) and the importance of photoperiod has also been demonstrated for stem growth (Rossi *et al.*, 2006c), the physiological or environmental cues driving growth cessation might be different.

Lupi *et al.* (2010) have demonstrated that cell production is closely related to xylem phenology. The date of onset of xylogenesis affects the number of cells produced by the cambium which, in turn, influences the ending of cell differentiation. As a result, earlier cambial resumptions lengthen the period available for cell division in the secondary meristem, increasing the growth potential during the year (Gričar *et al.*, 2005; Deslauriers *et al.*, 2008). In conifers, the larger amount of cells produced by cambium leads to greater accumulations of cells in the developing xylem, increasing the time spent differentiating and maturing the tracheids and delaying the ending of wood formation. As a result, any environmental factor affecting the resumption of growth in spring could indirectly influence the production and temporal dynamics of cell differentiation by affecting all successive phenological phases of xylem (Rossi *et al.*, 2006b). This hypothesis provides valuable cues for identifying the relative importance of the factors affecting timings and dynamics of xylem growth, and makes the simple relationships between the temperatures occurring in late-summer and the date of ending of xylem growth more complex.

Thermal predictors of the growing season

Several methods have been applied to investigate plant growth and its changes over time. Definitions of the growing season differ according to plant species, and are calculated in different ways, either directly (bud or cambial phenology), or indirectly (thermal sums, days experiencing

air and soil temperatures above certain thresholds, freezing days) (Nizinski & Saugier, 1988, Körner & Paulsen, 2004; Schwartz *et al.*, 2006; Seo *et al.*, 2008). In our reconstruction of the past cambial phenology, the applied thresholds of temperature were not defined a priori. Instead, the thresholds were statistically assessed on a wide dataset of observations collected weekly from four permanent plots during nine years, by defining a binary response of presence or absence of growth, and modeling the logistic response probability according to a vector of explanatory variable, either minimum or maximum temperature. The resulting temperature thresholds have the advantage of being objectively assessed and statistically validated, and are as close as possible to the biological limits of the growth process in the stem. In this study, the minimum and maximum temperature thresholds allowing xylogenesis ranged between 4-5 °C and 15-16 °C, respectively, which confirm previous findings from other conifer species of cold climates (Rossi *et al.*, 2008b, Swidrak *et al.*, 2011). Cambium is a sink for non-structural carbohydrates, and its activity requires a continuous supply of energy in the form of sucrose which, for the first cells to be formed, is extracted from the storage tissues or produced by photosynthesis (Oribe *et al.*, 2003; Deslauriers *et al.*, 2009). During cell maturation, trees assign a large amount of carbon obtained from photosynthesis to the deposition of cellulose microfibrils in order to provide the developing cells with secondary walls. The thresholds estimated in this paper could represent the critical temperatures limiting the demand for photo-assimilates by the metabolic processes involved in cell growth. Moreover, as xylogenesis is the most important net accumulation of biomass in forest ecosystems, knowledge about the climatic factors on the verges of the growing season is crucial to determine the time window during which the carbon sequestered by the atmosphere is permanently stocked in trees.

The models using maximum and minimum temperature produced similar results in terms of onset of xylogenesis, with 0.5 and 0.8 days decade⁻¹ of earlier cambial activity, respectively. Nevertheless, different endings, and hence different durations of xylogenesis were calculated for the last 60 years, essentially because the slope of the ANCOVA regression for the ending of xylogenesis with maximum temperature was not significant (Table 2.5). In model validation, predictions were confirmed by observations in 94.9 and 95.0% of cases with minimum and maximum temperature, respectively (Table 2.4). This indicated that both models produced equally reliable estimations of xylem phenology, but prevented a definitive choice of the most suitable model. Unlike photosynthesis that is able to maintain high assimilation rates even at temperatures below 5 °C, xylem formation requires necessarily large amounts of available sucrose to be allocated in the growing tissues to complete growth, which is a temperature-limited process (Körner, 2003a; Deslauriers *et al.*, 2009). Comparing the daily growth responses of conifers to maximum and minimum temperatures, the better results were observed with the latter (Deslauriers & Morin, 2005; Wei *et al.*, 2007, Rossi *et al.*, 2008b). Moreover, cell doubling time remains quite constant at temperatures of 10-25 °C, but triplicates when temperatures fall from 10 to 5 °C, and approaches infinity at 1-2 °C (Körner, 2003b). There is evidence that minimum rather than maximum temperature constrains growth by acting on tissue formation. However, the effects of the two variables have still not been experimentally and definitively disentangled, and which temperature mostly controls the length of the growing period remains an unresolved question.

This paper used weekly observations performed during 9 years in four permanent sites in Quebec, Canada for defining a phenological model of black spruce and for reconstructing timings of

cambium phenology over the last 60 years using chronologies of temperature generated by the ANUSPLIN model (McKenney *et al.*, 2006). All sites exhibited increasing trends of both annual and May-September temperatures, with the greatest changes occurring for maximum temperature at the higher latitudes. Accordingly, earlier cambial resumptions by 0.5-0.8 days decade⁻¹ were estimated, while significant delays for the ending of xylogenesis were calculated only with the model using minimum temperatures. Phenological events in spring were confirmed to be more variable and changing faster than those occurring in autumn. Results clearly showed a lengthening in duration of xylogenesis since 1950, although contrasting extents were observed, ranging between 0.07 and 1.5 days decade⁻¹, calculated with the model based on maximum and minimum temperatures, respectively. To our knowledge, this is the first time that past cambial phenology has been modelled and reconstructed. According to the findings reported for leaf and flower buds, changes in cambial phenology revealed increasing trends in length of the growing season, demonstrating the effects of the recent global warming on secondary meristems of trees. The present reconstruction of cambial phenology applied and validated a model based on growth thresholds statistically assessed on a wide dataset of observations, rather than defined a priori. As a result, the temperature thresholds used were representative of the biological limits of the growth process of xylem, thus providing suitable estimations of the timings of past cambial phenology.

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CHAPITRE III

CONCLUSION GÉNÉRALE

3.1. Conclusion générale

Principale contribution et originalité de l'étude

Le modèle que nous avons développé s'est révélé un bon outil pour l'estimation journalière des changements de la phénologie du passé, mais aussi, il pourrait être utilisé pour faire des estimations sur l'évolution future de la phénologie en fonction des prévisions de la hausse de la température avec une approche à échelle journalière. Bien qu'il y ait différentes études à propos de l'influence de la température sur la phénologie, il n'y a pas d'études sur l'évolution historique de la phénologie du cambium. Le présent travail est basé sur l'analyse d'une base de données phénologiques qui s'étale sur neuf ans, mais une telle période n'est pas suffisante pour établir des tendances de la croissance. C'est pourquoi ce modèle a été élaboré pour effectuer l'estimation de la phénologie des soixante dernières années afin que nous soyons en mesure de dégager des tendances de la phénologie d'un méristème secondaire, le cambium.

À notre connaissance, ce travail est le premier à effectuer une modélisation et une estimation du passé de la phénologie du cambium. Cette estimation est basée sur des seuils de températures statistiquement évalués avec l'aide des données observées plutôt que sur des seuils définis a priori. En conséquence, les seuils de températures utilisés sont représentatifs des limites biologiques du processus de croissance du xylème, fournissant ainsi des estimations appropriées de l'évolution de la phénologie cambiale durant les soixante dernières années.

Résumé des principaux résultats sur les tendances de la température et les changements de la phénologie

Au cours des 60 dernières années, tous les sites ont affiché une tendance croissante dans les températures annuelles et ainsi que pour la période de mai à septembre. Un changement plus évident a été observé pour la température maximale aux latitudes élevées (2.8 °C par 100 ans). Nos tendances de changements de température sont plus élevées que celles rapportées par Zhang *et al.* (2000), qui se situent entre 1 et 1.5 °C, mais plus conservatrices que celles rapportées par Plummer *et al.* (2006), qui sont de 6.0 °C.

En ce qui concerne la xylogénèse, on a observé des changements plus marqués pour le début de la xylogénèse au printemps, comparativement à la fin de la xylogénèse. En effet, la fin de la formation du cerne de croissance survient l'été lorsque les températures sont encore élevées. Nos résultats concordent tout de même avec ceux de Sparks et Menzel (2002), rapportant que les événements printaniers ont une plus grande variabilité et changent plus vite que les événements survenant ultérieurement dans la saison de croissance. Nos résultats ont illustré que depuis 1950, on observe, principalement, un début précoce de l'activité cambiale (6.5 jours par 100 ans), une fin tardive (1.5 jours par 100 ans) et, par conséquent, un allongement de la durée (8 jours par 100 ans) de la xylogénèse.

Perspectives de recherche

Dans cette recherche, nous avons travaillé avec l'épinette noire (*Picea mariana*) dans la région du Saguenay-Lac-Saint-Jean, mais il sera intéressant de savoir, premièrement, si nos seuils de température sont applicables aux autres régions de distribution de l'épinette noire et, également, d'être en mesure de reconnaître si ces seuils de température correspondent aux autres espèces ayant une distribution semblable à l'épinette noire, comme par exemple l'épinette blanche (*Picea glauca*) et le sapin baumier (*Abies balsamea*).

Une relation entre la fonte de neiges et la phénologie a été établie (Kirdyanov *et al.*, 2003; Vaganov *et al.*, 1999). Puis, on a observé que la fonte des neiges a un effet linéaire positif sur la saison de croissance (Forrest et Miller-Rushing, 2010; Ellebjerg *et al.*, 2008; Inouye, 2008). Dans la présente recherche, nous avons travaillé sur la température, mais une augmentation de la température peut favoriser une fonte anticipée de la neige. Donc, une étude qui considère à la fois l'influence de la fonte de la neige et celle de l'augmentation de la température sur la phénologie cambiale serait intéressante et nécessaire pour mieux comprendre la dynamique des différents facteurs qui affectent ou peuvent affecter la croissance à court et long termes (Lupi *et al.*, 2011).

Une autre étude qui est importante à développer est la relation entre la phénologie et la croissance. Plus précisément, on cherche à savoir si la largeur du cerne de croissance chez l'épinette noire est influencée par le début, la fin ou la durée de la xylogénèse. En ayant comme

hypothèse que lors d'un début précoce de la saison de croissance, la largeur du cerne peut être allongée. On peut travailler avec l'estimation de la phénologie de la période de 1950 à 2010 de nos quatre sites d'échantillonnage et des mesures de largeur des cernes de rondelles à hauteur de poitrine pour chaque site afin de chercher les possibles relations entre la phénologie de la xylogénèse et la croissance.

3.2. Références

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