UNIVERSITÉ DU QUÉBEC À MONTRÉAL

VARIATION INTRA-ANNUELLE DE LA FORMATION DU BOIS, DU DÉVELOPPEMENT DE LA POUSSE ET DES FEUILLES DE TROIS ESPÈCES MAJEURES DANS LA FORÊT BORÉALE

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN BIOLOGIE

PAR

LIHONG ZHAI

JUILLET 2009

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

VARIATIONS IN INTRA-ANNUAL WOOD FORMATION, AND DEVELOPMENT OF FOLIAGE AND SHOOT OF THREE MAJOR BOREAL TREE SPECIES

THESIS

PRESENTED

AS A PARTIAL REQUIREMENT

FOR THE MASTER IN BIOLOGIE

BY

LIHONG ZHAI

JULY 2009

PREFACE

This thesis presents the results of a study conducted as part of my master in biology that began in January 2007. The results are presented in the form of a scientific article. A general introduction precedes the section in Chapter 1 and develops the basic concepts and issues related to this study. A general conclusion follows Chapter 1. It brings together the conclusions of the scientific article and a link with the various objectives mentioned in the introduction. The scientific article will be submitted in summer 2009.

I would like to thank my supervisor, Frank Berninger, for guidance throughout this project. I thank my co-supervisor Yves Bergeron for guiding and funding this project. I thank the late Dr. Bernhard Denneler (Bergeron, 2007) for giving me an opportunity to know wood anatomy science and introducing me the basic techniques in this field. I thank my committee members, Jacques Tardif, Christian Messier, Daniel Kneeshaw, and Martin J. Lechowicz for their feedback, comments and corrections on this thesis, and Anne Jetté, Jian-Guo Huang, Danielle Charron for field assistance. I thank Venceslas-Claude Goudiaby for technical advice on collecting field data and translation of the abstract into French. I would also like to thank my husband, Jian-Guo Huang, and my family for their support and patience. This study was funded by the Fonds québécois pour la sciences et la technologies (FQRNT), programme en équipe and the Canada Chair in Forest Ecology and Management.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

RÉSUMÉ

L'étude de la formation intra-annuelle de bois, du développement des pousses annuelles et des feuilles pourrait fournir des informations quant à la dynamique de la croissance des arbres au cours de la saison de croissance. La formation intra-annuelle de bois et le développement des pousses annuelles et des feuilles sont des processus complexes contrôlés à la fois par des facteurs physiologiques et environnementaux.

Les objectifs de cette étude étaient (i) d'étudier le patron annuel et la dynamique de formation du bois de même que le développement des pousses annuelles et des feuilles chez trois espèces majeures de la forêt boréale (i.e., *Pinus banksiana* Lamb., *Populus tremuloides* Michx., et *Betula papyrifera* Marsh.) au cours de la saison de croissance 2007 dans le Nord-Ouest du Québec, Canada et (ii) d'identifier les relations entre d'une part la formation intra-annuelle de bois, le développement des pousses annuelles et des feuilles et d'autre part les facteurs climatiques ; on s'intéressera en même temps aux facteurs météorologiques limitant leur croissance durant la saison de croissance.

Des micro-carottes de bois ont été prélevées une fois par semaine au niveau des tiges de ces trois espèces pendant la saison de croissance 2007. Des coupes transversales ont ensuite été effectuées au niveau des micro-carottes puis colorées avec du violet de crésyl et de la safranine afin d'identifier les stades de formations des cellules du bois et le nombre de cellules produit. La phénologie (débourrement du bourgeon), l'élongation des pousses annuelles et l'accroissement des feuilles/aiguilles ont aussi été mesurés trois fois par semaine. La production hebdomadaire de cellules, l'élongation des pousses annuelles et l'accroissement des feuilles ont été ajustés grâce à la fonction de Gompertz et les indices de croissance hebdomadaires ont été calculés afin d'éliminer des changements de croissance d'origine endogène. Une analyse de corrélation simple a été utilisée pour déterminer les facteurs météorologiques majeurs qui influencent la production des cellules du xylème, de l'élongation des pousses annuelles et de l'accroissement des feuilles durant la saison de croissance.

Il ressort des résultats obtenus que les dates de début d'élongation des pousses annuelles et d'accroissement des feuilles sont plus précoces que la date reprise de croissance de la tige chez *B. papyrifera*. Contrairement à ce qui a été observé chez *B. papyrifera*, les dates de début d'élongation des pousses annuelles et de croissance des feuilles ont été plus tardives que la date de reprise de croissance de la tige chez *P. banksiana* et *P. tremuloides*. L'arrêt de la formation de nouveau xylème intervient aux alentours de la mi-août pour les trois espèces. La fin de la maturation des cellules a été noté le 15 septembre chez *P. banksiana* et *P. tremuloides* et le 6 septembre chez *B. papyrifera*. Concernant les trois espèces, la durée de formation du bois au niveau de la tige a été plus longue chez *P. banksiana* et plus courte chez *B. papyrifera*. Durant la période de production des cellules, la corrélation entre d'une part les températures du sol et de l'air et d'autre part la production des cellules du xylème a été positive chez *P. banksiana* et négative chez *P. tremuloides* et *B. papyrifera*. La corrélation entre les précipitations et la production des cellules du xylème a été positive chez *P. tremuloides* et *B. papyrifera*, toutefois aucune corrélation n'a été notée chez *P. banksiana*. De plus, il a été noté chez les trois espèces une corrélation positive entre la température de l'air et l'élongation des pousses annuelles. Toutefois chez les trois espèces, aucune corrélation n'a été notée entre la croissance des feuilles et les variables météorologiques.

Cette étude a montré que la formation intra-annuelle du bois, le développement des pousses annuelles et des feuilles de même que la phénologie est non seulement déterminés par l'espèce, mais de plus les facteurs limitants clés sont différents. Ces résultats relatifs aux patrons de croissance temporels des différents organes des arbres (tige, pousse annuelle et feuille) pourraient être utiles dans la compréhension des relations entre la croissance des arbres et les changements climatiques.

Mots-clés : la formation intra-annuelle du bois, la phénologie des arbres, la élongation de la tige, la dynamique de la croissance.

ABSTRACT

Studies on the intra-annual stem wood formation, shoot and foliage development could provide precise information on tree growth dynamics during a growing season. Intra-annual wood formation and development of shoot and foliage are complex processes, which are controlled by both physiological and environmental factors.

The goals of this study were (i) to explore the annual pattern and dynamics of stem wood formation and the development of shoot and foliage in three major boreal species (i.e., *Pinus banksiana* Lamb., *Populus tremuloides* Michx. and *Betula papyrifera* Marsh.) during the 2007 growing season in northwestern Quebec, Canada., and (ii) to identify the relationships between intra-annual wood formation, shoot and foliage development and weather factors, as well as to determine the major meteorological factors limiting their growth during the growing season.

Wood micro-cores were taken weekly from the stems of these three species during the 2007 growing season. Cross-sections of micro-cores were sectioned and stained with cresyl fast violet and safranin to identify the stages of wood cell formation and to count the total number of cells produced. Tree phenology (buds burst), shoot elongation, and leaves/needles enlargement were also recorded three times per week. Weekly cumulative cell production, shoot elongation, and foliage enlargement were fitted with the Gompertz function, and weekly growth index were calculated to detrend the endogenous origin which effects tree growth. Simple correlation analysis was used to explore the major meteorological factors influencing xylem cell production, shoot elongation, and foliage enlargement during the growing season.

The results showed that the onset date of shoot and foliage development for *B. papyrifera* was earlier than the onset date of stem growth. Unlike *B. papyrifera*, the onset date of shoot and foliage development of *P. banksiana* and *P. tremuloides* was later than their onset date of stem development. The cessation date of new xylem cell division of the three species was in mid August. The completion of cell maturation was observed on September 13th for *P. banksiana* and *P. tremuloides*, and on September 6th for *B. papyrifera*. Among the three species, the duration of stem wood formation of *P. banksiana* was the longest, whereas that of *B. papyrifera* was the shortest. During the cell production period, air and soil temperatures were positively correlated with the xylem cell production of *P. banksiana*, and negatively correlated with that of *P. tremuloides* and *B. papyrifera*. Precipitation was positively correlated with the xylem cell production of *P. tremuloides* and *B. papyrifera*, whereas no correlation was found for *P. banksiana*. Air temperature was positively correlated with shoot elongation of these three species. No significant correlation was found between leaf enlargement of the three species and the meteorological variables.

This study showed that intra-annual wood formation, shoot and foliage development, and tree phenology are species-specific, and thus, their major limiting factors are different. These findings on the temporal growth patterns of tree different organs (stem, shoot, and foliage) may be useful for understanding the relationships between tree growth and climate changes.

Key words: intra-annual wood formation, tree phenology, extension growth, growth dynamics.

GENERAL INTRODUCTION

The global average surface temperature increased about 0.6 °C during the 20th century and is projected to rise 1.8–4.0 °C during the 21st century (IPCC, 2007). In Canada, annual mean temperatures are increasing nationally; a linear trend of 1.3 °C is evident from 1948 to 2008 (Environment Canada, 2008). Over this period, the trend has been to warmer autumns, winters and springs (Environment Canada, 2008).

Climate warming has resulted in an earlier spring and later autumn, thus extending the growing season length and changing tree phenology since tree phenology is very sensitive to environmental factors such as growing degree days and temperature (Fritts, 1976; Schweingruber, 1996). For example, Menzel and Fabian (1999) reported that spring events, such as leaf unfolding, had advanced by 6 days and autumn events, such as leaf colouring, were delayed by 4.8 days, as well as an increase of 10.8 days detected in the mean annual growing season in Europe since the early 1960s. Earlier budburst, leafing, and flowering in several species were also observed from long phenological time series (Chmielewski and Rötzer, 2001). Climate change results in changes in tree and forest growth, and will likely to drive the migration of tree species, leading to shifts in the geographic distribution of forest types and new combinations of species within forests. In the long run, warmer temperature and increased or decreased precipitation are expected to change forest location, composition, and productivity. In North America, many tree species may shift northward or to higher elevations (IPCC, 2007). Therefore it is important to understand tree growth and the effect of climate change on tree growth.

A traditional way to study tree growth and its reactions to environmental factors is the tree-ring method (Fritts, 1976; Schweingruber, 1996). That is based on radial wood production at the yearly time scale, i.e., inter-annual ring growth, to study the influence of environmental factors on growth. Inter-annual ring growth has been extensively studied since the 1900s (Douglass, 1914; 1917; 1920). These studies showed that variations in inter-annual radial growth of trees in temperate and boreal forests could well reflect variations in climatic factors (temperature, precipitation, and drought or moisture index) at monthly, seasonal, annual or decadal scales (e.g., Douglass, 1920; Fritts, 1976; Cook et al., 1991; Archambault and Bergeron, 1992; Schweingruber, 1996; Tardif and Bergeron, 1993; Briffa et al., 1998; Berninger et al., 2004). However, tree growth information at a finer time scale such as daily, pentad, weekly, or monthly is limited. Also, it is not clear how these short term growth rates connect actually to annual growths. A recently developed intra-annual tree growth study can provide such detailed information on cambium dynamics and intra-annual xylem formation at those finer time scales.

Processes of intra-annual wood formation

Intra-annual wood formation in trees is initiated by cell division in the vascular cambium, and followed by differentiation of cambial derivations (Kozlowski and Winget, 1964; Schweingruber, 1996; Samuels et al., 2005; Marion et al., 2007). Differentiation of cambial derivations (xylem formation) was further defined to involve four major steps: (1) cell division and expansion, (2) production of secondary cell walls, (3) cell wall lignifications, and (4) programmed cell death (Plomion et al., 2001; Samuels et al., 2005).

Factors influencing the intra-annual wood formation

The dynamics of seasonal tree growth is influenced by both internal and external factors. Internal factors include genetics, age and the hormonal regulation of the tree. External factors include physical-geographical, soil, and weather factors (Fritts, 1976; Schweingruber, 1996). The internal factors determine the physiological condition of the tree, and regulate the biological growth curve (Fritts 1976; Schweingruber, 1996; Vaganov et al., 2006). The external factors provide physical conditions for the growth and development of trees, and essentially influence the size of cells, thickness of the cell wall, and finally the density of tree rings (Vaganov et al., 2006). The seasonal periodicity or rhythm of biological processes in a tree is determined by regular environmental fluctuations associated with the annual cycle. The onset of xylem formation is regulated by photoperiod, temperature, water availability (as external factors) (Hänninen, 1995; Leinonen et al., 1997), and internal factors such as auxin production (Wang et al., 1997).

Internal factors

The genetic constitution of tree is one of the major internal factors influencing the dynamics of seasonal growth in trees. The phenology, the timing of bud opening, and the initiation of meristem activities in shoots, stems and roots between different species is species-specific (Ladefoged, 1952). Differences between species are found not only in the timing of the initiation and termination of cell division in meristems, but also in the seasonal dynamics of growth. Ladefoged (1952) divided tree species into three groups on the basis of qualitative analysis of growth-rate curves: (1) with a growth rate maximum in the first third of the season, (2) with a more symmetrical growth curve, (3) with a uniform growth rate during the growing season. The distribution through the season of the rate of growth is related to the characteristics of the species.

The cambial age is also a major internal factor connected with the genotype and influencing the seasonal dynamics of growth processes in trees. The wood cells made by young cambium have smaller radial sizes, a smaller cell wall thickness, and a lower wood density, as well as more earlywood and less latewood (Telewski and Lynch, 1991). Young cambium is characterized by high activity, resulting in the production of more new wood cells and wider annual rings than those produced by older cambium.

External factors

Physical-geographical factors: among these factors, the most essential factors are regional climatology and topography. Local topography has a strong influence on the thermal regime (Fritts, 1976), so that eastern and southern slopes receive markedly more solar energy than western and northern slopes. This may result in very different seasonal courses of growth in shoots and stems of nearby trees of the same species.

Soil factors: the major soil factors influencing tree growth include temperature, water regime of the soil, composition (mechanical, chemical properties, and texture), and its content of mineral elements. In the boreal forest, the availability of soil water is a prerequisite for the recovery of photosynthetic capacity in spring and early summer (Bergh and Linder, 1999). Soil temperature is a major factor stimulating the onset of tree growth in the spring (Bergh and Linder, 1999). Soil mineral elements provide the necessary nutrients for tree to combine with sugars to produce proteins and other complex compounds which enable trees to grow and to function (Kramer and Kozlowski, 1979).

Weather factors: the temperature and precipitation. These factors are most important features for determining the dates of onset and end of cell division in meristems, the growth rate, and the overall seasonal course of the growth curve (Fritts, 1976; Fritts et al., 1991). Temperature may be considered as the most important single factor in the initiation of meristem growth activity (Larson, 1994). At the same time, low soil humidity can cause an earlier end of growth in a season (Fritts, 1956; 1976), or at least an earlier onset of latewood formation. A combination of temperature and humidity changes during a period of a growing season may cause acceleration or deceleration of growth processes (Vaganov et al., 1985; Schweingruber, 1996) and largely determines the overall result: the size and internal structure of the annual ring formed in that year. Boreal forests are generally believed to be mostly temperature and nutrient limited while drought limitations are considered to be minor.

Coordination between tree different organs

According to Kramer and Kozlowski (1979), a better understanding of what constitutes optimum allocation or partitioning of growth among the various organs of tree is one of the most important tasks of tree physiology. Information concerning the partition of growth among the leaves, branches, stems, and roots is necessary to an understanding of how various environmental and cultural practices affect growth.

Bud phenology of boreal trees is characterized by two major events. In the autumn, growth ceases and buds enter dormancy, a state that prevents growth even under environmental conditions favorable to growth (Vegis, 1964; Wareing, 1969). In the spring, bud break occurs once dormancy has been overcome, and favorable growth conditions allow ontogenetic development to proceed. Several studies have shown that, after release from dormancy, the rate of ontogenetic development in boreal trees depends largely on air temperature (e.g., Sarvas, 1972). The amount of chilling required to break bud dormancy varies with the species, genotype, location of the buds on the tree, and possibly the weather of the preceding summer (Kramer and Kozlowski, 1979).

Cambial reactivation is assumed to be promoted by auxin, produced in the younger shoots and exported basipetally along the stem to induce the production of xylem (Larson, 1969) and regulate xylem development (Uggla et al., 1998). Following the basipetal movement of the auxin, periclinal divisions in the cambium should begin close to buds, spread downwards toward branches and stem (Larson, 1969; Lachaud, 1989). Cambial activity and subsequent initiation of xylem cell production and development at the beginning of the growing season is sensitive to various environmental factors, primarily temperature, water availability, and/or photoperiod (Mäkinen et al., 2003). Generally, cell division initiation occurred while soil and air temperatures were increasing from mid May into June. Antonova and Stasova (1997) found a positive correlation between initial xylem cell production and air temperature. Spring reactivation of cambium activity and subsequence initiation of xylem cell production is typically preceded by the new growth of the buds and their release of auxin throughout the stem (Vaganov et al., 2006).

The leaves of a tree play a paramount role in photosynthesis, the process by which practically all energy enters our biosphere. The timing of leaf unfolding and leaf fall of deciduous tree species are most important phenological events, and directly affect the period in which light can be intercepted for growth. Cell division predominates during the early stages of development of leaf primordial. Subsequently, a leaf achieves its final shape and size by both cell division and expansion, with the latter predominating. Ultimate leaf size depends on the number of cells in the primordial, the rate and duration of cell division, and sizes of mature cells, but cell number appears to be most important (Kramer and Kozlowski, 1979). Leaf emergence has been classified into three types: the flush type, the intermediate type and the succeeding type (Kikuzawa, 1983). The flush type shows all leaves emerging simultaneously after budbreak with a short duration of shoot elongation. The succeeding type shows the leaves emerge one by one successively after budbreak with a long duration of shoot elongation. In the intermediate type, some leaves emerge simultaneously after budbreak. Afterwards, the remaining leaves emerge one by one successively with shoot elongation.

Stems of trees support the crown, conduct water and minerals upward from the roots, and conduct foods and hormones from points where they are manufactured to those where they are used in growth or stored for future use.

The size and structure of the xylem cells, as well as the rate of cell division, may also be controlled by these growth regulators, which are produced by the actively growing stem apex or by the leaves. The width and structure of the annual ring in trees are intimately related to the amount and duration of shoot growth (Kozlowski, 1971). The seasonal growth of shoot and foliage, through the hormonal control of cambial activity, is of central importance to the character and distribution of the seasonal growth rate of stem wood (Zimmermann, 1964; Savidge, 1996).

The coordination of the seasonal dynamics of growth of the various parts of woody plants results in allometric relations between them during the growth and development of the woody plant and the stand (Vaganov et al., 2006). The phenology of the boreal forest is mainly driven by temperature, which affects the timing of the start of the growing season and thereby its duration, and the level of frost hardiness and thereby the reduction of foliage area and photosynthetic capacity by severe frost events. To assess the possible impact of climate change on growth of boreal trees, it is important to understand the climate factors driving the growth of the different tree parts.

Study questions and objectives

Studies conducted on intra-annual wood formation have been reported in both conifer and broadleaf species in some regions in the past and were shown to be able to provide detailed information on tree radial growth at finer time scales (e.g., Deslauriers et al., 2003a; Schmitt et al., 2004; Deslauriers and Morin, 2005; Dufour and Morin, 2007; Ko Heinrichs et al., 2007; Rossi et al., 2007; Gruber et al., 2008). But previous intra-annual studies pay more attention to intra-annual stem growth, and less to intra-annual growth of other organs such as shoot and foliage development. To improve our ability to simulate tree growth and to achieve the goal of sustainable forest management, it is important to precisely characterize the intra-annual growth of different tree organs.

In the boreal forest of Canada, jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh.) are widely distributed boreal tree species. Jack pine is an ever-green, shade-intolerant coniferous species and usually grows on the sandy soil. Trembling aspen is a shade-intolerant and top-canopy deciduous species in the boreal forest. Compared with trembling aspen, white birch is a more shade-tolerant deciduous species. All three species are typical post-fire species in the boreal ecosystem. They are considered to be the most important species with respect to their abundance and forest yield and management (Bergeron and Harvey, 1997; Harvey et al., 2002). Hence understanding of how meteorological factors influence the intra-annual growth of their different parts and of their coordination is particularly important for the prediction of future forest productivity. In addition, to be able to observe the development of tree phenology during the growing season, therefore a young stand involving these three major boreal species at Lac Dances of northwestern Quebec was selected as our study site for this Master's project.

Our study objectives are 1) to explore the annual pattern and dynamics of stem wood formation and the development of shoot and foliage of three boreal tree species: Jack pine, trembling aspen and white birch, which will allow us to describe the developmental processes of xylem formation, shoot extension growth, and foliage enlargement, and to investigate the coordination between tree different organs in northwestern Quebec, Canada; 2) to identify the relationships between intra-annual wood formation, shoot extension growth, and foliage enlargement of these tree species and weather factors, as well as to determine the major meteorological factors influencing their growth during the 2007 growing season.

The following Chapter 1 will be presented as a paper for a scientific journal.

CHAPITRE I

VARIATIONS IN INTRA-ANNUAL WOOD FORMATION, AND DEVELOPMENT OF FOLIAGE AND SHOOT OF THREE MAJOR BOREAL TREE SPECIES

Lihong Zhai[1], Frank Berninger[1], Yves, Bergeron[1, 2]

[1]Centre d'étude de la forêt (CEF), Département des sciences biologiques, Université du Québec à Montréal, C.P. 8888, Succursale Centre-Ville, Montréal, Québec, Canada, H3C 3P8.

[2]Chaire industrielle CRSNG UQAT-UQAM en aménagement forestier durale, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, Québec, Canada, J9X 5E4.

1.1 RÉSUMÉ

La formation intra-annuelle du bois et le développement des pousses annuelles et des feuilles chez trois espèces majeures de la forêt boréale (i.e. *Pinus banksiana*, *Populus tremuloides* et *Betula papyrifera*), et leurs relations avec le climat ont été étudiées au cours de la saison de croissance 2007 dans le Nord-Ouest du Québec. Des micro-carottes de bois ont été prélevées une fois par semaine au niveau des tiges de ces trois espèces de mai à septembre 2007. Des coupes transversales ont ensuite été effectuées au niveau des micro-carottes puis colorées avec du violet de crésyl et de la safranine afin d'identifier les stades de formations des cellules du bois et le nombre de cellules produit. La phénologie (débourrement du bourgeon), l'élongation des pousses annuelles et l'accroissement des feuilles/aiguilles ont aussi été mesurées trois fois par semaine. Il ressort des résultats obtenus que les dates de début d'élongation des pousses annuelles et d'accroissement des feuilles sont plus précoces que la date reprise de croissance de la tige chez *B. papyrifera*. Contrairement à ce qui a été observé chez *B. papyrifera*, les dates de début d'élongation des pousses annuelles et de croissance des feuilles ont été plus tardives que la date de reprise de croissance de la tige chez *P. banksiana* et *P. tremuloides*. L'arrêt de la formation de nouveau xylème intervient aux alentours de la mi-août pour les trois espèces. La fin de la maturation des cellules a été noté le 15 septembre chez *P. banksiana* et *P. tremuloides* et le 6 septembre chez *B. papyrifera*. Concernant les trois espèces, la durée de formation du bois au niveau de la tige a été plus longue chez *P. banksiana* et plus courte chez *B. papyrifera*. Durant la période de production des cellules, la corrélation entre d'une part les températures du sol et de l'air et d'autre part la production des cellules du xylème a été positive chez *P. banksiana* et négative chez *P. tremuloides* et *B. papyrifera*. La corrélation entre les précipitations et la production des cellules du xylème a été positive chez *P. tremuloides* et *B. papyrifera*, toutefois aucune corrélation n'a été notée chez *P. banksiana*. De plus, il a été noté chez les trois espèces une corrélation positive entre la température de l'air et l'élongation des pousses annuelles. Toutefois chez les trois espèces, aucune corrélation n'a été notée entre la croissance des feuilles et les variables météorologiques.

Mots-clés : la formation intra-annuelle du bois, la phénologie des arbres, la élongation de la tige, la dynamique de la croissance.

1.2 ABSTRACT

The intra-annual xylem formation and development of foliage and shoot of three dominant boreal species jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), and white birch (*Betula papyrifera* Marsh.), and their relationships to climate in northwestern Quebec were investigated during the 2007 growing season. Wood micro-cores were taken weekly from the stems of these three species from May to September. Cross-sections of micro-cores were sectioned and stained with cresyl fast violet and safranin to identify the stages of wood cell formation and count total number of cells produced. Tree phenology (buds burst) and the growth of shoots and foliage were also recorded three times per week. The results showed that the onset date of shoot and foliage development for *B. papyrifera* was earlier than the onset date of the stem growth. Unlike *B. papyrifera*, the onset date of shoot and foliage development of *P. banksiana* and *P. tremuloides* was later than the onset date of the stem development. The ending date of new xylem cell division of the three species was in mid August. The completion of cells maturation was observed on September 13th for *P. banksiana* and *P. tremuloides*, and on September 6th for *B. papyrifera*. Among three species, the duration of stem wood formation of *P. banksiana* was the longest, whereas that of *B. papyrifera* was the shortest. During the cell production period, air and soil temperatures were positively correlated with cell production of *P. banksiana*, and negatively correlated with that of *P. tremuloides* and *B. papyrifera*. Precipitation was positively correlated with cell production of *P. tremuloides* and *B. papyrifera*, whereas no correlation was found for *P. banksiana*. Air temperature was positively correlated with shoot elongation of these three species. No significant correlation was found between leaf enlargement of the three species and the meteorological variables.

Key words: intra-annual wood formation, tree phenology, extension growth, growth dynamics.

1.3 INTRODUCTION

Climate controls the timing of tree growth by regulating the initiation and cessation, as well as growth processes of tree different organs (i.e., foliage, shoot, stem, and root) during a growing season. Since the timing of spring growth phases such as bud-break, leafing, shooting, and flowering, is primarily determined by the accumulated temperatures above a threshold value (Beaubien and Freeland, 2000), tree phenology may be advanced by warmer winter and spring temperatures during recent decades. Earlier bud burst, flowering, and leaf unfolding in several species have been observed from long phenological time series. For example, 8 days earlier leafing was observed in several European tree species (*Betula pubescens* Ehrh., *Prunus avium* L., *Sorbus aucuparia* L., and *Ribes alpinum* L.) from 1969 to 1998 (Chmielewski and Rötzer, 2001). In Canada, Beaubien and Freeland (2000) collected data on the first flowering date of trembling aspen and found a 26-day shift to earlier blooming from 1900 to 1997. They also found an 8-day advancement in first flowering date over the period 1936-1996 through analysis of the spring flowering index (mean of the first flowering dates of *Populus tremuloides* Michx., *Amelanchier alnefolia* Nutt., and *Prunus virginiana* L.). In addition, later leaf senescence and fall was also observed (Menzel and Fabian, 1999). Khanduri et al. (2008) summarized delayed autumn events reported in previous studies and found an average delay of 1.4 days per decade in autumn events. Earlier timing of spring phenology and later autumn events demonstrates a longer duration of wood formation during a growing season. This longer duration might affect the intra-annual growth pattern in shoot, leaf, stem and roots, leading to a change in wood properties and tree productivity. Therefore it is very important to better understand intra-annual growth patterns in tree different organs and to explore how meteorological factors influence their development during a growing season.

During recent years, there has been an increasing number of studies focusing on intra-annual xylem formation (e.g., Tardif et al., 2001b; Deslauriers et al., 2003a; 2003b; Rossi et al., 2006b; 2008; Ko Heinrichs et al., 2007; Thibeault-Martel et al., 2008). Of the previous studies, some studies have analyzed cambial activity and xylem formation, and described the dynamics of xylem development and cell differentiation over time (Deslauriers et al., 2003a).

Some studies investigated the endogenous (Nobuchi et al., 1995; Rossi et al., 2008) or exogenous factors controlling intra-annual xylem formation (Savidge, 1996; Deslauriers et al., 2003b; 2008; Rossi et al., 2006b; 2007). A few studies investigated cambial activity and intra-annual xylem formation in roots (Hitz et al., 2008; Thibeault-Martel et al., 2008). In addition, shoot elongation was also documented (Junttila and Heide, 1981; Kanninen, 1985; Ozawa et al., 2000; Chuine et al., 2001). However, all of the above studies essentially focused on the stem or shoot, or root radial growth, but few studies attempt to investigate the intra-annual growth in stems in combination with the intra-annual growth in other parts of the tree, such as in leaves and shoots.

In this study, an investigation of intra-annual xylem formation and foliage and shoot development of one conifer species jack pine and two broadleaf species trembling aspen and white birch was conducted in northwestern Quebec during the 2007 growing season. The purposes of this study were i) to explore the annual pattern and dynamics of stem wood formation and the development of shoot and foliage in these three major boreal tree species during 2007 growing season; ii) to identify the relationships between intra-annual wood formations, shoot and foliage development and weather factors, as well as to determine the major meteorological factors limiting their growth during the growing season.

1.4 MATERIALS AND METHODS

1.4.1 Study site and tree selection

The study area is a part of the Lake Duparquet Teaching and Research Forest of northwestern Quebec, Canada (Harvey, 1999). This region is dominated by continental cold, dry air from the arctic in winter and by warm, moist air from the south in the summer (Sheridan, 2002). Climate observations from the LaSarre meteorological station (about 42 km northward) showed that the mean annual temperature from 1971-2008 was around 0.7 °C, and the average annual total precipitation was around 889.8 mm, with 27.7% in the form of snow (Environment Canada, 2008). In this climate transition zone, there exists a vegetation transition zone from broadleaf and coniferous mixed forests in the south to coniferous dominated boreal forests in the north. The common tree species in this vegetation transition zone include trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), balsam popular (*Populus balsamifera* L.), balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss.), eastern white cedar (*Thuja occidentalis* L.), and Jack pine (*Pinus banksiana* Lamb.) (Bergeron et al., 2004).

In order to easily monitor tree phenology (bud burst, leaf/needle, and shoot development), our study site was selected in a young jack pine plantation forest at Lake Dances (48°31'25"N, 79°25'13"W). In our study site, jack pine trees were planted around 1992 and the clear cut was in 1979 (Claude-Michel Bouchard personal comm.). To avoid the impacts of both natural and human disturbances on tree growth, we chose 10 healthy trees for each species as our study trees to investigate tree phenology (bud burst), the cambium dynamics and intra-annual xylem formation, and the development of shoot and foliage during the 2007 growing season.

1.4.2 Data collection

Field sampling

Micro cores:

To monitor the cambial activity and xylem formation of these three species during the 2007 growing season, wood micro-cores (2.5 mm in diameter and 20-25mm in length) were taken weekly at 1 m above ground in a spiral up the stem of 10 trees per species using Trephor (Rossi et al., 2006a), starting from May 3rd to the end of September, 2007. In order to avoid any disturbance from injury wood (Forster et al., 2000), at least 20-30mm distance was maintained between adjacent sampling locations. Each micro-core was stored immediately in a microtube with 50% aqueous ethanol and stored at 5°C in order to avoid tissue deterioration. In total, 630 samples were taken during 21 weeks growing season of 2007 for these three species.

Tree phenology and the development of shoot and foliage:

Tree phenology (bud burst), shoot elongation and needle/leaf enlargement were recorded for the three species (10 trees per species) from May 3rd to September 27th at the site Lac Dances.

For each jack pine tree, two main branches were chosen from the middle canopy to measure the length of new shoots growth three times per week; For each trembling aspen and white birch tree, five main branches were chosen from the middle canopy to measure the length of new branches and to count the number of the new leaves produced on these new branches three times per week.

In order to measure the leaf area and leaf biomass of new leaves produced during the growing season and to avoid negative impacts of manual defoliation on the study trees, six reference trees were randomly chosen in the same plot three times per week. Leaves from one new shoot per tree were removed to measure the needle/leaf area and needle/leaf biomass each time.

In addition, DBH and tree height were measured for each studied tree. Increment cores were taken at DBH from each tree to determine the exact age of the studied trees. Tree age, height and DBH are reported in Table 1.

Table 1: Tree characteristics with standard deviations of sampled trees.

	Jack pine n=10	White birch n=10	Trembling aspen n=10
Mean DBH (cm)	10.18±1.58	6.82±1.94	8.31±1.56
Mean height (m)	6.59±1.01	7.54±1.84	7.46±0.89
Mean age (year)	14±2	15±2	17±3

Climate data

The weather variables including daily maximum, minimum, mean air and soil temperature, maximum and minimum relative humidity, and precipitation in 2007 were obtained from the weather station at the Lake Duparquet Research Station, which is 2 km from our study site. The detailed variations in meteorological factors in 2007 were shown in Appendix 1.

1.4.3 Laboratory preparation

Collected wood micro-cores were prepared for microscopy according to the following steps (Schweingruber, 1980; Deslauriers et al., 2003b): 1) the wood micro-cores were embedded in paraffin by means of dehydration with ethanol and D-limonene, and were immersed in liquid paraffin successively; 2) to facilitate cutting, wood and cell lumens in both xylem and phloem were well penetrated by liquid paraffin and the microcores were then fixed on biocassettes (support) by means of paraffin blocks; 3) transverse sections of 12 μm were cut with a rotary microtome. In order to identify difference phases of xylem cell development (i.e. radial enlargement, cell wall thickening and mature cell) and count total cell number, the sections were stained with cresyl fast violet (0.05%), and Safranin (1%). When observing the sections under the light microscope, the cells during the cell enlargement phase have pink cell walls, the cell walls of the cell wall thickening phase is violet, and the mature cell wall is complete in blue. The images of all slices were taken with a digital camera under the microscope. Three radial files were selected randomly from each slice. The software Wincell™ (Régent Instruments, Inc. 2007) was used to analyze the images and obtain a series of xylem formation parameters such as cell number, cell size, cell wall thickness, and intra-annual radial width.

1.4.4 Standardization

Due to eccentric growth, trees may produce different tree-ring widths at various places around the circumference of their trunks. The width of annual rings varied within the tree circumference and along the stem, among the different samples (Schmitt et al., 2004). According to Rossi et al. (2003), the number of cells of the three previous years was counted on three radial files per sample and used to standardize the cell number around the circumference of each stem. A ratio was obtained for each sample by dividing the mean cell number of the sample by the mean cell number of all samples per tree. The number of cells in each xylem formation phase (i.e. cell enlargement, cell wall thickening, and mature cell) was then multiplied by the ratio to standardize the data according to the sample's relative position on the stem (Deslauriers et al., 2003). According to the relative position of the sample, the standardized number of cells in each *j*-sample and *i*-phase (nc_{ij}) was calculated as:

$$nc_{ij} = n_{ij} (a_m/a_i)$$

with

$$am = \frac{\sum_{j=1}^{N} a_j}{N}$$

Where n_{ij} was the number of cells counted, a_j the mean cell number of the previous rings for each *j*-sample, *N* the number of *j*-samples and *am* the mean cell number of the previous rings of all *j*-samples.

1.4.5 Statistical analysis

1.4.5.1 Growth fitted by the Gompertz function

The dates for the onset of xylem cell production were compared among three species using the nonparametric Kruskal-Wallis one-way analysis of variances by ranks test (Sheskin, 1997). The xylem cell formation was modeled using a sigmoidal function, specifically the Gompertz function (Gompertz, 1825). Tree-ring increment pattern was determined by fitting the Gompertz function (Deslauriers et al., 2003; Rossi et al., 2006) on the data (weekly cell number, cell size) obtained by the micro-cores measurements. All analyses were conducted using the Sigma Plot statistical package (Sigma Plot Version 10, Systat Software Inc). The Gompertz function is described by Cheng and Gordon (2000) as follows:

(1) $y = a \exp(-e^{(\beta - \kappa t)})$

in which,

y: the cumulative sum of growth;

t: the time computed in day of the year;

a: the upper asymptote of the maximum growth where at $t_i y \approx a$;

β: the x-axis placement parameter;

k: the rate of change parameter.

Through fitting of the Gompertz function, the critical points and phases of intra-annual xylem development such as the onset date of cell formation, the timing of maximum cell numbers, the ending date of cell formation, the rate of cell production during different phases, etc. were determined.

From the estimated constants, the weighted mean absolute rate of cell production (r) was calculated according to Richards (1959):

(2) $r = ak/(2(v+2))$

Where the parameter v was set at 0.0001, since the Gompertz function is a special case of the Richards function when v=0 (Deslauriers et al., 2003):

(3) $r = ak/4$

1.4.5.2 Growth indices

Wood cell formation may be controlled by both endogenous and exogenous factors. In order to detect which exogenous influences are operating during wood formation, the sigmoid trend of endogenous origin has to be removed, as it is common practice in dendrochronology (Fritts, 1976). Detrending processes involve transforming the value of ring width into a dimensionless index value through dividing the observed ring widths by the expected ring widths (Fritts, 1976) given by the spline function. The Gompertz function could well fit the seasonal cell development curve.

All data in Figure 1 (i) were converted to weekly increments of cell growth (Figure 1 (ii)) by taking the vertical difference between two subsequent points.

(4) $WRG = CN_t - CN_{t-1}$

WRG: Weekly Relative Growth

CN: Cumulative Number of cells

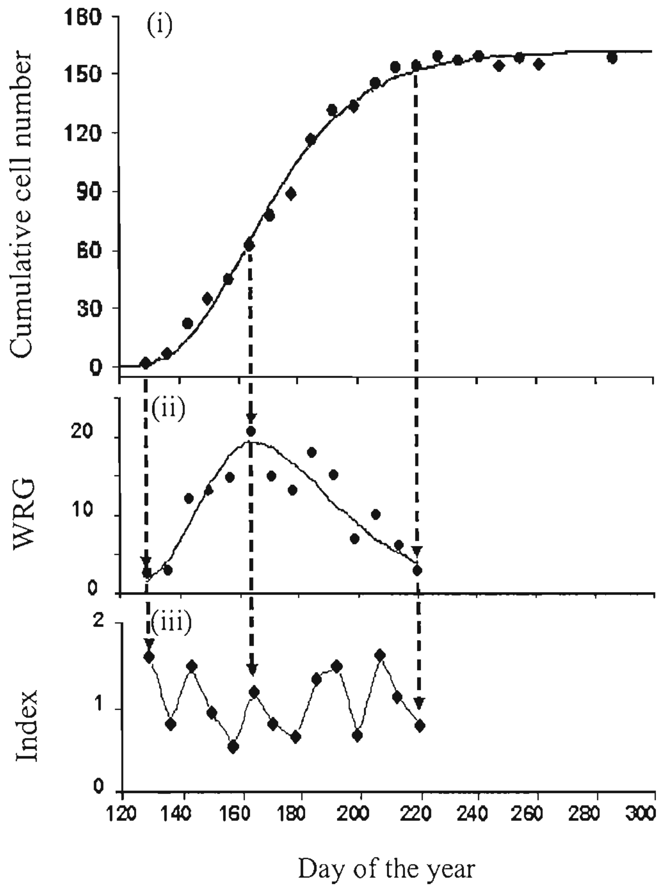


Figure 1: Data measurement and transformation: (i) the dots represent the weekly cumulative cell production during the growth period; the solid line represents the fitted Gompertz function, (ii) the dots are the weekly relative growth values (WRG) and the bell-shaped line represents the estimated WRG value derived from the Gompertz function, and (iii) time series of the weekly index (WI) as ratio between the measured and the estimated WRG.

Here, the endogenous trend still exists but becomes bell shaped (the solid line in the figure 1 (ii)). Then the endogenous trend is removed by dividing the measured weekly relative growth by the estimated weekly relative growth from the Gompertz function.

(5) Weekly Index $=WRG_m/WRG_g$

WRG_m: Weekly Relative Growth by measurement

WRG_g: Weekly Relative Growth estimated by the Gompertz function

So the weekly growth index (Figure 1 (iii)) is free of any trend and the fluctuations of indices around the mean values of 1 are assumed to reflect the expected environmental signal.

1.4.5.3 Climate dependence

Based on the different phases identified, the relationships of these phases with meteorological factors on a weekly basis, including minimum, maximum, and mean air and soil temperature, precipitation, daily minimum and maximum VPD, and relative humidity (RH) were explored by correlation and regression analyses by statistical software. The limiting factors for different phases were determined. The relationships of intra-annual xylem formation of these three species with meteorological factors were also explored by correlation and regression analysis.

The growth of new shoots and foliage during the whole growing season was also fit by the Gompertz function to assess the processes of shoot extension growth and foliage expansion growth. The relationships between weekly shoot and foliage growth and meteorological factors were explored by correlation and regression analysis.

Comparisons among species in timing of onset, duration and ending of xylogenesis, final number of cells produced, and the rate of cell production were performed using analysis of variance (ANOVA).

1.5 RESULTS

1.5.1 Dynamics of intra-annual wood formation

The number of cambial cells and xylem cells of the three species in difference stages was presented throughout the 2007 growing season in Figure 2. Similar annual cambium dynamics were observed in the cambial zones of the three tree species (Figure 2). The dormant cambium consisted of six to eight cells when cell production did not occur from the end of August to the next beginning of May. In May, the number of cells in the cambial zone had increased to 10-15, indicating the onset of cambial activity. The earliest increases in the number of cambium cells were observed in jack pine at the beginning of May, which was 2-3 weeks earlier than trembling aspen and 3-4 weeks earlier than white birch. Cambium cells of jack pine, trembling aspen, and white birch reached their maximum on May 31, June 14, and June 21, respectively. Once annual cambium activity had finished, the number of cambium cells fell to the minimum value which corresponded to the dormant condition of the cambium with 6-8 cambium cells. Termination of cambium activity of the three species occurred about mid August.

The three species showed the same dynamics of xylem cell differentiation which is characterized by delayed bell-shaped curves of enlarging and wall thickening cells, and an S-shaped curve of mature cells. The onset of xylem cell enlargement of the three species, corresponding to the beginning of xylem differentiation, started 2-3 weeks later than the onset of cambium activity. The greatest rate of cell enlargement of the three species was observed in June. It took about a week for the xylem cells of all three species to progress from the cell enlargement phase to the cell thickening phase. The jack pine cell wall thickening phase to mature cell phase took two weeks, but trembling aspen and white birch took one week only. The first mature jack pine, trembling aspen and white birch xylem cells were detected on May 31, June 7 and June 14, respectively.

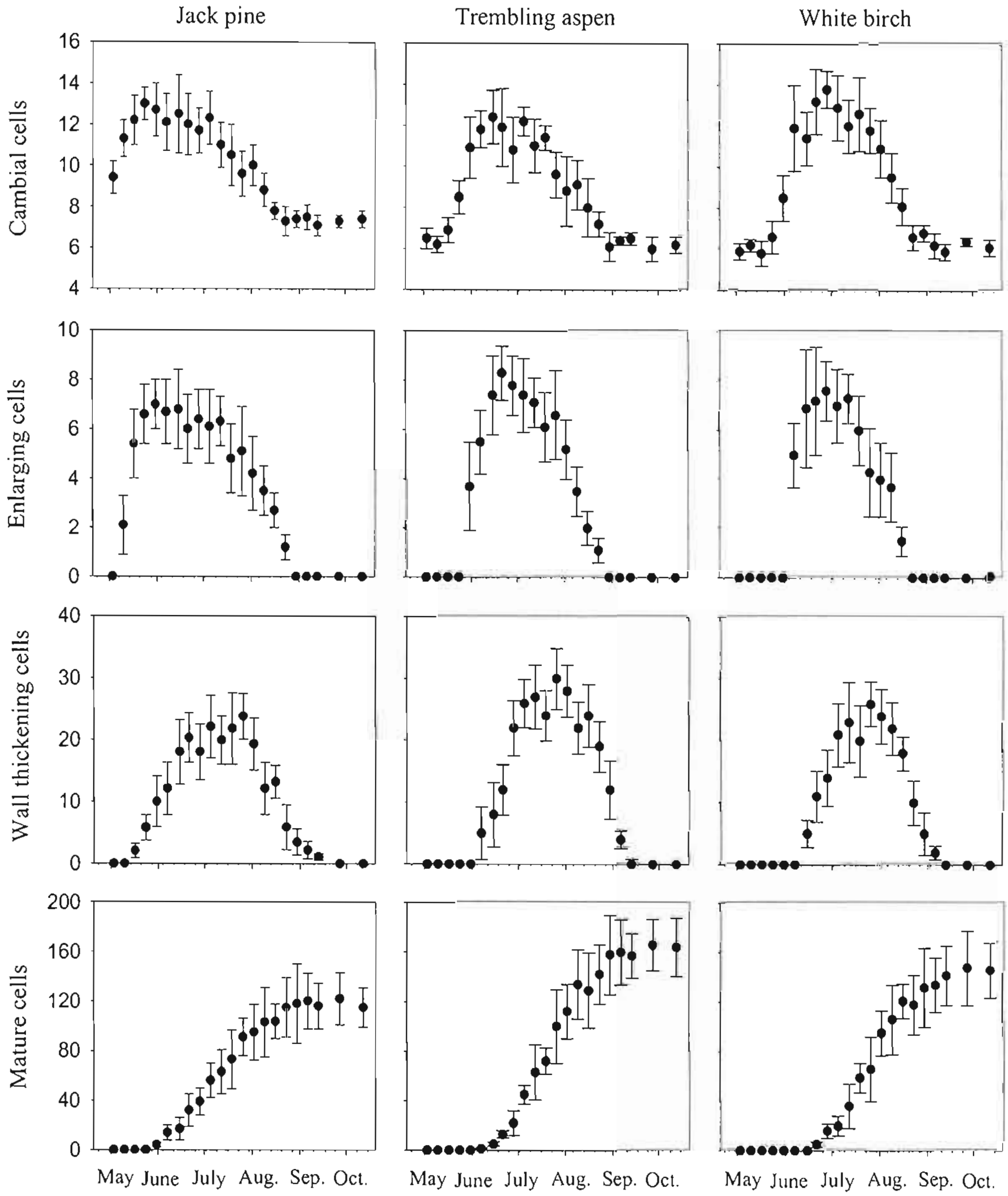


Figure 2: Number of cells in the cambial zone, radial enlargement, secondary cell wall thickening, and mature cells in jack pine, trembling aspen, and white birch during the 2007 growing season. Dots represent the average cells and bars indicate the standard deviations among trees.

Weekly cumulative cell production was well fit with the Gompertz function as shown by the R^2 values of 0.93, 0.94 and 0.92 for jack pine, trembling aspen and white birch, respectively (Figure 3). The parameters of the Gompertz function fit to the cell formation data of the three species are listed in Table 2.

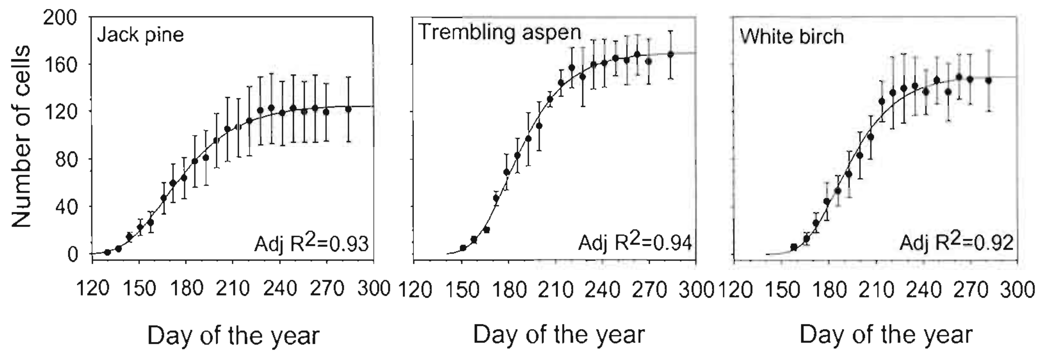


Figure 3: Number of xylem cells over time and the Gompertz curve fit to cumulative cell production for the three species during the 2007 growing season. The dots represent the average cells, and the bars indicate standard deviations among trees.

Table 2: Parameters of the Gompertz function fit to the cell formation data of the three species, Adj.R^2 and the rate of the cell formation (r) of jack pine, white birch and trembling aspen in the 2007 growing season.

	a	β	κ	r	Adj. R^2
Jack pine	125.8	6.45	0.0387	1.22	0.93
Trembling aspen	166.2	8.39	0.0473	1.97	0.94
White birch	150.2	8.92	0.0481	1.81	0.92

The onset, duration and ending of cell differentiation were computed in days of the year for each tree of the three species. Averages were reported in Figure 4, where the bars correspond to the mean value and the error bars to the standard deviation among trees. The onset of cell formation of jack pine, trembling aspen and white birch, corresponding to the first xylem cell observed in the cell enlargement phase, occurred on May 7, May 28, and June 5, respectively. It was significantly different among the three species (ANOVA, F=8.30, P<0.01). The earliest start of cell formation was observed in jack pine. The latest start of cell formation occurred in white birch. Both jack pine and trembling aspen terminated cell formation (i.e. the lignifications of the xylem cell is completed) on September 13, which was one week later than white birch. The duration of cell differentiation was between 98 and 126 days and was significantly different among the three species (ANOVA, F=9.68, P<0.01). Jack pine had the longest growing season, and white birch had the shortest growing season among three species. The total number of cell production for jack pine, trembling aspen and white birch was 125, 166 and 150, respectively, and no significant difference was detected between the two broadleaf species (ANOVA, F=1.15, P>0.05). The average rate of cell production for jack pine, white birch and trembling aspen was 1.22, 1.81, and 1.97 cells per day, respectively, and also no significant difference was detected between the two broadleaf species (ANOVA, F=0.24, P>0.05).

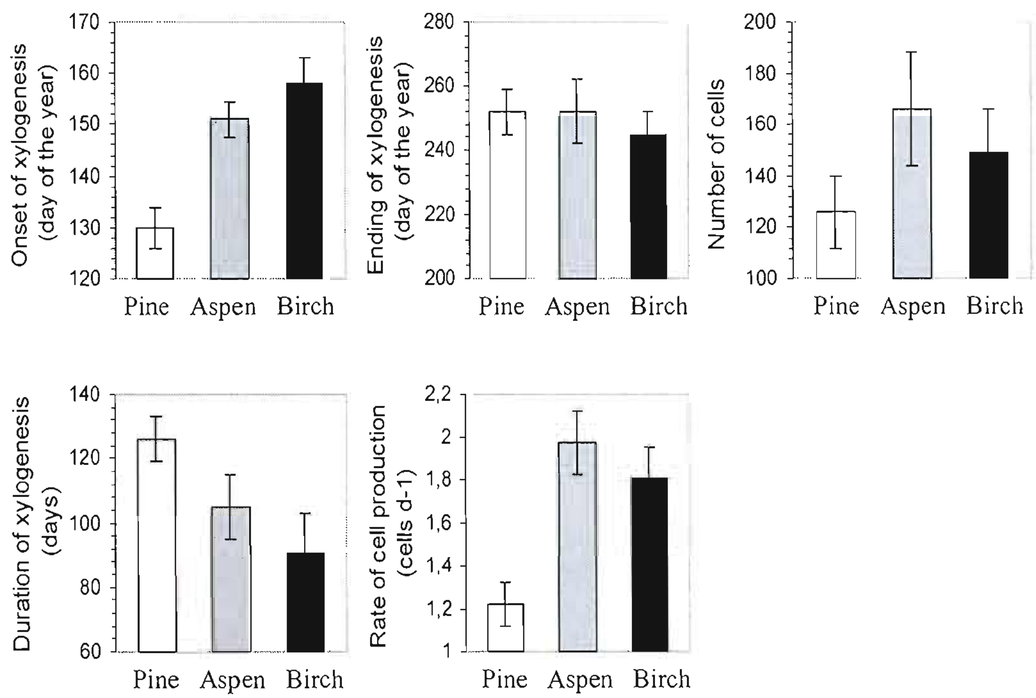


Figure 4: Onset, ending and overall duration of cell differentiation, number of cells producted and the rate of cell production for jack pine, trembling aspen, and white birch during the 2007 growing season. The bars show the standard deviation among trees.

1.5.2 Development of shoot and foliage and wood formation

The three species showed clear differences in the onset, duration and cessation of shoot elongation, of leaf enlargement, and of stem cell division (Figure 5).

In the field, we considered the timing of budburst as the timing of the onset of shoot elongation and foliage enlargement of the three species. Within a species, the onset of shoot elongation and leave enlargement was different when compared to the onset of stem cell division (Figure 5A). The onset of shoot elongation and foliage enlargement was on May 20, May 22, and May 27 for jack pine, white birch and trembling aspen, respectively. However, the onset of xylem cell division was detected on May 7, June 5 and May 28 for jack pine, white birch and trembling aspen, respectively. As a consequence, the onset of stem cell division of jack pine and trembling aspen was, respectively, 13 days and 1 day earlier than that of shoot elongation and needle/leaf enlargement. However, the onset of stem cell division of white birch was 14 days later than that of shoot elongation and leaf enlargement.

The shoot elongation and needle enlargement of jack pine finished on June 28 and August 2, respectively. The end of shoot elongation and leaf enlargement was on June 21 and July 10 for trembling aspen, and on July 12 and July 30 for white birch, respectively. The three species showed the same order in the ending date of shoot elongation, leaf enlargement, and stem cell division, i.e., ending of shoot elongation earlier than that of foliage enlargement, and ending of foliage enlargement earlier than that of stem cell division.

Between the two broadleaf species, the onset of shoot elongation and leaf enlargement of trembling aspen were 5 days later than that of white birch. But the ending date of shoot elongation and leaf enlargement of trembling aspen was 21 days earlier than that of white birch. This indicates that the duration of shoot elongation and leaf enlargement of trembling aspen is shorter than that of white birch (Figure 5B). The three species also showed that the duration of shoot elongation is shorter than the duration of stem cell division and leaf enlargement.

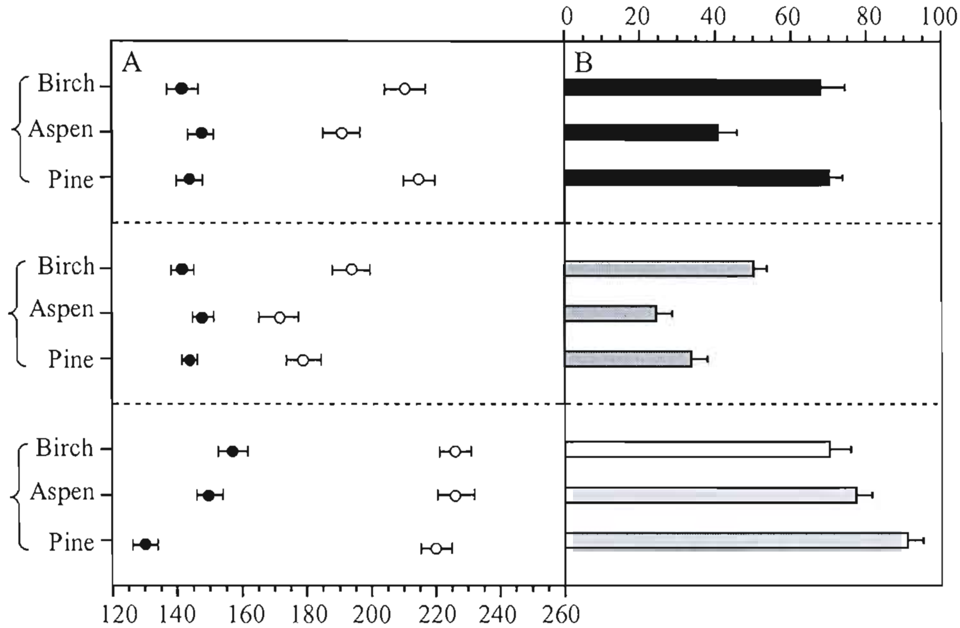


Figure 5: Onset date, ending date (A) and duration (B) of the principal phenological events (i. e. stem xylem cell division, shoot elongation, foliage enlargement) of the three species during the 2007 growing season. The closed cycle represents the onset date; the open cycle represents the termination date. The bars correspond to the mean value of duration and the error bars correspond to the standard deviation among trees.

In Figure 6, the results showed similar growth pattern but delayed growth dynamics in shoot elongation, needle/leaf enlargement and stem cell production during the growing period in our studied species. Jack pine had a delayed S-shaped curve for stem and needle developments compared with an S-shaped curve for shoot development. White birch demonstrated a delayed S-shaped curve of stem growth in comparison with the S-shaped curves of shoot and leaf growth. Trembling aspen was in turn found to have delayed S-shaped curves for shoot, leaf, and stem development.

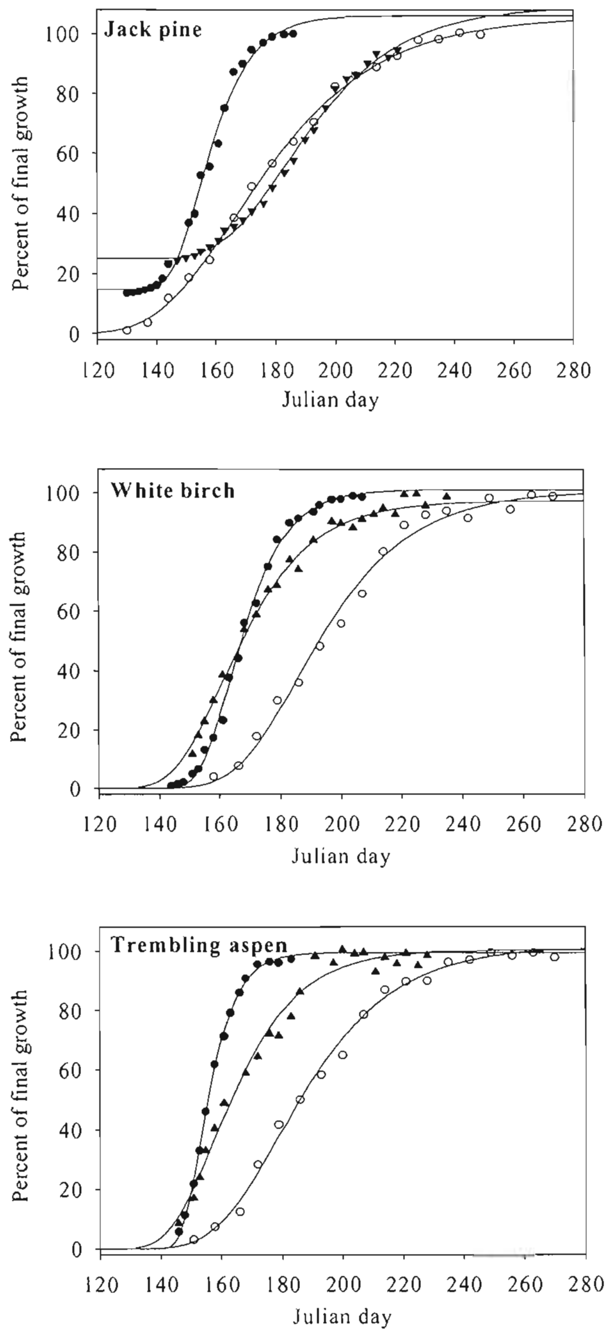


Figure 6: Growth pattern of wood cell formation (open circles), shoot elongation (closed circles), and leaf enlargement (triangle) and its Gompertz curve of the three species during the 2007 growing season.

1.5.3 Relationships between meteorological factors and intra-annual xylem formation, shoot and foliage development

The immediate response of these three species to ambient weather conditions is clear from the result of the climate-growth analysis (Figures 7-9). Correlation analysis results showed that minimum air temperatures and minimum soil temperatures were significantly positively correlated with jack pine cell production (Figure 7). Other meteorological variables such as mean and maximum air temperatures, precipitation, RH, or VPD were not statistically significant correlated with jack pine wood cell formation of. Maximum air temperature was negatively correlated with cell production of trembling aspen. Precipitation was positively correlated with both trembling aspen and white birch cell production. No significant correlations were found between wood formation of trembling aspen and white birch and soil temperature, RH, and VPD.

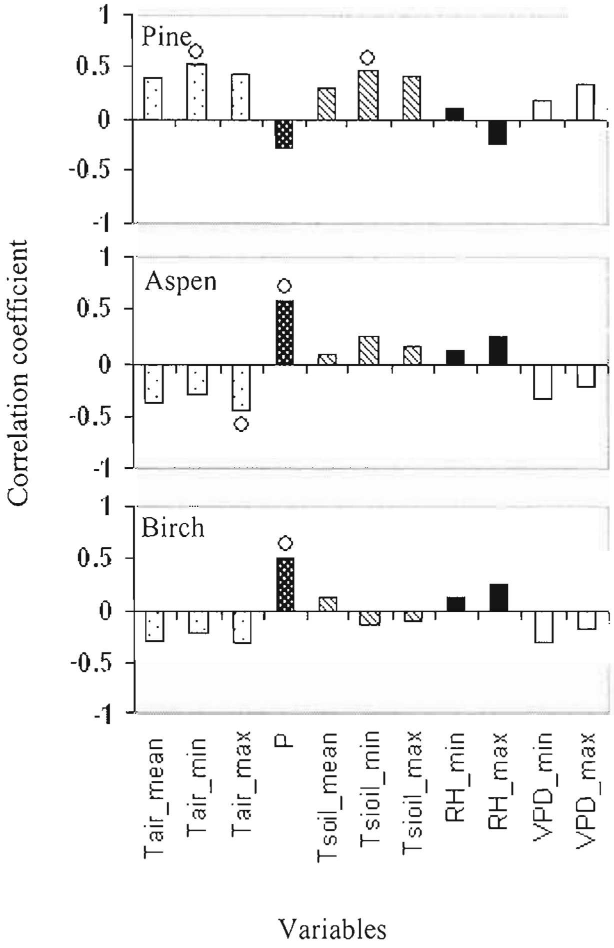


Figure 7: Simple correlation coefficients (Pearson, $p<0.05$) between the rate of intra-annual wood formation and meteorological factors during the 2007 growing season. T_{air} (air temperature), T_{soil} (soil temperature), P (precipitation), RH (relative humidity), and VPD (vapor pressure deficit). Significant results ($p<0.05$) are marked by open cycles.

In Figure 8, the results show that mean, minimum, and maximum air temperatures significantly correlate with shoot elongation of jack pine during the growth period. Maximum air temperature was positively correlated with shoot elongation of trembling aspen and white birch. No significant correlation was found between shoot elongation of the three species and other meteorological variables.

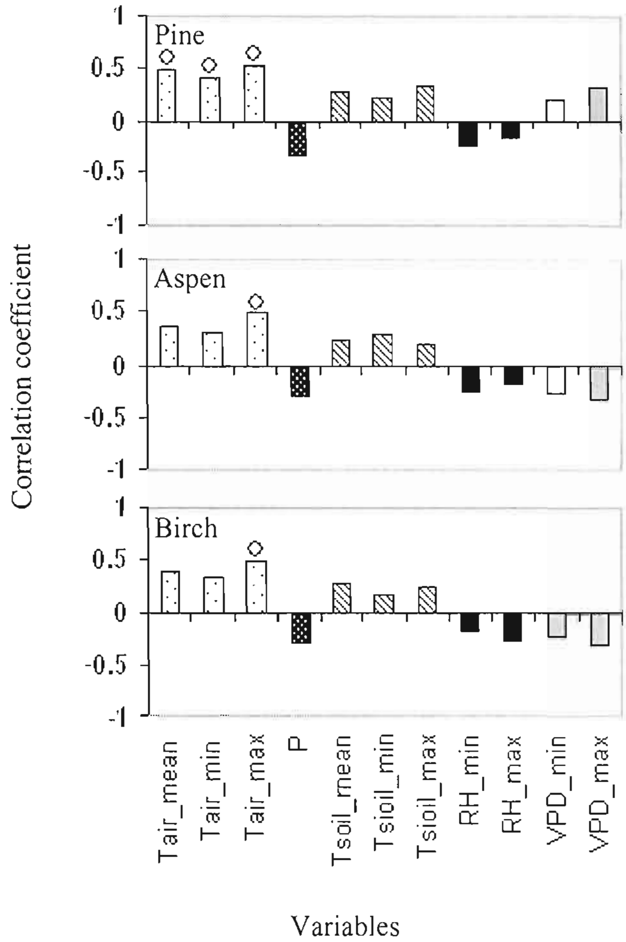


Figure 8: Simple correlation coefficients (Pearson, p<0.05) between the rate of shoot extension growth and meteorological factors during the 2007 growing season. T_{air} (air temperature), T_{soil} (soil temperature), P (precipitation), RH (relative humidity), and VPD (vapor pressure deficit). Significant results ($p<0.05$) are marked by open cycles.

Our results show no significant correlation between leaf enlargement of the three species and meteorological variables (Figure 9). But most of the meteorological variables were positively correlated with leaf enlargement except for the negative correlation observed between leaf enlargement and maximum and minimum VPD.

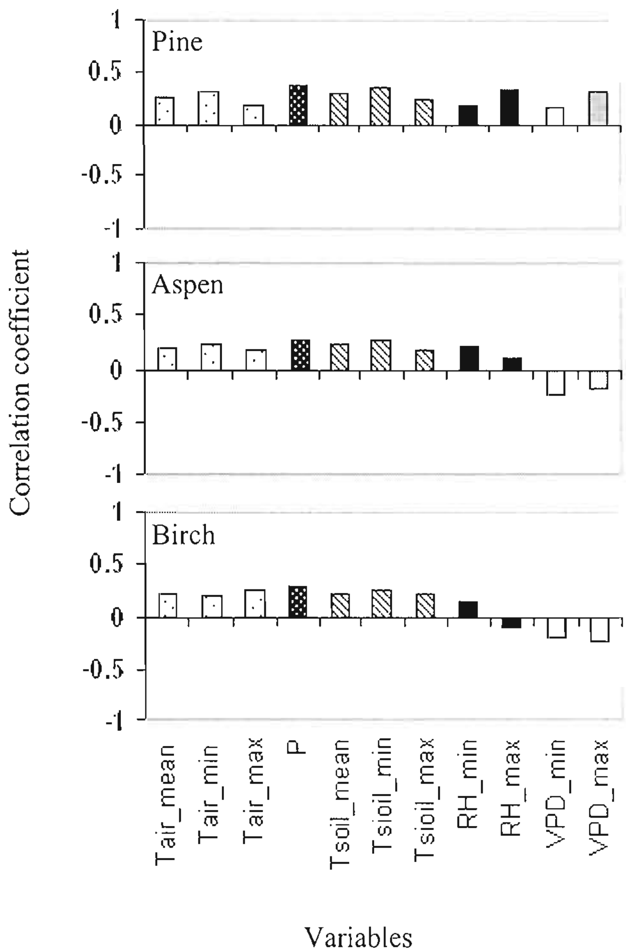


Figure 9: Simple correlation coefficients (Pearson, $p<0.05$) between the rate of foliage enlargement and meteorological factors during the 2007 growing season. T_{air} (air temperature), T_{soil} (soil temperature), P (precipitation), RH (relative humidity), and VPD (vapor pressure deficit). Significant results ($p<0.05$) are marked by open cycles.

1.6 DISCUSSION

Trees are vulnerable to climate extremes such as drought and frost during a growing season. Climate warming might result in increased frequency and amplitude of climate extremes such as drought and frost during the growing season (IPCC, 2007; Huntington, 2004). In our study, we found that different climate factors affect the intra-annual growth of the tree and of different tree parts. Difference in timing of intra-annual growth for each species might cause different growth periods among species. Thus trees that are affected by different climate factors and undergone different growth periods might be subjected to a different period of vulnerability to drought and frost under climate warming.

1.6.1 Intra-annual growth pattern and dynamics

Past studies on the physiology of cambial activity suggested that, in conditions where temperature strongly limits the radial growth of trees, the temperature must be higher than a given threshold and the thawing of the upper soil layer after snow melt must have begun so that radial growth can begin (Vaganov et al., 1999; Kirdyanov et al., 2003). In this study, the onset of the first xylem cell formation for jack pine was observed approximately on May 7th, when minimum air temperature during consecutive days from May 6th-10th was above 5°C (5-days mean temperature was 5.3°C), and warmer than before. This temperature is consistent with the threshold temperature triggering tree growth in spring reported in previous studies. Schmitt et al. (2004) documented that at the tree line growth occurred when the daily temperature was above 5°C. Rossi et al. (2007) reported that xylogenesis was active when the mean daily air temperature was 5.6°C-8.5°C. However, minimum air temperature for the onset of new xylem cell production of trembling aspen and white birch was approximately 8.2°C-10.4°C. We do not know if these different temperature thresholds are real or coincidental and the result of the climate pattern during the year in question. The different temperature triggering the onset of the xylem formation between jack pine and the two broadleaf species indicates that the onset of the xylem formation of broadleaf trees might be controlled by a different interaction between air temperatures, and external factors (e.g. photoperiod, water availability (Hänninen, 1995; Leinonen et al., 1997)) and internal factors (e.g. auxin production (Wang et al., 1997)).

We found that the onset date of shoot and foliage development for trembling aspen was later than the onset date of the stem development, indicating that the carbohydrate reserved in the previous growth year played an important role in producing new xylem cells. This supports the well known fact that conditions of the previous year are of critical importance for radial growth of the current year (Hogg et al., 2005; Leonelli et al., 2008), since a good portion of the xylem growth precedes leaf extension. The onset date of shoot and foliage development for white birch was earlier than the onset date of stem growth, suggesting that the formation of early xylem cells might be triggered by photosynthesis in new leaves formed during early growing season. This supports the findings of some tree-ring studies that found that the climate conditions in the current growth year are important for radial growth of white birch (Tardif et al., 2001b; Levanič and Eggertsson, 2008). Unlike many hardwoods, foliage development of most pine is a slow process. The onset date of the shoots and needles for jack pine was later than the date of onset of the stem, suggesting that the carbohydrate reserves in the previous year and photocarbohydrates produced by old needles might together stimulate new xylem cells formation during the early growing season. Our results show that the coordination of different organs in a given tree species is species-specific. In our study, the data of jack pine agreed with the study of Vaganov et al. (1999) who reported that the timing of the thaw in spring is critical for cambial initiation of boreal forests. Compared with the ever-green boreal conifers, broadleaf trees need a higher temperature for bud burst (about 6°C, Grace et al., 2002) after the soil thawing in spring because photosynthesis cannot occur while the new leaves are not produced.

Among the three species, the duration of leaf enlargement for trembling aspen was shorter than the other two species. Since trembling aspen's all leaves emerge simultaneously after budbreak with a short duration of shoot elongation, if late spring frost occurs after leaf emergence, subsequent tree growth during the growing season will be suffered seriously. The IPCC (2007) reported that there will be more frequent climate events such as spring frost, thus affecting trembling aspen growth. In contrast, the leaves of white birch emerge one by one successively after budbreak with a long duration of shoot elongation. Therefore subsequent white birch growth will be less suffered by late spring frosts. Trembling aspen is a shade intolerant species, and the short duration of its shoot elongation and leaf enlargement could help trees to occupy the upper canopy space and thus avoid the shade of other tree species. However, white birch is a more shade tolerant species than trembling aspen and the long duration of its shoot and leaf development could allow the trees to invade new habitats by expanding photosynthetic organs as widely as possible using the current year's products or by using newly-formed leaves (Kikuzawa, 1982). Therefore, white birch could often coexist with trembling aspen in the boreal forest (Bergeron, 2000).

We found that the shoot elongation was complete earlier than foliage enlargement and stem cell production. In the forest, due to species competition, trees attempt to reach maximum shoot length and tree height during a short time period to occupy a favourable spatial condition for photosynthesis.

Intra-annual variations in the rate of cell division and differentiation determine variations among the cell queues, resulting in a typical annual pattern consisting of three bell-shaped curves (cambial, cell enlargement, and cell wall thickening cells) and a growing S-shaped curve (mature cells). The bell-shaped patterns are connected with the number of cells passing through each differentiation phase, whereas the S-shaped curves are associated with the gradual accumulation of mature cells in the tree ring. Similar bell-shaped curves of cambial cells and enlarging cells suggest that an increase in the rate of formation of new xylem cells was always accompanied by an increase in the number of cells in the cambial zone (Vaganov et al., 2006).

A shorter duration of cell changing from the wall thickening phase to the mature phase for trembling aspen and white birch than that of jack pine suggests that broadleaf species had faster maturation rate than jack pine. This might be caused by higher photosynthesis of broadleaf species than that of jack pine. Broadleaf species have a larger leaf area than jack pine, thus producing greater carbohydrates in a short time period than jack pine. Thus their cells become mature faster than jack pine. Great annual total cell production might be due to high cell production rate. Among three studied species, the highest cell production rate of trembling aspen could result in the greatest total cell number, whereas the lowest cell production rate of jack pine might lead to the smallest cell number.

The ending date of new cell production of jack pine, trembling aspen, and white birch was on August 9th, 16th, and 16th, respectively. Our results are consistent with Vaganov et al. (2006), who reported that at high latitude new cell production of tree species usually ceased in about mid-August. Thus the duration of new xylem cell division is mainly determined by the onset date of new cell division (Vaganov et al., 2006). The modelled date of the first cell division depends on the estimated dates of the end of constant snow cover and threshold values of air temperature and effective temperature sum (Vaganov et al., 1999). Jarvis and Linder (2000) suggested that the timing of the thaw in spring is critical because neither cambial cell division nor uptake of nutrients and carbon dioxide can occur while the soil is frozen. Thus both spring temperature and the date of snow melt (relative with winter precipitation) are critical for not only the onset of new cell production, but also the duration of the cell production period. A warmer and earlier spring combined with less winter precipitation could result in a longer duration of cell production. In addition, minimum air temperature was about 11.2°C when the new cell production of three species ceased at our study site, indicating that the new cell production ceased at a much higher temperature than it necessary for its initiation in the spring.

When new xylem cell production ceases, the annual tree ring width almost reached final width because cell wall thickening occurs at the inside of the cell wall but does not affect cell size. Therefore in the current growing season, annual ring width is primarily influenced by the meteorological factors during the new cell production period, i.e., from mid-May to mid-August. Dendroclimatic studies of birch in north Iceland found that June and July temperature positively influence tree ring width (Levanič and Eggertsson, 2008). Cell wall thickness is related to wood density. Cell wall thickening is operated throughout the whole cell formation period. This indicates that wood density might be controlled by climate factors (mostly summer temperatures suggested in the past study (Wang et al., 2002)) from the onset of cell formation to the ending of cell lignification (May-September).

1.6.2 Climate dependence

Intra-annual wood formation is controlled by both endogenous (age, size, gene) and exogenous factors (climate and disturbances). However, previous studies investigated the effect of meteorological factors on intra-annual wood formation without removal of endogenous origin trend (Gruber et al., 2008). Thus their results are questionable. In this study, we found that the weekly cell index calculated after removal of the largely endogenously determined growth pattern performed better than other studies. Therefore removal of endogenous origin trend in the weekly cell growth is needed when exploring the effects of climate variables on the intra-annual xylem formation.

During the period of xylem cell production of jack pine from May 7th to August 9th, a positive correlation between the weekly cell increment index and air and soil minimum temperatures indicates that temperature was a dominant factor for positively controlling cell production of jack pine. Past studies found that the tracheids mainly divide and enlarge during the warmest period of the growing season (Wang et al., 2002) because temperature has a strong effect on assimilate and phytohormone production in needles (Lachaud, 1989). Gruber et al. (2008) also found that air and soil temperatures were shown to positively control xylem development of stone pine (*Pinus cembra* L.) in western Austria. Other studies also documented that temperature (Antonova and Stasova, 1993), especially night temperature (Richardson and Dinwoodie, 1959), is a critical factor for influencing radial cell enlargement, which is consistent with previous dendroclimatological studies of these three boreal tree species (Tardif et al., 2001a). The positive effect of temperature on radial cell growth was also supported by many tree-ring studies that found positive effect on radial growth of jack pine during the growing season (Hofgaard et al., 1999; Tardif et al., 2001a). Warmer soil temperature could favour root activity and thus transport more water and nutrients for cell growth.

Shoot elongation of jack pine was positively limited by temperature during the growth period. Kanninen (1985) documented that night temperature positively affected the shoot elongation rate more than day temperature through analysis of shoot elongation in *Pinus sylvestris* during the period of maximum elongation rate. Our study showed that the needle area was positively correlated with temperature, but did not reach a significant level at $p<0.05$. Junttila and Heide (1981) reported that the needle length of *Pinus sylvestris* was significantly positively associated with the mean temperature of the growing season, especially Junc-August temperature in Northern Fennoscandia. The non-significant correlation might result from insufficient weekly data or artificial errors during needle collection from the reference trees over the growing season.

Cell production of trembling aspen was found to be positively correlated with precipitation, and negatively correlated with maximum air temperature from May 28th to August 16th. This indicates that trembling aspen was water-limited during cell production period in the summer. Schweingruber (1996) observed that there was a negative correlation between xylem formation of trembling aspen and air temperature. He further interpreted that the negative effect of high temperature could be due to temperature-caused drought stress in trees, which in turn reduces photosynthesis production. White birch was also shown to be water-limited during cell production period from June 4th to August 16th. Our results together indicate that cell production of two broadleaf species were mainly water-limited during the cell production period in the growing season. Sufficient precipitation may be able to meet their water demands during leaf elongation in hot summer. Tardif et al. (2001a) also revealed that white birch was positively limited by June precipitation. Broadleaf species have been extensively reported to be water-limited during the growing season in many studies (Tardif et al., 2001a; 2001b; 2006; Hogg et al., 2005).

Shoot elongation of trembling aspen and white birch was shown to be positively associated with air temperature. Leaf area growth of two broadleaf species was found to have non significant ($P<0.05$) positive correlation with temperature. We attributed this insignificant correlation to insufficient leaf area data collected during the summer because the duration of leaf elongation (from the timing of the budburst to the timing of the maximum leaf size) of trembling aspen and white birch was short, around 43 days and 69 days, respectively. Since leaf measurements are destructive and we cannot remeasure the leaf area of the same leaf the scatter in the leaf area data is larger and we, therefore, failed to establish a significant correlation with climate.

1.7 CONCLUSIONS

In this study, we investigated the intra-annual growth of stem, shoot, and foliage of three major boreal tree species jack pine, trembling aspen, and white birch in northwestern Quebec during the 2007 growing season. Our results showed that soil and air temperature during the intensive growth period from mid-May to mid-August was a primary factor for positively affecting stem, shoot and needle growth of jack pine. The atmospheric and soil moisture conditions during the growth period were important for stem growth of trembling aspen and white birch, whereas June-August temperatures were critical for the shoot elongation and perhaps also for the foliage enlargement. The coordination among stem, foliage and shoot for a given species was species-specific. For example: the budburst was earlier in white birch than in trembling aspen, but the leaves are growing more rapidly and the maximum leaf area was attained earlier in trembling aspen than in white birch. The different timings of these phenological events show that trees will be sensitive to climate events during different time periods and will have different periods of climatic vulnerability. This study provides us some clues for the allocation of carbohydrates among different tree organs during the growth period. An extended growing season as a consequence of climate warming might lead to earlier budburst, shoot elongation, leaf enlargement, and stem cell division. But they also might be suffered from some spring frosts, thus resulting in growth interruptions or reductions, which will have important impacts on forest productivity. Hence future more intra-annual growth of tree organs during subsequent several growing seasons will be needed to improve our understanding of tree growth and to better simulate and predict tree growth in the boreal forest

1.8 ACKNOWLEDGEMENTS

This work was funded by the Fonds québécois pour la sciences et la technologie (FQRNT), programme en équipe and the Canada Chair in Forest Ecology and Management. We thank Danielle Charron, Jianguo Huang, Anne Jetté, and Alain Leduc for their assistance during fieldwork. We also thank Venceslas-Claude Goudiaby for technical advice on collecting field data.

1.9 REFERENCES

Antonova, G.F., and Stasova, V.V. 1993. Effects of environmental factors on wood formation in Scots pine stems. Trees 7: 214-219.

Beaubien, E.G., and Freeland, H.J. 2000. Spring phenology trends in Alberta, Canada: links to ocean temperature. International Journal of Biometeorology 44(2): 53-59.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Québec's southern boreal forest. Ecology 81(6): 1500-1516.

Bergeron, Y., Gauthier, S., Flannigan, M., and Kafka, V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in Northwestern Quebec. Ecology 85(7): 1916-1932.

Cheng, C. and Gordon, I.L. 2000. The Richards function and quantitative analysis of germination and dormancy in meadow-foam (Limnanthes alba). Seed Science Research 10: 265-277.

Chmielewski, F. M., and Rötzer, T. 2001. Response of tree phenology to climate change across Europe. Agricultural and Forest Meteorology 108: 101-112.

Chuine, I., Aitken, S.N., and Ying, C.C. 2001. Temperature thresholds of shoot elongation in provenances of Pinus contorta. Canadian Journal of Forest Research 31: 1444-1455.

Deslauriers, A., Anfodillo, T., Rossi, S., and Carraro, V. 2007. Using simple causal modeling to understand how water and temperature affect daily stem radial ariation in trees. Tree Physiology 27: 1125-1136.

Deslauriers, A., Morin, H., and Bégin, Y. 2003a. Cellular phenology of annual ring formation of Abies balsamea in the Quebec boreal forest (Canada). Can. J. For. Res. 33: 190-200.

Deslauriers, A., Morin, H., Urbinati, C., and Carrer, M. 2003b. Daily weather response of balsam fir (Abies balsamea (L.) Mill.) stem radial increment from dendrometer analysis in the boreal forest of Quebec (Canada). Trees 17: 477-484.

Environment Canada (2008) Climate trends and variations bulletin for Canada. Environment Canada Atmospheric Environment Service Climate Research Branch, http://www.msc-smc.ec.gc.ca/ccrm/bulletin/regional_e.cfm.

Forster, T., Schweingruber, H.F., and Denneler, B. 2000. Increment puncher. A tool for extracting small cores of wood and bark from living trees. IAWA Journal 21: 169-180.

Fritts, H.C. 1976. Tree rings and Climate. Academic Press, New York.

Gompertz, B. 1825. On the nature of the function expressive of the law of human mortality and on a new mode of determining life contingencies. Phil. Trans. R. Soc. 2: 513-585.

Gruber, A., Baumgartner, D., Zimmermann, J., and Oberhuber, W. 2008. Temporal dynamics of wood formation in Pinus cembra along the alpine treeline ecotone and the effect of climate variables. Trees 23: 625-635.

Hänninen, H. 1995. Effects of climate changejon trees from cool and temperate regions: an ecophysiological approach to modelling of bud burst phenology. Can. J. Bot. 73: 183-199.

Harvey, B. 1999. The Lake Duparquet Research and Teaching Forest: Building a foundation for ecosystem management. For. Chron. 75(3): 389-393.

Hitz, O.M., Gärtner, H., Heinrich, I., and Monbaron, M. 2008. Wood anatomical changes in roots of European ash (Fraxinus excelsior L.) after exposure. Dendrochronologia 25: 145-152.

Hofgaard, A., Tardif, J., and Bergeron, Y. 1999. Dendroclimatic response of Picea mariana and Pinus banksiana along a latitudinal gradient in the eastern Canadian boreal forest. Canadian Journal of Forest Research 29: 1333-1346.

Hogg, E.H., Brandt, J.P., and Kochtubajda, B. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Canadian Journal of Forest Research 35: 610-622.

Huntington, T. G. 2004. Climate Change, Growing Season Length, and Transpiration: Plant Response Could Alter Hydrologic Regime. Plant Biology 6: 651-653.

IPCC (Intergovernmental Panel on Climate Change) 2007. Climatic Change 2007: the Physical Science Basis. In: Proceedings of the 10th Session of Working Group I of the IPCC, Paris, Feburary 2007.

Jarvis, P. and Linder, S. 2000. Constraints to growth of boreal forests. Nature 405: 904-905.

Junttila, O. and Heide, O.M. 1981. Shoot and needle growth in pinus sylvestris as related to temperature in northern Fennoscandia. For. Sci. 27: 423-430.

Kanninen, M. 1985. Shoot elongation in Scots pine: diurnal variations and response to temperature. Journal of Experimental Botany 36: 1760-1770.

Khanduri, V. P., Sharma, C. M., and Singh, S. P. 2008. Thc cffccts of climate change on plant phenology. Environmentalist 28: 143-147.

Kikuzawa, K. 1983. Leaf survival of woody plants in deciduous broad-leaved forests. 1. tall trees. Can. J. Bot. 61: 2133-2139.

Kirdyanov, A.V., Hughes, M., Vaganov, E.A., Schweingruber, F.H., and Silkin, P. 2003. The importance of early summer temperature and date of snow melt for tree growth in The Siberia Subarctic. Trees 17: 61-69.

Ko Heinrichs, D., Tardif, J., and Bergeron, Y. 2007. Xylem production in six tree species growing on an island in the boreal forest region of western Quebec, Canada. Can. J. Bot. 85: 518-525.

Lachaud, S. 1989. Participation of auxin and abscisic acid in the regulation of seasonal variations in cambial activity and xylogenesis. Trees 3: 125-137.

Leinonen, L., Repo, T. and Hanninen, H. 1997. Changing environmental effects on frost hardiness of Scots pine during dehardening. Ann. Bot. 79: 133-138.

Leonelli, G., Denneler, B., and Bergeron, Y. 2008. Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada. Canadian Journal of Forest Research 38: 1211-1222.

Levanič, T. and Eggertsson, O. 2008. Climatic effects on birch (Betula pubescens Ehrh.) growth in Fnjoskadalur valley, northern Iceland. Dendrochronologia 25: 135-144.

Menzel, A. and Fabian, P. 1999. Growing season extended in Europe. Nature 397: 659.

Nobuchi, T., Ogata, Y., and Siripatanadilok, S. 1995. Seasonal characteristics of wood Formation in Hopeaodorata and Shorea henryana. IAWA Journal 16: 361-369.

Ozawa, H., Itoh, K., and Hori, Y. 2000. Shoot structure and dynamics of saplings and canopies of three deciduous broad-leaved trees of a coppice forest in central Japan. Trees 14: 206-214.

Richardson, S.D., and Dinwoodie, J.M. 1959. Studies on the physiology of xylem development. I. The effects of night temperature on tracheid size and wood density in conifers. Journal of the Institute of Wood Science 6: 3-13.

Rossi, S., Deslauriers, A., Anfodillo, T., and Carrer, M. 2008. Age-dependent xylogenesis in timberline conifers. New Phytologist 177: 199-208.

Rossi, S., and Deslauriers, A. 2007. Intra-annual time scales in tree rings. Dendrochronolgia 25: 75-77.

Rossi, S., Deslauriers, A., Anfodillo, T., and Carraro, V. 2007. Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. Oecologia 152: 1-12.

Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R., and Borghetti, M. 2006a. Conifers in cold environments and synchronize maximum growth rate of tree-ring formation with day length. New Phytologist 170: 301-310.

Rossi, S., Anfodillo, T., and Menardi, R. 2006b. Trephor: a new tool for sampling Microcores from tree stems. IAWA Journal 27(1): 89-97.

Savidge, R.A. 1996. Xylogenesis, genetic and environmental regulation. IAWA Journal 17: 269-310.

Schmitt, U., Jalkanen, R., and Eckstein, D. 2004. Cambium dynamics of Pinus sylvestris and Betula spp. in the northern boreal forest in Finland. Silva Fennica 38(2): 167-178.

Schweingruber, F.H. 1996. Tree Rings and Environment: Dendroecology. Swiss Federal Institute for Forest, Snow and Landscape Research, Paul Haupt Publishers, Brimensdorf and Bern.

Schweingruber, F.H. 1978. Microscopic wood anatomy, mikroskopische Holzanatomie. Available at Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf.

Sheridan, S. C. 2002. The redevelopment of a weather-type classification scheme for North America. International Journal of Climatology 22: 51–68.

Tardif, J. and Bergeron, Y. 1993. Radial growth of Fraxinus nigra in a Canadian boreal floodplain in response to climatic and hydrological fluctuations. Journal of Vegetation Sciences 4: 751-758.

Tardif, J., Conciatori, F., and Bergeron, Y. 2001a. Comparative analysis of the climatic response of seven boreal tree species from northwestern Québec, Canada. Tree-ring Research 57: 169-181.

Tardif, J., Flannigan, M., and Bergeron, Y. 2001b. An analysis of the daily radial activity of 7 boreal tree species, northwestern Quebec. Environmental Monitoring and Assessment 67: 141-160.

Thibeault-Martel, M., Krause, C., Morin, H., and Rossi, S. 2008. Cambial activity and intra-annual xylem formation in roots and stems of Abies balsamea and Picea mariana. Annals of Botany 102: 667-674.

Vaganov, E.A., Hughes, M.K., Kirdyanov, A.V., Schweingruber, F.H., Silkin, P.P. 1999. Influence of snowfall and melt timing on tree grwoth in subarctic Eurasia. Nature 400: 149-151.

Vaganov, E.A., Hughes, M.K., and Shashkin, A.V. 2006. Growth Dynamics of Conifer Tree Rings: Images of Past and Future Environments. Springer Verlag. 354p.

Wang, Q., Little, C. H.A. and Odén, P.C. 1997. Control of longitudinal and cambial growth by gibberellins and indole-3-acetic acid in current-year shoots of Pinus sylvestris. Tree Physiology 17: 715-721.

Wang, L.L., Payette, S., and Bégin, Y. 2002. Relationships between anatomical and densitometric characteristics of black spruce and summer temperature at tree line in northern Quebec. Can. J. For. Res. 32: 477-486.

GENERAL CONCLUSION

Under climatic warming, changes in tree growth and wood properties may result in changes in forest productivity. To accurately assess forest growth and productivity for achieving the goal of sustainable forest management, we need to improve our understanding of tree growth in a detailed calendar. Investigation of intra-annual tree growth during a growing season can provide detailed information on how meteorological factors affect the growth of different organs and how these different organs coordinate with each other, which could improve our understanding of tree growth. In this study, we 1) investigated the intra-annual shoot, foliage, and stem growth for three major boreal tree species jack pine, trembling aspen and white birch in northwestern Quebec during the 2007 growing season, and how different organs coordinate with each other during the growing period; 2) explored how meteorological factors influence their growth, and determined the major limiting meteorological factors.

We found that the onset of xylem cell production for jack pine was triggered by temperature since May 7th, and during new cell production period from May 7th to August 9th air and soil minimum temperatures were dominant factors for positively controlling the xylem cell production of jack pine. Shoot growth of jack pine was also positively stimulated by summer temperature. During the growth period from May 28th to August 16th, the xylem cell production of trembling aspen was affected positively by precipitation and negatively by air temperature. During the cell production period from June 4th-August 16th, the xylem cell production of white birch was also positively regulated by precipitation. Therefore, we conclude that two broadleaf species were mainly limited by moisture conditions during cell production from June to August. Shoot growth of trembling aspen and white birch was positively correlated with air temperature. In addition, our study showed that the weekly cell increment indices calculated after the removal of endogenous origin in intra-annual cell growth were a good index for exploring the relationships between the intra-annual xylem cell production and meteorological factors.

Among the three species, the onset of xylem cell formation of jack pinc is earliest, and that of white birch is latest. The terminate date of xylem cell formation of white birch is earlier than that of jack pine and trembling aspen. Therefore, the duration of xylem cell formation of white birch is shortest among three species, and jack pine has a longest duration of xylem cell production.

We also found that the onset date of xylem cell formation and the development of shoot and foliage as well as the end date of cell, foliage and shoot development were different within intra- and inter- species. Therefore, the carbohydrates reserved in the previous growth year played an important role in producing new xylem cells for trembling aspen. The climate conditions in the current growth year are critical for producing new xylem cells for white birch. The carbohydrates reserves in the previous year and photocarbohydrates produced by old needles of jack pine in the current growing season might together stimulate new cells of the xylem during the early growing season.

Our study demonstrates that investigation of the intra-annual tree growth (shoot, leaf, and stem) at the weekly scale could be a valid tool to identify major climatic factors for influencing shoot, leaf and stem growth during a growing season. Future intra-annual tree growth studies should focus on not only stem growth, but also foliage and shoot growth during a growing season. This could give a clear picture about how tree organs react to meteorological factors and how they coordinate with each other under a warming climate.

In addition, our study could allow us to predict the potential effect of future climate warming on growth of these three boreal species in northwestern Quebec. In Quebec, Hulme and Shread (1999) reported that mean annual temperature in 2100 would be about 3.5°C higher than today, as much as 5°C greater in winter, and accompanied by increased precipitation of 10 to 25%. With the increased temperature and precipitation predicted and the prolonged growing season expected in northwestern Quebec in the near future, jack pine might take advantage of warming spring temperatures to increase stem cell production, shoot extension growth and needle area enlargement during a warmer growing season. Trembling aspen and white birch might benefit from increased temperature and precipitation to enhance their stem cell production, leaf enlargement (possiblc increased leaf numbers and area) and shoot extension during a longer growing season. These potential changes in xylem cell production of stem and development of shoot and foliage will be likely to lead to potential change in tree growth and forest productivity in the long term. Consequently it will be possible to result in shift in species range and forest structure, and composition. The results obtained from these intra-annual tree growth studies could improve our ability to simulate tree growth and forest growth, and will favour the sustainable forest management in the future. Therefore future more studies on intra-annual growth of tree different parts will be necessary to improve our understanding of tree growth and our ability to predict the tree growth and forest productivity in the boreal biome.

REFERENCES

Antonova, G.F., and Stasova, V.V. 1993. Effects of environmental factors on wood formation in Scots pine stems. Trees 7: 214-219.

Antonova, G.F., and Stasova, V.V. 1997. Effects of environmental factors on wood formation in larch (Larix sibirica Ldb.) stems. Trees 11: 462-468.

Archambault, S., and Bergeron, Y. 1992. An 802-year tree-ring chronology from the Quebec boreal forest. Can. J. For. Res. 22: 674-682.

Beaubien, E.G., and Freeland, H.J. 2000. Spring phenology trends in Alberta, Canada: links to ocean temperature. International Journal of Biometeorology 44(2): 53-59.

Belyea, R.M., Fraser, D.A., and Rose, A.H. 1951. Seasonal growth of some trees in Ontario. Forestry Chronicle 27: 300-305.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscape on boreal forest fire regimes. Ecology 72: 1980-1992.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology 81: 1500-1516.

Bergeron, Y. 2007. Bernhard Denneler 1963-2007. Tree-Ring Research 63 (1): 65.

Bergeron, Y., Gauthier, S., Flannigan, M., and Kafka, V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in Northwestern Quebec. Ecology 85(7): 1916-1932.

Bergeron, Y. and Harvey, B.D. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. Forest Ecology and Management 92: 235-242.

Bergeron, Y., Leduc, A., Harvey, B.D., and Gauthier, S. 2002. Natural fire regime: A guide for sustainable management of the Canadian boreal forest. Silva Fennica 36: 81-95.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., and Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. 31: 384-391.

Berninger, F., Hari P., Nikinmaa, E., M. Lindholm and Merilainen, J. 2004. Use of modeled photosynthesis and decomposition to describe tree growth at the northern tree line. Tree Physiology 24: 193-204.

Bergh, J. and Linder, S. 1999. Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands. Global Change Biology 5: 245–53.

Bicknell, S.H. 1982. Development of canopy stratification during early succession in northern hardwoods. Forest Ecology and Management 4: 41–51.

Bormann, F.H., and Kozlowski, T.T. 1962. Measurements of tree growth with dial gage Dendrometers and vernier tree ring bands. Ecology 43: 289-294.

Bouriaud, O., Leban, J.M., Bert, D., and Deleuze, C. 2005. Intra-annual variations in Climate influence growth and wood density of Norway spruce. Tree Physiology 25: 651-660.

Briffa, K.R., Jones, P.D., Schweingruber, F.H., Osborn, T.J., Shiyatov, S.G, and Vaganov, E.A. 1998. Reduced sensitivity of recent tree growth to temperature at high latitudes. Nature 391: 678-682.

Buhler, O., Nielsen, C.N., Kristoffersen, P. 2006. Growth and phenology of established Tilia cordata street trees in response to different irrigation regimes. Arboriculture an Urban Forestry 31: 3-9.

Camarero, J.J., Guerrero-Campo, J., and Gutiérrez, E. 1998. Tree-ring growth and Structure of Pinus uncinata and Pinus sylvestris in the Central Spanish Pyrenees. Arctic, Antarctic, and Alps Research 30: 1-10.

Chalk, L., and Phil, M.A. 1930. The formation of spring and summer wood in ash and Douglas fir. Oxford Forestry Memoirs No. 10, Oxford University Press, London.

Cheng, C. and Gordon, I.L. 2000. The Richards function and quantitative analysis of germination and dormancy in meadow-foam (Limnanthes alba). Seed Science 10: 265-277.

Chmielewski, F. M., and Rötzer, T. 2001. Response of tree phenology to climate change across Europe. Agricultural and Forest Meteorology 108: 101-112.

Chuine, I., Aitken, S. N., and Ying, C. C. 2001. Temperature thresholds of shoot elongation in provenances of Pinus contorta. Canadian Journal of Forest Research 31: 1444-1455.

Chuine, I., Cambon, G., and Comtois, P. 2000. Scaling phenology from the local to the regional level: advances from species-specific phonological models. Global Change Biology 6: 943-952.

Cook, E.R., Bird, T., Peterson, M., Barbetti, M., Buckley, B., D'Arrigo, R., Francey, R., and Tans, P. 1991. Climatic change in Tasmania inferred from a 1089-year tree-ring chronology of subalpine Huon pine. Science 253: 1266-1268.

D'Arrigo, R., Jacoby, G.C., and Free, R. 1992. Tree-ring width and maximum latewood density at the North American treeline: parameters of climatic change. Can. J. For. Res. 22: 1290-1296.

Daubenmire, R.F. 1945. An improved type of precision dendrometer. Ecology 26: 97-98.

Deslauriers, A., Anfodillo, T., Rossi, S., and Carraro, V. 2007. Using simple causal modeling to understand how water and temperature affect daily stem radial ariation in trees. Tree Physiology 27: 1125-1136.

Deslauriers, A. and Morin, H. 2005. Intra-annual tracheid production in balsam fir stems and the effect of meteorological variables. Trees 19: 402-408.

Deslauriers, A., Morin, H., and Bégin, Y. 2003a. Cellular phenology of annual ring formation of Abies balsamea in the Quebec boreal forest (Canada). Can. J. For. Res. 33: 190-200.

Deslauriers, A., Morin, H., Urbinati, C., and Carrer, M. 2003b. Daily weather response of balsam fir (Abies balsamea (L.) Mill.) stem radial increment from dendrometer analysis in the boreal forest of Quebec (Canada). Trees 17: 477-484.

Douglass, A.E. 1914. A method for estimating rainfall by the growth of trees. In: E. Huntington, The climatic factor as illustrated in arid America. Publication 192. Carnegie Institute of Washington, Washington, D.C. pp101-121.

Douglass, A.E. 1917. Climatic records in the trunks of trees. American Forestry 23(288): 732-735.

Douglass, A.E. 1920. Evidence of climatic effects in the annual rings of trees. Ecology 1(1): 24-32.

Dufour, B. and Morin, H. 2007. Focusing modelling on the tracheid development period – an alternative method for treatment of xylogenesis intra-annual data. Dendrochronologia 25: 125–133.

Eckstein, D. 2004. Change in past environments-secrets of the tree hydrosystem. New Phytologist 163: 1-4.

Environment Canada (2008) Climate trends and variations bulletin for Canada. Environment Canada Atmospheric Environment Service Climate Research Branch, http://www.msc-smc.ec.gc.ca/ccrm/bulletin/regional_e.cfm.

Flannigan, M.D., Bergeron, Y., Engelmark, O., and Wotton, B.M. 1998. Future wildlife in the circumboreal forests in relation to global warming. Journal of Vegetation Sciences 9: 469-476.

Forster, T., Schweingruber, H.F., and Denneler, B. 2000. Increment puncher. A tool for extracting small cores of wood and bark from living trees. IAWA Journal 21: 169-180.

Fritts, H.C. 1976. Tree rings and Climate. Academic Press, New York.

Fritts, H.C., and Fritts, E.C. 1955. A new dendrograph for recording radial changes of a tree. Forest Science 1: 271-276.

Gompertz, B. 1825. On the nature of the function expressive of the law of human mortality and on a new mode of determining life contingencies. Phil Trans R Soc 2:513-585.

Gartner, B.L., Aloni, R., Lichtfuss-Gautier, A.N., Roig, F.A. 2002. Clues for dendrochronology from studies of wood structure and function. Dendrochronologia 20(1-2): 53-61.

Girardin, M.P., Tardif, J., Flannigan, M.D., and Bergeron, Y. 2004a. Multicentury reconstruction of the Canadian Drought Code from eastern Canada and its relationship with paleoclimatic indices of atmospheric circulation. Climate Dynamics 23: 99-115.

Girardin, M.P., Tardif, J., Flannigan, M.D., Wotton, B.M., and Bergeron, Y. 2004b. Trends and periodicities in the Canadian Drought Code and their relationships with atmospheric circulation for the southern Canadian boreal forest. Can. J. For. Res. 34: 103-119.

Grace, J., Berninger, F., and Nagy, L. 2002. Impacts of climate change on the tree line. Annals of Botany 90: 537-544.

Graumlich, L.J. 1993. Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. Can. J. For. Res. 23: 133-143.

Gruber, A., Baumgartner, D., Zimmermann, J., and Oberhuber, W. 2008. Temporal dynamics of wood formation in Pinus cembra along the alpine treeline ecotone and the effect of climate variables. Trees 23: 625-635.

Hänninen, H. 1995. Effects of climate changejon trees from cool and temperate regions: an ecophysiological approach to modelling of bud burst phenology. Can. J. Bot. 73: 183-199.

Harvey, B. 1999. The Lake Duparquet Research and Teaching Forest: Building a foundation for ecosystem management. For. Chron. 75(3): 389-393.

Harvey, B.D., Leduc, A., Gauthier, S., and Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. Forest Ecology and Management 155: 369-385.

Hitz, O.M., Gärtner, H., Heinrich, I., and Monbaron, M. 2008. Wood anatomical changes in roots of European ash (Fraxinus excelsior L.) after exposure. Dendrochronologia 25: 145-152.

Hofgaard, A., Tardif, J., and Bergeron, Y. 1999. Dendroclimatic response of Picea mariana and Pinus banksiana along a latitudinal gradient in the eastern Canadian boreal forest. Canadian Journal of Forest Research 29: 1333-1346.

Hogg, E.H., Brandt, J.P., and Kochtubajda, B. 2005. Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. Canadian Journal of Forest Research 35: 610-622.

Horacek, P., Slezingerova, J., and Gandelova, L. 1999. Effects of environment on the xylogenesis of Norway spruce (Picea abies [L.] Karst.). In: R. Winner, and R.E., Vetter (eds.), Tree-ring analysis: 33-53. CAB International.

Huang, J.G., and Zhang, Q.B. 2007. Tree rings and climate for the last 680 years in Wulan area of northeastern Qinghai-Tibetan Plateau. Climate Change 80: 369-377.

Hulme, M. and Shread, N. 1999. Climate change scenarios for Canada. Climate Research Unit, UK.

Huntington, T. G. 2004. Climate Change, Growing Season Length, and Transpiration: Plant Response Could Alter Hydrologic Regime. Plant Biology 6: 651-653.

IPCC (Intergovernmental Panel on Climate Change) 2007. Climatic Change 2007: the Physical Science Basis. In: Proceedings of the 10th Session of Working Group I of the IPCC, Paris, February 2007.

Jarvis, P. and Linder, S. 2000. Constraints to growth of boreal forests. Nature 405: 904-905.

Jones, B., Tardif, J., and Westwood, R. 2004. Weekly xylem production in trembling aspen (Populus tremuloides) in response to artificial defoliation. Can. J. Bot. 82: 590-597.

Junttila, O. and Heide, O.M. 1981. Shoot and needle growth in pinus sylvestris as related to temperature in northern Fennoscandia. For. Sci. 27: 423-430.

Kanninen, M. 1985. Shoot elongation in Scots pine: diurnal variations and response to temperature. Journal of Experimental Botany 36: 1760-1770.

Keeland, B.D., and Sharitz, R.R. 1993. Accuracy of tree growth measurements using Dendrometer bands. Can. J. For. Res. 23: 2454-2457.

Khanduri, V. P., Sharma, C. M., and Singh, S. P. 2008. The effects of climate change on plant phenology. Environmentalist 28: 143-147.

Kikuzawa, K. 1983. Leaf survival of woody plants in deciduous broad-leaved forests. 1. tall trees. Canadian Journal of Botany 61: 2133-2139.

Kirdyanov, A.V., Hughes, M., Vaganov, E.A., Schweingruber, F.H., and Silkin, P. 2003. The importance of early summer temperature and date of snow melt for tree growth in The Siberia Subarctic. Trees 17: 61-69.

Ko Heinrichs, D., Tardif, J., and Bergeron, Y. 2007. Xylem production in six tree species growing on an island in the boreal forest region of western Quebec, Canada. Canadian Journal of Botany 85: 518-525.

Korpilahti, E. 1988. Photosynthetic production of Scots pine in the natural environment. Acta For. Fenn., Monograph No. 202, 71 p.

Kozlowski, T.T., and Winget, C.H. 1964. Diurnal and seasonal variation in radii of tree stems. Ecology 45: 149-155.

Kozlowski, T.T. 1971. Growth and developoment of trees. Vol. II. Combial growth, root growth, and reproductive growth. New York: Academic Press. 514 p.

Kramer, P. J., and Kozlowski, T. T. 1979. Physiology of woody plants. Academic Press, Inc. Harcourt Brace Jovanovich, Publishers, New York, USA.

Kramer, K., Leinonen, I., and Loustau, D. 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forest ecosystems: an overview. International Journal of Biometeorology 44: 67-75.

Kuroda, K. 1986. Wound effects on cytodifferentiation in the secondary xylem of woody plants. Wood Research 72: 67-117.

Lachaud, S. 1989. Participation of auxin and abscisic acid in the regulation of seasonal variations in cambial activity and xylogenesis. Trees 3: 125-137.

Ladefoged, K. 1952. The periodicity of wood formation. Det Kongel Danske Vidensk Selsk Skrift Dan Biol 7: 1-98.

Leinonen, L., Repo, T. and Hanninen, H. 1997. Changing environmental effects on frost hardiness of Scots pine during dehardening. Ann. Bot. 79: 133-138.

Leonelli, G., Denneler, B., and Bergeron, Y. 2008. Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada. Canadian Journal of Forest Research 38: 1211-1222.

Levanič, T. and Eggertsson, O. 2008. Climatic effects on birch (Betula pubescens Ehrh.) growth in Fnjoskadalur valley, northern Iceland. Dendrochronologia 25: 135-144.

Linkosalo, T. 1999. Mutual regularity of spring phenology of some boreal tree species: predicting with other species and phonological models. Can. J. For. Res. 30: 667-673.

MacDougal, D.T. 1921. Growth in Trees. Carnegie Inst. Pub. 307, Washington, D.C.

Mäkinen, H., Nöjd, P., and Saranpää, P. 2003. Seasonal changes in stem radius and production of new tracheids in Norway spruce. Tree Physiology 23: 959-968.

Marion, L., Gričar, J., and Oven, P. 2007. Wood formation in urban Norway maple trees studied by the micro-coring method. Dendrochronologia 25: 97-102.

Menzel, A. and Fabian, P. 1999. Growing season extended in Europe. Nature 397: 659.

Nobuchi, T., Ogata, Y., and Siripatanadilok, S. 1995. Seasonal characteristics of wood Formation in Hopeaodorata and Shorea henryana. IAWA Journal 16: 361-369.

Numainville, G., and Desponts, M. 2004. Les stades de débourrement des bourgeons foliaires de l'épinetter noire-Guide No.7. Gouvernement du Québec, Ministère des Ressources naturelles de la Faune et des Parcs, Direction de la recherche forestière. 24p.

Ozawa, H., Itoh, K., and Hori, Y. 2000. Shoot structure and dynamics of saplings and canopies of three deciduous broad-leaved trees of a coppice forest in central Japan. Trees 14: 206-214.

Phipps, R.L., and Gilbert, G.E. 1960. An electric dendrograph. Ecology 41: 389-390.

Plomion, C., Leprovost, G., and Stokes, A. 2001. Wood formation in trees. Plant Physiology 127: 1513-1523.

Reineke, L.H. 1932. A precision dendrometer. Journal of Forestry 30: 692-697.

Richardson, S.D., and Dinwoodie, J.M. 1959. Studies on the physiology of xylem development. I. The effects of night temperature on tracheid size and wood density in conifers. Journal of the Institute of Wood Science 6: 3-13.

Root, T.J., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., and Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. Nature 421: 57-60.

Rossi, S., Deslauriers, A., Anfodillo, T., and Carrer, M. 2008. Age-dependent xylogenesis in timberline conifers. New Phytologist 177: 199-208.

Rossi, S., and Deslauriers, A. 2007. Intra-annual time scales in tree rings. Dendrochronolgia 25: 75-77.

Rossi, S., Deslauriers, A., Anfodillo, T., and Carraro, V. 2007. Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. Oecologia 152: 1-12.

Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R., and Borghetti, M. 2006. Conifers in cold environments and synchronize maximum growth rate of tree-ring formation with day length. New Phytologist 170: 301-310.

Rossi, S., Anfodillo, T., and Menardi, R. 2006. Trephor: a new tool for sampling microcores from tree stems. IAWA Journal 27(1): 89-97.

Rossi, S., Deslauriers, A., and Morin, H. 2003. Applicaiton of the Gompertz equation for the study of xylem cell development. Dendrochronologia 21: 33-39.

Samuels, A.L., Kaneda, M., and Rensing, K.H. 2005. The cell biology of wood formation: from cambial divisions to mature secondary xylem. Can. J. Bot. 84: 631-639.

Sarvas, R. 1972. Investigations on the annual cycle of development of forest trees. Active period. Commun Inst For Fenn 76: 1-110

Savidge, R.A. 1996. Xylogenesis, genetic and environmental regulation. IAWA Journal 17: 269-310.

Schaber, J. and badeck, F.W. 2005. Plant phenology in Germany over the 20th century. Reg. Environ. Change 5: 37-46.

Schmitt, U., Jalkanen, R., and Eckstein, D. 2004. Cambium dynamics of Pinus sylvestris and Betula spp. in the northern boreal forest in Finland. Silva Fennica 38(2): 167-178.

Schmitt, U., Möller, R., and Eckstein, D. 2000. Seasonal wood formation dynamics of beech (Fagus sylvatica L.) and black locust (Robinia pseudoacacia L.) as determined by the 'pinning' technique. Journal of Applied Botany 74: 10-16.

Schmitz, N., Verheyden, A., Kairo, J.G., Beeckman, H., and Koedam, N. 2007. Successive cambia development in Avicennia marina (Forssk.) Vierh. is not climatically driven in the seasonal climate at Gazi Bay, Kenya. Dendrochronologia 25: 87-96.

Schwartz M.D., and Reiter, B.E. 2000. Changes in North American spring. International Journal of Climatology 20: 929-932.

Schweingruber, F.H. 1996. Tree Rings and Environment: Dendroecology. Swiss Federal Institute for Forest, Snow and Landscape Research, Paul Haupt Publishers, Brimensdorf and Bern.

Sheridan, S. C. 2002. The redevelopment of a weather-type classification scheme for North America. International Journal of Climatology 22: 51-68.

Sheskin, D.J. 1997. Handbook of parametric and nonparametric statistical procedure. CRC Press LLC, Boca Raton, Florida, 719p.

Skomarkova, M. V., Vaganov, E.A., Mund, M., Knol, A., Linke, P,. Boerner, A., Schulze, E. D. 2006. Inter-annual and seasonal variability of radial growth, wood density and carbon isotope ratio in tree rings of beech growing in Germany and Italy. Trees 20: 571-586.

Shukla, R. P. and Ramakrishnan, P. S. 1984. Leaf dynamics of tropical trees related to successional status. New Phytol. 97: 687–706.

Tardif, J. and Bergeron, Y. 1993. Radial growth of Fraxinus nigra in a Canadian boreal floodplain in response to climatic and hydrological fluctuations. Journal of Vegetation Science 4: 751-758.

Tardif, J., Conciatori, F., and Bergeron, Y. 2001a. Comparative analysis of the climatic response of seven boreal tree species from northwestern Québec, Canada. Tree-ring Research 57: 169-181.

Tardif, J., Flannigan, M., and Bergeron, Y. 2001b. An analysis of the daily radial activity of 7 boreal tree species, northwestern Quebec. Environmental Monitoring and Assessment 67: 141-160.

Telewski, F.W. and Lynch, A.M. 1991. Measuring growth and development of stems. In: Lassoie, J.P., Hinckley, T.M. (Eds.), Techniques and Approaches in Forest Tree Ecophysiology, 599 p.

Thibeault-Martel, M., Krause, C., Morin, H., and Rossi, S. 2008. Cambial activity and intra-annual xylem formation in roots and stems of Abies balsamea and Picea mariana. Annals of Botany 102: 667-674.

Thompson, A. 2007. Climate change: late leaf fall. Nature Reports Climate Change, 29 November 2007. doi:10.1038/ngeo.2007.61.

Uggla, A., Stenlund, S., Holmdahl, O.J.M., Jakubek, E.-B., Thebo, P., Kindahl H., and Björkman, C. 1998. Oral Neospora caninum inoculation of neonatal calves, Int. J. Parasitol. 28: 1467–1472.

Vaganov, E.A., Hughes, M.K., Kirdyanov, A.V., Schweingruber, F.H., Silkin, P.P. 1999. Influence of snowfall and melt timing on tree grwoth in subarctic Eurasia. Nature 400: 149-151.

Vaganov, E.A., Hughes, M.K., and Shashkin, A.V. 2006. Growth Dynamics of Conifer Tree Rings: Images of Past and Future Environments. Springer Verlag. 354p.

Vegis, A. 1964. Dormancy in higher plants. Ann. Rev. Plant Physiology 15: 185–215.

Wang, Q., Little, C. H.A. and Odén, P.C. 1997. Control of longitudinal and cambial growth by gibberellins and indole-3-acetic acid in current-year shoots of Pinus sylvestris. Tree Physiology 17: 715-721.

Wang, L.L., Payette, S., and Bégin, Y. 2002. Relationships between anatomical and densitometric characteristics of black spruce and summer temperature at tree line in northern Quebec. Can. J. For. Res. 32: 477-486.

Wareing, P.F. 1969. Germination and dormancy. In: Wilkins, M.B., Editor, 1969. Physiology of Plant Growth and Development, McGraw-Hill, London, pp.605–644.

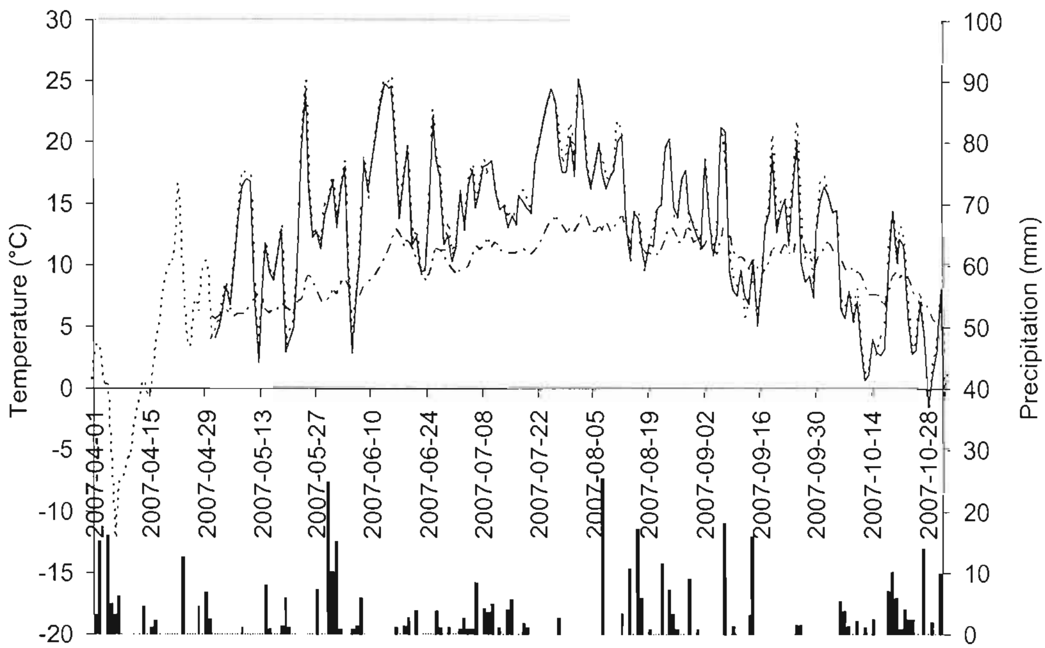
Wolter, K.E. 1968. A new method for marking xylem growth. Forest Science 14: 102-104.

Yoshimura, K.S., Hayashi, T. Itoh, and Shimaji, K. 1981. Studies on the improvement of the pining method for marking xylem growth. I Minute examination of pin marks in taeda pine and other species. Wood Research 67: 1-16.

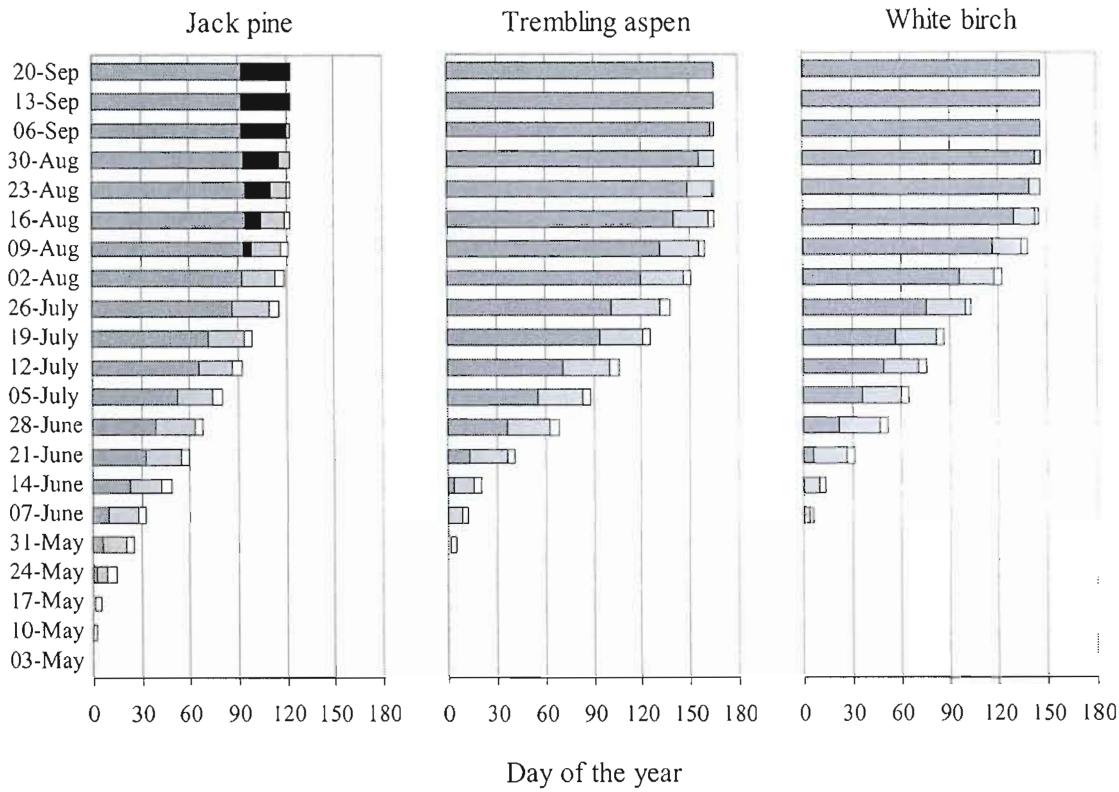
Zimmermann, M. H. 1964. The formation of wood in forest trees. Academic Press Inc., New York. 562 p.

APPENDICES

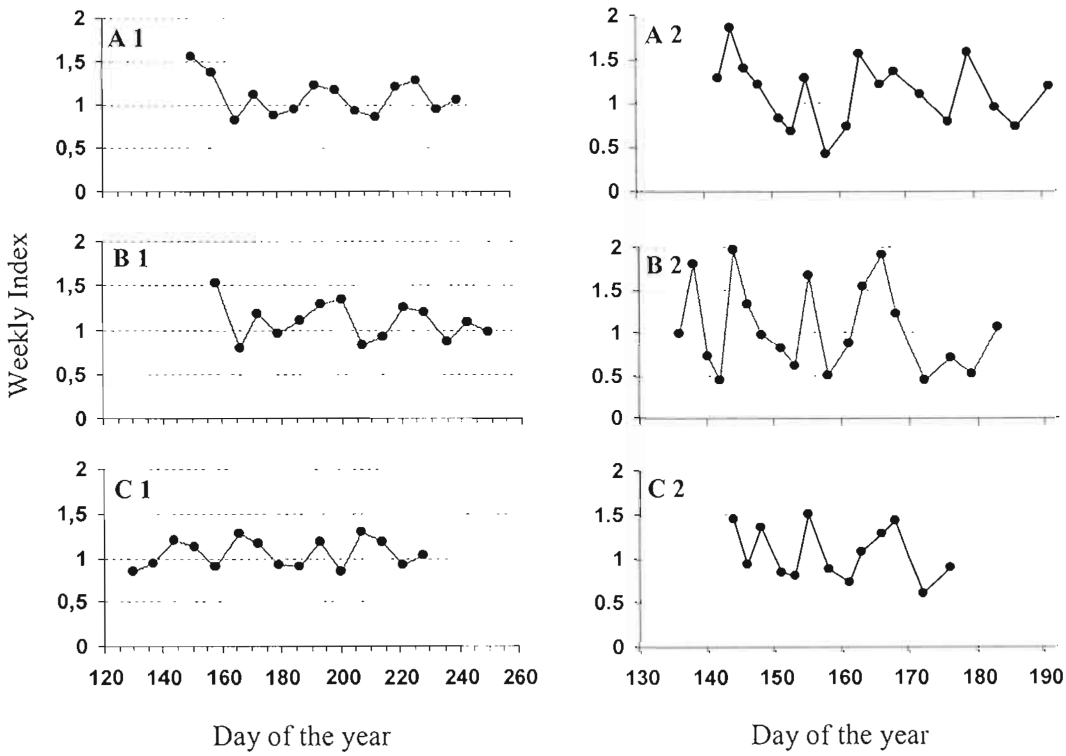
Appendix 1. Variations in meteorological variables during the 2007 growing season. (—): Mean air temperature in the site; (····): Mean air temperature at the weather station; (–·–·): Soil temperature; Solid bars: Precipitation.



Appendix 2. Number of cells in different phases of wood cell formation for Jack pine, trembling aspen, and white birch during the 2007 growing season. Latewood: ▩.
(Radial enlargement phase □, cell wall lignifications phase □, and mature cell phase □).

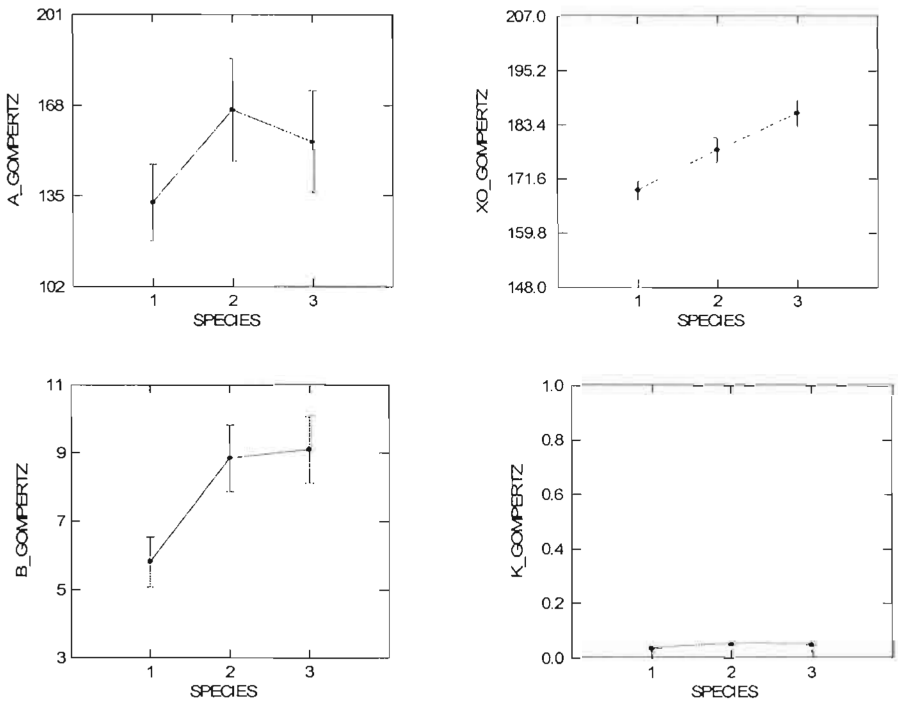


Appendix 3. Time series of the weekly index (WI) of stem wood cell formation and shoot extension growth of the three species. A: Trembling aspen; B: White birch; C: Jack pine. 1: wood cell formation; 2: shoot extension growth.



Appendix 4. F-statistic and resulting probability of the analysis of variance (ANOVA, P=0.05) of parameters of Gompertz function of the three species. X_0 is the date of the greatest cell production. Species 1: jack pine, Species 2: trembling aspen, Species 3: white birch.

	F	P
A	1.159	0.339
B	4.876	0.022
K	2.873	0.086
X_0	11.672	0.001



Appendix 5. Onset, ending and duration of xylem cell division, shoot elongation and foliage enlargement of the three species in 2007 (n=10 trees/species).

Observation	Jack pine	Trembling aspen	White birch
Onset of xylem cell division	127±3.6	147 ±2.8	154±6.5
End of new xylem cell division	221±4.2	228±5.1	228±7.0
Duration of xylem cell division	94 ±7.1	80 ±8.5	74±8.2
Onset of shoot elongation	140±3.1	149±2.7	142±2.0
End of shoot elongation	179±5.2	172±3.6	193±7.3
Duration of shoot elongation	39±6.4	24±4.8	51±8.2
Onset of leave enlargement	140±3.1	149±2.7	142±2.0
End of leave enlargement	218±4.7	191±4.0	211±6.7
Duration of leave enlargement	78±5.6	43±4.8	69±7.1